IMPACTS OF FLOW RELEASES ON INVERTEBRATE DRIFT AND JUVENILE CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) DIET ON THE TRINITY RIVER BELOW LEWISTON DAM

By

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ABSTRACT

IMPACTS OF FLOW RELEASES ON INVERTEBRATE DRIFT AND JUVENILE CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA) DIET ON THE TRINITY RIVER BELOW LEWISTON DAM

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Benthic macroinvertebrate (BMI) drift, species composition and abundance are specific to local hydrologic and habitat conditions, which can restrict or enhance availability to salmonids as a food resource. Currently, a knowledge gap exists on the Trinity River (northern California) in how flow releases from Lewiston Dam potentially impact BMI drift and feeding opportunities for juvenile salmonids. Samples of BMIs from drift, benthos, and diets of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) were collected from two sites in the upper Trinity River February-April 2018, during stable flow conditions (~8 m^3/s) and two increased flow conditions peaking at ~50 m^3/s. Chironomidae (Diptera) and Baetidae (Ephemeroptera) were dominant BMI taxa in the drift, benthos and diets. Although contributions to biomass were more even across BMI taxa in the drift, biomass consumed by fish was dominated by Chironomidae and Baetidae at both study sites. BMI taxonomic composition was more similar between benthic, drift and diet samples at the upstream study site below Lewiston Dam, whereas compositional similarities diverged during peak discharge conditions at the downstream study site. Although standardized drift rates (ex. mg/m^3) did not increase with increased flow, the total export of BMI drift increased significantly with increased flow ($p<0.05$). Consumption of BMIs by juvenile Chinook was not proportional to increased total BMI export during higher flow, suggesting fish responded more to standardized drift metrics. The findings of this study can inform future research and Trinity River water management on juvenile Chinook salmon responses to managed increases in flow and drift feeding dynamics.

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INTRODUCTION

The restoration of natural flow regimes on large rivers impacts a variety of resources including drinking water, hydropower, timber, minerals and fish (Jacobson et al. 2006). Because of the large economic value accrued through river management, restoration efforts are often small-scale and site-specific, focusing on ecosystem functions in selected sections of a river (Gore & Shields 1995). The restoration and rehabilitation of large-scale ecosystem functions (e.g., restoring a natural flow regime) is less common (Gore & Milner 1990), more expensive (Kern 1992) and near impossible on large managed rivers. However, altered flow regimes downstream of dams (e.g., the removal of periods of high flow for flood control or water storage), lead to impaired riparian-aquatic interactions that degrade wildlife, flood mitigation, bank stability, and nutrient cycling (Kominoski et al. 2013). Additionally, floods and experimental increases in discharge are associated with beneficial processes that enhance river diversity and resilience (Tonkin et al. 2018).

Dams and diversions can cause serious impacts to downstream sensitive species (Bruno et al. 2010), such as benthic macroinvertebrates. Dam management dampens natural flow variability (Olden et al. 2014), limiting aquatic and terrestrial organisms' ability to adapt and utilize disturbances such as increases in discharge (Lytle & Poff, 2004). One such instance of adaptation to flow variability is benthic macroinvertebrate (BMI) drift or the downstream movement of invertebrates in streams and rivers (Shearer et al. 2003). Drift of BMIs is a defining characteristic in lotic ecosystems (Leung et al.

2009), and is generally sensitive to environmental changes such as natural or managed flow alterations (Bruno et al. 2010), proximity to dams (Jones 2013), habitat type (i.e., pool, riffles, runs, glides; Leung et al. 2009), increases in temperature (Carolli et al. 2012) and season (Naman et al. 2016). Dynamics of drifting invertebrates have profound impacts on the transfer of energy from BMI primary consumers to secondary consumers such as fish and terrestrial predators (Leung et al. 2009). Additionally, BMI drift concentrations has been found to be positively correlated with fish production and distribution (Wilzbach et al. 1986).

Drift of BMIs occurs through passive and active processes, which vary in influence depending on the magnitude and frequency of streamflow. Passive drift is due to mechanical (grain movement) or flow turbulence that can dislodge BMIs from the streambed (Naman et al. 2016; Gibbins et al. 2007). There are generally two types of passive drift: (1) constant passive drift occurs below critical entrainment thresholds (Brittain and Eikeland 1988) and is often referred to as background drift irrespective of any periodicity (Waters 1965), and (2) catastrophic passive drift that results in a pulse of high drift density under increased discharge and turbulence (Anderson and Lehmukhl 1968; Gibbins et al. 2007). In contrast, active drift is a deliberate behavior of BMIs to emerge into adult life stages, avoid predation by benthic predators or foraging fish (Peckarsky 1980; Malmqvist and Sjostrom 1987, Hammock et al. 2012) or to maximize forage intake and colonize new areas downstream (Kohler 1985; Shearer 2003). Predation avoidance by BMIs often results in diel cycles of drift, with peaks in drift densities at night in streams with drift-feeding fish (Bishop 1969; Allan 1978). BMI drift patterns also vary seasonally and throughout the lifecycles of specific BMI taxa (O'Hop and Wallace 1983).

The effects of streamflow on BMI drift densities and flux have important management considerations regarding food-availability for drift feeding fish downstream of dams (Elliot 1967; Sagar & Glova 1998; Hayes et al 2007; Leung et al. 2009). Drift concentration (mg/m^3) and density (abundance/m^3) are measures of prey availability for drift-feeding salmonids (Nielsen 1992; Harvey and Railsback 2014). Drift of BMIs is a key parameter in habitat suitability for salmonids and is commonly measured as total flux (drift concentration multiplied by estimated discharge; Q) rather than a focus on any specific invertebrate taxa in the drift (Hughes and Dill 1990; Weber et al. 2014). Given suitable drift-foraging conditions to fish (i.e. water depth and velocity), the magnitude of drift flux has direct impacts on the growth and survival of drift-feeding salmonids (Rosenfeld et al. 2005; Weber et al. 2014). For example, steelhead growth rates can decrease with decreased drift forage availability as competition for food resources increases (Keeley 2001; Weber et al. 2014). Interestingly, salmonid growth can be more limited by prey availability than water temperature (Beauchamp 2009). Additionally, shifting from consuming lower-quality (e.g., aquatic invertebrate larvae and pupae) to higher-quality (e.g., adult aquatic and terrestrial invertebrates) invertebrate prey taxa in the drift can greatly improve juvenile growth, even if consumption rate is lower (Beauchamp 2009). Therefore, drift concentrations and drift flux as well as the composition of drifting invertebrates are key parameters in the suitability of habitat for salmonids.

Many studies have examined the relationship between flow manipulations and BMI densities in the drift and in the benthos (e.g., Perry & Perry 1986; Brittain et al. 1988; Rempel et al. 1999; Imbert & Perry 2000; Miller & Judson 2014). An unnaturally sharp decrease in discharge can strand BMIs in marginal areas (Corrarino & Brusven 1983), possibly decreasing drift densities. Conversely, flow reductions can induce elevated drift densities for certain taxa, and decreased drift densities for others (Poff & Ward 1991). Prolonged periods of scouring floods below dams (e.g., hydropeaking) may result in periods of increased catastrophic drift, but may also result in overall reductions in benthic populations (Brittain & Eikland 1988). However, non-scouring increases in discharge may also increase drift by agitating sediment or material that BMIs cling to, without actually entraining sediment in the water column (Poff & Ward 1991; Imbert & Perry 2000). Moreover, drift flux varies with the duration, rate of increase, and magnitude of discharge in a hydrograph (Brooker & Hemsworth 1977; Weisburg and Burton 1993; Imbert and Perry 2000).

In order to reduce the impacts of altered flow regimes on invertebrate drift, it is critical to maintain minimum baseflows for BMI production and a variable flow regime to provide drift feeding opportunities for salmonids in stream systems with regulated flows (Weisburg and Burton 1993; Bunn and Arthington 2002). In the short term, pulses in flow designed to mimic natural flow variability and increase water velocity can cause significant increases in invertebrate drift (Brittain & Eikeland 1988) compared to a prolonged and slow rise in discharge (Brooker and Hemsworth 1977; Imbert and Perry 2000).

Objectives and Hypotheses

The objectives of this study were to assess trends in drift, benthic densities and juvenile Chinook salmon (*Oncorhynchus tshawytscha*) diet during muted winter baseflow conditions and experimental spring pulse flow releases out of Lewiston Dam on the Trinity River in northern California, USA. In cooperation with the Trinity River Restoration Program (TRRP) and the Bureau of Reclamation (BR), I utilized two pulse flow dam releases, both peaking at approximately 50 m^3/s, to study impacts of pulse releases on drift and benthic densities, invertebrate composition and food delivery to juvenile Chinook salmon. I expected seasonal changes in invertebrate composition and transport to be reflected in the fish diet samples. Additionally, following a pulse flow I expected BMI drift rates to increase, supporting the hypothesis that experimental pulse flows can help in the delivery of food available to fish during critical rearing periods below a dam. Because the ability of a juvenile salmonid to survive to the adult stage critically depends on juvenile fish size (Thedinga and Koski, 1984), with higher survival for larger fish at entry to sea (Koenings et. al, 1984), this information will inform the TRRP toward meeting its goal of increased salmonid production in the Trinity River (McBain & Trush, 2000).

METHODS

Study Sites

The Trinity River is a 267-kilometer long tributary to the Klamath River in northern California, spanning Trinity and Humboldt Counties, including both Trinity and Lewiston lakes (Figure 1). The 7,690 km^2 Trinity River watershed is known for its natural resources including salmon, timber, minerals and water supply (DOI 2000). Hydraulic mining in the 1800s and 1900s washed sediment from hillslopes into waterways, dramatically altering river morphology and salmonid habitat (USFWS & Hoopa Valley Tribe 1999). Between 1963-1965, the Bureau of Reclamation constructed both the Lewiston and Trinity dams, diverting as much as 90% of the annual flows accreted above the dams to the Sacramento River (McBain & Trush, 2000; DOI 2000). Today, as much as 50% of the river's flows are still exported each year (McBain & Trush, 2000). Reduced flows in the Trinity River downstream of the dams led to increased channel confinement, reduced habitat complexity and altered sediment caliber downstream of the dams (USFWS & Hoopa Valley Tribe 1999: DOI 2000). Since 2000, the TRRP has focused on flow restoration, gravel augmentation and channel and floodplain habitat restoration to create a more natural alluvial river downstream of the dams (USFWS & Hoopa Valley Tribe 1999; Beechie et al. 2015).

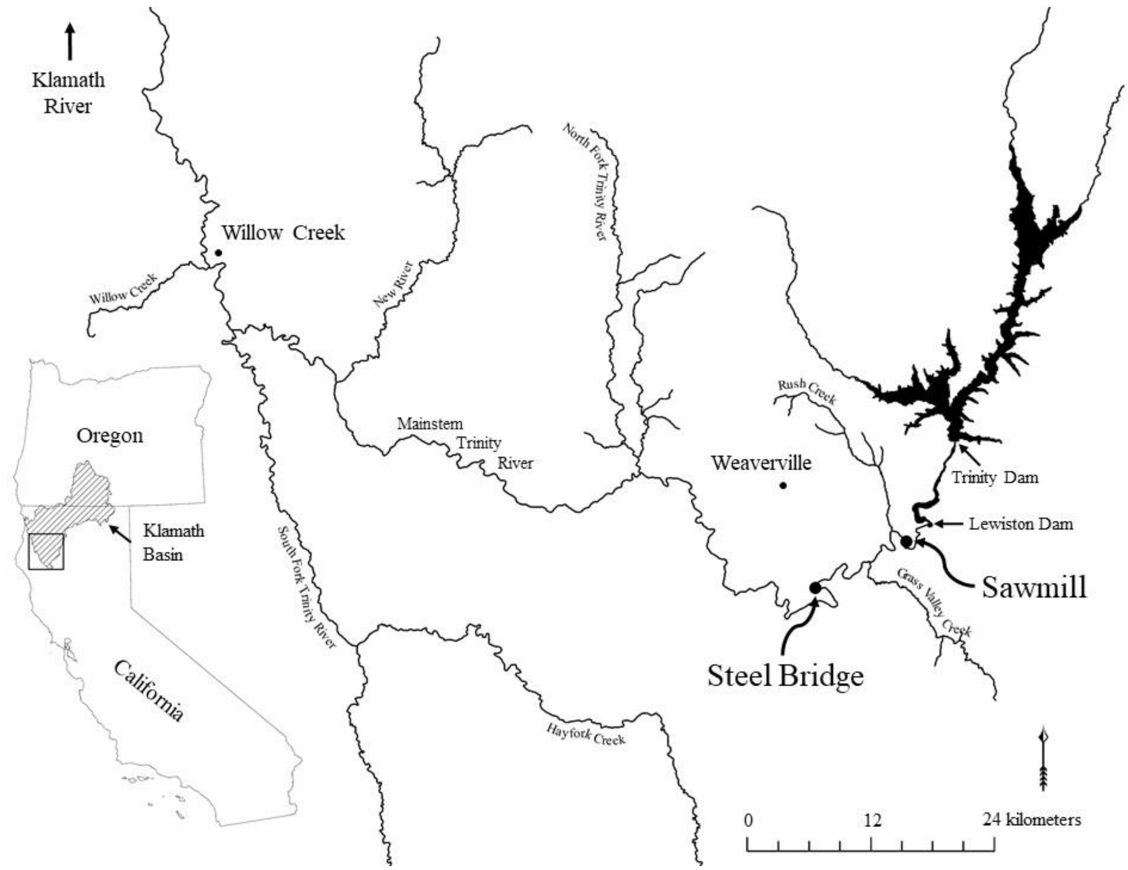

Figure 1. Map showing location of study sites within the Klamath Basin (inset) and on the mainstem Trinity River below Lewiston Dam. The locator square on the inset map represents the Trinity River sub-basin within the Klamath Basin. The Trinity River Restoration Reach begins at Lewiston Dam and flows to the confluence of the mainstem Trinity River and North Fork Trinity River.

This study was conducted on the mainstem Trinity River at two sites between Lewiston Dam and the North Fork Trinity River (hereafter "Restoration Reach"). Consultation with professionals from the TRRP, U.S. Fish and Wildlife Service (USFWS), the Yurok Tribe, and the Hoopa Valley Tribe led to the selection of two study sites: 1) Sawmill (~5 km downstream of Lewiston dam) and 2) Steel Bridge (~21 km downstream of Lewiston dam) (Figure 1). Sites were also selected based on ease of access and presence of a uniform riffle habitat for sampling BMIs from the benthos, drift and juvenile Chinook salmon diets. The downstream site, Steel Bridge, has inputs from two upstream tributaries: Rush Creek and Grass Valley Creek. In addition to Chinook salmon, other salmonids present at these sites include brown trout (*Salmo trutta*), steelhead trout (*Oncorhynchus mykiss*) and Coho salmon (*Oncorhynchus kisutch;* Beechie et al. 2015). Other species present in the Restoration Reach include Pacific lamprey (*Entosphenus tridentatus*), green sturgeon (*Acipenser medirostris*) and three-spined stickleback (*Gasterosteus aculeatus*). Riparian vegetation at both sites was composed of mixed coniferous and deciduous forests dominated by red alder (*Alnus rubra*), ponderosa pine (*Pinus ponderosa*), douglas fir (*Pseudotsuga menziesii*), bigleaf maple (*Acer macrophyllum*), and willow (*Salix* sp.; Beechie et al. 2015).

Study Site Characteristics

Impacts from a modified flow regime on the Trinity River are largely present at the downstream study site, Steel Bridge, resulting in incised channels, armoring of the stream bed, and vegetation encroachment close to the banks with approximately 25% riparian canopy cover. Annual average baseflow conditions at Steel Bridge range from ~8.5-13 m^3. The Restoration Reach has been grouped into classes of confinement, Steel Bridge is ranked as a confined, meandering channel with a slope of 0.0027 (Beechie et al. 2015).

The upstream study site, Sawmill, has a more gradually sloping cross-sectional profile and is thus more connected to its floodplain allowing for greater wetted area during periods of increased flow. Sawmill is ranked as a variably confined, meandering channel with a slope of 0.0029 (Beechie et al. 2015). Periodic gravel injections upstream of Sawmill allow for a greater proportion of alluvial material on the banks with 0% canopy cover. Annual average baseflow at Sawmill ranges from ~8-10 m^3.

Field Methods

Sampling occurred over a three-month period between February-April 2018 on a bi-weekly basis (n=28 total days of sampling). Each sampling occasion lasted four consecutive days at both study sites where samples were taken from the benthos, drift and juvenile Chinook salmon diets. Sampling periods during baseflow conditions in 2018 were: February 5-8, 20-23, March 5-8, 19-22 and April 2-5. The majority of data (~80%)

represent baseflow conditions, whereas ~20% of the data were collected during experimental pulse flow releases from Lewiston Dam (Figure 2). Sampling periods during experimental pulse flows were: April 16-18 and 22-28, with peak discharge of the first pulse flow on April 17, 2018 and the second pulse on April 28, 2018.

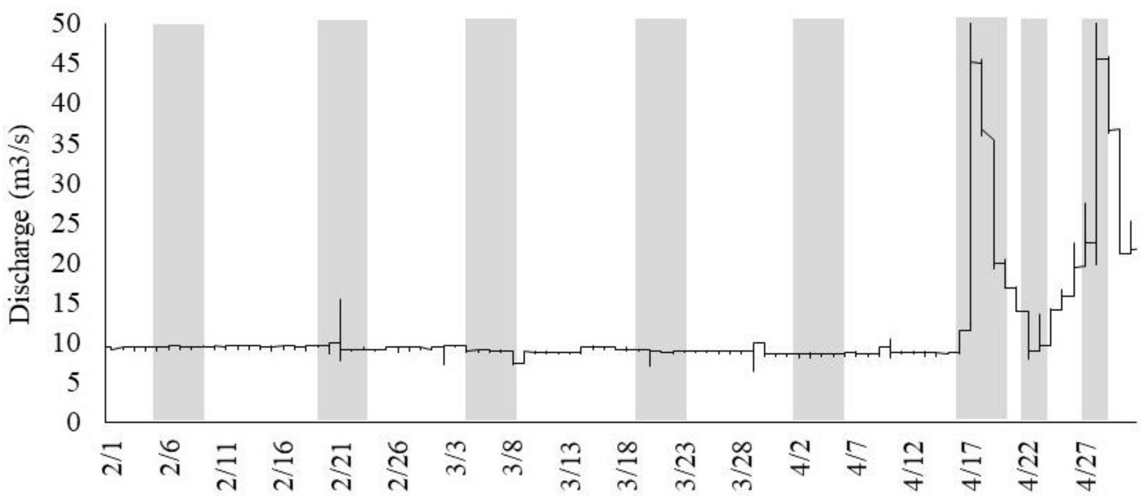

Figure 2. Average daily streamflow on the mainstem Trinity River, released from Lewiston Dam during the 2018 study period. Shaded regions represent sampling periods. The spikes in the hydrograph in April represent the two experimental pulse flows. Flow data are from the USGS gauging station in Lewiston, CA (USGS 11525500).

<u>Benthic sampling</u>

Benthic macroinvertebrates were sampled in the benthos at each study site to quantify densities of BMI taxa available for capture in the drift and to fish foraging in the benthos. Benthic samples were collected once per week over the course of the study period (February – April 2018) using a Surber net with a 0.31 m^2 standard sampling area and 500 μm mesh. Benthic sampling consisted of placing the Surber net on the streambed, scrubbing and removing large rocks with a wire brush within the sampling area upstream of the net, then disturbing the benthic substrate for a one-minute timed period. This procedure was repeated at three nearby locations within the same riffle and then composited into a single sample. Benthic samples were taken during baseflows as well as before and after the first experimental pulse flow out of Lewiston Dam to assess shifts in densities and composition of BMI taxa found in the benthos.

Drift sampling

Benthic macroinvertebrate drift samples were collected every 24 hours for four days in a row during each sampling week at both study sites. Benthic macroinvertebrates from the drift were sampled with two 0.31 m^2 drift nets with 500 µm mesh that were placed in the river for 2 hours before sunset. Benthic macroinvertebrate drift samples were collected simultaneously at both sites on each sampling day.

It is well-documented that sampling at dusk is appropriate for standardized sampling and capturing BMIs during periods of elevated drift rates (Elliott 1967; Chutter 1975; Collier & Wakelin 1992; Rincón & Lobón-Cerviá 1997). The peak in BMI drift at dusk is potentially a response to a reduction in light intensity and as a way for BMIs to avoid predation (Holt & Waters 1967; Bishop & Hynes 1969; Chaston 1969; Statzner & Mogel 1985; Flecker 1992; Forrester 1994; Dahl & Greenberg 1999). Therefore, drift nets were set out 2 hours before sunset in order to sample during this time of day when many taxa are actively drifting. Nets were checked and brushed periodically to discourage build-up of algae and other debris from creating backwaters at the opening of each drift net. Water velocity entering the drift nets was measured with a SonTek Flowtracker 2 at the beginning and end of each sampling period in order to determine the rate of flow in order to standardize BMI drift rates (concentrations= mg/m^3, density= $\#/m^3$) and drift flux (concentrations or density/Q). Temperature (°C) and dissolved oxygen (mg/L) were also measured adjacent to drift nets with a YSI ProODO at the beginning and end of each sampling period.

BMI drift concentrations can differ between the surface and the lower water column (Shearer et al. 2002); therefore, drift nets were raised approximately 1 inch from the stream bed to prevent non-drifting BMIs from crawling in the net, and the top of the net was positioned approximately 2.5 cm above the water surface to capture any terrestrial invertebrate inputs on the water surface. All BMI samples (benthic: n=18, drift: n=110) were rinsed in 500 μm sieves, transferred to appropriately-sized containers, and preserved in the field using a 90% ethanol solution.

Juvenile Chinook salmon diet sampling

Procedures for sampling and handling fish were approved under Humboldt State University IACUC Protocol 17/18.ESM-65-A. Prior to benthic and drift sampling, juvenile Chinook salmon were captured by 9.2 m seine nets with 3 mm mesh size. Captured juveniles ≥50 mm were anesthetized with buffered MS-222 (tricaine methanesulfonate) at a dosage of 100ppm. Each juvenile fish was measured for length (±1mm) and weight (±0.1g) and stomach contents collected via gastric lavage for a maximum ~15 juveniles per day, per site. Due to the smaller gape limitations of the juvenile fish sampled, a modified gastric lavage method outlined by Strange & Kennedy (1981) was used by attaching micro-pipettes with 1mm tip diameter to a hand bulb and rubber tubing leading to a water reservoir. The tip of the pipette was carefully inserted into the mouth and stomach. By squeezing the hand bulb, short pulses of water flushed stomach contents into funnels with 500μm sieves. After processing, juveniles were transferred to recovery buckets with river water and then returned to the approximate location where they were collected. Over the course of the study, 100 juvenile Chinook salmon individuals were sacrificed and dissected to confirm lavage efficiency in flushing stomach contents. All diet samples and sacrifices (n=580) were washed and transferred to Whirl-Paks®, and preserved in the field using a 90% ethanol solution.

Laboratory Methods

In the laboratory, BMI benthic and drift samples were sorted, enumerated and identified based on whole samples or subsamples at 1/2, 1/4, 1/8 or 1/16 of the original sample depending on total sample volume. Subsampling was conducted following a modified version of the protocols by Rosenberg et al. (1997) using a custom gridded tray to accommodate larger volumes of detritus and inorganic material collected in two-hour drift samples, ranging from approximately 200-2,000 milliliters. Small portions of the sample were placed in petri dishes for inspection under dissecting scopes with adjustable magnification (up to 100x). This process was repeated until the whole sample or subsample was processed. As with drift samples, stomach contents were emptied onto petri dishes and processed keeping track of individual fish IDs to standardize diet biomass (mg) with the gut mass (g) of each fish to assess relative gut fullness.

Aquatic BMIs were identified to family and terrestrial invertebrates to order or class using dichotomous keys in Merritt et al. (2008), Thorp & Covich (2009), McCafferty (1983) and online resources including the USGS North American Aquatic Macroinvertebrate Digital Reference Collection (Walters et al. 2017). Lengths of individual BMIs were measured in size classes to the nearest millimeter from head capsule to the end of abdomen excluding cerci and antennae. Maximum shell lengths were measured for Gastropoda and other Mollusca. Length-mass equations were used to predict mass as a power function of a linear dimension:

(1) $M = aL^b$

Using equation (1), an organism's mass (M) is predicted by taking a known length (L) to the power of b and multiplying by a, which are published constants (Wardhaugh 2013; Wisseman 2012, unpublished data; Sabo et al. 2002; Benke et al. 1999; Appendix A). After processing, BMIs were preserved in BEEM® capsules (Glauert 1991) with a 75% ethanol solution, separated by taxa, sampling date and sampling location.

Data Analysis

Multivariate and univariate analyses were conducted after arranging BMI composition, abundance and biomass between sample types (benthic, drift and diets) into community matrices with environmental variables including sampling site, sampling day (1-28), week (1-7), month (1-3), water temperature (Celsius), dissolved oxygen (mg/L), water velocity (m/s) and discharge (m^3/s). Additionally, BMI data were used to calculate common community metrics such as taxonomic richness, relative abundance of dominant taxon and the Shannon-Wiener diversity index. A random grouping structure was also included to account for the nested and non-independent nature or observations collected from each site on each day. All statistical analyses were performed with R version 3.6.1 (R Core Team 2019) in RStudio version 1.2.5019 (RStudio Team 2019).

Invertebrate drift & benthic samples

To assess the impacts of experimental pulse releases on BMI drift, total abundances and biomass (mg) of BMIs collected in drift samples were converted to drift concentration (total biomass of BMIs collected in drift nets divided by water volume that passed through the net), drift density (total number of invertebrates/water volume through the net) and drift flux (drift concentration and densities multiplied by the expected daily discharge). Using the lme4 package in R (Bates et al. 2015), the BMI drift metrics mentioned above were log-transformed to linearize their distribution and used as responses in linear mixed effects models to account for the nested data structure. For nested sampling designs, it is good practice to include streams and/or sampling sites as random effects in mixed-models to control for non-independence of observations within streams and sites (Louhi et al. 2011; Pinheiro & Bates 2000). However, due to the small number of sampling locations, site was treated as a fixed effect. To account for the nested and non-independent data structure, a random component was included and modeled as:

$$(2)\ \log(Y_{ij}) = \alpha + \beta_1(R_i) + \beta_2(Flow_{ij}) + \beta_3(Site_{ij}) * \beta_4(Week_{ij}) + \varepsilon_{ij}$$

Where α is the intercept and $\beta_1(R_i)$ is the random grouping structure treating each site on each sampling day as an individual group. $\beta_2 - \beta_4$ are the coefficients for the fixed structure of the model predicting log-transformed drift rates, $\log(Y_{ij})$, based on observations i while allowing for mixed effects per random group j (Zuur et al. 2009). In this case, each predictor is a categorical variable where Flow represents groups of observations made during baseflow conditions, Pulse 1 and Pulse 2. Site represents observations made at Sawmill and Steel Bridge. Week represents time, grouping observations made during each week of the sampling period (1-7). Lastly, ε_{ij} represents the residual error per individual observation i and random group j in the model.

In order to address assumptions of normally distributed residuals and homogeneity of variance about a fitted line, frequency residual plots and standardized residual vs fitted value plots were produced to check assumptions. Analysis of variance (ANOVA) was used with each linear mixed effects model to statistically test for differences in drift rate metrics between sampling locations (Site), sampling time (Week) and flow conditions (Flow) and interactions between site and time. To effectively test for significant interactions between sampling time and location, marginal sums of squares were used in ANOVAs which test for significant main effects only after other factors and their interactions were tested relative to the default method that sequentially tests for significance in the order they appear in the model (Bates et al. 2015). Additionally, stacked bar charts were used to visually assess the impact of averaged daily discharge on the composition and magnitude of BMI drift concentration, density and flux as well as benthic invertebrate densities (total number of BMIs collected in the benthos per standard unit area).

Juvenile Chinook salmon diet

Using the same fixed and random structures as the linear mixed effects models predicting drift rate metrics, BMI biomass (mg) and abundance extracted from diet samples were compared across sampling site (Site), time (Week) and flow condition (Flow) using a relative gut fullness index (mg/g) and total biomass consumed (mg) as responses. Juvenile Chinook gut fullness (mg/g) was determined by dividing total BMI biomass by the mass of each fish (g). Total invertebrate biomass consumed and gut fullness were log-transformed to meet assumptions for normally distributed variance and were compared using Analysis of Variance (ANOVA) with marginal sums of squares. Tukey HSD pairwise comparisons were made to further assess the differences in juvenile Chinook consumption between baseflow conditions, Pulse 1 and Pulse 2, separated by sampling site. Frequency residual plots and standardized residual vs fitted value plots were produced to check assumptions of normally distributed residuals and homogeneity of variance. Additionally, stacked bar charts separating total consumed biomass data by site and sampling day were used to visualize percent biomass contributions in the diets per BMI taxa.

Community Analysis

Non-metric multidimensional scaling (NMDS) ordination using the Bray-Curtis dissimilarity index (Bray & Curtis 1957) was used to visualize patterns in BMI community composition among sites, sample types (i.e., drift, benthos, fish diet) and discharge. Rare invertebrate taxa were defined as those comprising <5% of relative abundance by count in benthic, drift and diet samples and were removed from analysis to avoid rare taxa from influencing ordination results. NMDS was performed by standardizing community matrices so individual observations of invertebrate taxa were on a relative scale between 0 and 1 based on their abundance to allow for comparisons among benthic, drift and diet samples (Oksanen et al. 2019). The Bray-Curtis dissimilarity index was calculated as:

(3) $$D = \frac{\sum |a_d - a_b|}{\sum a_d + \sum a_b}$$

Where a_d is the proportion of a particular invertebrate taxa found in drift samples and a_b is the proportion of the same invertebrate taxa found in benthic samples. Measures of dissimilarity were given scores between 0 (samples completely similar) and 1 (samples are completely dissimilar). Calculations were made n times until all pair-wise comparisons were made between benthic and drift samples, drift and diet samples and benthic and diet samples.

Permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis dissimilarity index was used to partition the community matrices of invertebrate taxa to identify sources of variation in the data (Oksanen et al. 2019). Monte Carlo permutation tests at 1,000 random iterations were used to test for significance via pseudo-F ratios in order to determine the significance of continuous variables to describe trends in the community matrix. I included continuous variables sampling day, discharge, turbidity, water velocity, water temperature, dissolved oxygen, taxon richness and proportions of dominant invertebrate taxa across all sample types as predictors for Bray-Curtis dissimilarity in each PERMANOVA. Additionally, environmental vectors were fit onto ordinations of community matrices to visually assess the strength and correlation of continuous variables.

Multiple response permutation procedure (MRPP) was used to test whether there was a significant difference between groups given as categorical variables including sampling site (Sawmill and Steel Bridge), flow condition (baseflow, pulse 1 and pulse 2) and sample type (benthic, drift and diets). Similar to the PERMANOVA, 1,000 random iterations of Monte Carlo permutation tests were used in MRPP to test for significant differences in the community matrices between groups. If two or more groups were significantly different in invertebrate species composition, then mean within-group Bray-Curtis dissimilarities should be less than the mean Bray-Curtis dissimilarities between two random samples from the community matrix, given as the null hypothesis (Oksanen et al. 2019).

Dominant and/or noteworthy invertebrate taxa were analyzed independently, including Chironomidae, Baetidae and *Daphnia*. Before dropping rare taxa, invertebrate families that occurred in smaller proportions were grouped into their respecting orders for easier visualization and interpretation. Taxa were ordered into the following groups with the exception for Chrionomidae (Diptera), Baetidae (Ephemeroptera) and *Daphnia* (Cladocera) which were kept separate (Table 1).

Table 1. Groups in which taxa have been ordered are in bold. Families and/or orders not in bold are listed by their respective group.

Ephemeroptera:	Heptageniidae, Ameletidae, Leptophlebiidae, Ephemerellidae
Plecoptera:	Perlidae, Perlodidae, Pteronarcyidae, Chloroperlidae, Nemouridae
Trichoptera:	Glossosomatidae, Brachycentridae, Limnephilidae, Rhyacophilidae, Hydropsychidae, Lepidostomatidae
Diptera:	Simuliidae, Ceratopogonidae, Tipulidae, Empididae, Blephericeridae, Tanyderidae, Athericidae
Coleoptera:	Elmidae, Amphizoidae, Dryopidae, Hydrophilidae, Dytiscidae, Haliplidae
Non-insects:	Oligachaeta, Sphaeriidae, Ostracoda, Nematomorpha, Acari, Amphipoda, Copepoda, Isopoda
Terrestrials:	Araneae, Collembola, Orthoptera, Lepidoptera, Hymenoptera, Hemiptera, Staphylinidae, Thysanoptera, Crambidae, Staphylinidae, Carabidae

RESULTS

Daily average discharge during baseflow conditions was consistently higher at the downstream site, Steel Bridge, and was likely influenced by accreted streamflows from tributaries Grass Valley Creek and Rush Creek. Baseflow conditions (Feb – April) during the study period at the upstream site, Sawmill, ranged from 8.17-9.60 m^3/s and at the downstream site, Steel Bridge, ranged from 9.08-11.95 m^3/s (Table 2; Table 3). Experimental pulse flows released from Lewiston Dam in April 2018 increased discharge approximately 5x during the first pulse (Pulse 1) and the second pulse (Pulse 2), both peaking at approximately 50 m^3/s. The range in discharge during both pulses were similar between sites, however the shape of the hydrograph differed between the two pulses. Both study sites experienced a 5x increase in discharge over a 24-hour period during Pulse 1 with peak discharge on 4/17/18, followed by a 3-day descending limb in the hydrograph. Following a return to baseflow conditions, both study sites experienced a 5x increase in discharge over a 6-day period during Pulse 2 with peak discharge on 4/28/18 .

Table 2. Environmental variables measured at the upstream site, Sawmill, during benthic, drift and diet sampling; averaged per sampling month and flow condition. Environmental variables include: water temperature (°C), dissolved oxygen (mg/L), water velocity (m/s), discharge (m^3/s), and turbidity (NTU). Mean values are given as well as minimum and maximum values.

Sampling month	Flow condition	Days sampled	°C			mg/L			m/s			m^3/s			NTU		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
February	Baseflow	8	8.41	6.72	9.40	11.81	11.53	12.07	0.66	0.34	0.91	9.15	8.92	9.60	0.91	0.80	1.06
March	Baseflow	8	8.97	8.40	9.86	11.79	11.30	12.07	0.74	0.52	0.90	8.86	8.74	8.91	0.94	0.87	1.00
April	Baseflow	6	11.24	10.23	11.50	11.20	10.83	11.43	0.78	0.55	1.07	8.39	8.17	8.69	1.09	0.83	1.30
April	Pulse 1	3	10.12	9.73	10.63	11.51	11.47	11.53	1.21	0.61	1.41	36.15	22.79	48.86	7.26	1.40	17.93
April	Pulse 2	3	10.45	10.0	10.97	11.33	11.17	11.57	0.91	0.76	1.07	29.47	11.24	49.05	2.88	0.90	5.30

Table 3. Environmental variables measured at the downstream site, Steel Bridge, during benthic, drift and diet sampling; averaged per sampling month and flow condition. Environmental variables include: water temperature (°C), dissolved oxygen (mg/L), water velocity (m/s), discharge (m^3/s), and turbidity (NTU). Mean values are given as well as minimum and maximum values.

Sampling month	Flow condition	Days sampled	°C			mg/L			m/s			m^3/s			NTU		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
February	Baseflow	8	7.73	6.23	8.91	12.17	11.70	12.63	0.32	0.12	0.41	10.16	9.58	10.61	0.90	0.80	1.06
March	Baseflow	8	9.17	8.17	10.57	11.70	11.43	12.00	0.34	0.22	0.56	9.99	9.08	11.95	0.99	0.80	1.47
April	Baseflow	6	12.08	10.57	13.70	10.76	10.33	11.17	0.31	0.23	0.36	10.09	9.73	10.35	1.09	0.83	1.30
April	Pulse 1	3	11.72	10.90	12.33	10.97	10.77	11.20	0.75	0.67	0.79	39.88	27.75	52.80	7.26	1.40	17.93
April	Pulse 2	3	12.59	11.03	14.00	10.70	10.27	11.17	0.67	0.49	0.88	27.80	14.29	52.48	2.22	0.90	5.30

Water temperatures steadily increased during warmer months of the study period (Table 2; Table 3). Conversely, dissolved oxygen concentrations decreased during warmer months (Table 2; Table 3). The volume of debris and detritus captured in drift nets increased dramatically during Pulse 1. Up to 2,000 milliliters of material was captured in each drift net at Steel Bridge during peak discharge of Pulse 1, whereas approximately 1,000 milliliters was captured during peak discharge of Pulse 2. Additionally, turbidity sharply increased during pulse 1 and to a lesser degree during Pulse 2 (Table 2; Table 3).

The volume of debris captured in drift nets was greater at the upstream site, Sawmill, for the majority of the study period and was primarily fine particulate organic matter (FPOM) and the filamentous algae Cladophoraceae: *Cladophora.* The volume of debris at the downstream site, Steel Bridge, was primarily comprised of coarse particulate organic matter (CPOM) and BMI exuviae, only exceeding Sawmill in volume during peak discharge of Pulse 1 (4/17/18). Additionally, *Cladophora* was only captured in the drift at Steel Bridge during pulse flows.

Benthic Macroinvertebrates

A total of 133,990 individual invertebrates were estimated to have been captured between all sample types during the study period (benthic: 38,129, drift: 85,729, diet: 10,132 individuals). Fifty unique invertebrate taxa were identified and enumerated from benthic, drift and diet samples (Appendix B). Chironomidae (Diptera) and Baetidae (Ephemeroptera) were the most abundant families found in benthic, drift and diet samples across all sampling occasions with the exception of *Daphnia*, a genus under Cladocera also referred to as water fleas, which was a dominant taxon in terms of drifting BMI abundance during Pulse 1 and Pulse 2.

Benthic densities were relatively similar between study sites, but the numbers of BMIs collected following Pulse 1 at Sawmill was much greater than Steel Bridge, which exhibited a decreasing trend through time (Figure 3). Benthic densities at the upstream site, Sawmill, ranged from approximately 750-3,500/m^2 and approximately 500-4,000/m^2 at the downstream site, Steel Bridge (Figure 3). For the majority of benthic samples taken from both sites, Chironomidae larvae were the most influential family and life stage contributing to benthic densities (~10-74%, Figure 3). Baetidae larvae was the next most influential family contributing ~2-27% to benthic densities (Figure 3). The lowest benthic densities at both sites were recorded 5 days following Pulse 1 on 4/22/18 when discharge returned to baseflow conditions (Sawmill; ~750/m2, Steel Bridge; ~500/m^2, Figure 3). Taxonomic richness and was greater at the downstream site, Steel Bridge (Appendix B).

However, both pulse flows slightly reduced BMI taxonomic richness in the benthos at both sites (Appendix B).

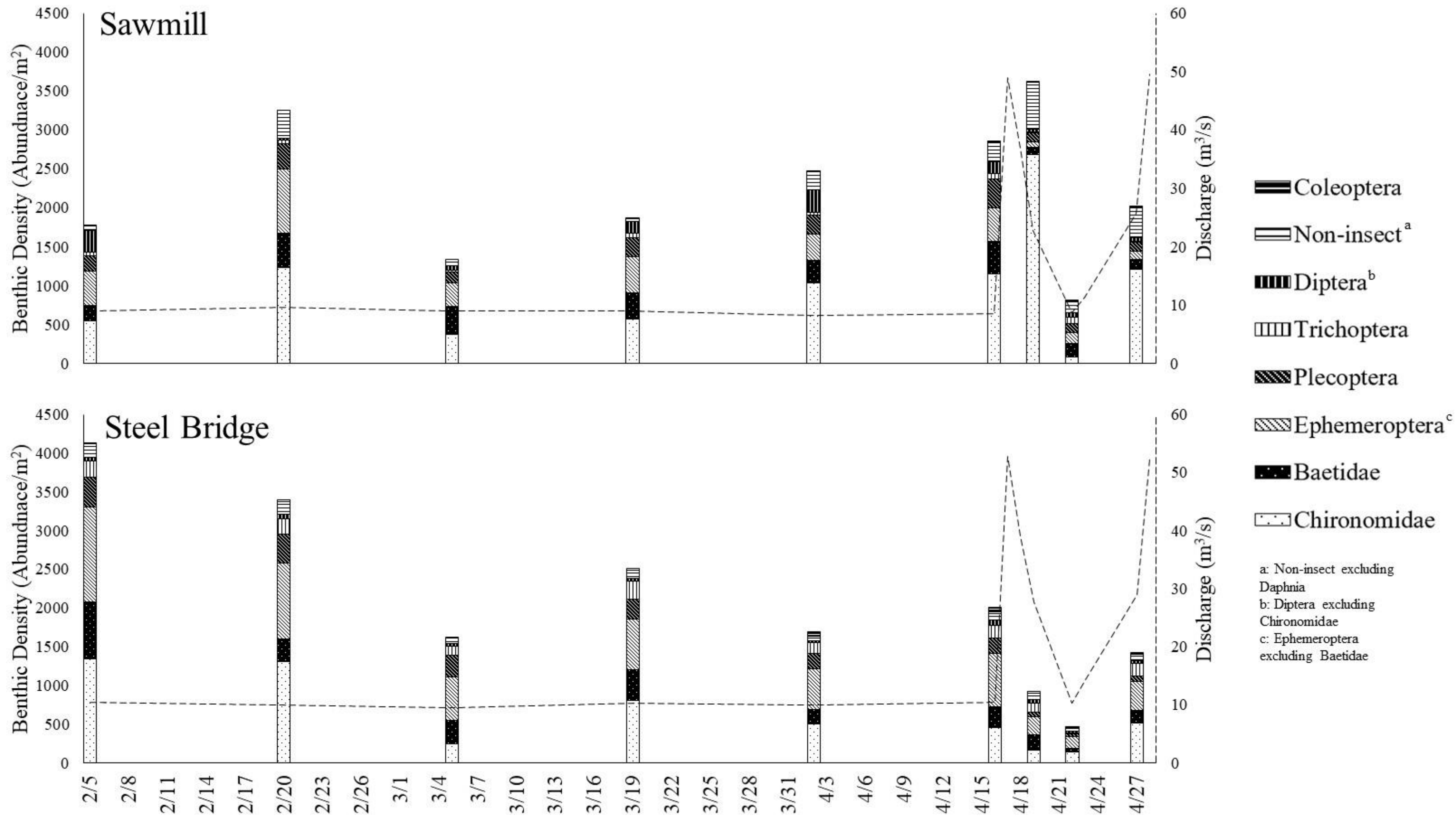

Figure 3. Changes in average benthic macroinvertebrate densities and composition from Feb-April 2018 at both study sites, Sawmill and Steel Bridge. The left y-axis represents benthic densities separated by invertebrate taxa. The right y-axis represents daily average discharge with a superimposed hydrograph and the x-axis represents sampling date.

Invertebrate Drift Rates

Invertebrate drift densities (abundance/m^3) and concentrations (mg/m^3) were highly variable at both study sites across the sampling period. Drift densities during the study period ranged 0.61-7.51 individuals/m^3 at Sawmill and 0.11-6.39 individuals/m^3 at Steel Bridge. Drift concentrations ranged 0.22-1.21 mg/m^3 at Samwill and 0.03-1.59 mg/m^3 at Steel Bridge.

ANOVA results suggest log-transformed drift densities and concentrations differed between sites depending on the week of sampling as suggested by significant interactions between sampling site and week (Table 4; Table 5). There was no evidence to support the hypothesis that flow condition has a significant impact of drift rates at both sites (Table 4; Table 5), however drift densities peaked at Steel Bridge during peak discharge of Pulse 1 (Figure 4). In general, drift rates at Steel Bridge gradually decreased from February to April, however drift rates were highly variable throughout the sampling period at the upstream site, Sawmill (Figure 4).

Table 4. Analysis of variance results from full linear mixed-effects models comparing log-transformed abundances BMI drift rates (density). Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	44	0.29	0.75
Site	1	36	0.01	0.96
Week	6	36	2.59	0.04
Site*Week	6	36	2.60	0.03

Table 5. Analysis of variance results from full linear mixed-effects models comparing log-transformed biomass BMI drift rates (concentration). Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	44	0.09	0.912
Site	1	36	0.02	0.881
Week	6	36	5.48	<0.001
Site*Week	6	36	3.50	0.010

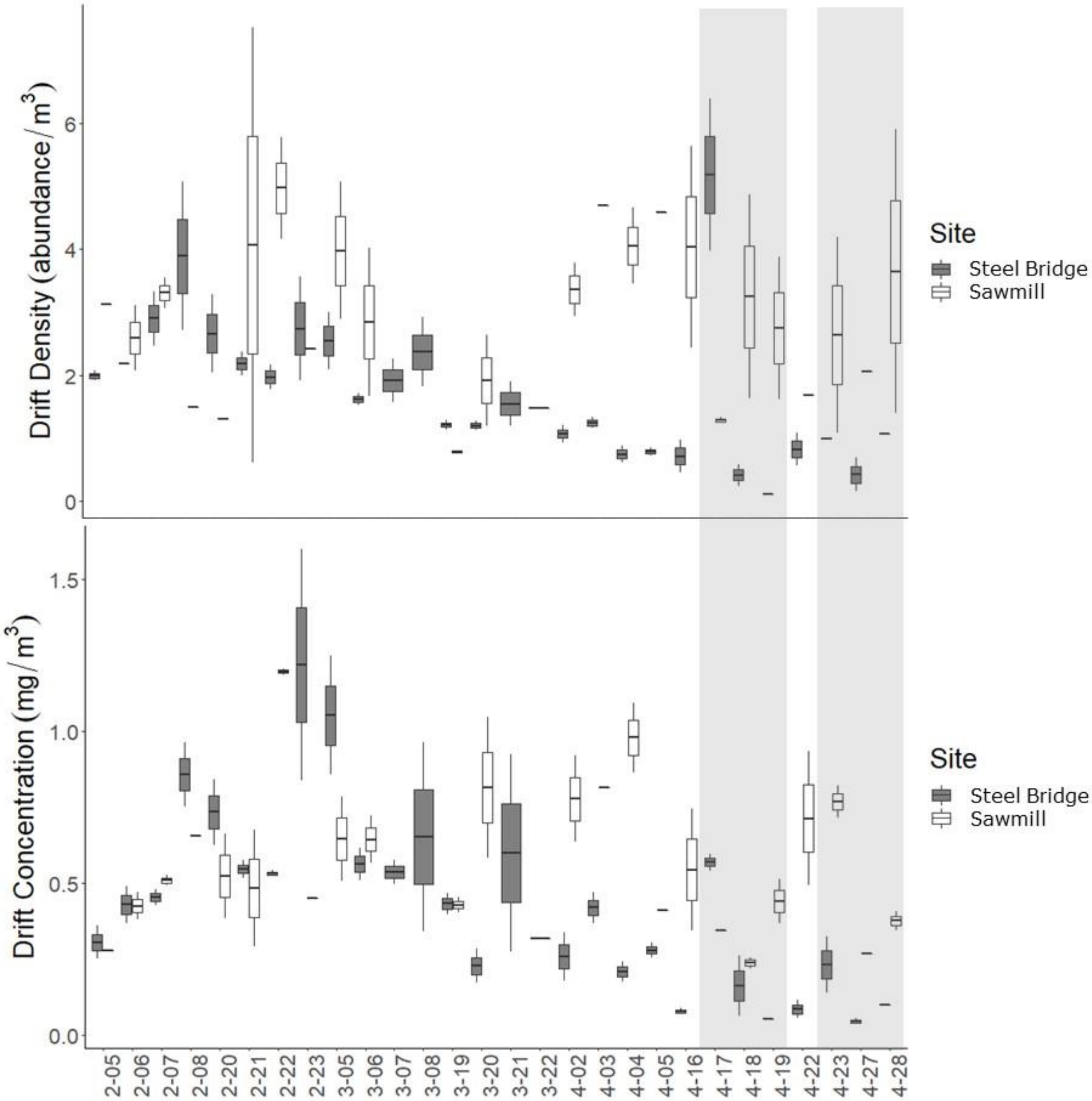

Figure 4. Box and whisker plots of macroinvertebrate drift density and drift concentration at both study sites, Sawmill and Steel Bridge from each day of sampling. Shaded regions represent periods of elevated discharge during pulse flows. Peaks in flow for Pulse 1 are on 4/17/18. A return to baseflows on 4/22/18 is followed by an increase and peak in flows for Pulse 2 on 4/28/18.

After converting densities and concentrations to flux, the total export of BMI abundance at Sawmill and Steel Bridge ranged from 5.89-380.83 individuals and 3.14-357.60 individuals, respectively. Drift flux biomass at Sawmill and Steel Bridge ranged from 2.48-20.21 mg/s and 0.58-34.88 mg/s, respectively. Average drift flux abundance at peak discharge at Sawmill was 73.28 individuals/s (Pulse 1) and 227.92 individuals/s (Pulse 2) individuals, representing a ~2.5x increase during Pulse 1 and ~8x increase in Pulse 2 in mean invertebrate abundance, relative to average baseflow conditions. Average invertebrate drift flux abundance at peak discharge at Steel Bridge was 286.68 individuals/Q (Pulse 1) and 71.78 individuals/Q (Pulse 2) individuals, representing a ~15x and ~4x increase in invertebrate flux respectively, relative to average baseflow conditions. The highest values, 286.68 individuals/s at 33.01 mg/s, were recorded at Steel Bridge during peak discharge of Pulse 1 (4/17/18; Figure 5).

ANOVA results suggests flow condition had the largest impact on the export of BMIs (Table 6; Table 7). However, a significant interaction between site and sampling week suggests the export of the biomass of BMIs differs between sites depending on when the samples were taken (Table 6; Table 7).

Table 6. Analysis of variance results from full linear mixed-effects model comparing log-transformed export of BMI abundance per second in the drift (flux). Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	44	3.63	0.034
Site	1	36	0.09	0.763
Week	6	36	1.83	0.120
Site*Week	6	36	1.82	0.124

Table 7. Analysis of variance results from full linear mixed-effects model comparing log-transformed export of BMI biomass per second in the drift (flux). Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	44	7.89	0.001
Site	1	36	0.22	0.646
Week	6	36	4.62	0.001
Site*Week	6	36	2.89	0.021

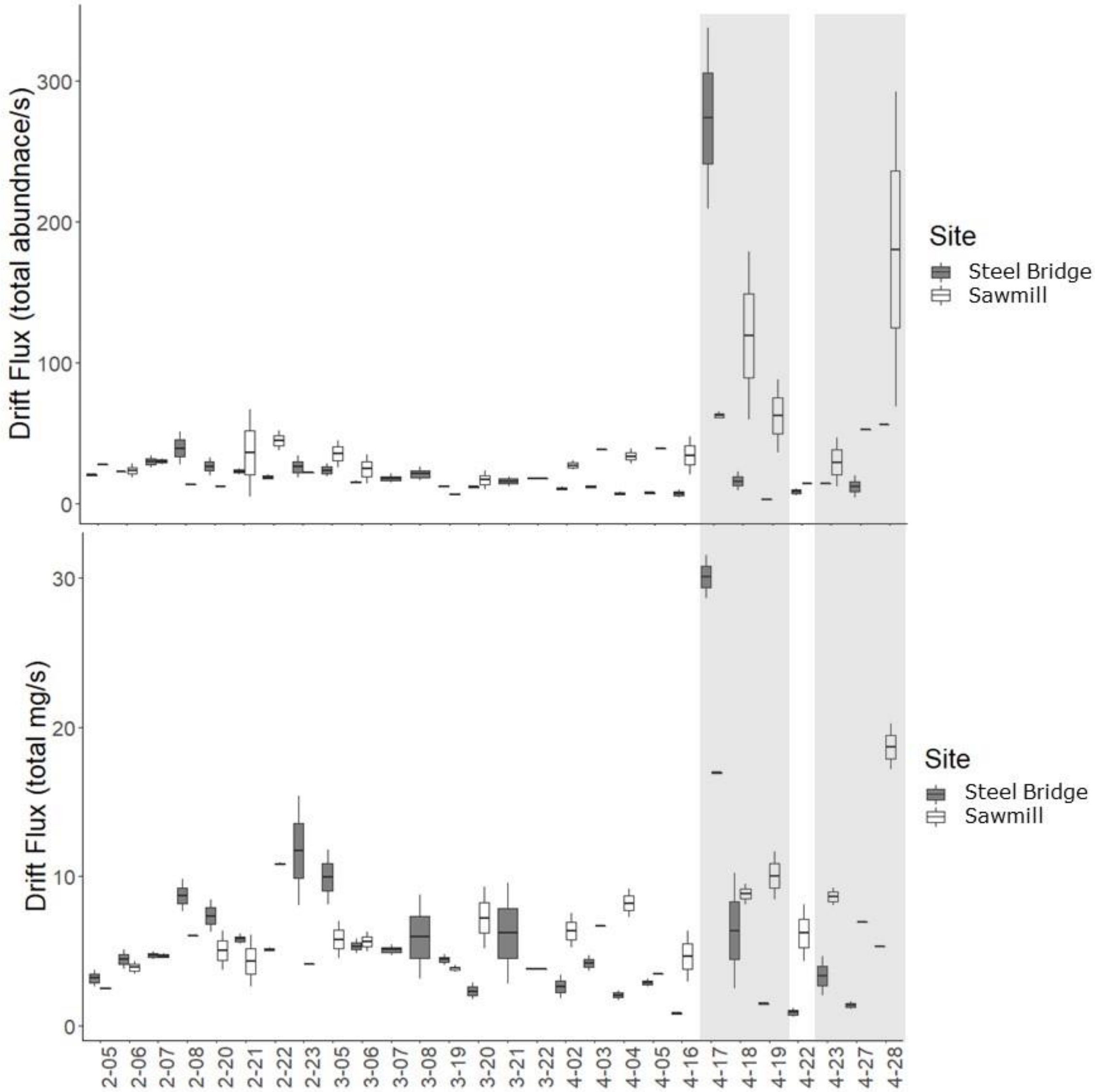

Figure 5. Total export of drifting BMI abundance and biomass represented by drift flux at both study sites, Sawmill and Steel Bridge, from each day of sampling. Shaded regions represent periods of elevated discharge during pulse flows. Peaks in flow for Pulse 1 are on 4/17/18. A return to baseflows on 4/22/18 is followed by an increase and peak in flows for Pulse 2 on 4/28/18.

Invertebrate Drift Composition

Daphnia, Chironomidae, non-insects (notably Oligachaeta, Nematomorpha and Acari), Ephemeroptera adults, and Diptera adults increased in relative abundance during both pulse flows at both study sites (Figure 6). *Daphnia* alone constituted 30% and 50% of invertebrate abundances in drift flux at Sawmill and Steel Bridge, respectively during the peak discharge of Pulse 1, a 20x and 30x increase, respectively relative to average baseflow conditions. Interestingly, Baetidae abundance remained relatively constant in the drift at the upstream site, Sawmill, but decreased in abundance over time at the downstream site, Steel Bridge (Figure 6). Taxonomic richness in the drift at both sites were constantly higher during baseflow conditions at both sites, relative to pulse flows where drops in the number of BMI taxa were observed (Appendix B). Additionally, taxonomic richness in drift was consistently higher at Sawmill during both pulse flows (Appendix B).

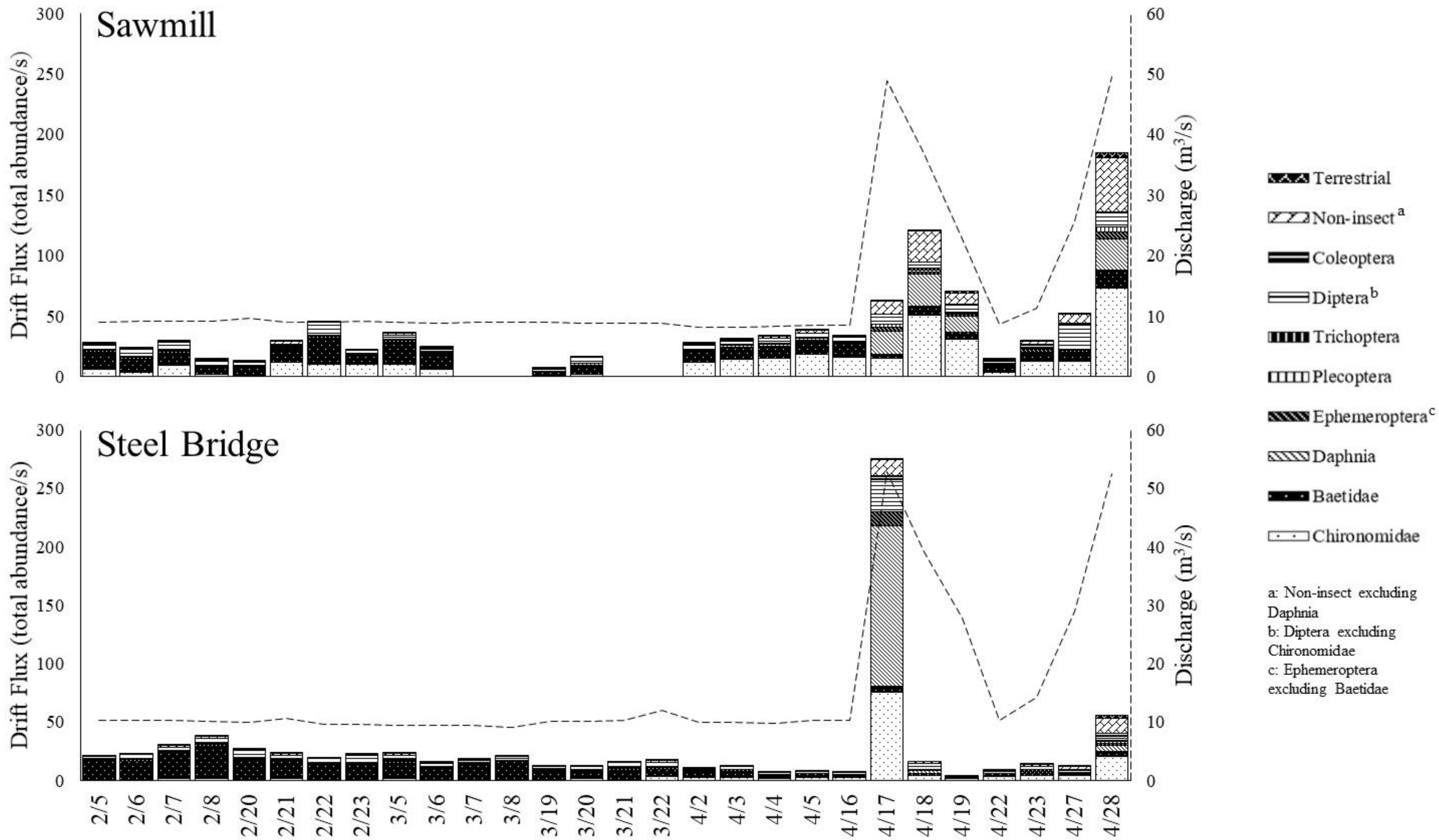

Figure 6. Mean invertebrate abundance in drift flux at both sites over time separated by taxa contribution in stacked bar. The left y-axis is drift flux magnitude (stacked bars), the right y-axis is daily average discharge (dotted line) and sampling date is on the x-axis.

Only a few taxa (e.g., Chironomidae, Baetidae, *Daphnia*) constituted the majority of drifting invertebrate abundances throughout the study period, however taxa contributions in drifting invertebrate biomass were more similar across taxa (Figure 7). Invertebrate taxa and life stages contributing to increases in drifting invertebrate biomass at Sawmill during both pulse flows included Chironomidae (9.43%), Ephermeroptera (14.15%, namely Heptageniidae and Ephemerellidae), Plecoptera larvae (22.92%, namely Perlodidae), Diptera adults (14.10%, namely Chironomidae), Trichoptera larvae (7.45%, namely Glossosomatidae), non-insects (9.96%), Coleoptera (3.19%) and terrestrial invertebrate inputs (4.21%; Figure 7). Invertebrate taxa that were dominant with increases in drifting invertebrate biomass at Steel Bridge during both pulse flows included Chironomidae (13.71%), *Daphnia* (15.13%), Ephermeroptera larvae (13.64%, namely Ephemerellidae), Plecoptera larvae (9.53%, namely Perlodidae), Diptera adults (18.91%, namely Chironomidae), non-insects (5.18%), Coleopterans (6.98%) and terrestrial invertebrate inputs (4.13%; Figure 7).

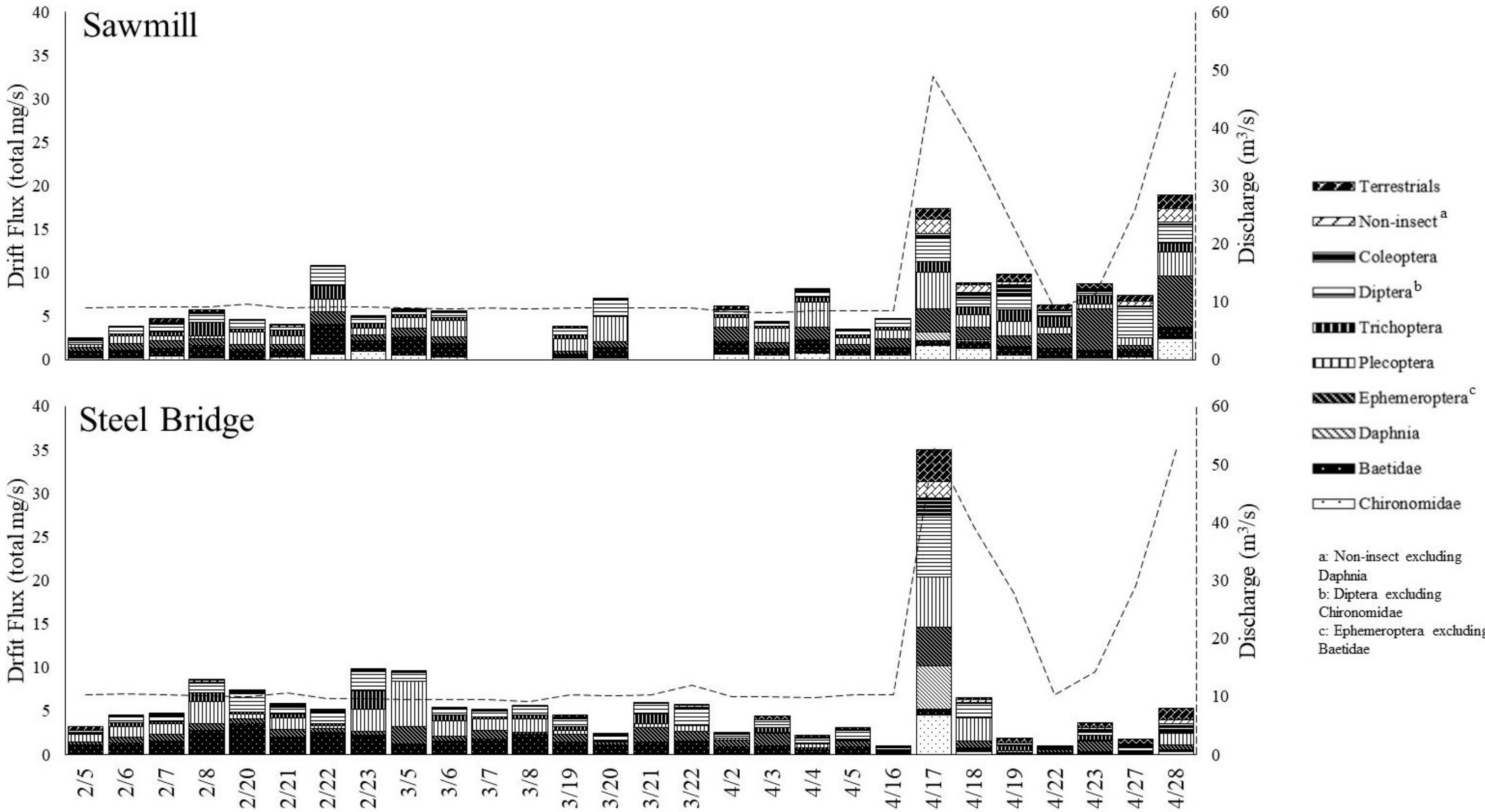

Figure 7. Mean invertebrate biomass in drift flux at both sites over time separated by taxa contribution. The left vertical axis represents drift flux magnitude, the right vertical axis represents daily average discharge and the horizontal axis represents sampling date.

Juvenile Chinook Salmon Diet

A total of 580 juvenile Chinook diet samples were processed to examine consumption and composition of BMIs in diets (Table 8; Table 9). Juvenile lengths and weights slightly increased throughout the sampling period. More juvenile Chinook were sampled via gastric lavage in March and April compared to February due to the lack of availability of ≥50 mm long fish in February 2018 (Table 8; Table 9).

Table 8. Number and size of juvenile Chinook salmon captured and lavaged/dissected from the upstream site, Sawmill, Feb-April 2018. Sampling month, number of days sampled and sample size (N) are given as well as mean, min and max fish length and mass.

			Length (mm)			Mass (g)		
Sampling month	Days sampled	N	Mean	Min	Max	Mean	Min	Max
February	8	30	47.30	38	54	1.05	0.4	1.6
March	8	100	50.81	36	66	1.28	0.3	3
April	12	159	53.09	38	72	1.50	0.3	3.5

Table 9. Number and size of juvenile Chinook salmon captured and lavaged/dissected from the downstream site, Steel Bridge, Feb-April 2018. Sampling month, number of days sampled and sample size (N) are given as well as mean, min and max fish length and mass.

			Length (mm)			Mass (g)		
Sampling month	Days sampled	N	Mean	Min	Max	Mean	Min	Max
February	8	31	50.97	41	57	1.33	0.6	2.2
March	8	102	52.51	36	68	1.39	0.4	2.8
April	12	158	55.54	38	75	1.86	0.4	4.7

Results from ANOVA suggest log-transformed diet metrics did not change between flow conditions when sampling site, time and their interactions are considered (Table 10; Table 11). These results indicate that juvenile Chinook did not consume more

BMI biomass during pulse flows, rather highly variable data was observed during pulse flows similar to standardized drift concentration (mg/m^3) and density (abundance/m^3). Additionally, total BMI biomass consumed and gut fullness did not respond to the increases in total export of BMI abundance and biomass in drift flux. Although assumptions of homogeneity of variance were satisfied, there was some skewness evident in the distribution of the residuals, but the impact of this would be more concerning if at least marginal evidence for significant impacts on diets were found.

Table 10. Analysis of variance results from full linear mixed-effects models comparing log-transformed total BMI biomass consumed (mg) of juvenile Chinook salmon. Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	39	2.49	0.100
Site	1	39	0.21	0.647
Week	6	39	1.69	0.148
Site*Week	6	39	0.48	0.818

Table 11. Analysis of variance results from full linear mixed-effects models comparing log-transformed gut fullness (mg/g) of juvenile Chinook salmon. Fixed effects include site, time (week), flow condition (baseflow, Pulse 1, Pulse 2) and their interactions. A random grouping structure has been included to account for the nested and non-independent nature of observations collected from each site on each day. F-value test statistics, numerator and denominator degrees of freedom (Df) and significance (p) are given.

Variable	numDf	denDf	F	*p*
Flow	2	39	2.51	0.094
Site	1	39	0.60	0.444
Week	6	39	2.06	0.081
Site*Week	6	39	0.83	0.558

Tukey HSD results suggest the total consumption of BMI biomass was slightly higher at Sawmill during Pulse 2 relative to baseflow conditions (Table 12). Additionally, the total consumption of BMI biomass and gut fullness during Pulse 2 at the downstream site, Steel Bridge, was higher relative to Pulse 1, but not significantly different relative to baseflow conditions (Table 12; Table 13). However, these findings are most likely due to the highly variable nature of the diet data collected, as there is no evidence that flow condition had a significant impact on juvenile Chinook diet when sampling site and time are taken into consideration (Table 10; Table 11).

Table 12. Tukey pairwise comparisons of log transformed total biomass (mg) of invertebrates consumed by juvenile Chinook salmon at both study sites on the Trinity River. Comparisons are between sampled flow conditions.

	Sawmill		Steel Bridge	
Comparison	Difference	*p*	Difference	*p*
Pulse 1-Baseflow	0.007	0.999	-0.181	0.423
Pulse 2-Baseflow	0.327	0.034	0.330	0.126
Pulse 2-Pulse 1	0.320	0.131	0.512	0.018

Table 13. Tukey pairwise comparisons of log transformed gut fullness (mg/g) of juvenile Chinook salmon at both study sites on the Trinity River. Comparisons are made between sampled flow conditions.

	Sawmill		Steel Bridge	
Comparison	Difference	*p*	Difference	*p*
Pulse 1-Baseflow	-0.011	0.931	-0.072	0.118
Pulse 2-Baseflow	0.066	0.097	0.052	0.318
Pulse 2-Pulse 1	0.077	0.137	0.123	0.023

The total consumption of invertebrate biomass (mg) and juvenile gut fullness (mg/g) was highly variable between sites throughout the sampling period (Figure 8).

Total biomass consumed by juvenile Chinook at Sawmill ranged from 0-27.02 mg with a mean 3.51 mg and gut fullness ranged from 0-1.87 mg/g with a mean 0.26 mg/g. Total biomass consumed by juveniles at Steel Bridge ranged 0-38.88 mg with a mean 5.51 mg and gut fullness ranged 0-2.46 mg/g with a mean of 0.34 mg/g (Figure 8).

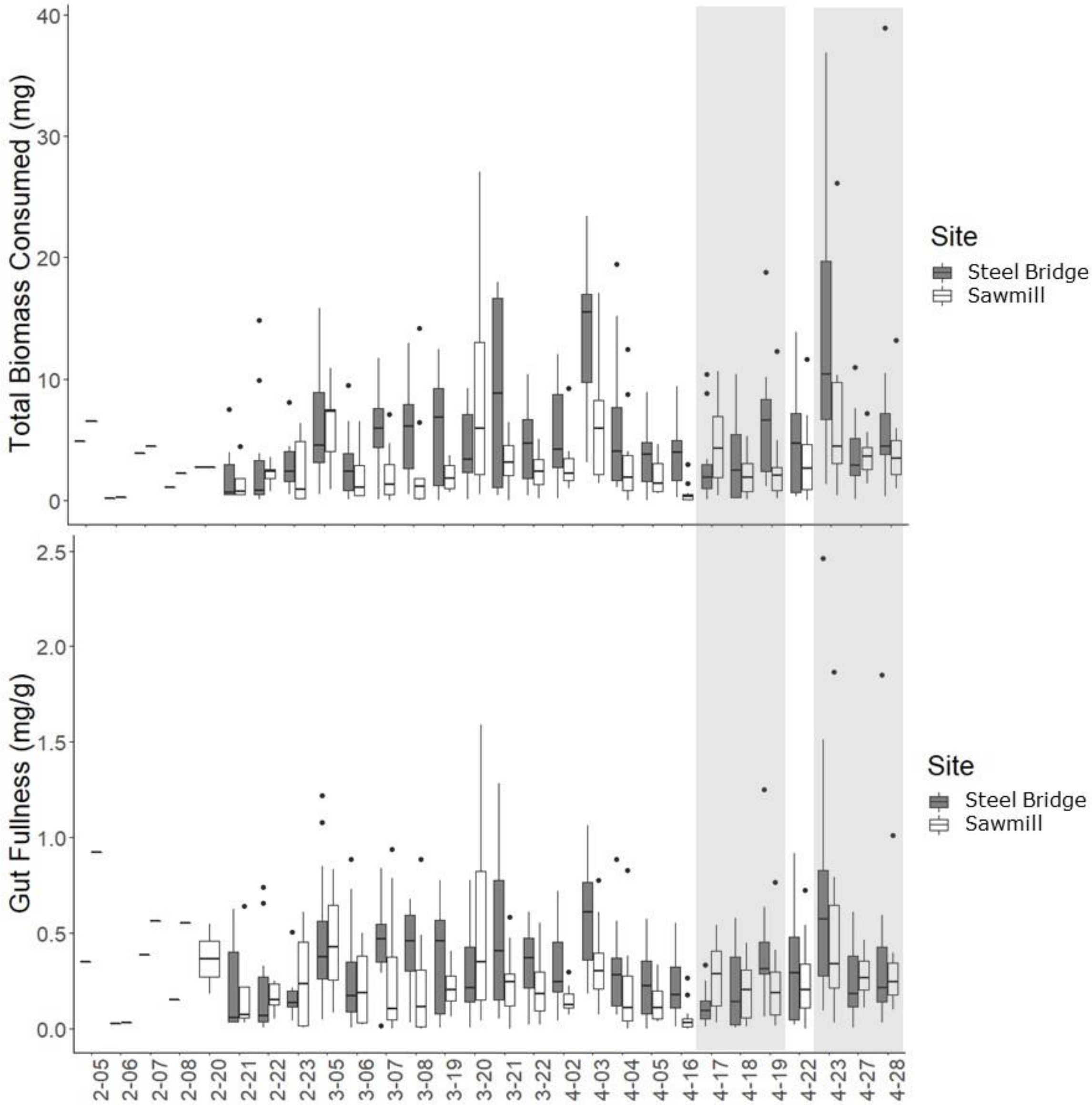

Figure 8. Juvenile Chinook diet data collected February-March 2018 from both study sites combined, Sawmill and Steel Bridge. Total biomass (mg) consumed by fish and gut fullness (mg/g) on each day of sampling. Shaded regions represent periods of elevated discharge during pulse flows. Peaks in flow for Pulse 1 are on 4/17/18. A return to baseflows on 4/22/18 is followed by an increase and peak in flows for Pulse 2 on 4/28/18.

Juvenile Chinook Diet Composition

Similar to invertebrate taxa collected from the benthos, taxonomic richness ($F=16.5$, $p<0.001$) and diversity ($F=40.51$, $p<0.001$) collected from diets were significantly greater at Steel Bridge during baseflow conditions. However, diets collected during both pulses had lower invertebrate taxonomic richness at both sites (Appendix B). Interestingly, the upstream site, Sawmill, had significantly higher invertebrate diversity collected from diets during both pulses relative to Steel Bridge ($F=17.07$, $p<0.001$), but taxonomic richness in diets was similar between sites (Appendix B).

Chironomidae (Diptera) and Baetidae (Ephemeroptera) constituted the vast majority of biomass consumed by juvenile Chinook salmon at both sites throughout the study period. After diet data were combined per day for each site, Chironomidae contributions to biomass consumed at the upstream site, Sawmill, ranged from ~3-86% and ~2-42% at the downstream site, Steel Bridge (Figure 9). Baetidae contribution to biomass consumed at Sawmill range from ~5-96% and ~3-80% at Steel Bridge (Figure 9). All other taxa contributions to biomass consumed at Sawmill ranged from <2%-68% and ~12-65% at Steel Bridge (Figure 9).

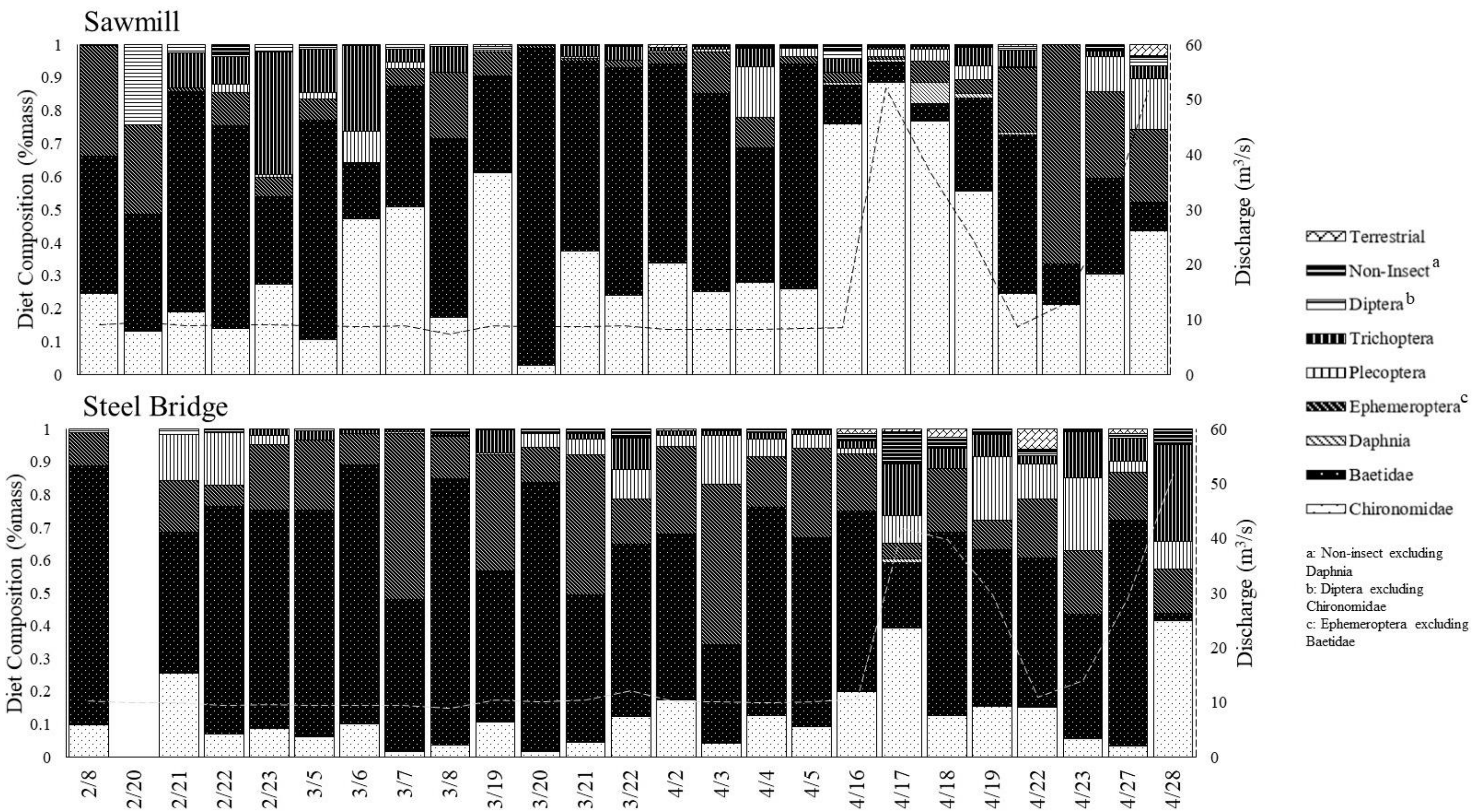

Figure 9. Invertebrate composition in juvenile Chinook salmon diets separated by taxa from both study sites during the study period (Feb-April 2018). The left y-axis is diet composition (%biomass), the right y-axis is daily average discharge (dashed line) and sampling date is on the x-axis. Missing data on 2/20/18 indicates no invertebrates were collected from diets at the study site and time.

Community Analysis

Invertebrate composition in standardized sample types (i.e., drift, benthic, fish diet) differed among site ($A=0.06$, $p<0.001$), sample type ($A=0.06$, $p<0.001$; Table 14) and flow condition ($A=0.04$, $p<0.001$; Table 15). However, the A values per MRPP result suggests that a small amount a variability was explained by grouping the data into sample types (Table 14) and flow condition (Table 15). Additionally, there was a relatively large degree of overlap among groupings in the NMDS ordination, especially in diets (Figure 10; Figure 11) due to the high degree of variability common in BMI and diet data (Santos et al. 2013).

Table 14. MRPP results of weighted mean within-group dissimilarity values between all flow conditions for each sample type (benthic, drift, diet) based on the Bray-Curtis index where 0 is completely similar and 1 is completely dissimilar. Number of samples and sample type scores are given per site and between sites. H_o represents the expected dissimilarity given the null hypothesis of no group dissimilarity between random samples. A is the proportion of dissimilarity distances explained by the group (analogous to R^2). P is the significance of the random permutation test based on 1,000 iterations.

	N	Benthic	Drift	Diet	H_o	A	p
Sawmill	300	0.32	0.46	0.38	0.48	0.07	<0.001
Steel Bridge	350	0.25	0.61	0.41	0.61	0.07	<0.001
Both sites	650	0.33	0.58	0.42	0.59	0.06	<0.001

Table 15. MRPP results of weighted mean within-group dissimilarity values between all sample types for each flow condition based on the Bray-Curtis index where 0 is completely similar and 1 is completely dissimilar. Number of samples and flow condition scores are given per site and between sites. H_o represents the expected dissimilarity given the null hypothesis of no group dissimilarity between random samples. A is the proportion of dissimilarity distances explained by the group (analogous to R^2). P is the significance of the random permutation test based on 1,000 iterations.

	N	Baseflow	Pulse 1	Pulse 2	H_o	A	p
Sawmill	300	0.46	0.38	0.50	0.48	0.05	<0.001
Steel Bridge	350	0.57	0.65	0.67	0.61	0.03	<0.001
Both sites	650	0.56	0.56	0.61	0.57	0.04	<0.001

Mean within-group Bray-Curtis dissimilarity values after 1,000 random permutations indicate benthic samples were the least variable sample type throughout the study period at both sites (Table 14). Interestingly, MRPP results suggest diet samples contained less variable invertebrate compositions compared to drift samples throughout the study period (Table 14). Additionally, drift samples at both sites contained the most variable invertebrate composition at both sites (Table 14). When compared across flow condition, all sample types (benthic, drift and fish diets) were less variable in invertebrate composition during Pulse 1 at Sawmill, whereas at Steel Bridge sample types diverged in similarity during pulse flows (Table 15). Additionally, diet composition at Sawmill during Pulse 1 was most similar to benthic invertebrate composition (Appendix C). Conversely, during the same time at Steel Bridge, diet compositions became relatively more dissimilar to benthic invertebrate composition (Appendix C).

Environmental vectors in the NMDS ordination and PERMANOVA results of both sites suggest that compositional variables (Chironomidae, Baetidae) included in the vector analysis described the most variability relative to all other taxa considered (Table 16; Table 17). Chironomidae relative abundance was correlated (p<0.001, $R^2 = 0.81$; Table 16) with periods of elevated discharge, especially at Sawmill (Pulse 1 & Pulse 2; Figure 10; Figure 11), whereas Baetidae relative abundance was correlated (p<0.001, $R^2 = 0.83$; Table 16) with baseflow conditions at both sites (Figure 10; Figure 11). However, the large variability in taxonomic composition of diet samples collected during periods of elevated discharge suggest a high degree of variability, especially at Steel Bridge where ordination results suggest increased discharge did not impact invertebrate composition in diets to the same degree as Sawmill (Figure 11). Compositional variables (e.g., Chironomidae; $R^2 = 0.81$, Baetidae; $R^2 = 0.83$, Richness; $R^2 = 0.18$) and environmental variables (e.g., day; $R^2 = 0.18$, discharge; $R^2 = 0.15$) explained the most variability in the community data set (Table 16; Table 17).

Table 16. Results from NMDS environmental vector fit on continuous environmental and community variables between both study sites on the Trinity River. R^2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	NMDS1	NMDS2	R^2	*p*
Day	-0.66610	0.74580	0.1930	<0.001
Temperature	-0.47734	0.87872	0.0796	<0.001
DO	0.42135	-0.90690	0.0652	<0.001
Turbidity	-0.86067	0.50917	0.0893	<0.001
Discharge	-0.74714	0.66467	0.1474	<0.001
Richness	0.10042	-0.99494	0.1794	<0.001
Diversity	0.99060	0.13681	0.0388	<0.001
Chironomidae	-0.98500	-0.17257	0.8141	<0.001
Baetidae	0.66531	-0.74657	0.8295	<0.001
Daphnia	-0.95528	-0.29571	0.0234	<0.001
Ephemeroptera	0.46386	0.88591	0.5285	<0.001

Table 17. Results from permutational multivariate ANOVA (PERMANOVA) on continuous environmental and community variables between both study sites on the Trinity River. R^2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	Df	SS	MS	F	R^2	*p*
Day	1	9.169	9.169	170.29	0.0716	<0.001
Temperature	1	1.371	1.371	25.47	0.0107	<0.001
DO	1	0.313	0.313	5.82	0.0024	0.002
Turbidity	1	2.234	2.234	41.48	0.0174	<0.001
Discharge	1	0.445	0.445	8.27	0.0034	<0.001
Richness	1	6.435	6.435	119.51	0.0502	<0.001
Diversity	1	7.663	7.663	142.32	0.0598	<0.001
Chironomidae	1	36.267	36.267	673.57	0.2831	<0.001
Baetidae	1	18.499	18.499	343.56	0.1444	<0.001
Daphnia	1	3.057	3.057	56.78	0.0238	<0.001
Ephemeroptera	1	8.265	8.265	153.49	0.0645	<0.001
Residuals	638	34.352	0.054		0.2682	
Total	649	128.069			1.0000	

Environmental vectors in the NMDS ordination of Sawmill (Figure 10) suggest increases in Chironomidae relative abundance in all sample types during periods of elevated discharge (Pulse 1 & Pulse 2). Similarly, increases in Chironomidae relative abundance were found in drift samples during periods of elevated discharge at Steel Bridge, while benthic and diet samples remained largely unchanged in invertebrate composition (Figure 11). Both Chironomidae and Baetidae relative abundance described a high degree of variability in NMDS ordinations of Sawmill (Chironomidae; $R^2 = 0.69$, Baetidae; $R^2 = 0.85$, Table 18; Table 19) and Steel Bridge (Chironomidae; $R^2 = 0.81$, Baetidae; $R^2 = 0.83$, Table 20; Table 21) relative to the other invertebrate taxa included in the analysis. Chironomidae were more associated with higher discharge and Baetidae were more associated with baseflow conditions in the drift at Steel Bridge (Figure 11).

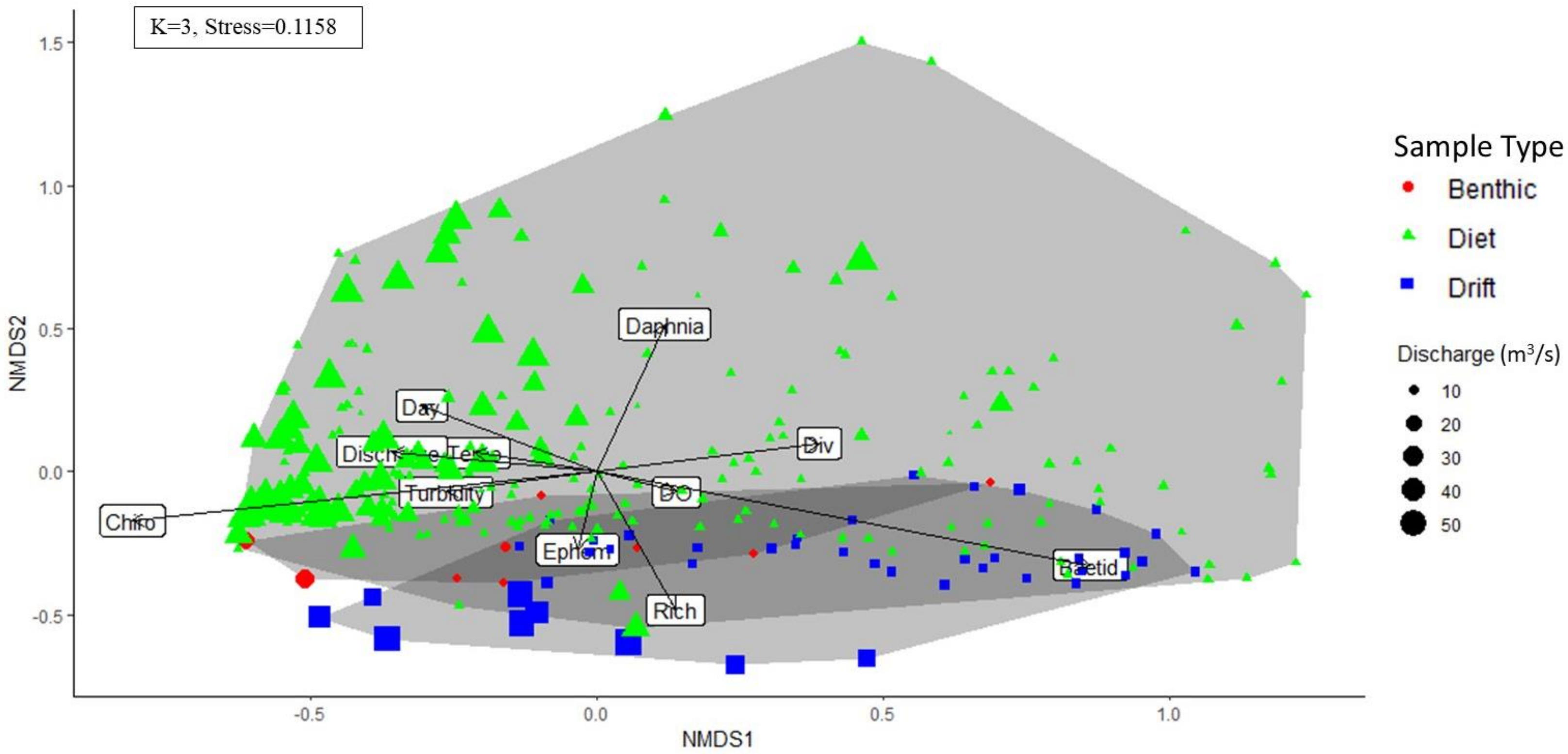

Figure 10. NMDS ordination plot of standardized benthic, drift and diet samples from the upstream site, Sawmill, on the Trinity River sample type (symbol shape and color) and the discharge when the sample was collected (symbol size). Continuous variables are vectors that represent correlations within the community matrix (direction) and the correlations strength (length). Rich=taxonomic richness, Div= diversity, DO=dissolved oxygen, Temp=temperature, Baetid=Baetidae relative abundance, Chiro=Chironomidae relative abundance, Daphnia=*Daphnia* relative abundance.

Table 18. Results from NMDS environmental vector fit and permutational multivariate ANOVA (PERMANOVA) on continuous environmental and community variables at the upstream site, Sawmill, on the Trinity River. R2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	NMDS1	NMDS2	R^2	*p*
Day	-0.78903	-0.61436	0.1508	<0.001
Temperature	-0.94393	-0.33013	0.0514	<0.001
DO	0.87539	0.48342	0.0254	0.020
Turbidity	-0.96998	0.24317	0.0747	<0.001
Discharge	-0.97579	-0.21870	0.1344	<0.001
Richness	0.27200	0.96230	0.2568	<0.001
Diversity	0.96971	-0.24424	0.1586	<0.001
Chironomidae	-0.97695	0.21347	0.6900	<0.001
Baetidae	0.93664	0.35029	0.8484	<0.001
Daphnia	-0.11436	0.99344	0.0768	<0.001
Ephemeroptera	0.21891	-0.97574	0.2818	<0.001

Table 19. Results from permutational multivariate ANOVA (PERMANOVA) on continuous environmental and community variables at the upstream site, Sawmill, on the Trinity River. R2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	Df	SS	MS	F	R^2	*p*
Day	1	2.849	2.8485	69.807	0.06856	<0.001
Temperature	1	0.321	0.3208	7.863	0.00772	<0.001
DO	1	0.191	0.1912	4.685	0.00460	0.003
Turbidity	1	0.778	0.7782	19.071	0.01873	<0.001
Discharge	1	0.440	0.4395	10.771	0.01058	<0.001
Richness	1	2.860	2.8595	70.076	0.06882	<0.001
Diversity	1	4.451	4.4509	109.076	0.10712	<0.001
Chironomidae	1	9.722	9.7220	238.253	0.23398	<0.001
Baetidae	1	4.772	4.7716	116.936	0.11484	<0.001
Daphnia	1	1.599	1.5985	39.174	0.03847	<0.001
Ephemeroptera	1	1.818	1.8176	44.543	0.04374	<0.001
Residuals	288	11.752	0.0408		0.28284	
Total	299	41.550			1.00000	

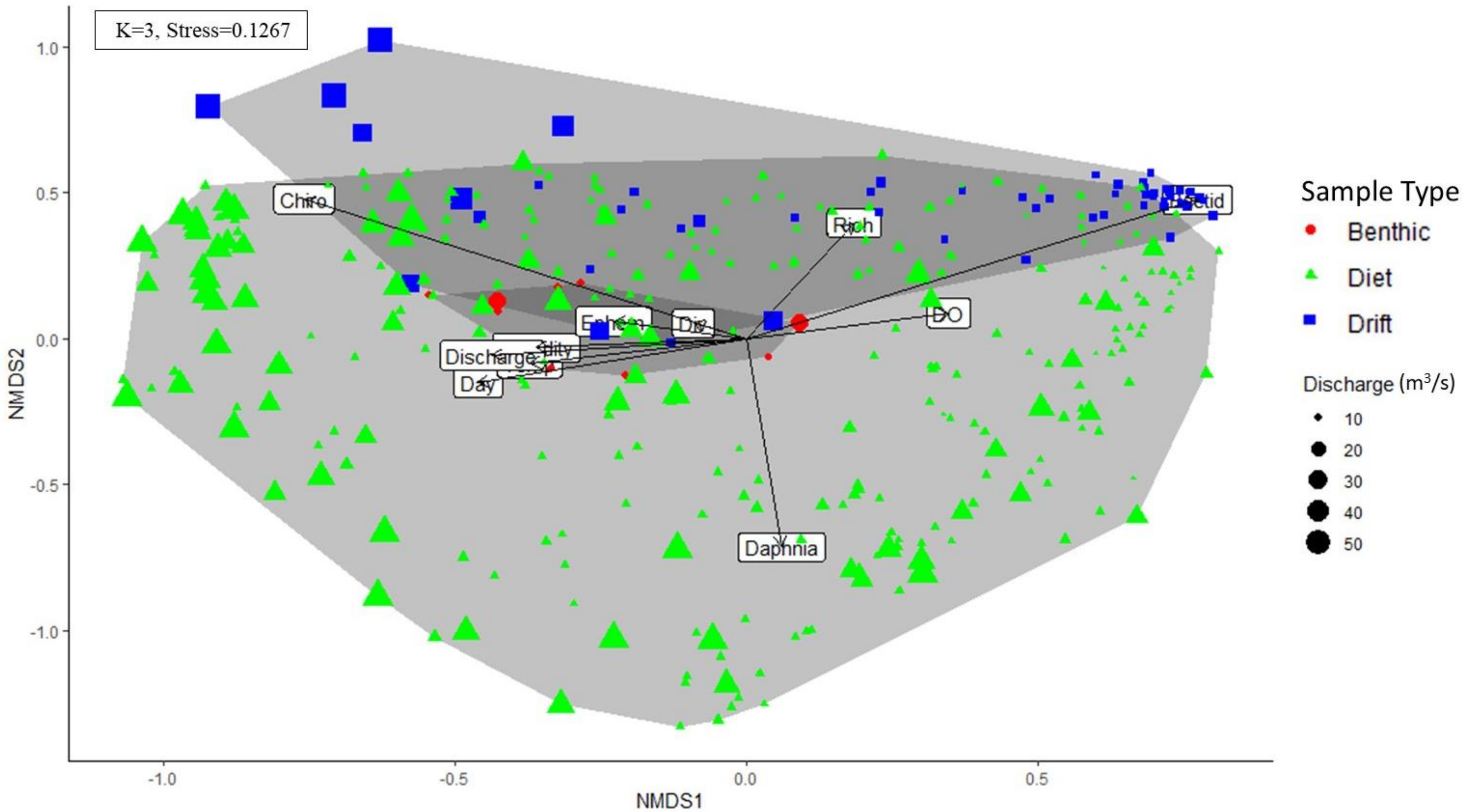

Figure 11. NMDS ordination plot of standardized benthic, drift and diet samples from the downstream site, Steel Bridge, on the Trinity River sample type (symbol shape and color) and the discharge when the sample was collected (symbol size). Continuous variables are vectors that represent correlations within the community matrix (direction) and the correlations strength (length). Rich=taxonomic richness, Div= diversity, DO=dissolved oxygen, Temp=temperature, Baetid=Baetidae relative abundance, Chiro=Chironomidae relative abundance, Daphnia=*Daphnia* relative abundance.

Table 20. Results from NMDS environmental vector fit on continuous environmental and community variables at the downstream site, Steel Bridge, on the Trinity River. R2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	NMDS1	NMDS2	R^2	p
Day	-0.94966	-0.31328	0.2349	<0.001
Temperature	-0.97557	-0.21969	0.1452	<0.001
DO	0.96945	0.24529	0.1286	<0.001
Turbidity	-0.99642	-0.08449	0.1310	<0.001
Discharge	-0.99160	-0.12937	0.1937	<0.001
Richness	0.42293	0.90616	0.1914	<0.001
Diversity	-0.86480	0.50212	0.0110	0.153
Chironomidae	-0.84562	0.53379	0.8056	<0.001
Baetidae	0.85187	0.52375	0.8272	<0.001
Daphnia	-0.96770	0.25209	0.0551	<0.001
Ephemeroptera	0.08449	-0.99642	0.5151	<0.001

Table 21. Results from permutational multivariate ANOVA (PERMANOVA) on continuous environmental and community variables at the downstream site, Steel Bridge, on the Trinity River. R2 represents each variables' relative contribution to explaining relative groupings in the corresponding ordination. P represents each variables' significance in explaining variation per 1,000 random permutations. Df is degrees of freedom taken per variable. SS is sums of squares and MS is mean of squares.

Variable	Df	SS	MS	F	R^2	*p*
Day	1	5.975	5.9745	100.791	0.08173	<0.001
Temperature	1	0.782	0.7820	13.193	0.01070	<0.001
DO	1	0.289	0.2890	4.876	0.00395	<0.001
Turbidity	1	1.778	1.7777	29.991	0.02432	<0.001
Discharge	1	0.331	0.3313	5.589	0.00453	<0.001
Richness	1	3.915	3.9154	66.054	0.05356	<0.001
Diversity	1	2.122	2.1224	35.805	0.02903	<0.001
Chironomidae	1	17.867	17.8671	301.420	0.24441	<0.001
Baetidae	1	12.876	12.8760	217.220	0.17614	<0.001
Daphnia	1	1.373	1.3732	23.165	0.01878	<0.001
Ephemeroptera	1	5.758	5.7584	97.146	0.07877	<0.001
Residuals	338	20.035	0.0593		0.27407	
Total	349	73.103			1.00000	

DISCUSSION

Drift Response to Experimental Pulse Flows

Numerous studies have implied that dam operations and seasonal changes in benthic densities together influence the total BMI drift export and likely the diet and feeding behavior of drift feeding fish (e.g., Poff & Ward 1991; Mckinney et al. 1999). This study found that the magnitude of total drifting BMIs (drift flux) on the Trinity River, below Lewiston Dam is most related to immediate increases in discharge, whereas the density (#/m^3) and concentration (mg/m^3) of BMIs in drift is highly variable throughout the study period with the exception for peak drift densities at the downstream site, Steel Bridge, following peak discharge of Pulse 1. These findings are similar to other studies that have observed increases in drift flux following increases in discharge and water velocity (Bond & Downes 2003; Gibbons et al. 2007). However, despite previous observations of higher drift concentrations with higher water velocity (Brittain & Eikeland 1988; Miller & Judson 2014), our study did not find relationships between invertebrate drift concentration and water velocity or discharge. Similarly, Leung et al. (2009) found no relationship between drift abundance and velocity at sampled riffles of Hudson Creek in British Columbia (Leung et al. 2009).

Logically it follows that if invertebrate entry into the drift remains at a constant rate during periods of increased discharge, then drift concentrations will decrease due to the dilution of BMIs in a larger volume of water (Hayes et al. 2019). However, if invertebrate entry into the drift increases (actively or passively) and remain proportional to the increase in water volume, then drift concentrations will increase with increasing discharge (Kennedy et al. 2014). The results of this study were in-between these two hypothetical situations where the relationship between drift concentration and discharge was variable between study sites over time, but the total increase in drift flux was observed at both sites during pulse flows. However, the response of drift flux to peak discharge varied between sites. For example, peaks in drift flux were recorded at Steel Bridge during the onset of Pulse 1 (4/17/18), whereas at Sawmill, peaks in drift flux were recorded one day following peak discharge (4/18/18). Similarly, drift flux at Sawmill responded to peak discharge of pulse 2, whereas drift flux values recorded at Steel Bridge during pulse 2 were comparable to baseflow conditions (Figure 5). The continuous increase in drift flux with increasing discharge recorded at Sawmill between 4/22-4/28/18, suggests elevated drift flux throughout the entire six-day period.

Many studies have linked the movement of periphyton, detritus and fine particulate organic matter (FPOM; Towns 1981; Tonkin et al. 2009) or the movement and deposition of sediment (Gomi et al. 2010) with increases in invertebrate drift rates. Others have noted that the movement of algae that accompanies increases in discharge does not appear to be a mechanism for drift entry by common invertebrate taxa like Chironomidae, Simuliidae and non-insects (Kennedy et al. 2014). However, in this study, a significant relationship between increasing discharge and increased drift flux at Steel Bridge during Pulse 1, but not Pulse 2, suggests that the large influx of drifting BMIs, especially *Daphnia* and Chironomidae, might have been influenced by the movement of detritus and algae asscociated with Pulse 1.

Drift distance varies considerably in the literature (Brittain & Eikeland 1988; Naman et al. 2016), and can range from centimeters at low water velocity to several hundred meters at high water velocity. While this implies the source of invertebrates in drift may be relatively close to their point of deposition in small streams (Hollis 2018), larger bodies of water with elevated velocities may transport invertebrates considerable distances form their point source. Thus, the increased drift rates of Chironomidae and *Daphnia* at the downstream site, Steel Bridge, are likely imports from upstream sources of marginal sections of river and side-channels that became inundated during Pulse 1, and flushed detritus and periphyton downstream colonized with Chironomidae larvae and *Daphnia*. Although increased Chironomidae and *Daphnia* significantly increased the total export of BMIs at Steel Bridge, the consumption of BMIs and diet composition during Pulse 1 did not respond in the same way. Power (1999) suggests the webbed architecture of filamentous algae, although densely populated with Chironomidae, may offer protection to invertebrates, thus making them unavailable to fish as a food source.

As mentioned earlier, drift samples collected at Steel Bridge during the peak discharge of Pulse 1 (4/17/18) were the largest samples by volume of the entire study period. Over 2,000 mL of detritus, algae and FPOM were collected from drift samples during Pulse 1 at Steel Bridge. The resulting drift samples also contained the highest invertebrate abundance (mostly Chironomidae and *Daphnia*) and biomass of the entire study period (Figure 6; Figure 7). *Daphnia* tend to be most abundant in lakes, ponds or lentic reservoirs above dams, but *Daphnia* are also known to also occupy marginal habitats of fast-moving rivers and streams (Thorp et al. 1994). Some species of Cladocerans can even live in groundwater, especially in the substrate of rivers (Dumont, 1987). However, it should also be considered that the large volume of algae and detritus captured during Pulse 1 could have functionally decreased the mesh size of the drift nets used allowing for a larger number of smaller BMI taxa to be captured. Especially those taxa known to colonize floating mats of algae like Chironomidae.

Benthic and Drift Dynamics

Drift samples included a greater variety of invertebrate taxa (richness) compared to benthic and diet samples (Appendix B). This is likely due to greater terrestrial input as well as the greater spatial scale that drift encounters. For example, invertebrates sampled from the drift will have likely traveled a farther distance and have originated from a more diverse range of sources than those collected in the benthos or diets (Shearer et al. 2003). Observations of positive relationships between benthic densities and drift densities are mixed in the literature (Shearer et al. 2003; Kennedy et al. 2014). Additionally, the responses of BMIs downstream of dams is not universal (Jones 2013), and can be highly dependent on site-specific ratios of low to high flow conditions (Trotzky & Gregory 1974). The highly variable nature of the relationships between benthic and drift densities is further corroborated by the findings of this study in that the upstream study site, Sawmill, did not have any significant relationship with the number of BMIs collected in the benthos and drift. Conversely, benthic and drift communities at Steel Bridge both exhibited decreasing trends over time, with the exception of increased in drift rates and flux at peak discharge of Pulse 1. Moreover, caution should be taken when comparing benthic densities to drift densities due to their relationship being complex and highly dependent on taxon-specific interactions, considering invertebrates will actively enter the drift (Shearer et al. 2003).

During the study period, a natural rain event occurred in between sampling efforts from 4/7-4/12/18. The volume of water accrued by Rush Creek and Grass Valley Creek increased discharge at the downstream site, Steel Bridge, approximately 4.5x but the rain event did not influence discharge at the upstream site, Sawmill, which more closely reflects discharge released from Lewiston Dam. Although sampling was not conducted during the rain event, the additional increase in discharge at Steel Bridge is a good example in how natural accretion of flows may have a greater influence on BMI communities with increasing distance downstream of Lewiston Dam. Conversely, the upstream site Sawmill had 0% canopy cover and suppressed flow variability for the majority of the year, allowing for a higher density of filamentous algae to persist (primarily Cladophoraceae: *Cladophora*). Furthermore, peak flow suppression on regulated rivers can induce higher algal production (Dufford et al. 1987), thus altering BMI communities while allowing Chironomidae and other generalist taxa to dominate in areas closer to dams with %EPT in benthic communities increasing with distance downstream of dams (Tonkin et al. 2009). The relative benthic abundance and biomass in drift of sensitive taxa (ex. %EPT) was consistently higher at the downstream site, Steel

Bridge, suggesting additional flows accrued by tributaries may reduce the standing crop of algae, allowing for sensitive invertebrate taxa to persist.

Strong correlations between benthic algae and the prevalence of Chironomidae (Diptera) larvae have been recorded by multiple studies (Power 1990; Tonkin et al. 2009), as well as negative relationships between algae density and sensitive invertebrate species like Ephemeroptera, Plecoptera and Trichoptera (Harding et al. 1990; Shearer et al. 2003; Tonkin et al. 2009). The presence of thick periphyton and floating algal mats common at the upstream site, Sawmill, may reduce the availability of substrate for sensitive species (e.g., Ephemeroptera, Harding et al. 1990) while collecting diatoms and detritus in favor of more hardy, generalist taxa like Chironomidae that feed from the algal mats (Pinder 1986; Power 1990). Although Chironomidae were present in the benthos and drift at both study sites, the family comprised a much smaller proportion of total invertebrate abundance in the benthos at the downstream site, Steel Bridge. Additionally, Chironomidae only became a dominant taxon in the drift at Steel Bridge during peak discharge of both pulse flows (4/17 & 4/28/18; Figure 6), suggesting elevated transport of Chironomidae to Steel Bridge in the drift from upstream sources. These findings suggest peak discharge of Pulse 1 (4/17/18) induced a flushing action, forcing a large mass of detritus and algae downstream that had been accumulating during the lengthy period of unnaturally low, winter baseflow conditions.

Chironomidae larvae and pupae are classified as weak swimmers (Merrit et al. 1996), and likely inhabit lower velocity sections at Sawmill, possibly contributing to the invertebrate taxonomic response in diets at Sawmill where fish were able to consume higher proportions of Chironomidae in marginal and lower velocity sections of riffle habitat. Conversely, the banks at Steel Bridge are more confined with less marginal habitat for refugia during high flows, deterring the high abundance of invertebrates in the drift during Pulse 1 (Figure 6) to be deposited in the benthos (Figure 3) and presumably reducing the amount of available feeding locations during periods of elevated discharge relative to Sawmill. It is therefore not surprising that fish diets did not respond to the increase of Chrinomidae relative abundance in the drift during pulse flows to that same extent as the upstream site, Sawmill.

Juvenile Chinook Salmon Diet Response to Experimental Pulse Flows

The response in consumption rate by juvenile Chinook to increased periods of discharge was highly variable. Larrarrigue et al. (2002) suggest that juvenile trout do not respond to increased drift rates following a hydropeaking event in mountain streams. Additionally, juvenile trout reduced in density and biomass seemingly due to the high energetic costs from increases in water velocity (Larrarrigue et al. 2002). Conversely, Miller & Judson (2014) observed significant increases in juvenile gut fullness following similar hydropeaking conditions with elevated drift rates. My study on the Trinity River did not find any evidence of increased or decreased consumption rates during periods of elevated discharge. Even though drift rates and flux peaked at Steel Bridge during the onset of Pulse 1, these findings support Larrarrigue et al.'s (2002) suggestion that juvenile fish do not utilize increased drift rates associated with peak flows because of the instinct to seek flow refugia, the increased energetic costs to feed at higher flows, the inability to capture prey at higher velocities (Miller & Judson 2014) or because consumption rates remained variable, regardless of flow and drift rates.

Chironomidae and Baetidae were the two most dominant invertebrate taxa collected from juvenile Chinook diets throughout the study period at both sites (Figure 9). The percent composition of Chironomidae in fish diets increased during both pulse flows at the upstream site, Sawmill (Figure 9). However, the percent composition of Chironomidae in fish diets remained relatively constant at the downstream site, Steel Bridge (Figure 9). The dominance of Chironomidae and Baetidae in juvenile salmonid diet is well-established (Armitage 1985; Leung et al. 2009; Baxter et al. 2017). Additionally, Chironomidae and Baetidae have been classified together as some of the most abundant and universally available taxa for consumption by fish in riffle habitats (Rader 1997).

Community Responses to Experimental Pulse Flows

Of the taxa used to run ordinations, Chrionomidae and Baetidae described the most variability as environmental vectors over all other taxa (Figure 11; Figure 12; Table 8). Additionally, increases in discharge were associated with increases in Chironomidae relative abundance, but inversely related to Baetidae relative abundance (Figure 10). This is likely due to Baetidae generally being categorized as intentional drifters (Rader 1997), and they are more likely to enter the drift behaviorally rather than catastrophically (Peckarsky 1980) in order to avoid predation by drifting at night (Peckarsky & Penton

1989; Poff & Ward 1991) or to colonize new areas (Corrarino & Brusven 1983). Conversely, Chironomidae are generally categorized as un-intentional drifters (Rader 1997), being more associated with catastrophic drift by entrainment into the water column following increases in discharge and disturbance (Lancaster 1990).

Contrary to expectation, fish diets did not necessarily reflect invertebrate composition in the drift throughout the study period at both sites. Site differences in dissimilarity values were recorded, where all sample types at Sawmill were generally more similar to each other throughout the study period relative to Steel Bridge (Table 5). This trend is further supported by between-group dissimilarity values among sample types during both pulse flows where juvenile diet composition was found to be more similar to benthic invertebrate composition during Pulse 1 at Sawmill relative to baseflow conditions (Appendix C). Conversely, juvenile diets diverged in compositional similarity during Pulse 1 at Steel Bridge relative to baseflow conditions (Appendix C).

Periods of increased discharge below dams are energetically costly for juvenile salmonids, but profitable feeding stations occupied by territorial juveniles can offset energetic costs, especially if feeding requirements are met via increased food availability and quality (Armstrong et al. 1998; Rosenfeld et al. 2005; Beauchamp 2009). In Newfoundland, Canada, a study was conducted in 2002 to record the response of Atlantic Salmon to periods of hydropeaking below dams. As discharge increased, researchers observed the range of velocity and depth occupied by juveniles increased by behaviorally increasing their contact with the benthos where water velocities were lowest (Scrunton et al. 2008). Additionally, substrate and marginal habitat can provide velocity refuge for stream salmonids, allowing them to integrate more behaviors such as search foraging (Scuton et al. 2008). The results of my study suggest juvenile Chinook salmon consumption rates from both study sites largely remained constant regardless of discharge and total export of drift (flux), most likely responding to standardized drift rates, which largely did not increase with increasing discharge. However, diet composition from the upstream site, Sawmill, shifted towards the Chironomidae-dominated drift composition during both pulses. Juvenile Chinook from Sawmill were likely able to cope with higher water velocities during pulse flows by increasing their contact with substrate and/or moving to marginal areas to consume higher proportions of drift-sensitive BMI taxa (Chironomidae) that were being deposited in large quantities.

Conversely, no metric of compositional similarity between drift and diets (Table 7, Figure 12, Appendix C), total invertebrate biomass consumed (Table 3, Figure 8) or gut fullness of juvenile Chinook (Table 4, Figure 8) responded to pulse flows at Steel Bridge, relative to baseflow conditions. This suggests fish at the downstream site were unable to exhibit the same compositional shifts found in the drift during pulse flows possibly due to the large volumes of detritus and algae transported from upstream sources. However, caution should be taken when inferring beyond site-level variability due to sampling from only two locations.

Recommendations for Future work

The results from this preliminary study on BMI drift and juvenile Chinook salmon diet on the Trinity River Restoration Reach can serve as baseline data for future work with experimental flow manipulations below Lewiston Dam. Primary limitations of this study included only two sampling locations, the energy intensive nature of collecting drift and diet samples as well as the contention of flow management in California when attempting to design a more natural flow regime on the Trinity River.

Future work should continue to study BMI drift in consecutive pulse flows designed to mimic a more natural hydrograph as well as benthic invertebrate densities to better understand the relationship between BMI production and their availability to juvenile salmonids. In addition, more robust sampling of BMI drift can shed light on the spatial variability of the movements of BMIs in the Restoration Reach, therefore better informing food availability metrics in fish production models. Future studies should further identify better control sites on the South or North Fork Trinity River to compare BMI assemblages in the benthos, drift and juvenile salmonid diets between dammed and undammed sections of river.

CONCLUSION

This study observed benthic densities between the two study sites, Sawmill and Steel Bridge, were variable. However, drastic increases in the deposition of Chrionomidae was observed at Sawmill during peak discharge of pulse 1. Neither drift concentrations or drift densities responded to pulse flows, with the exception of increased drift densities at Steel Bridge during pulse 1. This was influenced by an abundance on drifting Chironomidae and *Daphnia* that were unable to settle out of the drift due to the incised channel at Steel Bridge. Total drift flux dramatically increased at both sites during pulse 1, but did not respond at Steel Bridge during pulse 2 likely due to the decreased movement of detritus and algae that had been flushed downstream during pulse 1. Consumption by juvenile Chinook salmon remained highly variable and did not increase with increasing drift flux. However, fish at Sawmill fed more on Chironomidae during both pulses. The findings of this study can inform future research and Trinity River water management on juvenile Chinook salmon responses to managed increases in flow and drift feeding dynamics.

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APPENDIX A

Length-weight regression constants a & b for individual BMI taxa and life stage based of body length. Equations are in the form $Biomass = aLength^b$, unless otherwise noted. The primary sources for regression constants are given.

Taxon/Group	Life Stage	a	b	Source
Diptera	*adults*	0.0400	2.2600	Sabo et al. 2002
Chironomidae	*larvae*	0.0018	2.6170	Benke et al. 1999
	pupae	0.0018	2.6170	Wisseman 2012
Simuliidae	*larvae*	0.0020	3.0110	Wisseman 2012
	pupae	0.0020	3.0110	Wisseman 2012
Ceratopogonidae	*larvae*	0.0025	2.4690	Benke et al. 1999
	pupae	0.0025	2.4690	Wisseman 2012
Tipulidae	*larvae*	0.0029	2.6810	Benke et al. 1999
	pupae	0.0029	2.6810	Wisseman 2012
Empididae	*larvae*	0.0054	2.5460	Wisseman 2012
	pupae	0.0054	2.5460	Wisseman 2012
Blephericeridae	*larvae*	0.0067	3.2920	Wisseman 2012
	pupae	0.0067	3.2920	Wisseman 2012
Tanyderidae	*larvae*	0.0025	2.6920	Wisseman 2012
	pupae	0.0025	2.6920	Wisseman 2012
Athericidae	*larvae*	0.0038	2.5860	Benke et al. 1999
	pupae	0.0038	2.5860	Wisseman 2012
Ephemeroptera	*adults*	0.0140	2.4900	Sabo et al. 2002
Baetidae	*larvae*	0.0053	2.8750	Benke et al. 1999
Heptageniidae	*larvae*	0.0108	2.7540	Benke et al. 1999
Ameletidae	*larvae*	0.0077	2.5880	Benke et al. 1999
Leptophlebiidae	*larvae*	0.0047	2.6860	Benke et al. 1999
Ephemerellidae	*larvae*	0.0103	2.6760	Benke et al. 1999
Plecoptera	*adults*	0.2600	1.6900	Sabo et al. 2002
Perlidae	*larvae*	0.0099	2.8790	Benke et al. 1999
Perlodidae	*larvae*	0.0196	2.7420	Benke et al. 1999
Pternonarcyidae	*larvae*	0.0324	2.5730	Benke et al. 1999
Chloroperlidae	*larvae*	0.0065	2.7240	Wisseman 2012
Nemouridae	*larvae*	0.0056	2.7620	Wisseman 2012

Taxon/Group	Life Stage	a	b	Source
Trichoptera	*adults*	0.0100	2.9000	Sabo et al. 2002
Glossosomatidae	*larvae*	0.0082	2.9580	Benke et al. 1999
	pupae	0.0082	2.9580	Wisseman 2012
Brachycentridae	*larvae*	0.0083	2.8180	Benke et al. 1999
	pupae	0.0025	3.4430	Wisseman 2012
Limnephilidae	*larvae*	0.0040	2.9330	Benke et al. 1999
	pupae	0.0040	2.9330	Wisseman 2012
Rhyacophilidae	*larvae*	0.0099	2.4800	Benke et al. 1999
	pupae	0.0099	2.4800	Wisseman 2012
Hydropsychidae	*larvae*	0.0046	2.9260	Benke et al. 1999
	pupae	0.0046	2.9260	Wisseman 2012
Lepidostomatidae	*larvae*	0.0079	2.6490	Benke et al. 1999
	pupae	0.0079	2.6490	Wisseman 2012
Non-Insects				
Oligachaeta	*Unknown*	0.0758	0.7400	Wisseman 2012
Sphaeriidae	*Unknown*	0.0163	2.4770	Wisseman 2012
Ostracoda	*Unknown*	0.0068	2.2700	Wisseman 2012
Collembola	*Unknown*	0.0024	3.6760	Wisseman 2012
Nematomorpha	*Unknown*	0.0758	0.7400	Wisseman 2012
Gastropoda*	*Unknown*	-3.3600	3.3800	Wardhaugh 2013
Acari	*Unknown*	0.0530	2.4940	Wisseman 2012
Daphnia	*Unknown*	0.0068	2.2700	Wisseman 2012
Amphipoda	*Unknown*	0.0050	3.0100	Benke et al. 1999
Copepoda	*Unknown*	0.0068	2.2700	Wisseman 2012
Coleoptera	*adults*	0.0400	2.6400	Sabo et al. 2002
Elmidae	*larvae*	0.0074	2.8790	Benke et al. 1999
Amphizoidae	*larvae*	0.0077	2.9100	Benke et al. 1999
Dryopidae	*larvae*	0.0400	2.6400	Benke et al. 1999
Hydrophilidae	*larvae*	0.0077	2.9100	Benke et al. 1999
Dytiscidae	*larvae*	0.0077	2.9100	Wisseman 2012
Haliplidae	*larvae*	0.0077	2.9100	Wisseman 2012
Terrestrials				
Orthoptera	*adults*	0.0300	2.5500	Sabo et al. 2002
Lepidoptera*	*adults*	-3.8300	2.7700	Wardhaugh 2013
Hymenoptera	*adults*	0.5600	1.5600	Sabo et al. 2002
Araneae	*adults*	0.0500	2.7400	Sabo et al. 2002

Taxon/Group	Life Stage	a	b	Source
Hemiptera	*adults*	0.0050	3.3300	Sabo et al. 2002
Crambidae	*adults*	0.0720	2.4010	Wisseman 2012
Staphylinidae	*adults*	0.0010	4.0260	Sabo et al. 2002
Carabidae	*adults*	0.0720	2.4010	Sabo et al. 2002
Thysanoptera*	*adults*	-5.1800	1.8900	Wardhaugh 2013
Isopoda*	*Unknown*	-4.8100	3.4400	Wardhaugh 2013

*Regression equation in the form $\ln Biomass = \ln a + b(\ln Length)$

APPENDIX B

1. Averaged BMI densities ($\#/m^2$) in the benthos at the upstream site, Sawmill, during each flow condition. Values in (x) are standard deviations. Missing sd values (NAs) are due to only one sample taken during each pulse flow. Total number of samples (n) and their taxonomic richness are given. Orders/groups are bold, followed by each respective BMI Family/group

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	7		1		1	
	Richness	34	(3)	25	NA	24	NA
Diptera	Chironomidae	713.286	(432.706)	2680.000	NA	1204.000	NA
	Simuliidae	130.571	(110.542)	14.000	NA	6.000	NA
	Ceratopogonidae	4.857	(9.582)	2.000	NA	0.000	NA
	Tipulidae	1.429	(1.512)	16.000	NA	32.000	NA
	Empididae	1.286	(2.215)	4.000	NA	6.000	NA
	Blephericeridae	0.429	(0.787)	0.000	NA	0.000	NA
	Tanyderidae	0.000	(0.000)	0.000	NA	0.000	NA
	Athericidae	4.143	(3.078)	4.000	NA	0.000	NA
Ephemeroptera	Baetidae	315.143	(104.492)	90.000	NA	132.000	NA
	Heptageniidae	297.857	(140.134)	58.000	NA	72.000	NA
	Ameletidae	0.286	(0.756)	0.000	NA	0.000	NA
	Leptophlebiidae	6.286	(5.589)	4.000	NA	14.000	NA
	Ephemerellidae	117.000	(80.843)	16.000	NA	20.000	NA
Plecoptera	Perlidae	71.571	(36.487)	42.000	NA	34.000	NA
	Perlodidae	47.286	(31.319)	0.000	NA	10.000	NA
	Pternonarcyidae	51.286	(25.487)	2.000	NA	14.000	NA
	Chloroperlidae	40.000	(19.698)	8.000	NA	22.000	NA
	Nemouridae	23.714	(36.958)	64.000	NA	38.000	NA
Trichoptera	Glossosomatidae	41.143	(18.216)	2.000	NA	0.000	NA
	Brachycentridae	0.143	(0.378)	0.000	NA	2.000	NA
	Limnephilidae	1.429	(2.992)	2.000	NA	2.000	NA
	Rhyacophilidae	6.429	(6.214)	4.000	NA	8.000	NA
	Hydropsychidae	1.143	(2.268)	0.000	NA	0.000	NA
	Lepidostomatidae	0.000	(0.000)	0.000	NA	0.000	NA
Non-Insect	Oligachaeta	138.571	(96.358)	522.000	NA	272.000	NA
	Sphaeriidae	2.143	(4.413)	4.000	NA	2.000	NA
	Ostracoda	25.000	(25.449)	40.000	NA	76.000	NA
	Collembola	0.429	(0.787)	0.000	NA	0.000	NA

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Nematomorpha	1.714	(1.799)	2.000	NA	8.000	NA
	Gastropoda	0.571	(0.976)	0.000	NA	0.000	NA
	Acari	4.286	(3.352)	12.000	NA	26.000	NA
	Daphnia	1.143	(2.268)	8.000	NA	2.000	NA
	Amphipoda	0.571	(0.976)	2.000	NA	0.000	NA
	Copepoda	0.286	(0.756)	4.000	NA	2.000	NA
Coleoptera	Elmidae	0.429	(1.134)	0.000	NA	2.000	NA
	Amphizoidae	0.000	(0.000)	0.000	NA	0.000	NA
	Dryopidae	0.143	(0.378)	0.000	NA	0.000	NA
	Hydrophilidae	0.000	(0.000)	0.000	NA	0.000	NA
	Dytiscidae	0.000	(0.000)	0.000	NA	0.000	NA
	Haliplidae	0.000	(0.000)	0.000	NA	0.000	NA
Terrestrial	Orthoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Lepidoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Hymenoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Araneae	0.000	(0.000)	0.000	NA	0.000	NA
	Hemiptera	0.000	(0.000)	0.000	NA	0.000	NA

2. Averaged BMI densities ($\#/m^2$) in the benthos at the downstream site, Steel Bridge, during each flow condition. Values in (x) are standard deviations. Missing sd values (NAs) are due to only one sample taken during each pulse flow. Total number of samples (n) and their taxonomic richness are given. Orders/groups are bold, followed by each respective BMI Family/group

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	7		1		1	
	Richness	32	(2)	24	NA	27	NA
Diptera	Chironomidae	686.571	(486.006)	158.000	NA	508.000	NA
	Simuliidae	2.286	(2.928)	8.000	NA	2.000	NA
	Ceratopogonidae	0.000	(0.000)	0.000	NA	0.000	NA
	Tipulidae	3.571	(3.457)	0.000	NA	0.000	NA
	Empididae	7.857	(4.634)	18.000	NA	12.000	NA
	Blephericeridae	0.286	(0.756)	0.000	NA	0.000	NA
	Tanyderidae	0.714	(0.951)	0.000	NA	0.000	NA
	Athericidae	27.286	(12.737)	18.000	NA	20.000	NA
Ephemeroptera	Baetidae	315.429	(211.760)	198.000	NA	170.000	NA
	Heptageniidae	394.857	(176.227)	178.000	NA	254.000	NA
	Ameletidae	4.143	(3.848)	0.000	NA	0.000	NA
	Leptophlebiidae	115.000	(57.472)	38.000	NA	90.000	NA
	Ephemerellidae	171.143	(149.795)	28.000	NA	28.000	NA
Plecoptera	Perlidae	74.286	(37.317)	20.000	NA	26.000	NA
	Perlodidae	59.714	(42.672)	8.000	NA	16.000	NA
	Pternonarcyidae	58.286	(38.043)	8.000	NA	10.000	NA
	Chloroperlidae	53.857	(28.997)	10.000	NA	14.000	NA
	Nemouridae	0.429	(0.787)	6.000	NA	6.000	NA
Trichoptera	Glossosomatidae	19.286	(11.528)	34.000	NA	66.000	NA
	Brachycentridae	5.143	(10.123)	0.000	NA	18.000	NA
	Limnephilidae	23.714	(25.283)	2.000	NA	14.000	NA
	Rhyacophilidae	1.571	(1.813)	4.000	NA	0.000	NA
	Hydropsychidae	103.000	(61.906)	80.000	NA	68.000	NA
	Lepidostomatidae	0.000	(0.000)	0.000	NA	0.000	NA
Non-Insect	Oligachaeta	19.429	(14.046)	28.000	NA	18.000	NA
	Sphaeriidae	3.571	(3.457)	6.000	NA	8.000	NA
	Ostracoda	17.857	(15.668)	6.000	NA	4.000	NA
	Collembola	0.714	(1.496)	2.000	NA	2.000	NA
	Nematomorpha	6.857	(10.189)	0.000	NA	4.000	NA
	Gastropoda	9.286	(7.274)	12.000	NA	14.000	NA
	Acari	39.714	(17.680)	32.000	NA	30.000	NA
	Daphnia	0.000	(0.000)	0.000	NA	0.000	NA

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Amphipoda	0.714	(0.951)	0.000	NA	0.000	NA
	Copepoda	0.000	(0.000)	0.000	NA	0.000	NA
Coleoptera	Elmidae	29.143	(23.724)	24.000	NA	12.000	NA
	Amphizoidae	0.000	(0.000)	0.000	NA	2.000	NA
	Dryopidae	2.429	(4.614)	0.000	NA	4.000	NA
	Hydrophilidae	0.000	(0.000)	0.000	NA	0.000	NA
	Dytiscidae	0.000	(0.000)	0.000	NA	0.000	NA
	Haliplidae	0.000	(0.000)	0.000	NA	0.000	NA
Terrestrial	Orthoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Lepidoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Hymenoptera	0.000	(0.000)	0.000	NA	0.000	NA
	Araneae	0.000	(0.000)	0.000	NA	0.000	NA
	Hemiptera	0.000	(0.000)	0.000	NA	0.000	NA

3. Daily average drift flux export (abundance/s) at the upstream site, Sawmill, during each flow condition. Standard deviations are indicated by (x). Total number of samples (n) and their taxonomic richness are given. Orders/groups are bold, followed by each respective BMI Family/group

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	40		6		6	
	Rich	42	(3)	38	(2)	30	(1)
Diptera	Adults	2.602	(2.137)	6.043	(1.504)	10.519	(10.060)
	Chironomidae	6.946	(6.117)	31.975	(17.977)	32.732	(34.873)
	Simuliidae	0.698	(0.715)	0.436	(0.073)	0.773	(0.754)
	Ceratopogonidae	0.012	(0.044)	0.039	(0.067)	0.000	(0.000)
	Tipulidae	0.001	(0.004)	0.028	(0.025)	0.148	(0.222)
	Empididae	0.001	(0.004)	0.029	(0.051)	0.321	(0.428)
	Blephericeridae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Tanyderidae	0.015	(0.071)	0.000	(0.000)	0.000	(0.000)
	Athericidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Ephemeroptera	Adults	0.152	(0.135)	0.148	(0.166)	0.753	(0.837)
	Baetidae	7.950	(5.610)	5.880	(2.183)	9.390	(4.791)
	Heptageniidae	0.235	(0.191)	0.425	(0.128)	0.719	(0.603)
	Ameletidae	0.034	(0.046)	0.078	(0.134)	0.000	(0.000)
	Leptophlebiidae	0.001	(0.004)	0.078	(0.134)	0.000	(0.000)
	Ephemerellidae	0.518	(0.371)	1.307	(0.563)	1.776	(1.955)
Plecoptera	Adults	0.028	(0.061)	0.078	(0.134)	0.067	(0.116)
	Perlidae	0.000	(0.000)	0.015	(0.025)	0.000	(0.000)
	Perlodidae	0.499	(0.398)	0.851	(0.887)	0.534	(0.587)
	Pternonarcyidae	0.074	(0.139)	0.866	(0.448)	1.082	(1.187)
	Chloroperlidae	0.064	(0.120)	0.029	(0.051)	0.065	(0.081)
	Nemouridae	0.003	(0.014)	0.000	(0.000)	0.000	(0.000)
Trichoptera	Adults	0.108	(0.145)	0.000	(0.000)	0.159	(0.143)
	Glossosomatidae	0.090	(0.074)	0.401	(0.397)	0.159	(0.143)
	Brachycentridae	0.002	(0.007)	0.078	(0.134)	0.000	(0.000)
	Limnephilidae	0.034	(0.041)	0.068	(0.061)	0.052	(0.090)
	Rhyacophilidae	0.020	(0.033)	0.056	(0.062)	0.000	(0.000)
	Hydropsychidae	0.014	(0.060)	0.000	(0.000)	0.000	(0.000)
	Lepidostomatidae	0.005	(0.014)	0.000	(0.000)	0.000	(0.000)
Non-Insects	Oligachaeta	0.225	(0.322)	1.363	(0.774)	1.459	(1.893)
	Sphaeriidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Ostracoda	0.024	(0.114)	1.854	(1.094)	2.067	(3.279)
	Collembola	0.038	(0.060)	0.309	(0.289)	0.523	(0.774)

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Nematomorpha	0.015	(0.031)	0.000	(0.000)	0.000	(0.000)
	Gastropoda	0.002	(0.010)	0.351	(0.311)	1.761	(3.016)
	Acari	0.315	(0.230)	6.225	(3.188)	6.820	(7.812)
	Daphnia	0.177	(0.168)	19.586	(6.888)	9.136	(14.092)
	Amphipoda	0.087	(0.229)	4.534	(5.122)	5.182	(8.265)
	Copepoda	0.049	(0.125)	0.439	(0.382)	1.092	(1.892)
Coleoptera	Adults	0.042	(0.072)	0.289	(0.071)	0.395	(0.077)
	Elmidae	0.004	(0.009)	0.126	(0.123)	0.000	(0.000)
	Amphizoidae	0.000	(0.000)	0.014	(0.024)	0.013	(0.023)
	Dryopidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hydrophilidae	0.001	(0.005)	0.015	(0.025)	0.104	(0.180)
	Dytiscidae	0.000	(0.000)	0.029	(0.051)	0.000	(0.000)
	Haliplidae	0.002	(0.007)	0.000	(0.000)	0.000	(0.000)
Terrestrials	Orthoptera	0.000	(0.000)	0.027	(0.047)	0.000	(0.000)
	Lepidoptera	0.003	(0.007)	0.000	(0.000)	0.000	(0.000)
	Hymenoptera	0.071	(0.099)	0.346	(0.251)	0.346	(0.312)
	Araneae	0.014	(0.026)	0.145	(0.177)	0.013	(0.023)
	Hemiptera	0.039	(0.059)	0.353	(0.309)	1.048	(0.790)

4. Daily average drift flux export (abundance/s) at the downstream site, Steel Bridge, during each flow condition. Standard deviations are indicated by (x). Total number of samples (n) and their taxonomic richness are given. Orders/groups are bold, followed by each respective BMI Family/group.

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	46		6		6	
	Rich	39	(3)	22	(3)	23	(4)
Diptera	Adults	2.570	(1.498)	9.752	(12.644)	1.356	(0.277)
	Chironomidae	1.575	(0.887)	27.003	(42.059)	9.561	(9.561)
	Simuliidae	0.464	(0.415)	1.019	(1.572)	0.851	(0.655)
	Ceratopogonidae	0.005	(0.016)	0.000	(0.000)	0.000	(0.000)
	Tipulidae	0.003	(0.011)	0.000	(0.000)	0.000	(0.000)
	Empididae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Blephericeridae	0.001	(0.005)	0.000	(0.000)	0.000	(0.000)
	Tanyderidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Athericidae	0.004	(0.010)	0.000	(0.000)	0.191	(0.194)
Ephemeroptera	Adults	0.125	(0.146)	0.064	(0.086)	0.000	(0.000)
	Baetidae	10.753	(6.692)	2.213	(2.229)	2.497	(1.305)
	Heptageniidae	0.404	(0.277)	0.758	(0.988)	0.258	(0.341)
	Ameletidae	0.061	(0.060)	0.526	(0.775)	0.000	(0.000)
	Leptophlebiidae	0.105	(0.095)	0.379	(0.494)	0.000	(0.000)
	Ephemerellidae	0.320	(0.196)	2.646	(4.252)	0.604	(0.584)
Plecoptera	Adults	0.078	(0.141)	0.000	(0.000)	0.000	(0.000)
	Perlidae	0.004	(0.010)	0.000	(0.000)	0.130	(0.224)
	Perlodidae	0.099	(0.092)	0.222	(0.227)	0.000	(0.000)
	Pternonarcyidae	0.014	(0.021)	0.000	(0.000)	0.451	(0.301)
	Chloroperlidae	0.015	(0.030)	0.000	(0.000)	0.389	(0.673)
	Nemouridae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Trichoptera	Adults	0.054	(0.107)	0.000	(0.000)	0.000	(0.000)
	Glossosomatidae	0.075	(0.075)	0.000	(0.000)	0.437	(0.462)
	Brachycentridae	0.007	(0.015)	0.000	(0.000)	0.000	(0.000)
	Limnephilidae	0.049	(0.079)	0.000	(0.000)	0.252	(0.219)
	Rhyacophilidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hydropsychidae	0.056	(0.050)	0.010	(0.018)	0.031	(0.053)
	Lepidostomatidae	0.027	(0.055)	0.000	(0.000)	0.000	(0.000)
Non-Insects	Oligachaeta	0.089	(0.113)	1.132	(1.882)	0.407	(0.323)
	Sphaeriidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Ostracoda	0.010	(0.034)	0.010	(0.018)	2.462	(3.932)
	Collembola	0.019	(0.044)	0.157	(0.273)	0.389	(0.673)
	Nematomorpha	0.025	(0.055)	0.000	(0.000)	0.000	(0.000)

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Gastropoda	0.005	(0.023)	0.108	(0.187)	0.000	(0.000)
	Acari	0.441	(0.327)	2.147	(2.661)	2.553	(1.830)
	Daphnia	0.036	(0.048)	46.824	(78.845)	2.203	(3.165)
	Amphipoda	0.007	(0.019)	0.000	(0.000)	0.087	(0.150)
	Copepoda	0.000	(0.000)	1.899	(3.262)	0.000	(0.000)
Coleoptera	Adults	0.063	(0.089)	1.207	(1.817)	0.383	(0.390)
	Elmidae	0.016	(0.029)	0.000	(0.000)	0.981	(1.507)
	Amphizoidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dryopidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hydrophilidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dytiscidae	0.011	(0.047)	0.000	(0.000)	0.000	(0.000)
	Haliplidae	0.001	(0.005)	0.000	(0.000)	0.000	(0.000)
Terrestrials	Orthoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Lepidoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hymenoptera	0.022	(0.044)	0.168	(0.264)	0.308	(0.070)
	Araneae	0.006	(0.014)	0.010	(0.018)	0.000	(0.000)
	Hemiptera	0.036	(0.055)	0.031	(0.053)	0.605	(0.833)

5. Daily average of total consumed invertebrates summed across all juvenile Chinook diets sampled during each flow conditions at the upstream site, Sawmill. Number of juveniles sampled (n) is given as well as invertebrate taxonomic richness per flow condition. Orders/groups are bold, followed by each respective BMI Family/group.

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	178		40		39	
	Rich	32	(0.563)	29	(0.584)	28	(0.311)
Diptera	Adults	0.947	(1.268)	0.667	(0.577)	0.667	(1.155)
	Chironomidae	198.368	(201.366)	375.3	(205.838)	87.333	(13.65)
	Simuliidae	4.158	(5.167)	1.000	(1.000)	1.000	(1.000)
	Ceratopogonidae	0.263	(0.733)	0.333	(0.577)	1.333	(1.528)
	Tipulidae	0.053	(0.229)	0.333	(0.577)	0.333	(0.577)
	Empididae	0.053	(0.229)	0.333	(0.577)	1.000	(1.732)
	Blephericeridae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Tanyderidae	0.000	(0.000)	0.333	(0.577)	0.000	(0.000)
	Athericidae	0.053	(0.229)	0.000	(0.000)	0.000	(0.000)
Ephemeropter	Adults	4.421	(10.123)	0.000	(0.000)	0.000	(0.000)
	Baetidae	49.368	(51.365)	19.00	(14.731)	18.667	(12.34)
	Heptageniidae	2.368	(2.454)	1.333	(0.577)	4.667	(0.577)
	Ameletidae	0.105	(0.315)	0.333	(0.577)	1.000	(1.000)
	Leptophlebiidae	0.211	(0.713)	0.667	(0.577)	0.333	(0.577)
	Ephemerellidae	3.053	(3.135)	8.333	(3.055)	17.333	(6.658)
Plecoptera	Adults	0.526	(1.124)	2.000	(1.000)	11.333	(6.658)
	Perlidae	0.421	(0.902)	1.333	(0.577)	0.667	(0.577)
	Perlodidae	1.000	(1.453)	2.000	(1.000)	12.333	(5.859)
	Pternonarcyidae	0.263	(0.653)	1.000	(1.000)	0.667	(1.155)
	Chloroperlidae	0.211	(0.419)	3.000	(1.732)	2.333	(2.517)
	Nemouridae	0.263	(0.806)	0.667	(0.577)	0.667	(1.155)
Trichoptera	Adults	0.737	(1.327)	0.000	(0.000)	0.000	(0.000)
	Glossosomatidae	7.684	(12.802)	21.00	(26.851)	7.667	(7.234)
	Brachycentridae	0.105	(0.315)	0.000	(0.000)	0.000	(0.000)
	Limnephilidae	0.105	(0.315)	0.333	(0.577)	0.333	(0.577)
	Rhyacophilidae	0.105	(0.315)	0.000	(0.000)	0.333	(0.577)
	Hydropsychidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Lepidostomatidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Non-Insect	Oligachaeta	0.105	(0.315)	1.000	(1.000)	1.333	(1.155)
	Sphaeriidae	0.000	(0.000)	0.333	(0.577)	0.000	(0.000)
	Ostracoda	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Collembola	0.895	(1.243)	24.00	(32.357)	1.667	(2.887)
	Nematomorpha	0.526	(0.612)	1.333	(2.309)	1.000	(1.000)

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Gastropoda	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Acari	0.053	(0.229)	2.667	(3.055)	0.333	(0.577)
	Daphnia	1.368	(4.798)	23.33	(18.930)	0.333	(0.577)
	Amphipoda	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Copepoda	0.000	(0.000)	0.667	(0.577)	0.000	(0.000)
Coleoptera	Elmidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Amphizoidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dryopidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hydrophilidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dytiscidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Haliplidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Terrestrial	Orthoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Lepidoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hymenoptera	0.105	(0.459)	0.000	(0.000)	0.333	(0.577)
	Araneae	0.158	(0.375)	2.333	(3.215)	0.333	(0.577)
	Hemiptera	0.263	(0.733)	1.333	(0.577)	2.000	(1.000)

6. Daily average of total consumed invertebrates summed across all juvenile Chinook diets sampled during each flow conditions at the downstream site, Steel Bridge. Number of juveniles sampled (n) is given as well as invertebrate taxonomic richness per flow condition. Orders/groups are bold, followed by each respective BMI Family/group.

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	n	212		39		39	
	Rich	32	(0.624)	25	(0.504)	24	(1.050)
Diptera	Adults	0.053	(0.229)	0.000	(0.000)	1.333	(1.528)
	Chironomidae	30.842	(24.685)	37.667	(14.189)	28.333	(11.547)
	Simuliidae	2.053	(2.818)	2.667	(2.082)	4.333	(5.859)
	Ceratopogonidae	0.158	(0.375)	0.333	(0.577)	0.000	(0.000)
	Tipulidae	0.105	(0.315)	0.000	(0.000)	0.333	(0.577)
	Empididae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Blephericeridae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Tanyderidae	0.105	(0.315)	0.000	(0.000)	0.000	(0.000)
	Athericidae	0.053	(0.229)	0.000	(0.000)	0.000	(0.000)
Ephemeropter	Adults	0.684	(1.204)	0.333	(0.577)	0.000	(0.000)
	Baetidae	41.895	(24.729)	16.333	(15.275)	16.000	(13.000)
	Heptageniidae	16.526	(14.615)	5.333	(2.517)	16.000	(12.490)
	Ameletidae	0.842	(1.015)	0.667	(0.577)	0.667	(0.577)
	Leptophlebiidae	1.737	(2.130)	1.667	(2.082)	1.667	(1.528)
	Ephemerellidae	4.421	(4.046)	6.667	(4.509)	8.333	(4.041)
Plecoptera	Adults	0.737	(1.327)	2.667	(2.309)	2.333	(1.528)
	Perlidae	0.263	(0.562)	0.000	(0.000)	1.000	(0.000)
	Perlodidae	1.789	(1.653)	3.000	(2.646)	3.000	(2.646)
	Pternonarcyidae	0.211	(0.535)	0.333	(0.577)	0.000	(0.000)
	Chloroperlidae	0.789	(0.918)	1.667	(1.528)	5.333	(5.033)
	Nemouridae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Trichoptera	Adults	0.158	(0.375)	0.000	(0.000)	0.000	(0.000)
	Glossosomatidae	2.632	(3.593)	2.667	(2.887)	3.667	(2.082)
	Brachycentridae	0.105	(0.459)	0.000	(0.000)	0.333	(0.577)
	Limnephilidae	0.368	(0.597)	0.333	(0.577)	0.000	(0.000)
	Rhyacophilidae	0.211	(0.713)	0.000	(0.000)	0.000	(0.000)
	Hydropsychidae	1.684	(1.945)	5.333	(4.041)	11.000	(11.790)
	Lepidostomatidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Non-Insect	Oligachaeta	0.474	(0.697)	4.333	(4.041)	1.667	(1.528)
	Sphaeriidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Ostracoda	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Collembola	2.474	(5.571)	4.000	(6.928)	3.000	(3.606)

Group	Taxa	Baseflow		Pulse 1		Pulse 2	
	Nematomorpha	1.474	(1.775)	2.000	(1.000)	1.333	(1.155)
	Gastropoda	0.000	(0.000)	0.667	(0.577)	0.667	(1.155)
	Acari	0.053	(0.229)	0.667	(1.155)	1.000	(1.732)
	Daphnia	0.263	(0.562)	2.000	(2.000)	0.333	(0.577)
	Amphipoda	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Copepoda	0.000	(0.000)	0.333	(0.577)	0.000	(0.000)
Coleoptera	Elmidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Amphizoidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dryopidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hydrophilidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Dytiscidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Haliplidae	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Terrestrial	Orthoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Lepidoptera	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
	Hymenoptera	0.053	(0.229)	0.333	(0.577)	0.333	(0.577)
	Araneae	0.053	(0.229)	0.000	(0.000)	0.000	(0.000)
	Hemiptera	0.053	(0.229)	0.333	(0.577)	2.667	(3.055)

APPENDIX C

1. Bray-Curtis dissimilarity matrix between sample types and flow conditions at Sawmill. Within group dissimilarities are in bold. Missing values (NAs) are due to a single sample being collected, therefore unable to calculate within-group dissimilarity.

Flow Condition	Sample Type	Benthic	Drift	Diet
Baseflow	Benthic	**0.2655**	0.5156	0.5222
	Drift	0.5156	**0.2977**	0.5033
	Diet	0.5222	0.5033	**0.4475**
Pulse 1	Benthic	**NA**	0.5312	0.3120
	Drift	0.5312	**0.3438**	0.5405
	Diet	0.3120	0.5405	**0.3396**
Pulse 2	Benthic	**NA**	0.4738	0.4959
	Drift	0.4737	**0.4320**	0.5682
	Diet	0.4959	0.5682	**0.4830**

2. Bray-Curtis dissimilarity matrix between sample types and flow conditions at Steel Bridge. Within group dissimilarities are in bold. Missing values (NAs) are due to a single sample being collected, therefore unable to calculate within-group dissimilarity.

Flow Condition	Sample Type	Benthic	Drift	Diet
Baseflow	Benthic	**0.2412**	0.6754	0.5975
	Drift	0.6754	**0.2743**	0.5798
	Diet	0.5975	0.5798	**0.5731**
Pulse 1	Benthic	**NA**	0.7028	0.6709
	Drift	0.7028	**0.5401**	0.6698
	Diet	0.6709	0.6698	**0.6383**
Pulse 2	Benthic	**NA**	0.5093	0.6275
	Drift	0.5093	**0.4549**	0.6742
	Diet	0.6275	0.6742	**0.6714**

3. Bray-Curtis dissimilarity matrix between sample types and flow conditions at both study sites. Within group dissimilarities are in bold.

Flow Condition	Sample Type	Benthic	Drift	Diet
Baseflow	Benthic	**0.2926**	0.6073	0.5715
	Drift	0.6073	**0.3132**	0.5696
	Diet	0.5716	0.5696	**0.5592**
Pulse 1	Benthic	**0.6423**	0.6145	0.5734
	Drift	0.6145	**0.4453**	0.6184
	Diet	0.5734	0.6184	**0.5453**
Pulse 2	Benthic	**0.3889**	0.5056	0.5922
	Drift	0.5056	**0.4472**	0.6327
	Diet	0.5922	0.6327	**0.6122**