Responses of macroinvertebrate drift, benthic assemblages and trout foraging to hydropeaking below Flaming Gorge Dam, Utah

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Abstract

The tailwaters of Flaming Gorge Dam (FGD) support a blue-ribbon trout fishery that experiences thousands of angler hours per year and generates significant revenue for Dagget County, Utah. Given this socially valued resource, there are concerns that the reimplementation of double-peak release patterns could be detrimental to the health of the trout fishery below FGD. Predicting the ecological impacts of double-peaking requires an explicit understanding of the habitat parameters that sustain the growth, reproduction and survival of fish populations across multiple life stages. Principal among these habitat variables is food resource availability, as the growth of brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout below FGD is sustained by a relatively narrow diet of drifting macroinvertebrates. Despite the documented dependence of salmonids on drifting invertebrates, we lack a thorough understanding of how macroinvertebrate drift responds to hydropeaking operations of varying frequency, magnitude and duration to accurately parameterize models of fish performance under different flow scenarios. This uncertainty was highlighted in the development of an individual-based model for the trout fishery below FGD and is the primary focus of this report. Specifically, we utilized variability in hydropeaking operations and experimental flows to quantify how macroinvertebrate drift, benthic assemblages and fish consumption patterns respond to double-peaking at both short (hourly) and long (years) time scales. Our results suggest that changes in discharge have a greater impact on drift density than absolute flow levels, such that drift density was significantly higher during double-peaking as compared to single-peak release patterns. Furthermore, at hourly time-scales, drift density was highest during the rising limb of the hydrograph and increases were not sustained for the duration of individual peaks. Contrary to our expectations, significant increases in daily macroinvertebrate export did not significantly reduce the density or richness of benthic assemblages. Finally, drift feeding salmonids appeared to respond to increased prey resource availability, as gut fullness was significantly greater following periods of peak flow compared to base flow. These results suggest that the effects of food resource availability on trout fitness cannot be considered independent of discharge fluctuations at both daily and monthly time-scales.

Introduction

The construction and management of over 7,700 large dams (> 15 m high) throughout the United States has fundamentally altered the chemical, physical and biological regimes of lotic ecosystems (Collier et al. 1996, Vinson 2001, Poff et al. 2007, Ligon et al. 2011). In some instances, the novel environmental conditions downstream from dams, particularly cold and clear water with high primary and secondary production (Baxter 1977, Allan 1995), are capable of supporting economically valuable native and/or non-native cold-water fisheries. However, fisheries

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and the ecosystem processes that sustain them are often secondary management priorities to water storage and/or hydropower production, two of the principal societal benefits of large dams (Jager and Smith 2008). Consequently, balancing societal needs with those of freshwater ecosystems requires accurate models of organismal responses to altered flow regimes (Richter 2003, Konrad et al. 2011).

Predicting the ecological effects of flow alteration is particularly important for managers of hydroelectric dams since maximizing the market value of generated power is achieved through releasing frequent, large discharge pulses (i.e., hydropeaking or load following flows) (Cushman 1985, Gore et al. 1989). Hydropeaking is most commonly achieved through releasing either a single, long-duration daily peak or preferably, by releasing two short-duration peaks of increased magnitude that coincide with peak energy demand (i.e., double-peaking – Fig. 1). In either scenario, hydropeaking operations can significantly increase daily hydrologic variation, which can adversely impact downstream fish populations (Moog 1993, Lagarrigue et al. 2002, Young et al. 2011).

Mitigating the ecological impacts of hydropower projects requires an explicit understanding of the habitat parameters that sustain the growth, reproduction and survival of fish populations across multiple life stages. Fisheries and dam managers model flow mediated species-habitat relationships using physical habitat models that focus primarily on depth and velocity (Jowett 1997, Bovee et al. 1998) or more complex niche models that also incorporate prey resource availability and biotic interactions (Railsback et al. 1995). The incorporation of biotic variables, particularly food resource availability, has greatly increased our predictive capabilities due to the strong dependency of trout on drifting macroinvertebrates (Filbert and Hawkins 1995, Hayes et al. 2011). Despite the documented dependence of salmonids on drifting invertebrates, we lack a thorough understanding of how macroinvertebrate drift responds to hydropeaking operations of varying frequency, magnitude and duration to accurately parameterize models of fish performance. For example, Railsback et al. (2006) identified uncertainties in the intra- and inter-daily responses of drifting macroinvertebrates to hydropeaking as a primary limitation to modeling changes in brown trout production below Flaming Gorge Dam, Utah.

A multitude of studies have documented responses of drifting macroinvertebrates to both low and high discharge events (Minshall and Winger 1968, Poff and Ward 1991, Robinson et al. 2004, Gibbins et al. 2007), but only a small fraction have explicitly addressed the novel hydrologic conditions imposed by hydropeaking. The few studies conducted to date have produced equivocal results, with some studies observing significant increases in drift density or richness (Irvine and Henriques 1984, Perry and Perry 1986) and others finding little to no impact (Shannon et al. 1996, Mckinney et al. 2009). Disparity in the direction and magnitude of responses among studies can likely be explained by variability in the rate (i.e., ramp rate), frequency,

duration and/or magnitude of discharge increases (Irvine and Henriques 1984, Shannon et al. 1996, Imbert and Perry 2000), but we have only begun to test these hypotheses. For example, in an experimental manipulation of ramp rates, Imbert and Perry (2000) found macroinvertebrate density and richness significantly increased following discharge increases, but only density exhibited differential responses between gradual and abrupt ramp rates. Furthermore, we know of only one study that has attempted to link changes in food resource availability associated with hydropeaking to fish foraging behavior (Lagarrigue et al. 2002).

In this study, we utilized variability in hydropeaking operations and experimental flows to quantify how macroinvertebrate drift, benthic assemblages and fish consumption patterns respond to non-bed mobilizing hydropeaking operations at both short (hourly) and long (years) time scales. Specifically, we asked: 1. Does macroinvertebrate drift density, biomass and composition differ between single and double-peak release patterns; 2. How does macroinvertebrate drift density and biomass respond to peaks of varying magnitude; 3. What are the intra- and inter-daily temporal dynamics of drift under a hydropeaking regime; 4. How does hydropeaking affect benthic macroinvertebrate assemblages; and 5. Does fish foraging behavior differ between base and peak flows?

Materials and methods

Study area

Our study focused on the Green River, a large (115,800 km^2) snow-melt driven system originating in the Wind River Range of northwestern Wyoming, USA (   ). The Green River flows through the high desert plains of Wyoming, Colorado and Utah before joining the Colorado River and alternates between low gradient, broad alluvial valleys and higher gradient, confined canyons (Schmidt and Grams 1999). The hydrologic regime of the Green River is altered by two major dams, Flaming Gorge dam (FGD) and Fontenelle. Fontanelle dam is located approximately 200 stream kilometers upstream from FGD and primarily functions to store water for downstream power production and agricultural water needs and therefore has relatively constant discharge rates. FGD is located in northwestern Utah, approximately 85 km upstream of the Yampa River, and was completed in 1963 for hydroelectric power generation and water storage to support irrigated agriculture. FGD imparts the largest single effect on the hydrology of the Green River, with an annual storage capacity of 4.67 x 10^9 cubic meters relative to a mean annual flow of 52 cubic meters per second (cms). Specifically, FGD has reduced the annual hydrologic variability of the Green River by decreasing the mean annual peak flow by more than 50%, increasing baseflows and altering the seasonal timing of high and low flow events (Andrews 1986). Cumulatively, the construction and management of FGD has significantly altered the hydrologic, thermal and sediment regimes, in addition to the flora and fauna of the Green River

(Andrews 1986, Merritt and Cooper 2000, Vinson 2001, Grams and Schmidt 2002).

Following the construction of FGD, daily double-peak release patterns were common throughout the 1970s and 80s as a way to more efficiently meet daily patterns of electrical demand. However, concerns over impacts to native fishes (e.g., Colorado pikeminnow, humpback chub, razorback sucker, bonytail) in the lower portions of the river and decadal drought promoted daily single-peak or steady daily flows, depending on the season of operation, over the last two decades. More recently, daily double-peaking was intermittently resumed because of both increased water availability and power demand. Specifically, starting in 2006, double-peak release patterns were implemented seasonally from October through March, pending water availability. Below FGD, double-peak flows consist of two hydroelectric generation peaks per day, morning and evening, with baseflows averaging 28 cms or less and peaks exceeding 75 cms for a sustained period of two to four hours (Fig. 1). Ramp rates are constrained such that differences in mean daily flow between consecutive days cannot exceed 3% (Muth et al. 2000).

The tailwaters of FGD support a blue-ribbon trout fishery that experiences thousands of angler hours per year and generates significant revenue for Dagget County, Utah. Given this socially valued resource, there are concerns that the reimplementation of double-peak release patterns could be detrimental to the growth, survival and reproduction of trout below FGD. Specifically, the growth of brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout is sustained by a relatively narrow diet of drifting macroinvertebrates (Filbert and Hawkins 1995, Vinson et al. 2006), for which responses to double-peaking are undocumented. This uncertainty was highlighted in the development of an individual-based model for the trout fishery below FGD (Railsback et al. 2006) and is the primary focus of this report.

Sampling Design

To investigate the effects of double-peaking on macroinvertebrates, we employed a before-after-control-impact (BACI) study design with one control and two treatment sites (   ). Weeping Rock (WR) was selected as the control site to characterize daily and seasonal fluctuations in macroinvertebrate drift where macroinvertebrate assemblages have been altered by dam construction, but flows exhibit nominal diel and seasonal fluctuations. WR is located immediately downstream of Fontanelle Dam, and experiences relatively consistent daily flow rates, which averaged 25 cms over the course of the study (e.g., Fig. 1). Immediately downstream of FGD, two sites were selected to represent the two dominant channel morphologies: laterally constrained canyons and broad alluvial valleys. Specifically, Tail Race (TR) is located < 1 km downstream of FGD and is a higher gradient (0.002 %), constrained canyon with an average wetted width of 45 m and a relatively coarse bed that is heavily armored (Vinson 2001, Railsback et al. 2006). In contrast, Little Hole (LH) is a lower gradient reach (0.0008 %) located approximately 10 km downstream from FGD that has an

average wetted width of 63 m and finer bed material consisting of coarse gravel, cobble and boulders.

Each site was sampled from October to March of both the 2010 and 2011 water years. Specifically, we sampled a total of two pre- and five post-double-peak sample cycles (see detailed description below) at weekly to monthly intervals to quantify the short- and long-term effects of double-peaking on macroinvertebrate drift and benthic densities (Table 1). In addition to monitoring conditions before and after double-peaking, we requested two experimental flow manipulations to test hypotheses related to single- versus double-peak release patterns (hiatus experiment), as well as variation in the magnitude of peak flows (peak magnitude experiment). Specifically, in 2010, double-peaking was interrupted after one month and returned to pre double-peaking flow conditions for a period of one week (Fig. 3c). Sampling cycles occurred at all sites immediately before and two days into the hiatus to quantify whether total daily macroinvertebrate export returned to pre double-peaking levels following the cessation of double-peaking (Table 1). Additionally, in November 2011 as double-peaking was implemented, we requested experimental releases in which the magnitude of the evening peak was gradually increased by 14 cms per day, culminating in a peak daily discharge of 75 cms (Fig. 4). Sampling was conducted at both TR and LH during each day of the four day experiment, with emphasis on targeting the increasingly larger evening peak, for a total of 5 samples per day (Table 1).

A sampling cycle consisted of seven to eight drift samples collected over a 24 hour time period. Drift sampling was synchronized among the three sites, with the objective of sampling base flow conditions, the rising limb and peak discharge of each daily double-peaking event. To accomplish this, a single drift sample was collected during each hydrologic stage except during peak flows, when we sampled twice to capture potential within-peak hysteresis. Discharge was monitored using data from USGS gauges 09234500 (TR) and 09211200 (WR), while flows at LH were estimated based on a two hour time of concentration from TR.

Macroinvertebrate and Fish Sampling
During each collection time per 24-hour sample cycle, macroinvertebrate drift was quantified using seven drifts nets (45 x 20 cm, 500 μm mesh) unless safe access was impeded by high flows, in which case a minimum of four nets were deployed. Drift nets were secured with metal rebar stakes, placed 10 cm off the stream bottom and deployed for 40 minute intervals. At the start and end of each deployment, we measured velocity with a digital flow meter at the vertical mid-point of each drift net (20 cm from the stream bottom) to obtain the average velocity among all nets. The contents from the nets for a given collection time, including vegetation and other debris, were composited and preserved in 95% ethanol. Drift sampling was constrained to the bottom third of a single representative riffle per site, which permitted safe wading conditions during peak discharge events and yet still maintained

representative habitat conditions at baseflows. However, a single riffle did not meet this criterion at TR and thus two separate riffles within 500 m of one another were sampled during high and low flow events.

To assess the impacts of double-peaking on benthic density and composition, we utilized two separate datasets: a long-term dataset of January and April benthic samples collected at both TR and LH since 1995 and benthic samples collected at each of WR, TR and LH once during each sample cycle. Benthic macroinvertebrates were sampled using a Hess (0.08 m^2, 250 µm mesh) or Surber sampler (0.09 m^2, 500 µm mesh) to collect eight randomly located samples from riffle habitats that were composited (0.64 m^2 and 0.72 m^2, respectively) and preserved in 95% ethanol.

Benthic and drift samples were processed using a subsampling procedure where a minimum of 200 organisms (or a minimum split of 1.5% of the total sample) were randomly extracted from all samples (Caton 1991, Vinson and Hawkins 1996). We identified macroinvertebrates to genus (Rogers 2005, Merritt et al. 2008), however, Chironomidae were identified to subfamily, and all non-insect taxa were identified to coarser levels, typically order or family. Prior to analysis, identifications were standardized to operational taxonomic units (OTUs, Cuffney et al. 2007), typically at genus level.

The dry mass of drifting macroinvertebrates was determined at the order level due to low within-order richness (average of 3 OTUs per order; Table 2) and high dominance (>90%) of one or two OTUs per order. Specifically, all individuals within a particular order (Amphipoda, Diptera, Ephemeroptera, etc.) were pooled, oven dried at 100°C for 48 hours and weighed to the nearest tenth of a milligram. Finally, the blotted wet weight of all vegetative biomass captured in individual drift samples was also obtained. The total biomass was computed as milligrams per cubic meter of water (for drift samples), as follows:

$$D_{drift}\left(^{mg}/_{m^3}\right) = \frac{N}{(t)(A)(V)(^{3600s}/_h)}$$

where N is the weight (mg) of organisms in a sample (corrected for field and/or lab subsampling splits); t is the time (hours) that the net was deployed; A is the area of the net opening (m^2); and V is the mean water velocity at the net mouth (m/s). Density was computed similarly for all samples by substituting the number of individuals in place of milligrams, and for benthic samples by omitting velocity variables, with final units as density per area (m^2).

To investigate the response of fish foraging behavior to double-peaking, rainbow and brown trout gut fullness and composition was compared between base and peak flow periods at both TR and LH. Specifically, fishes at LH were sampled during baseflow (23.5 cms) on November 15th, 2010 at 08:00 following a 16 hour hiatus from

hydro-peaking and at 13:00 following a four hour peak flow event (60.8 cms). Similarly, TR baseflow fish diets were sampled the next day at 11:00 following a 24 hour hiatus from hydropeaking and at 15:00 following a three hour peak flow event. Disparate sampling times between sites and dates were required to maximize the baseflow period prior to diet sampling, complete fieldwork during daylight hours and yet operate within flow release constraints established by FGD operations. During each sampling event, fish were collected using a combination of backpack and boat-mounted electroshockers, with a target of 15 replicates per species and size class (<200, 201 – 400, > 400 mm). Captured fishes were euthanized using a lethal dose of MS-222, identified to species, weighed to the nearest tenth of a gram, measured to the nearest millimeter (total length) and the stomach extracted and preserved in 95% ethanol. Each stomach was blotted dry and weighed to the nearest milligram, the contents filtered through a 250 μm sieve and the stomach re-weighed once empty. As with drift samples, the contents were identified to the lowest possible taxonomic resolution and dry mass was determined at the order level. In addition we performed dry mass estimates of unidentifiable organic matter and vegetation. Gut fullness (mg g^{-1}) was determined as the total macroinvertebrate biomass (mg), including fish eggs but omitting organic matter and fish adults which caused outliers in the analyses, standardized to the emptied gut weight (grams) of each fish.

Analyses

To quantify responses of drifting macroinvertebrates to double-peaking, we tested for disparate temporal trends among sites using nonparametric analysis of covariance (ANCOVA). A nonparametric ANCOVA was chosen in lieu of more traditional ANOVA models because of the paucity of temporal independence among sample cycles at a site. Specifically, we compared temporal trends for each treatment site (TR and LH) to the control (WR) using pairwise tests of equality with day of year as the covariate to account for observed seasonal effects. Individual sites and sample years were analyzed separately because we anticipated differential responses based on disparate geomorphologies and hydrographs. We used total daily macroinvertebrate export (mg m^{-3}) as the response variable, which was computed by summing the biomass of all collected samples per 24 hour sample cycle per site. In addition to running ANCOVAs for total daily macroinvertebrate export per sample cycle, we also tested the homogeneity of temporal trends for the two dominant taxa (> 90% of total biomass on average) at TR and LH: Amphipoda and Diptera. The extreme dominance and ubiquity of these two orders among all samples, contrasted with the rarity and low biomass of other orders precluded the use of multivariate analyses to test for differences in assemblage composition through time.

ANCOVA models were fit in R (version 2.14.1, R Development Core Team 2011) using the sm package (version 4.1,Young and Bowman 1995). We tested multiple values of the kernel density estimation smoothing parameter (*h*) to confirm significance at different values and according to various methods. The Sheather-Jones method

(Sheather and Jones 1991) was selected for visual representation of the smoothed estimators and resulting reference band. Specifically, the reference band graphically represents the acceptance region for the null hypothesis of no difference in the temporal trend between sites and is directly related to the error differences between the actual data points and the smoothed fit. We adopted the methodology of Bowman and Young (1996) and interpreted deviations of the smoothed curve from the reference band as statistically significant departures of individual sample periods. The p-value for this test, however, is based on the entire dataset and the deviation from reference bands is intended to inform local interpretation. The alpha level for all ANCOVAs, as well as all other statistical analyses, was set to 0.1 due to natural variation anticipated in drift data. Although we recognize that the probability of finding significant results by chance increases as more tests are conducted, we did not adjust alpha levels using Bonferroni procedures because they are overly conservative and therefore increase the chance of ignoring ecologically meaningful results (Moran 2003). Complete input data and analysis R script are available upon request from the authors.

To analyze the relationship of intra-daily drift patterns with discharge, as well as temporal patterns during the two experimental releases from FGD, we relied on both qualitative analyses and simple linear regression. In particular, we graphically examined relationships between intra-daily drift patterns and discharge using the seven to eight drift samples collected during each sample cycle. We were specifically interested in assessing the degree of diel periodicity at both the control and treatment sites and how double-peaking altered the magnitude and timing of daily drift patterns. Furthermore, we qualitatively evaluated how daily drift patterns changed during the one-week hiatus from double-peaking in 2010 and the peak magnitude experiment in 2011. Lastly, we quantified the response of drift during the rising limb of the peak magnitude experiment to peaks of increasing magnitude using simple linear regression.

We used random forest (RF) regression models to elucidate potential drivers of intra- and inter-daily variation in macroinvertebrate drift, where biomass from individual drift samples collected during each 24 hour sample cycle was used as the response variable. Models were developed individually for the control and two treatment sites for the 2010 water year only, given that 2010 was the only true double-peak year (see results). The predictor variables included time of day, day of year, instantaneous discharge corresponding to individual drift samples, the change in flow occurring two hours prior to sample collection, Froude number (computed from average velocity and depth following Statzner et al. (1988)), vegetative biomass contained within individual drift samples and benthic densities collected once during each 24 hour sample cycle. No final predictors had Pearson correlation coefficients exceeding 0.50.

RF was chosen over more traditional linear regression models because predictor variables exhibited both linear and non-linear relationships with the response variables

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and we anticipated complex interactions among variables. RF combines the results of multiple un-pruned classification trees based on independent bootstrapped samples of the original data to generate more stable and accurate model results (Cutler et al. 2007, Siroky 2009). An additional layer of randomness is added by basing each split of the regression tree on a subset of predictors randomly chosen at each node. We used the randomForest package within program R (version 2.14.1, R Development Core Team 2011), with model results averaged across 500 trees and the default values for the bootstrapped sample size and number of predictors tried at each node. Overall model performance was assessed using a cross-validated r-squared (R^2) computed by applying the final model to the data withheld from the bootstrap sample. Individual variable importance was assessed by computing increases in the mean squared error when the validation data for an individual variable was permutated, while all others remained unchanged. We did not seek to optimize model accuracy by successively removing predictors having poor predictive power, but rather included all predictors in all models because our primary goal was to compare the relative importance of predictors within and among models. Final relationships were visually assessed using partial dependency plots, which plot the marginal effect of an individual predictor variable when other predictor variables are held constant.

To assess the effects of double-peak release patterns on benthic macroinvertebrate assemblages, we utilized a 17 year record (1995 – 2011) of macroinvertebrate benthic samples to test for relationships between the variation in daily flow and macroinvertebrate density and richness at both TR and LH. We used hourly discharge measurements to compute the mean daily coefficient of variation (CV) for each year for two time periods coinciding with double-peaking and the timing of benthic macroinvertebrate sampling: October 1st – December 31st and January 1st – March 31st. Relationships between macroinvertebrate benthic densities and richness with the mean daily CV were quantified using simple linear regression.

Differences in gut fullness between base and peak flows was quantified using both univariate and multivariate analyses. Specifically, a two-way factorial design in a generalized linear model (GLM) with a log (Y+c) transformation was used to compare gut fullness between flow levels (High or Low), fish species (*S.trutta* and *O. mykiss*) and the flow by species interaction. Sites and years were run in separate models and sample sizes within distinct size classes were not sufficient to be included as a factor in the model.

The extent of compositional diet differences (biomass standardized by gut weight) between flow levels for individual fish species and sites were quantified using a multiple response permutation procedure (MRPP) (Mielke and Berry 2001), where individual fishes of the same species and flow were considered replicates. MRPP is a nonparametric permutation procedure that tests for differences among two or more groups. A p-value assesses the probability of observed group differences under the

null hypothesis, while an *A*-statistic (range: 0 – 1) quantifies the effect size and within group homogeneity (McCune and Grace 2002).

Results

We observed significant increases in intra-day hydrologic variability below FGD during double-peak years (*t* = 5.8; *d.f.* = 8.2; *p*-value < 0.001) with the mean daily CV greater than 30% on average compared to less than 10% during non-double-peak years (Fig. 5). However, double-peak releases from FGD were not consistent between the two study periods (Fig. 1). In 2010, pre-double-peak release patterns consisted of relatively high, steady flows between 50 and 60 cms, which were lowered to 30 cms between 01:00 and 06:00 each day. Starting in October and continuing through March, double-peaking consisted of two daily peaks of equal magnitude, but of disparate durations between the morning (3.5 hours) and evening (5 hours) peaks. Both peaks ranged from 60 to 70 cms and had ramp rates ranging from 10.5 to 13 cms per hour.

In contrast, both the 2011 pre- and actual double-peak release patterns differed from those in 2010. Specifically, pre-double-peak flows consisted of a single evening peak (magnitude: 51 cms; duration: ~3 hours) followed by a period of relatively constant discharge (25-30 cms). Double-peaking persisted from October to March, but differed from 2010 release patterns in the duration and magnitude of peaks (Fig. 1), as well as the disparity between morning and evening peaks within a day. The morning peak was the smallest observed (range: 42 – 50 cms) and was followed by a larger afternoon peak (range: 57 – 71 cms), with ramp rates ranging from 11 – 13 cms and peaks lasting < 3 hours on average; a daily pattern very similar to pre-treatment flows.

Biomass and composition of drifting macroinvertebrates between single and double-peak release patterns

We collected a total of 69 taxa that were reduced to 37 OTUs from 385 drift samples among all sites and dates, including experiments (Table 2). Total richness and average sample richness was lowest at TR (18 OTUs total, 5 per sample) followed by LH (27 OTUs, 8 per sample) and WR (26 OTUs, 11 per sample). Four orders comprised 99% of macroinvertebrate drift density among all sites (e.g., Fig. 6): Amphipoda (73.3%), Diptera (17.6%), Ephemeroptera (5.1%) and Trichoptera (3.6%). Considering double-peaking sites alone, Amphipoda (specifically *Hyallela*) comprised the majority of the assemblage (~85%) and Diptera, primarily Chironomidae and some Simullidae, made up an additional 10% of the assemblage. In contrast, the control site had higher levels of Diptera (60.8%), moderate levels of Ephemeroptera and Trichoptera (~28%) and low, but consistent densities of Amphipoda (5.2%) in the drift.

Average drift in 2010 was 0.18 milligrams per cubic meter (1.98 # individuals m^{-3}) at TR, 0.24 mg m^{-3} (2.81 # m^{-3}) at LH and 0.11 mg m^{-3} (1.02 # m^{-3}) at WR. In 2011, average drift was elevated at TR (0.45 mg m^{-3}, 4.92 # m^{-3}), but remained steady or

were slightly elevated at LH and WR as compared to 2010. Maximum observed drift, excepting experimental flows and overall elevated levels at Tail Race in 2011, occurred during double-peaking in 2010 with values of 1.03 mg m^{-3} (11.69 # m^{-3}) and 1.55 mg m-3 (22.88 # m^{-3}) at TR and LH, respectively. On average, double-peaking increased the biomass of drifting invertebrates by over 200% compared to pre-double-peaking levels. WR had consistent levels of background drift, with maximum drift not exceeding 1.38 mg m^{-3} (6.38 # m^{-3}) in either year.

Temporal patterns of total daily export of drifting macroinvertebrates differed between the 2010 and 2011 water years (Fig. 7). In 2010, we observed significant, short-term increases in drift biomass with the initiation of double-peaking at both TR and LH; however, the overall temporal drift patterns did not significantly differ from the control (Table 3). Specifically, control and double-peak sites significantly diverged for 60 – 80 days following the initiation of double-peak flows, with total daily export exceeding 2.65 mg m^{-3} at both TR and LH, an average increase of 171% relative to pre-double-peaking samples, while total daily export remained constant or even decreased at the control site (Fig. 7). In contrast, responses of total daily export to double-peaking during the 2011 water year were highly variable. The temporal patterns of total daily export significantly differed between TR and the control, but significant differences existed prior to the initiation of double-peaking, after which the two sites began to converge through time (Fig. 7). In contrast, total daily export did not significantly differ between LH and the control in 2011 and exhibited similar temporal patterns as in 2010.

The observed short-term increases in total daily drift export were primarily driven by Amphipoda, which exhibited significantly different temporal patterns from the control during all site by year combinations (Table 3). Amphipoda was the dominant taxa downstream from FGD and exhibited short-term increases in total daily export exceeding 183 % (> 1.11 mg m^{-3}) of pre-double-peaking conditions on average (Fig. 6). Similarly, the temporal patterns of Diptera, the second most dominant group (Fig. 6), exhibited marginal differences between control and downstream sites across all site by year combinations, except for TR in 2010 (Table 3).

Intra-daily drift patterns during double-peaking
Drift at the control site (WR) was relatively constant and did not exhibit evidence of diel fluctuations on a daily time-scale. In contrast, for a given double-peak event drift exhibited considerable temporal variability, with increases in drift biomass during the rising limb of the hydrograph or at the onset of peak flows constituting the greatest contributions to total daily export (Fig. 3b). However, after approximately two hours of peak flows, we observed hysteresis, in which elevated drift biomass was not sustained despite persistent high discharge exceeding 50 cms. For example, following one-month of double-peaking at TR in 2010, drift increased from 0.11 mg m^{-3} at baseflow (35 cms) to 0.64 mg m^{-3} within one hour of discharge reaching 70 cms (Fig. 3b).

However, drift approached pre-peak conditions (0.25 mg m^{-3}) prior to the descending limb of the hydrograph.

In December of 2010, when flow release patterns were returned to single-peaking for a one-week period (i.e., the hiatus experiment), we observed a total daily export of 0.97 and 0.72 mg m^{-3} at TR and LH, respectively (Fig. 3c). This export rate was equivalent to pre-double-peak levels and substantially lower than the elevated export (2.91 mg m^{-3}) observed one week prior during double-peaking (Fig. 3b). During the hiatus, maximum drift at any single time did not exceed 0.25 mg m^{-3} and the maximum occurred when flows increased in the evening from 30 to 50 cms, but was not markedly elevated from baseflow levels, which were 0.14 mg m^{-3} on average (Fig. 3c).

The influence of peak magnitude and other factors on macroinvertebrate drift rates

During the experimental increase in the magnitude of afternoon peaks, we observed proportional increases in maximum drift density that exceeded 3.02 mg m^{-3} (49.7 # m^{-3}); an increase of over 400% during the course of the experiment (Fig. 4). At TR, drift biomass at peak initiation was strongly related to peak discharge (R^2=0.94) and for every increase of 10 cms, biomass was predicted to increase by 0.81 mg (y=0.081x-2.25). Responses at LH showed similar, but more variable (R^2=0.67) and muted (y=0.036x -0.63), with a maximum drift biomass of 1.39 mg m^{-3}. At finer temporal scales, the degree of within peak hysteresis appeared to also intensify, as the magnitude of peak discharge increased (Fig. 4).

Our ability to explain variation among all drift samples collected at a site during the 2010 water year varied among sites, with the TR random forest model having the highest precision (R^2 = 43.4%) followed by LH (R^2 = 35.24%) and WR (R^2 = 30.41%) (Fig. 8). Drift density at WR was most sensitive (i.e., greatest percent increase in mean square error [MSE]) to daily benthic densities and to a lesser extent Froude number, day of year and flow (Fig. 8). In contrast, vegetative export was the single best predictor for both TR and LH (Fig. 8), with drift biomass exhibiting a threshold response to vegetative drift, but the range of observed values and subsequent thresholds differed dramatically between sites (Fig. 9). Subsequent predictors of importance at both TR and LH were day of year and measures of discharge. Specifically, drift biomass increased when discharge levels exceeded 60 cms at TR or discharge increased more than 25 cms in two hours at LH; however, drift increases were only sustained for 70 to 80 days from the start of double-peaking (Fig. 9), as observed in daily total export results (Fig. 7).

Hydropeaking effects on benthic macroinvertebrate assemblages

We observed relatively weak and variable responses of benthic macroinvertebrates to the degree of intra-daily flow variability across the 17 year period of record: 12 years of single-peak or steady flows and five years of double-peaking (   ). Taxa richness exhibited the only consistent response with richness inversely related to the mean daily coefficient of variation for both the January and April TR samples (R^2=0.25

and 0.3, respectively), while LH exhibited no discernible patterns. Benthic densities were not negatively correlated with increasing daily CVs, except over the short-term at TR in the January samples.

Fish foraging responses to hydropeaking

The stomach contents of 242 fishes were analyzed at both TR and LH, with between 20 to 40 fish processed per species and flow levels (   ). Brown trout were captured in lower numbers than rainbow trout at TR and the converse was true at LH. Within a site, a particular fish species was caught at approximately the same frequency during both low and high flow levels. The average length and weight of captured fish was 340 g and 460 mm, with the majority of fish in the middle size class (200-400 mm).

Gut fullness was significantly greater following peak versus base flows at both TR and LH (   ), however, a significant species by flow interaction was observed for TR, with only rainbow trout showing significant increase in gut fullness following peak flows (   ). On average, gut fullness increased by 3.66 mg g^{-1} following high flows for both sites and species. Amphipoda and Diptera dominated the composition of fish diets, with occasional occurrences of snails, fishes and fish eggs (   ). While the total biomass of consumed invertebrates increased following peak flows, we observed no significant differences in the relative abundance of diet composition between flow levels for both rainbow and brown trout at either site (all *A*-statistics < 0.05); two p-values were less than 0.05 (data not shown), but the ecological significance was very weak as indicated by the very low *A*-statistics. Lastly, because of the large amount of ingested organic matter, particularly filamentous algae, we tested for differences in organic matter consumption between species and flow treatments. Rainbow trout had significantly greater quantities of ingested vegetation as compared to brown trout at both TR and LH (,   ). Furthermore, organic matter consumption appeared higher following peak flows, although brown trout at TR did not show significant increases (   ).

Discussion

Hydropeaking has been shown to alter the density and composition of macroinvertebrate assemblages, which play critical roles in river ecosystems by serving as important conduits of energy between basal resources and higher trophic levels (Cummins and Klug 1979, Nakano and Murakami 2001, Baxter et al. 2005). In this study we sought to quantify the structural responses of drifting and benthic macroinvertebrate assemblages to hydropeaking, as well as the functional implications for fish foraging behavior and subsequent fitness. In the succeeding sections we discuss intra- and inter-daily patterns in macroinvertebrate drift, the mechanisms likely driving the observed patterns and the implications of increased drift density for the

fishery below FGD. We focus specifically on the 2010 water year since the annual hydrograph was more characteristic of double-peaking, as well as the experimental flows and fish diet study conducted in 2011.

Biomass and composition of drifting macroinvertebrates between single and double-peak release patterns

Similar to other studies, we found that double-peaking significantly increased the degree of intra-daily hydrologic variability (Cushman 1985, Gore et al. 1989, 1994), which more than doubled the daily export of drifting macroinvertebrates for a 60 – 80 day time period. Despite the sustained high flows typical of single-peaking (Fig. 3a), we believe total daily export was greater during periods of double-peaking because invertebrates were responding to the frequent, rapid rises in discharge. For example, the change in flow two hours prior to drift sampling was a good predictor of differential drift biomass at LH (Fig. 9), with drift increases observed when flow changes exceeded 20 cms. Increases in drift density have been repeatedly observed in response to sudden discharge rises associated with experimental floods(Irvine 1985, Poff and Ward 1991), natural floods (Robinson et al. 2004, Callisto and Goulart 2005) and hydropeaking (Irvine and Henriques 1984, Perry and Perry 1986, Cereghino et al. 2004, Mckinney et al. 2009). Drift increases are thought to result from the 'shaking' and/or transport of benthic sediments in the case of catastrophic drift (Allan 1995, Gibbins et al. 2007) and less dramatically, as passive or involuntary drift when individuals are dislodged from the benthos (Allan 1995). Given the relatively coarse substrate and heavy armoring immediately below FGD (Railsback et al. 2006), our study mainly focused on non-bed scouring flows and thus drift was likely the product of both the dislodgement of individual invertebrates and/or the mechanical shearing of the thick algal mats, which blanket much of the river.

Despite the observed drift responses, we found that drift increases were only sustained for a period of 60 -80 days. Decreases in daily macroinvertebrate export through time, in the absence of discharge changes, may result from several factors including the depletion or seasonal decline of benthic densities (Irvine 1985, Allan 1987, Cereghino et al. 2004, Callisto and Goulart 2005); redistribution of benthic assemblages to the stream margins or other refugia (Ciborowski and Clifford 1983, Ciborowski 1987, Rempel et al. 1999) or temporal trends in a covariate such as vegetative export and/or stream temperature (Irvine and Henriques 1984, Irvine 1985, Shannon et al. 1996, Tockner and Wagner 1997). Results from random forest modeling suggest that temporal variability in macroinvertebrate drift was tightly linked to patterns in vegetative export and not changes in the density or distribution of benthic macroinvertebrates (Fig. 8). Specifically, we failed to detect changes in benthic densities at both short (data not shown) and long time-scales and with benthic densities exceeding 50,000 individual per square meter it is unlikely that adequate refugia existed to accommodate the redistribution of all individuals. Rather, the dominant taxa at treatment sites, *Hyallela* and Chironmidae midges, are commonly

found at high densities in mats of Cladophora glomerata (Power 1990, Shannon et al. 1996), the main filamentous algae within the Green River.

Hydropeaking has been shown to increase the export of benthic organic matter, with the rate of macroinvertebrate drift strongly correlated with the timing and magnitude of organic matter export (Irvine and Henriques 1984, Irvine 1985, Shannon et al. 1996, Tockner and Wagner 1997). In our study, the biomass of drifting organic matter appeared to interact with day of year to explain the ephemeral nature of drift increases. Specifically, the export of drifting organic matter rapidly increased following the initiation of double-peaking and subsequently declined after approximately 60 to 80 days (data not shown), although responses were more variable at LH. We believe that drift decreased at LH, despite rising quantities of drifting vegetative biomass, because the downstream position of LH relative to FGD allowed it to continue to receive sloughed, senesced algae that was locally stored in upstream backwaters and subsequently transported by the changes in stage height associated with double-peaking (Shannon et al., 1996; S.W. Miller, personnel observation). Furthermore, invertebrate densities were likely low in the sloughed algal mats because once senesced, the algae no longer continued to be a good source of epiphytic diatoms for Amphipoda and Chironomidae midges.

Alternatively, water temperature was highly correlated with day of year (r = -0.96) and was not included in the RF models because data was not available for WR and LH. When included in the TR model, temperature was one of the top predictors, with drift precipitously declining below $7^{o}C$ (data not shown). Seasonal drift patterns below FGD have been linked to changes in stream temperature (Railsback et al. 2006), but it is unclear whether temperature is the proximate cause or a spurious correlation resulting from other temporal covariates. Temperature has been shown to influence diel patterns of macroinvertebrate drift, with the larger drift peak at dusk attributed to warmer afternoon temperatures and increased macroinvertebrate activity rates (Brittain and Eikland 1988, Allan 1995). Such mechanisms could be operating at longer time-scales to explain the reduced drift throughout the winter months, but it appears unlikely given the relatively steady drift rates at WR, which likely experiences similar seasonal temperature declines. Rather, we believe decreasing temperatures interacted with reduced light availability, both of which decreased with day of year, to increase the rate and short-term export of senescing algae to temporarily increase drift rates (reviewed in Allan, 1995).

Intra-daily drift patterns during double-peaking
Similar to results from other studies, drift increases were associated with the rising limb of the hydrograph, but were not sustained for the duration of daily peak events (Perry and Perry 1986, Imbert and Perry 2000, Robinson et al. 2004, Mochizuki et al. 2006). This trend is similar to the pattern of hysteresis observed for sediment (Asselman 1999, Lenzi and Marchi 2000) and organic matter transport (Irvine and

Henriques 1984) during flood events, but it is unclear whether the mechanisms explaining cyclical macroinvertebrate drift patterns are similar to those observed for organic matter and sediment transport. Hysteresis in macroinvertebrate drift is typically attributed to either reductions in benthic densities and/or behavioral adaptations (Irvine and Henriques 1984, Perry and Perry 1986). As previously noted, persistent, high benthic densities in our study suggests the supply of invertebrates was not likely the driver nor the limiting factor, but rather, the supply of drifting vegetative biomass. We found vegetative export to be the top predictor of drift rates, which exhibited concordant patterns of daily hysteresis with invertebrate drift (data not shown). Similarly, Irvine and Henriques (1984) observed that organic matter export was highly correlated (> 0.83) with short-term increases in macroinvertebrate drift. Furthermore, during the experimental increase in peak magnitude, the pattern of within peak hysteresis intensified, suggesting supply limitation of drifting organic matter. Alternatively, behavioral adaptations, specifically the redistribution of *Hyallela* and Chironomidae midges to areas of lower shear stress, could interact with the supply of vegetative material to explain the observed patterns. Several studies have observed that a variety of taxa including snails, mayflys, caddisflys and true flies actively seek flow refugia during periods of increased velocity (Hart and Finelli 1999, Holomuzki and Biggs 1999, 2000). However, this explanation seems less plausible for Amphipoda and Chironomidae midges, since they appeared to largely inhabit algal mats, which are subject to considerable shear and transport.

The influence of peak magnitude and other factors on macroinvertebrate drift rates

Previous studies have examined how drift rates vary as a function of ramp rate and to a lesser extent the magnitude and duration of high flows in experimental (Irvine 1985, Imbert and Perry 2000)and regulated systems (Irvine and Henriques 1984, Perry and Perry 1986). Ward (1976) hypothesized that slower, more gradual ramp rates might minimize the impacts to drifting invertebrates; however, tests of this hypothesis have produced equivocal results. For example, Imbert and Perry (2000) observed significantly greater drift increases during abrupt versus step-wise increases in experimental stream channels, while in natural settings, Perry and Perry (1986) did not observe differential drift densities among ramp rates. In contrast, systematic evaluations of how drift density varies as a function of the magnitude and/or duration of peak flows have not been explicitly addressed (but see Irvine & Henriques, 1984), despite the fact that ramp rates are often restricted by environmental flow regulations and the amount and value of generated power is controlled more by the magnitude and duration of peaks than the ramp rate.

We utilized experimental flows from FGD to evaluate changes in drift density as a function of the magnitude of peak discharge. Our results suggest that drift increases in proportion to the magnitude of peak flows (Fig. 4), although with only four data points it was difficult to discern proportional from exponential increases. Our results are somewhat surprising, as past studies failed to detect sustained drift increases following

successive natural or experimental floods of increasing magnitude because of reductions in benthic densities and/or the acclimation of benthic assemblages (Irvine and Henriques 1984, Poff and Ward 1991, Imbert and Perry 2000). In contrast, with the high benthic densities observed below FGD and no apparent long-term reductions, source populations appeared adequate to sustain increased drift densities over the course of the four day experiment, although more pronounced hysteresis was observed as the experiment continued and flow increased. More extensive experiments over a greater range of discharges would be required to determine whether drift increases are only initiated above some threshold or absolute change in discharge (Imbert and Perry 2000, Robinson et al. 2004, Mochizuki et al. 2006) and if drift plateaus or is otherwise unsustainable above certain magnitudes or varied ramp rates. Our random forest modeling of drift samples during the 2010 water year suggest significant increases in drift biomass occur above 60 cms and following flow changes exceeding 10 cms (Fig. 9). However, the flow change threshold varied between sites and is likely artificially low because of persistent drift increases for approximately two hours, during which no change in flow occurred (e.g., Fig. 3). We attribute the low sensitivity of drift biomass to discharge and flow change to both short- and long-term patterns of hysteresis, which resulted in variable drift responses despite similar discharge levels.

Hydropeaking effects on benthic macroinvertebrate assemblages

Despite short-term increases in drift density exceeding 22 individuals per cubic meter of water (172% increase), we failed to detect significant short- or long-term decreases in benthic densities. This finding contrasts those of other studies finding reductions in benthic densities in response to both flood events (Grimm and Fisher 1989, Shannon et al. 2001, Robinson et al. 2004) and hydropeaking operations (Cereghino and Lavandier 1998, Blinn et al. 2012). The resistance of benthic densities to double-peaking below FGD is likely a result of non-bed mobilizing flows and the extremely high benthic densities relative to observed drift rates; drift density never exceeded 1% of benthic densities when scaled to total daily export over a 24 hour time period following Elliott (1967). Furthermore, benthic assemblages below FGD are dominated by *Hyalella*, Chironomidae midges and a small proportion Baetidae mayflys, all of which are highly productive and disturbance adapted organisms (Vinson 2001).

In contrast to the response of benthic densities, the increased hydrologic variability associated with double-peaking over the last five of 17 years considered by this study was associated with statistically significant, but ecologically questionable declines in taxa richness at TR. Specifically, the rate of species loss was less than 0.10 taxa, but with an assemblage of only five taxa on average, the loss of any taxa can be significant. Although the hyper abundant assemblage dominants, Amphipoda and Diptera, do not appear impacted by double-peaking, taxa with significantly lower benthic densities might be more susceptible to increased drift rates.

Fish foraging responses to hydropeaking

The impacts of hydopeaking on trout populations have been widely studied in terms of alterations to physical habitat, while a paucity of studies have directly addressed how altered prey resource availability effects foraging behaviors and subsequent fitness (but see Lagarrigue et al. 2002). It has been suggested that trout do not utilize the increased drift densities associated with peak flows because of the instinct to seek flow refugia, the increased energetic costs of foraging at high flows and/or the inability to capture prey at higher velocities (Lagarrigue et al. 2002, Railsback et al. 2006). In contrast, we observed significant increases in gut fullness following peak flows which exceeded 3.7 mg g^{-1} on average, an increase of over 83%. Our results are similar to those of Lagarrigue et al., (2002) who observed significant increases in brown trout gut fullness two to four hours following catastrophic drift associated with hydropeaking events. However, we cannot be certain as to precisely when rainbow and brown trout increased consumption rates in relation to a hydropeaking event. Specifically, foraging behavior might have initially decreased during the ascending limb and only resumed once flows stabilized, during which time drift remained elevated for approximately two hours. Lagarrigue et al., (2002) sampled at four hour intervals and speculated that brown trout did not feed during peak flows. In contrast, Flodmark et al., (2006) observed no differences in brown trout behavior (e.g., movement rates, feeding or agnostic) in response to simulated hydropeaking in experimental channels. Understanding trout behavior throughout a peaking event is critical, as our results suggest that peaks of increased magnitude result in higher, but shorter duration drift increases. Thus, the extent of increased foraging behavior might vary as a function of peak magnitude and duration.

Although significant, the results of our study should be interpreted with caution as they represent only a single instance of fish foraging behavior at two different sites. For example, because of safety concerns, we requested that daily peaks occur in the early to late afternoon, as opposed to the early evening or morning when peaks normally occur. This difference is significant and could influence the transferability of our results to natural double-peak flows. Specifically, increased light availability coinciding with peaks occurring earlier in the day could have influenced the foraging efficiencies and preferences of drift feeding salmonids (Allan 1995) and thus artificially inflated brown and rainbow trout responses. Furthermore, it is unclear of the net benefit of increased consumptions given the likely increased energetic costs of foraging at higher velocities and of increased vegetation consumption. Additional work is needed to incorporate our drift results with the observational studies of fish behavior conducted by Argonne National Laboratory to further refine the individual based models developed by Railbacks et al (2006).

Conclusion

In efforts to predict the ecological effects of double-peaking on the fitness of trout below FGD, an individual-based modeling approach has been adopted (Railsback et al. 2006). Preliminary results from these models suggest that trout production is more sensitive to food availability than to flow fluctuations. However, in making these conclusions, the authors recognized three primary assumptions that needed backed by empirical observations. In this study, we explicitly address two of these assumptions: intra- and inter-daily variations in drift and benthic densities and fish foraging behaviors during double-peaking. Our results suggest that under a double-peaking release pattern macroinvertebrate drift is significantly increased for a period of 60 – 80 days. Drift increases were strongly related to the magnitude and frequency of peak flows, while the duration of individual peaking events appeared less influential. In our snapshot of trout foraging responses to double-peaking we provide evidence that trout feeding patterns are strongly influenced by the drift pulses resulting from peaking events. Thus, the effects of food resource availability on trout fitness cannot be considered independent of discharge fluctuations at both daily and monthly time-scales. We recommend integrating these results with other studies of fish behavior below FGD to reparameterize the individual-based model in hopes of increasing the accuracy of model predictions. Furthermore, we strongly recommend the continued monitoring of macroinvertebrate assemblages to assess both the short and long-term responses of the food base to different release patterns.

Bibliography

Allan, J. 1995. Stream ecology: structure and function of running waters. Springer.

Allan, J. D. 1987. Macroinvertebrate drift in a Rocky Mountain stream. Hydrobiologia 144:261-268.

Andrews, E. D. 1986. Downstream effects of Flaming Gorge Reservoir on the Green River , Colorado and Utah. Geological Society Of America Bulletin 97:1012-1023.

Asselman, N. E. M. 1999. Suspended sediment dynamics in a large drainage basin : the River Rhine Abstract : 1450:1437-1450.

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Baxter, R. M. 1977. Environmental effects of dams and impoundments. Annual Reviews of Ecology and Systematics 8:255-283.

Blinn, A. W., J. P. Shannon, L. E. Stevens, J. P. Carder, and D. W. Blinn. 2012. Consequences of fluctuating discharge for lotic communities. Journal of the North American Benthological Society 14:233-248.

Bovee, K., B. Lamb, J. Bartholow, C. B. Stalnaker, J. Taylor, and J. Henriksen. 1998. Stream habitat analysis using the instream flow incremental methodology. Page 130. Fort Collins, CO.

Bowman, A., and S. G. Young. 1996. Graphical Comparison of Nonparametric Curves. Journal of the Royal Statistical Society. Series C (Applied Statistics) 45:83-98.

Brittain, J. E., and T. J. Eikland. 1988. Invertebrate drift - A review. Hydrobiologia 166:77-93.

Callisto, M., and M. Goulart. 2005. Invertebrate drift along a longitudinal gradient in a Neotropical stream in Serra do Cipo National Park , Brazil. Hydrobiologia 539:47-56.

Caton, L. 1991. Improved subsampling methods for the EPA "Rapid Bioassessment" benthic protocols. Bulletin of the North American Benthological Society 8:317–319.

Cereghino, R., M. Legalle, and P. Lavandier. 2004. Drift and benthic population structure of the mayfly Rhithrogena semicolorata (Heptageniidae) under natural and hydropeaking conditions. Hydrobiologia 519:127-133.

Cereghino, R., and P. Lavandier. 1998. Influence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream. Freshwater Biology 40:385-399.

Ciborowski, J. J. H. 1987. Dynamics of Drift and Microdistribution of Two Mayfly Populations: A Predictive Model. Canadian Journal of Fisheries and Aquatic Sciences 44:832-845.

Ciborowski, J. J. H., and H. F. Clifford. 1983. Life histories, microdistribution and drift of two mayfly (Ephemeroptera) species in the Pembina River, Alberta, Canada. Ecography 6:3-10.

Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: a primer on the downstream effects of dams. Reston, VA.

Cuffney, T. F., M. D. Bilger, and A. M. Haigler. 2007. Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. Journal of the North American Benthological Society 26:286–307.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology, Evolution, and Systematics 10:147-172.

Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. North American Journal of Fisheries Management 5:330–339.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783-92.

Elliott, J. 1967. Invertebrate drift in a Dartmoor stream. Archiv für Hydrobiologie:201-308.

Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. Transactions of the American Fisheries … 124:824-835.

Gibbins, C., D. Vericat, and R. J. Batalla. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. Freshwater Biology 52:2369-2384.

Gore, J. A., J. M. Nestler, J. Layzer, and others. 1989. Instream flow predictions and management options for biota affected by peaking-power hydroelectric operations. Regulated Rivers: Research & Management 3:35–48.

Gore, J. A., S. Niemela, V. H. Resh, and B. Statzner. 1994. Near-substrate hydraulic conditions under artificial floods from peaking hydropower operation: A preliminary

analysis of disturbance intensity and duration. Regulated Rivers: Research & Management 9:15-34.

Grams, P. E., and J. C. Schmidt. 2002. Streamflow regulation and multi-level flood plain formation : channel narrowing on the aggrading Green River in the eastern Uinta Mountains, Colorado and Utah. Geomorphology 44:337-360.

Grimm, N. B., and S. G. Fisher. 1989. Stream Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293-307.

Hart, D. D., and C. M. Finelli. 1999. Coupling in Streams : The Pervasive Effects of Flow on Benthic Organisms. Annual Reviews of Ecology and Systematics 30:363-395.

Hayes, J. W., J. D. Stark, and K. A. Shearer. 2011. Transactions of the American Fisheries Society Development and Test of a Whole-Lifetime Foraging and Bioenergetics Growth Model for Drift-Feeding Brown Trout. Transactions of the American Fisheries Society:37-41.

Holomuzki, J. R., and B. J. F. Biggs. 1999. Distributional responses to flow disturbance Distributional responses by a stream-dwelling snail. Oikos 87:36-47.

Holomuzki, J. R., and B. J. F. Biggs. 2000. Persistence Taxon-specific responses to high-flow disturbance in streams : implications for population persistence. Journal of the North American Benthological Society 19:670-679.

Imbert, J., and J. Perry. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. Hydrobiologia 436:191-208.

Irvine, J. R. 1985. Effects of Successive Flow Perturbations on Stream Invertebrates. Canadian Journal of Fisheries and Aquatic Sciences 42:1922-1927.

Irvine, J. R., and P. R. Henriques. 1984. A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. New Zealand Journal of Marine and Freshwater Research 18:283-290.

Jager, H. I., and B. T. Smith. 2008. Sustainable Reservoir Operation : Can We Generate Hydropower and Preserve Ecosystem Values? River Research and Applications 352:340-352.

Jowett, I. G. 1997. Instream Flow Methods : A Comparison of Approaches. Regulated Rivers: Research & Management 13:115-127.

Konrad, C. P., J. D. Olden, D. A. Lytle, T. S. Melis, J. C. Schmidt, E. N. Bray, M. C. Freeman, K. B. Gido, N. P. Hemphill, M. J. Kennard, L. E. McMullen, M. C. Mims,

M. Pyron, C. T. Robinson, and J. G. Williams. 2011. Large-scale Flow Experiments for Managing River Systems. BioScience 61:948-959.

L.E.W., F., T. Forseth, J. H. L'Abee-Lund, and L. A. Vollestad. 2006. Behaviour and growth of juvenile brown trout exposed to fluctuating flow. Eocology of freshwater fih 15:57-65.

Lagarrigue, T., R. Cereghino, P. Lim, P. Reyes-Marchant, R. Chappaz, P. Lavandier, and A. Belaud. 2002. Diel and seasonal variations in brown trout (Salmo trutta) feeding patterns and relationship with invertebrate drift under natural and hydropeaking conditions in a mountain stream. Aquatic Living Resources 15:129-137.

Lenzi, M. A., and L. Marchi. 2000. Suspended sediment load during floods in a small stream of the Dolomites (northeastern Italy). Catena 39:267-282.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 2011. Effects Downstream Ecological of Dams A geomorphic perspective. BioScience 45:183-192.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Page 284. MjM Software Design.

Mckinney, T., A. D. Ayers, and R. S. Rogers. 2009. Macroinvertebrate drift in the tailwater of a regulated river below Glen Canyon Dam , Arizona. Southwestern Naturalist 44:205-210.

Merritt, D. M., and D. J. Cooper. 2000. Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. Regulated Rivers: Research & Management 16:543–564.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An Introduction to the Aquatic Insects of North America, 4th edition. Kendall Hunt Publishing.

Mielke, P. W., and K. J. Berry. 2001. Permutation methods: a distance function approach. Page 363. Springer Verlag.

Minshall, G. W., and P. V. Winger. 1968. The Effect of Reduction in Stream Flow on Invertebrate Drift. Ecology 49:580-582.

Mochizuki, S., Y. Kayaba, and K. Tanida. 2006. Drift patterns of particulate matter and organisms during artificial high flows in a large experimental channel. Limnology 7:93-102.

Moog, O. 1993. Quantification daily peak hydropower flows on aquatic fauna and management to minimize environmental impacts. Regulated Rivers: Research & Management 8:5-14.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 2:403-406.

Muth, R. T., L. W. Crist, K. E. LaGory, J. W. Hayse, K. R. Bestgen, T. P. Lyons, J. K. Ryan, and R. A. Valdez. 2000. Flow Recommendations for Endangered Fishes in the Green River Downstream of Flaming Gorge Dam, Final Report to Upper Colorado River Endangered Fish Recovery Program. Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies : Dynamic interdependence. Proceedings of the National Academy of Sciences of the United States of America 98:166-170.

Perry, S. A., and W. B. Perry. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. Hydrobiologia 134:171-182.

Poff, N. L. ., and J. V. Ward. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. Canadian Journal of Fisheries and Aquatic Sciences 48:1926–1936.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104:5732-7.

Power, M. E. 1990. Benthic turfs vs floating mats of algae in river food webs. Oikos 58:67-79.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Railsback, S. F., B. C. Harvey, S. K. Jackson, and R. H. Lamberson. 1995. InSTREAM : The Individual-Based Stream Trout Research and Environmental Assessment Model.

Railsback, S. F., J. W. Hayes, and K. E. LaGory. 2006. Simulation Analysis of Within-Day Flow Fluctuation Effects on Trout below Flaming Gorge Dam. Page 52 Argonne National Laboratory.

Rempel, L. L., J. S. Richardson, and M. C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. Journal of the North American Benthological Society 18:34-48.

Richter. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. Ecological Applications 13:206-224.

Robinson, C. T., S. Aebischer, and U. Uehlinger. 2004. Immediate and habitat-specific responses of macroinvertebrates to sequential, experimental floods. Journal of the North American Benthological Society 23:853-867.

Rogers, C. D. 2005. Identification Manual to the Freshwater Crustacea of the Western United States and Adjacent Areas Encountered During Bioassessment. Page 81. EcoAnaylsts, Inc.

Schmidt, J. C., and P. E. Grams. 1999. Geomorphology of the Green River in the Eastern Uinta Mountains, Dinosaur National Monument, Colorado and Utah. Pages 81-111 *in* A. J. Miller and A. Gupta, editors. Varieties of Fluvial Form. John Wiley & Sons.

Shannon, J. P., D. W. Blinn, P. L. Benenati, and K. P. Wilson. 1996. Organic drift in a regulated desert river. Canadian Journal of Fisheries and Aquatic Sciences 1369:1360-1369.

Shannon, J. P., D. W. Blinn, T. Mckinney, E. P. Benenati, K. P. Wilson, and C. O'Brien. 2001. Aquatic food base response to the 1996 test flood below Glen Canyon dam, Colorado River, Arizona. Ecological Applications 11:672-685.

Sheather, S. J., and M. C. Jones. 1991. A Reliable Data-Based Bandwidth Selection Method for Kernel Density Estimation. Journal of the Royal Statistical Society. Series B (Methodological) 53:683-690.

Siroky, D. S. 2009. Navigating Random Forests and related advances in algorithmic modeling. Statistics Surveys 3:147-163.

Statzner, B., J. A. Gore, V. H. Resh, S. Journal, N. American, and B. Society. 1988. Hydraulic Stream Ecology : Observed Patterns and Potential Applications Hydraulic stream ecology : observed patterns and potential applications. Journal of the North American Benthological Society 7:307-360.

Tockner, K., and J. A. Wagner. 1997. Measuring drift during a receding flood: Results from an Austrian mountain brook (Ritrodat-Lunz). International Review of Hydrobiology 82:1-13.

Vinson, M. R. 2001. Long-term dynamics of an invertebrate assemblage downstream from a large dam. Ecological Applications 11:711–730.

Vinson, M. R., E. C. Dinger, and M. Baker. 2006. Flaming Gorge Tailwater Aquatic Biota Monitoring Program , 1994-2005. Page 54.

Vinson, M. R., and C. P. Hawkins. 1996. Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. Journal of the North American Benthological Society 15:392–399.

Ward, J. V. 1976. Effect of flow patterns below large dams on stream benthos: a review. Pages 235-253 *in* J. F. Osborn and C. H. Allman, editors. Instream Flow Needs Symposium. American Fisheries Society, Bethesda Maryland.

Young, P. S., J. J. Cech, and L. C. Thompson. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. Reviews in Fish Biology and Fisheries 21:713-731.

Young, S. G., and A. W. Bowman. 1995. Non-Parametric Analysis of Covariance. Biometrics 51:920-931.

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Table 1: Sample types, dates and total number of drift samples collected per sampling cycle (date) at the control (WR) and two treatment sites (TR and LH) during the 2010 and 2011 water years.The pre/post time frame indicates the time relative to double peaking initiation. The two experimental flow types were 1. 'Hiatus': double-peaking was interrupted after one month and single-peak flows implemented for one week and 2. 'Experiment': at the initiation of double-peak flows in 2011, the magnitude of peaks flows was increased by 14 cms per day, culminating in a peak daily discharge of 75 cms.

Flow Type	Pre/post time frame	Date	LH	TR	WR
2010 Water Year					
Pre	2 week	2009-10-27	8	6	8
Pre	1 week	2009-11-03	8	8	8
Post	1 week	2009-11-10	8	8	8
Post	1 month	2009-12-01	8	8	8
Hiatus	1 month	2009-12-07	7	7	7
Post	2 months	2010-01-05	8	7	8
Post	3 months	2010-02-02	8	8	8
Post	4 months	2010-03-02	8	8	8
2011 Water Year					
Pre	2 week	2010-10-19	7	7	7
Pre	1 week	2010-10-26	7	7	7
Experiment	Day 1	2010-11-01	5	5	0
Experiment	Day 2	2010-11-02	5	5	0
Experiment	Day 3	2010-11-03	5	5	0
Experiment	Day 4	2010-11-04	5	5	0
Post	1 week	2010-11-09	7	7	7
Post	1 month	2010-12-07	8	8	8
Post	2 months	2011-01-04	8	8	8
Post	3 months	2011-01-28	8	8	8
Post	4 months	2011-02-25	8	8	8

Table 2: Drifting macroinvertebrates collected at each of WR, TR and LH during the 2010 and 2011 water years. All taxa are standardized to Operational Taxonomic Units (OTU). An 'X' is used to denote the presence of a particular taxa at a site.

Order	Taxon	LH	TR	WR
	Turbellaria	X		
Amphipoda	Gammarus			X
Amphipoda	Hyalella	X	X	X
Basommatophora	Lymnaea	X	X	
Basommatophora	Physa	X	X	X
Basommatophora	Planorbidae	X		X
Coleoptera	Heterelmis		X	
Coleoptera	Liodessus			X
Coleoptera	Optioservus	X	X	X
Cypriniformes	Catostomus			X
Decapoda	Cambaridae			X
Diptera	Chironominae	X	X	X
Diptera	Culicidae		X	
Diptera	Hemerodromia			X
Diptera	Muscidae		X	X
Diptera	Orthocladiinae	X	X	X
Diptera	Simuliidae	X	X	X
Diptera	Tanypodinae	X	X	X
Ephemeroptera	Baetis	X	X	X
Ephemeroptera	Callibaetis	X		X
Ephemeroptera	Epeorus	X	X	X
Ephemeroptera	Ephemerella			X
Ephemeroptera	Tricorythodes	X	X	X
Hemiptera	Corixidae	X		X
Neotaenioglossa	Potamopyrgus antipodarum	X	X	
Plecoptera	Chloroperlidae	X		X
Plecoptera	Hesperoperla	X		
Plecoptera	Isoperla	X		X
Trichoptera	Brachycentrus	X		
Trichoptera	Glossosoma	X		
Trichoptera	Helicopsyche			X
Trichoptera	Hydropsyche	X		X
Trichoptera	Hydroptila	X	X	X
Trichoptera	Lepidostoma	X		
Trichoptera	Oecetis	X	X	
Trombidiformes	Acari	X	X	X
Veneroida	Pisidiidae	X		

Table 3: ANCOVA results (p-values) comparing temporal drift patterns in total daily export between the control site (WR) and each treatment by year combination. Also included are ANCOVA results for each of the two dominant taxa, Amphipoda and Diptera, analyzed separately.

Site Comparison	Year	Total Export	Amphipoda	Diptera
TR-WR	2010	0.31	0.09	0.26
TR-WR	2011	0.07	0.06	0.11
LH-WR	2010	0.14	0.08	0.11
LH-WR	2011	0.35	0.10	0.07

Table 4: Total number of rainbow and brown trout sampled per size class (mm) at both TR and LH during each of the two sampled flow stages: base and peak.

		Rainbow trout			Brown trout		
Site Flow	Flow	<200	200-400	>400	<200	200-400	>400
LH	Peak	2	20	2	3	18	12
LH	Base	0	16	2	1	14	18
TR	Peak	14	27	0	0	14	6
TR	Base	15	30	1	0	19	8

Table 5: ANOVA results for the comparison of rainbow and brown trout gut fullness, omitting organic matter and fishes, between base and peak flow events at both TR and LH. Response variable is fish gut content biomass standardized by empty gut weight. Method = Generalized Linear Model (GLM) using gaussian distribution and log (Y+c) transformation, run separately for each site.

Site/Factor	F statistic	P-value
TR		
Flow	10.423	0.002
Species	40.414	0.000
Flow:Species	4.756	0.031
LH		
Flow	18.015	0.000
Species	0.287	0.594
Flow:Species	0.026	0.872

Table 6: ANOVA results for the comparison of rainbow and brown trout organic matter consumption between base and peak flow events at both TR and LH. Response variable is consumed organic matter biomass standardized by empty gut weight. Method = Generalized Linear Model (GLM) using gaussian distribution and log (Y+c) transformation, run separately for each site.

Site/Factor	F statistic	P-value
TR		
Flow	3.168	0.077
Species	38.120	0.000
Flow:Species	8.645	0.004
LH		
Flow	6.579	0.012
Species	117.613	0.000
Flow:Species	0.053	0.819

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Figure 1: Example flow regimes for the 2010 (a) and 2011 (b) water years. Shown are daily hydrographs of representative dates for a single treatment site (black lines) located immediately downstream of FGD (TR) and the control site (dotted, gray line) located downstream from Fontenelle dam (WR). For the treatment site, daily hydrographs are shown for conditions one-week prior (dashed, black lines) and one-week during (solid, black lines) double-peaking.
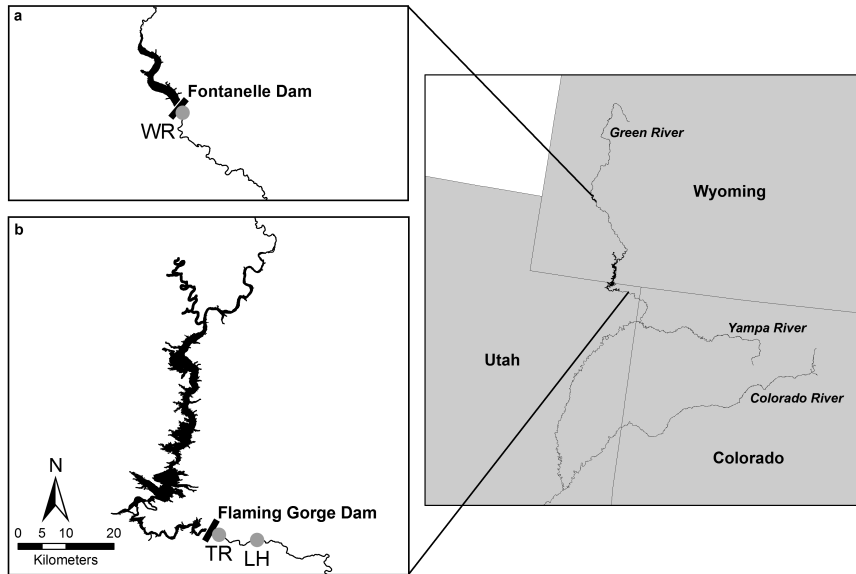
Figure 2: Location of the Green River within Wyoming, Utah and Colorado. Panel b shows the location of the double-peaking sites, located immediately (TR) and 10 km downstream (LH) of Flaming Gorge Dam. The contol site (WR, panel a) is located immediately downstream from Fontanelle Dam, approximately 200 km upstream from FGD.
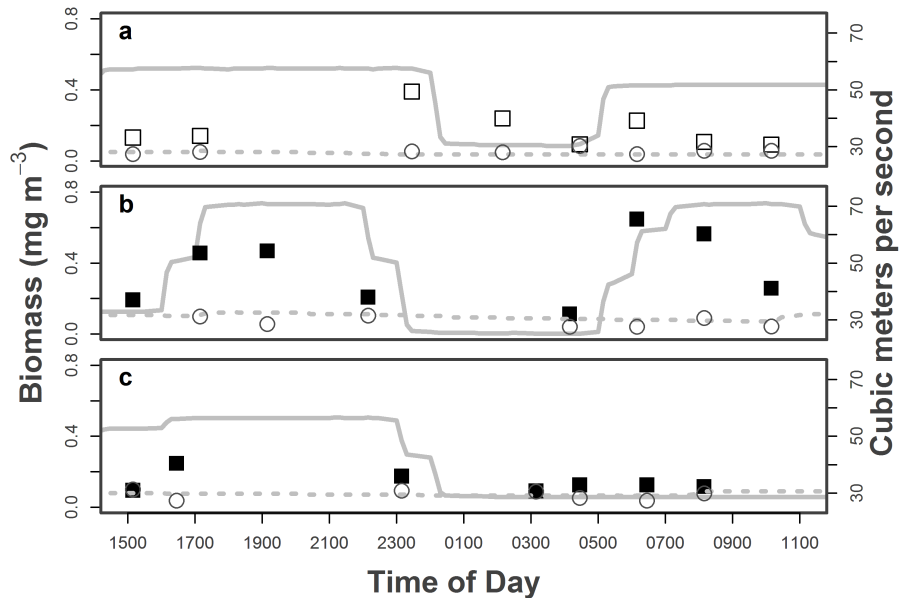
Figure 3: Within-day relationships between drift biomass and discharge at WR (circles, dotted line) and TR (squares/solid line) during pre- (a: 11/03/2009) and post-double-peaking (b: 12/01/2009), as well as during the hiatus experiment (c; 12/07/2009). Drift and flow at WR (circles/dotted) are provided for illustration of corresponding control responses.
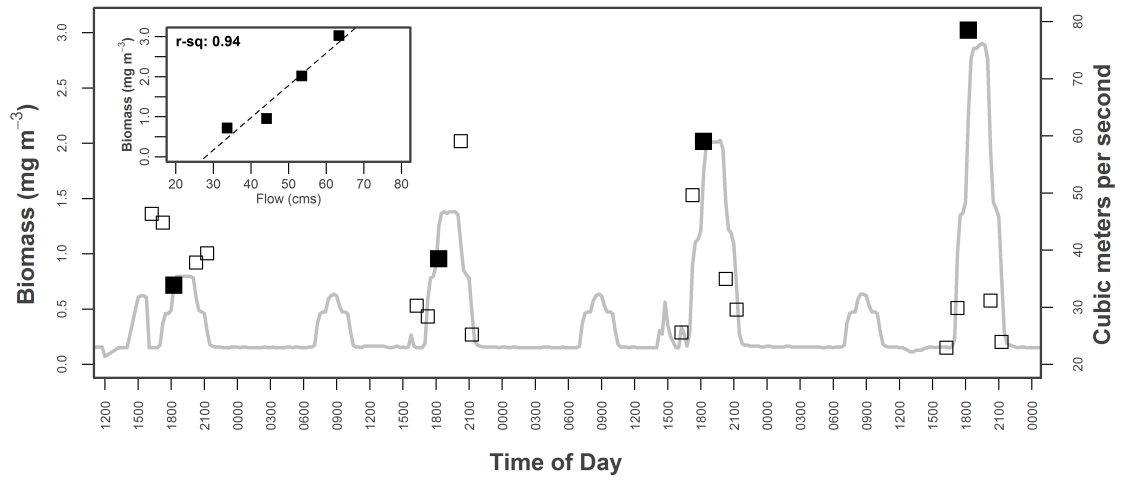
(a)
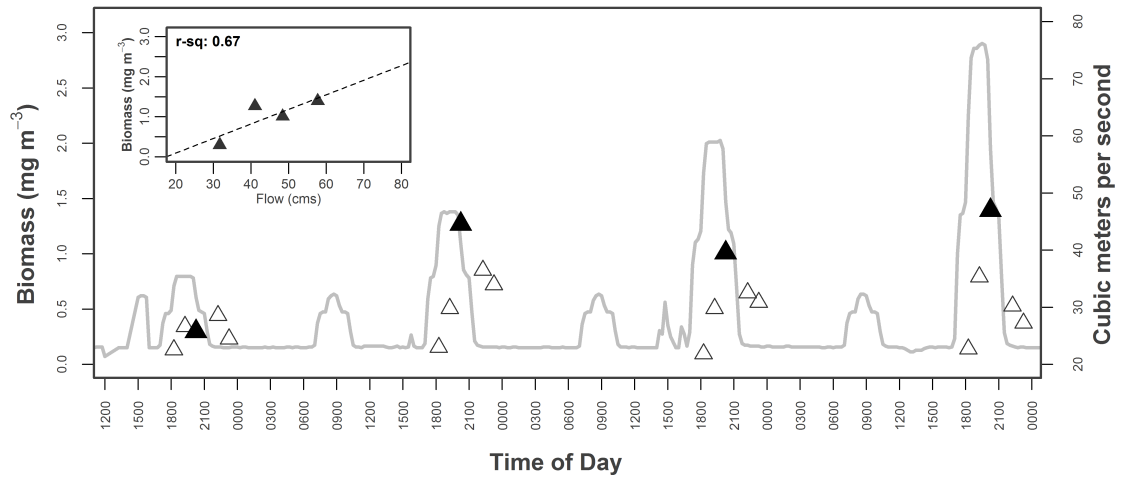
(b)

Figure 4: Inter- and intra-daily responses of drift biomass to experimental afternoon peaks of increasing magnitude from 11/01/2011 to 11/04/2010. Inset shows the relationship between drift biomass during the rising limb of the hydrograph (filled points corresponding between figures) and peak discharge for both TR (y=0.081x-2.25, R-squared=0.94) and LH (y=0.036x -0.63, R-squared=0.67).
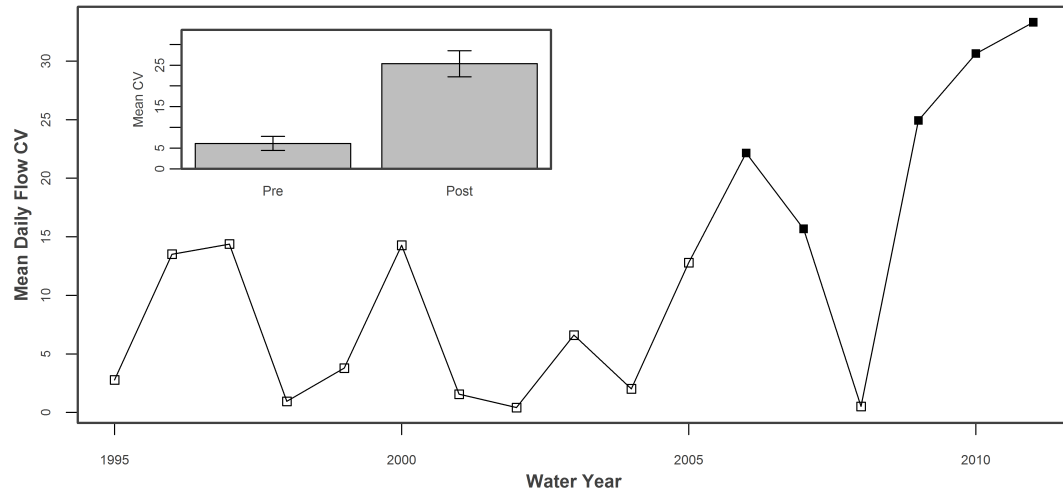
Figure 5: Mean daily coefficient of variation in discharge from October – March (i.e., typical period of double-peak releases) compared among years (1995-2011) and between non-double-peak and double-peak winters (inset).
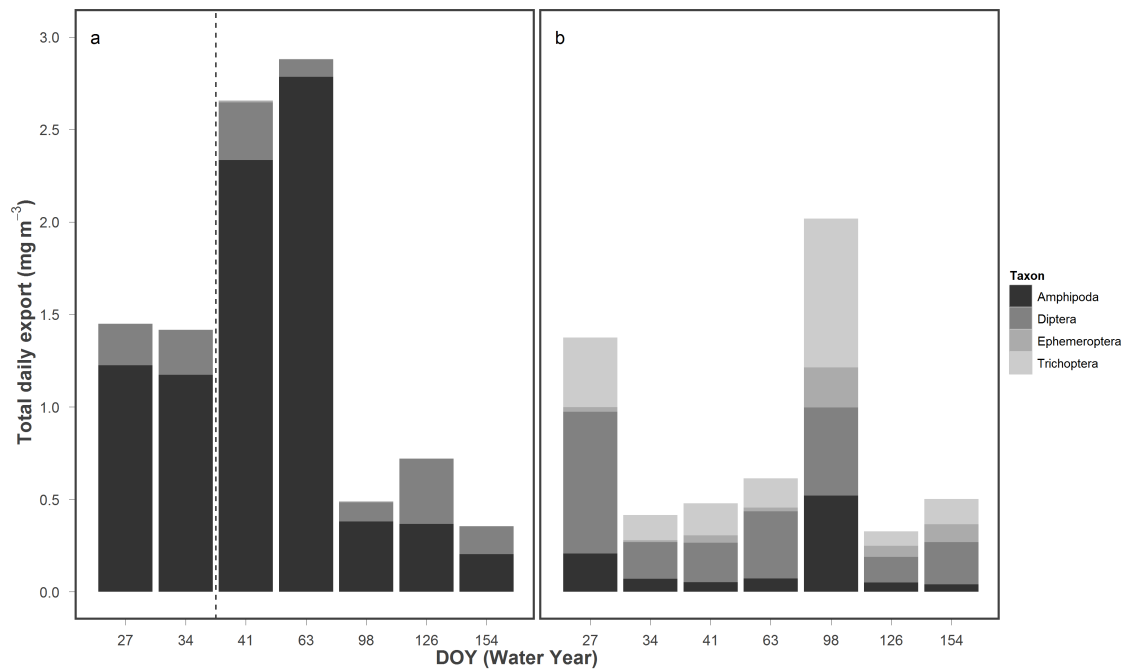
Figure 6: Change in drift assemblage composition through time for both TR (a) and WR (b) for the 2010 water year. The dashed line separates pre- and post- double-peaking samples, with no double-peaking at WR.

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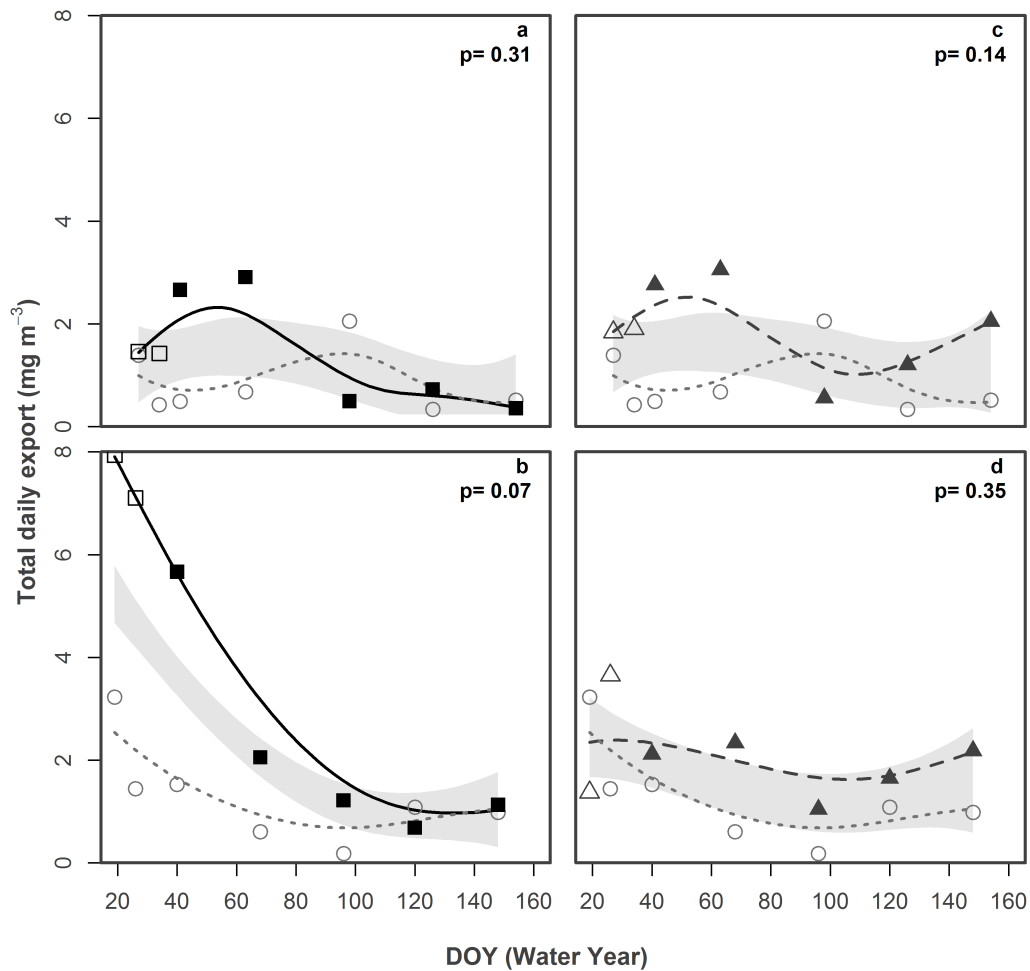
Figure 7: ANCOVA pairwise comparisons of the temporal patterns in total daily export (mg m^{-3}) of drifting macroinvertebrates between each control (circles/dotted=WR) and treatment (a-b/squares/solid=TR; c-d/triangles/dashed=LH) pair during both 2010 (top) and 2011 (bottom). Filled symbols indicate double-peaking conditions and hollow circles indicate pre-double-peaking or control conditions. The reference band graphically represents the acceptance region for the null hypothesis of no difference in the temporal trend between sites and is directly related to the error differences between the actual data points and the smoothed fit.
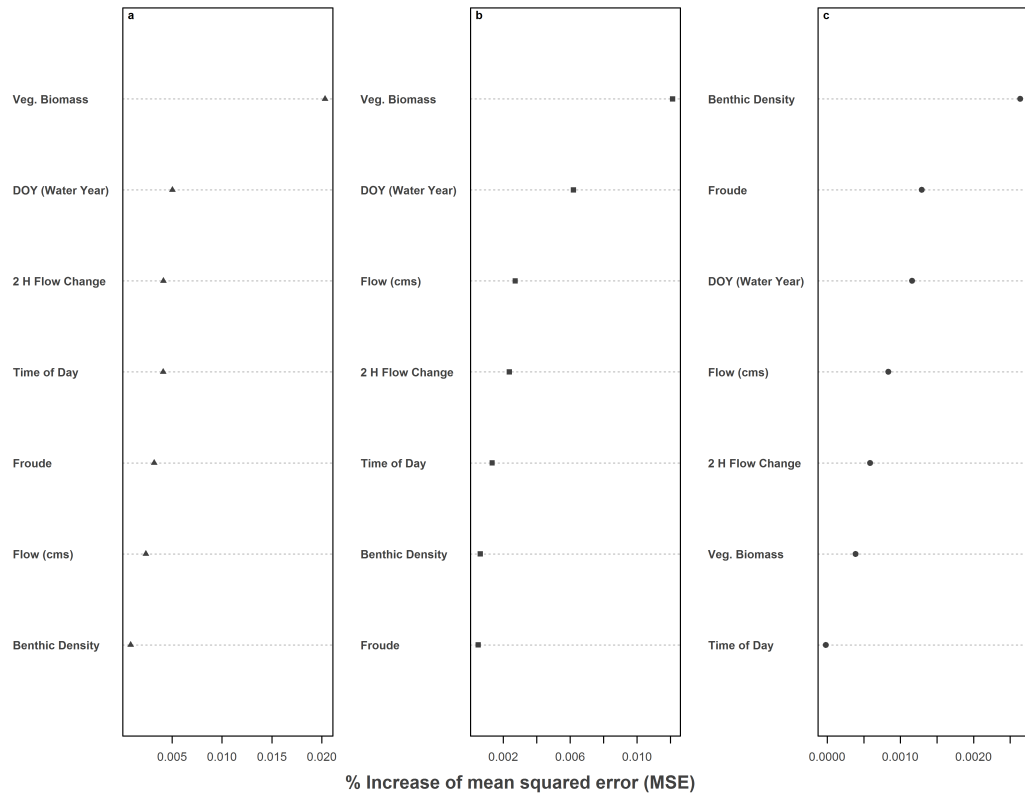
Figure 8: Variable importance plots for the random forest models developed to explain inter- and intra-daily variation in drift biomass for LH (a), TR (b), and WR (c), during the 2010 water year, including the hiatus experiment. The sensitivity of drift biomass to individual predictors was assessed by quantifying the percent increase in mean square error (MSE) when the validation data for an individual predictor was permutated.
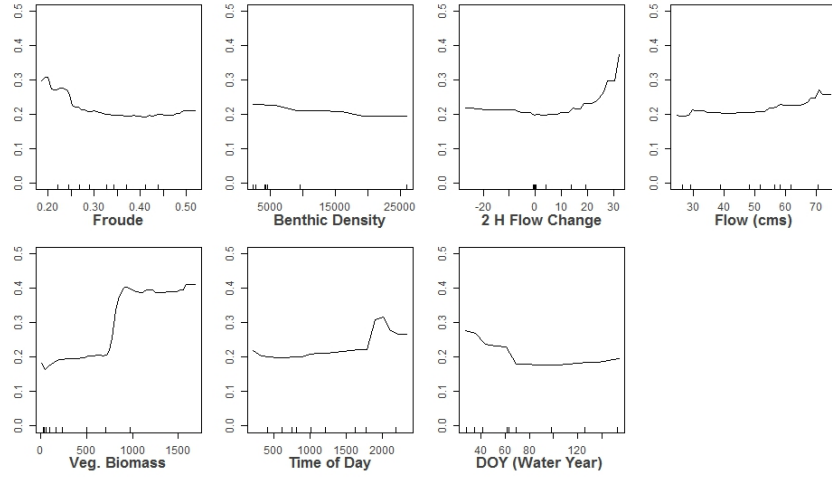
(a) Little Hole
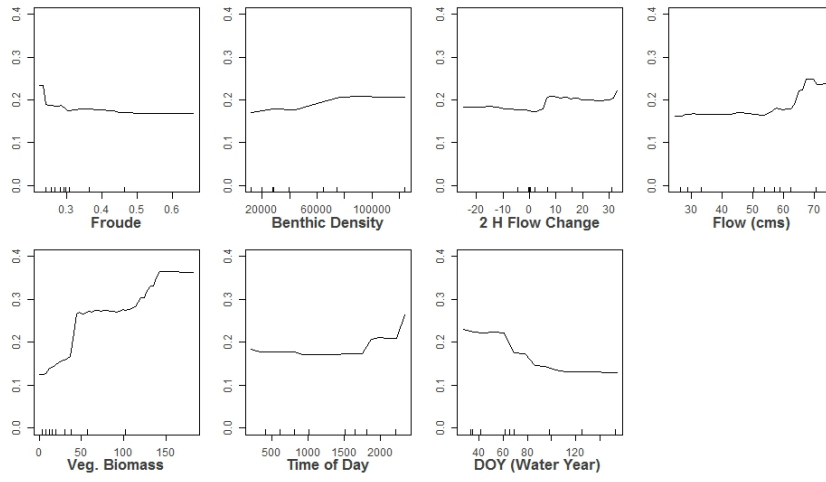
(b) Tail Race
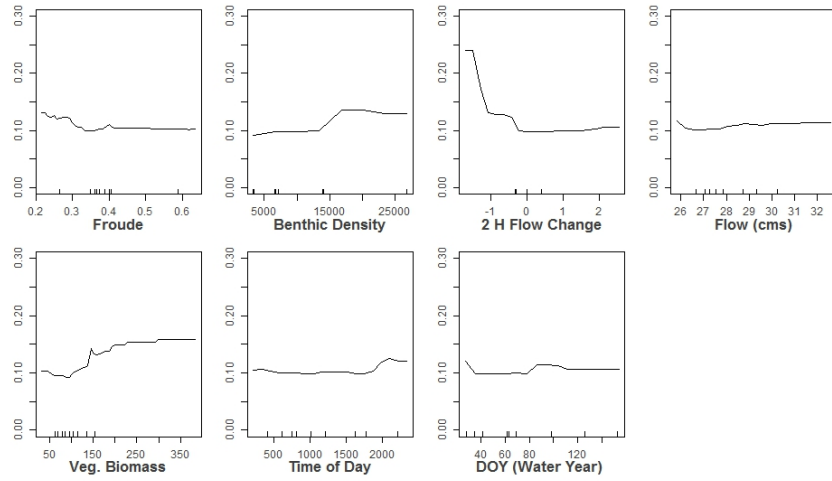
(c) Weeping Rock

Figure 9: Partial plots of variables in random forests models. Note that the y-axis (partial dependence) is scaled within, but not among, sites.
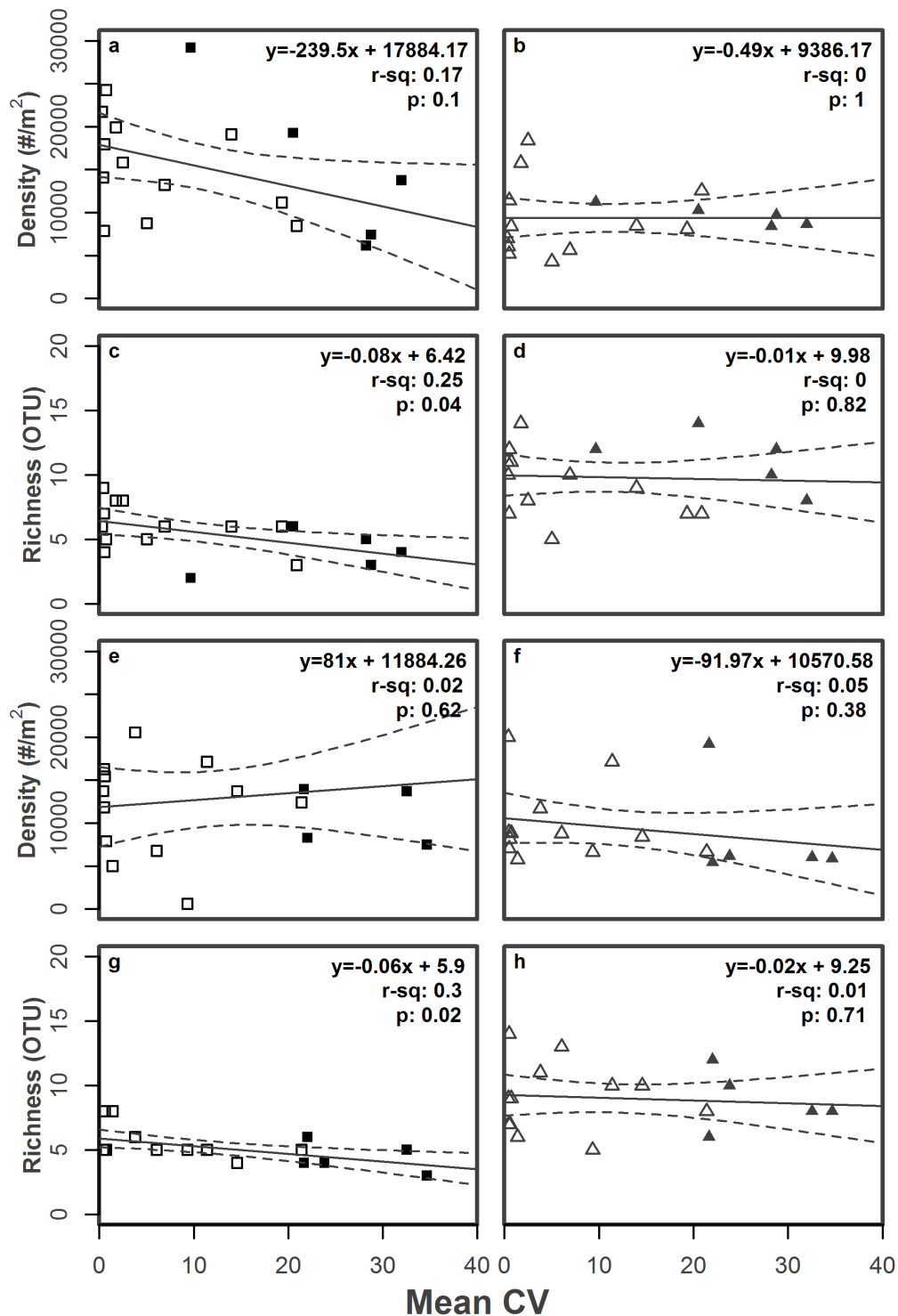
Figure 10: Relationship between macroinvertebrate taxa richness/density and the mean daily coefficient of variation (CV) compared among Tail Race (left) and Little Hole (right) for the January (a-d) and (e-h) April sampling events from 1995-2012. The mean daily CV was computed for: October – December (a-d) and January – April (e-h). The least squared regression line, 95 percentile confidence intervals, regression equations, coefficient of determination (r-sq) and p values (p) are provided.
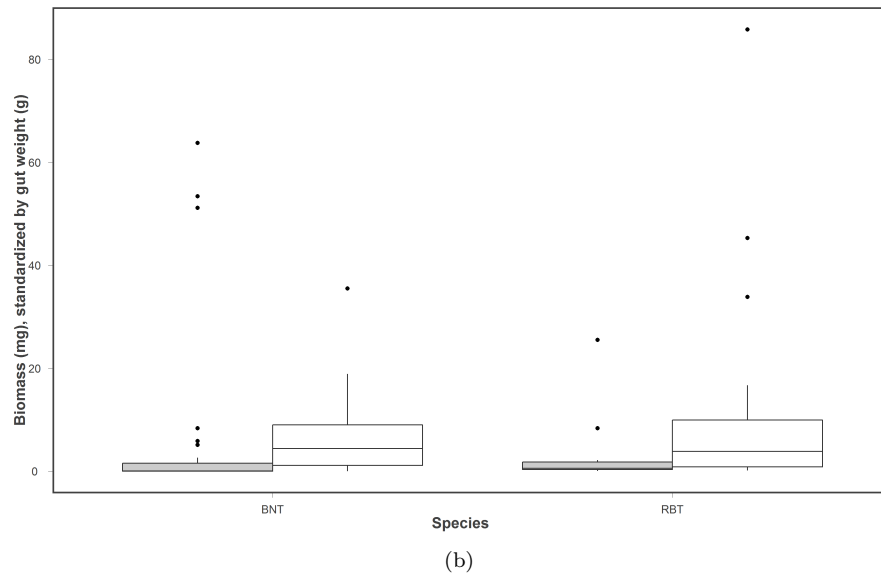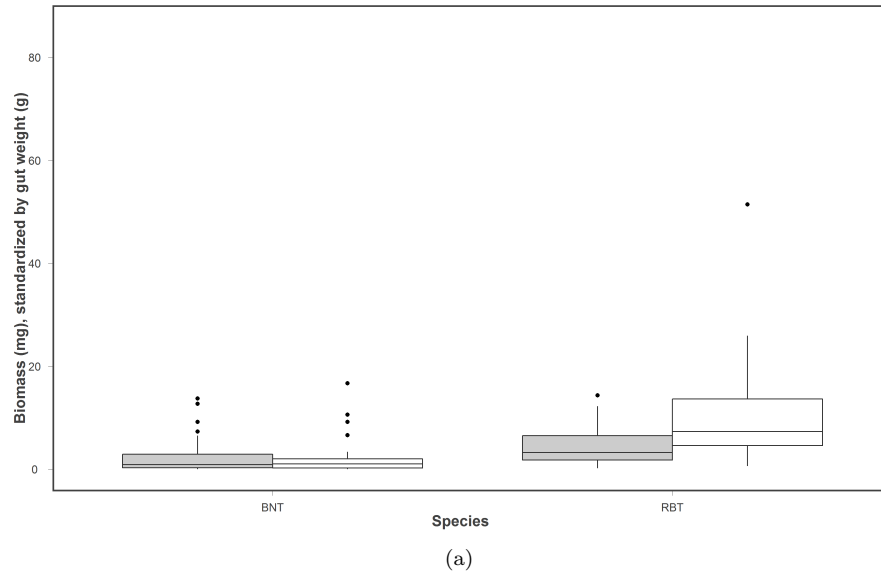
(a)

(b)

Figure 11: Differences in gut fullness between peak (white) and base (grey) flows by species for both TR (a) and LH (b). Macroinvertebrate biomass, including fish eggs but excluding fish adults and organic matter, was significantly ($p<0.01$) increased at both sites during peak flows (white) as compared to base flows (gray). Brown (BNT) and rainbow (RBT) trout had significantly different responses at TR ($p<0.001$), with an interaction between flow and species ($p<0.05$). ANOVA model results presented in Table 5.
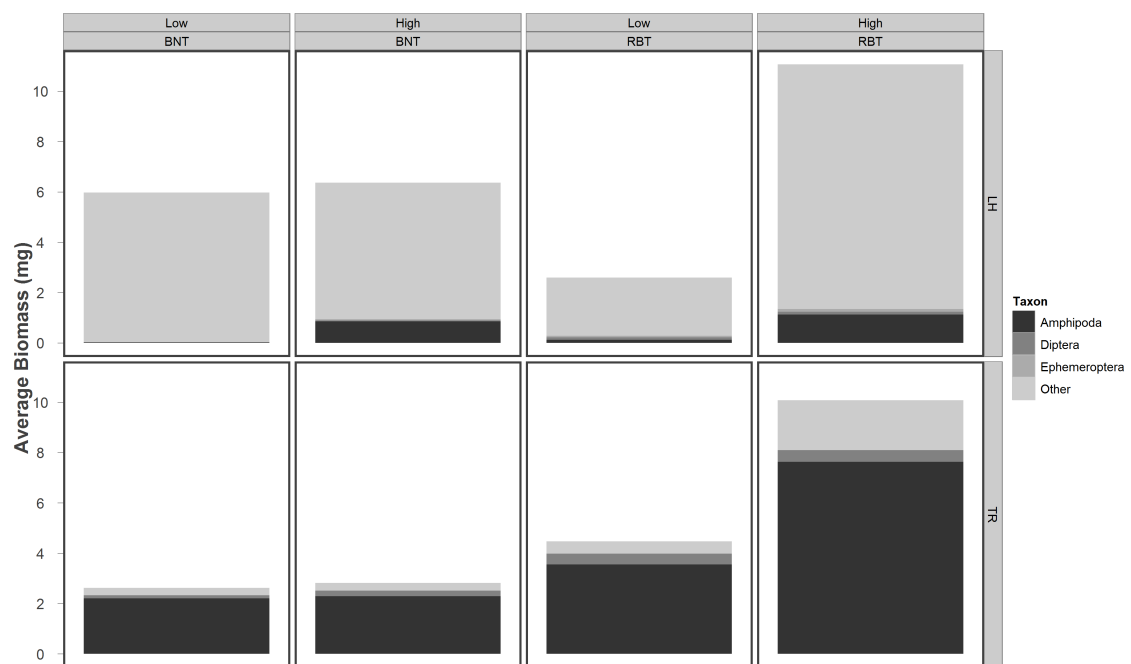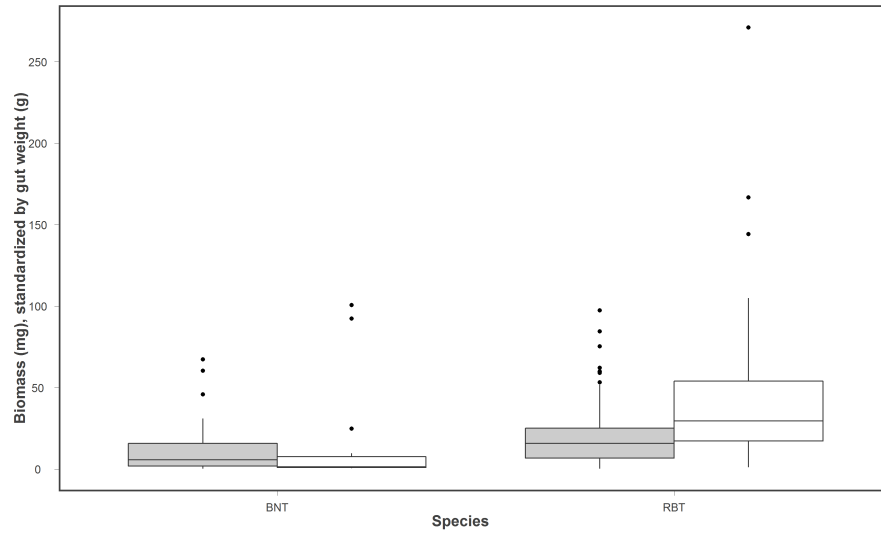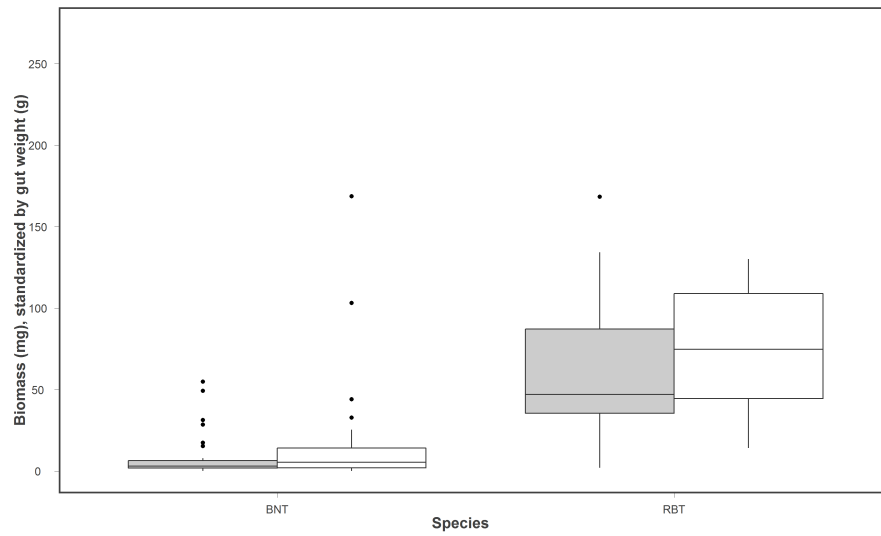
Figure 12: Macroinvertebrate prey resources utilized by brown (BNT) and rainbow (RBT) trout compared between low and high flow treatments for both Tail Race (TR) and Little Hole (LH). The "Other" category contains Gastropoda, Coleoptera, and fish eggs but excludes fish adults.

(a)

(b)

Figure 13: Differences in organic matter consumption between peak (white) and base (gray) flows by species for both TR (a) and LH (b). At both sites, species differentially consumed vegetation (p<0.001). At LH, both species had significant responses (p<0.01) to peak flows. At TR, BNT and RBT responded differentially to flow treatments (p<0.01). ANOVA model results presented in Table 5.