

# Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking

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**Abstract:** We utilized both hydropeaking and experimental flows to quantify responses of macroinvertebrate drift, benthic assemblages, and fish consumption to double-peak release patterns. Our results suggest that changes in discharge may have a greater impact on macroinvertebrate drift than absolute flow levels, such that mean daily drift biomass was significantly higher during double-peaking; however, drift increases were sustained for only 30–60 days despite ongoing hydropeaking. Drift increases were proportional to peak magnitude, with drift biomass peaking during the rising limb of the hydrograph and declining prior to the cessation of peak flows. Both within- and among-day drift hysteresis appeared related to patterns in vegetative export, principally *Cladophora* and *Amblystegium*. Increases in macroinvertebrate drift were not associated with detectable reductions in benthic densities, while we observed inconsistent and modest taxa richness reductions. Lastly, gut fullness for both brown and rainbow trout increased significantly following periods of hydropeaking, suggesting that the effects of double-peaking can propagate through tail-water food webs.

**Résumé :** Nous avons utilisé des lâchés d'eau liés à la demande hydroélectrique et des débits expérimentaux pour quantifier les réactions de la dérive de macroinvertébrés, des assemblages benthiques et de la consommation des poissons à des motifs de lâchés doubles. Nos résultats portent à croire que les variations de débit pourraient avoir une plus grande incidence sur la dérive de macroinvertébrés que la valeur absolue des débits, la biomasse dérivante quotidienne étant significativement plus grande quand des lâchés doubles étaient utilisés; cela dit, les augmentations de la dérive n'étaient maintenues que de 30 à 60 jours, même si les lâchés se poursuivaient sur une plus longue période. Les augmentations de la dérive étaient proportionnelles à la magnitude des lâchés, la biomasse dérivante atteignant son maximum pendant la branche montante de l'hydrogramme, puis diminuant avant la cessation des débits de pointe. Des hystérésis quotidiennes et sur plusieurs jours étaient associées à des motifs d'exportation végétale, principalement de *Cladophora* et d'*Amblystegium*. Si les augmentations de la dérive de macroinvertébrés n'étaient pas associées à des réductions perceptibles des densités benthiques, des réductions modestes et non uniformes de la richesse taxonomiques ont été observées. Enfin, le contenu du tube digestif augmentait significativement tant pour la truite brune que pour la truite arc-en-ciel dans la foulée de périodes de lâchés liés à la demande, ce qui donne à penser que les effets des lâchés doubles peuvent se propager dans les réseaux trophiques des eaux d'aval. [Traduit par la Rédaction]

## Introduction

The construction and management of over 7700 large dams (>15 m high) throughout the United States has fundamentally altered the chemical, physical, and biological components of many lotic ecosystems (Collier et al. 1996; Ligon et al. 1995; Vinson 2001; Poff et al. 2007). In some instances, the novel environmental conditions created downstream from bottom-release dams, particularly cold, clear water with high primary and secondary production (Baxter 1977; Blinn et al. 1998), are capable of supporting economically valuable fisheries. However, fisheries and the ecosystem processes that sustain them are often secondary management priorities to water storage and hydropower production (Jager and Smith 2008). Consequently, balancing societal needs with those of freshwater ecosystems requires accurate models of organismal responses to altered flow regimes (Richter et al. 2003; Konrad et al. 2011).

Predicting the ecological effects of flow alterations 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). 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). In either scenario, hydropeaking operations can substantially increase daily hydrologic variability (Cushman 1985; Gore et al. 1994), which can adversely impact downstream algal, macroinvertebrate, and fish assemblages (Moog 1993; Blinn et al. 1995; Young et al. 2011).

Mitigating the ecological impacts of hydrologic alterations requires an explicit understanding of the habitat parameters that sustain organismal growth, survival, and reproduction. Discharge-mediated changes in habitat suitability are typically modeled based on changes to water depth, velocity, or bed substrate (Jowett 1997; Bovee et al. 1998). In more complex niche models, temperature, prey resource availability, and (or) biotic interactions are also considered (Van Winkle et al. 1998; Railsback et al. 2009). The incorporation of biotic variables, particularly food resource availability, has greatly increased the predictive capabilities of such models because of the strong dependency of trout on drifting macroinvertebrates (Filbert and Hawkins 1995; Hayes et al. 2000). Despite the documented dependence of salmonids on drifting invertebrates, we lack a thorough understanding of how macroinvertebrate drift responds to hydropeaking operations of varying

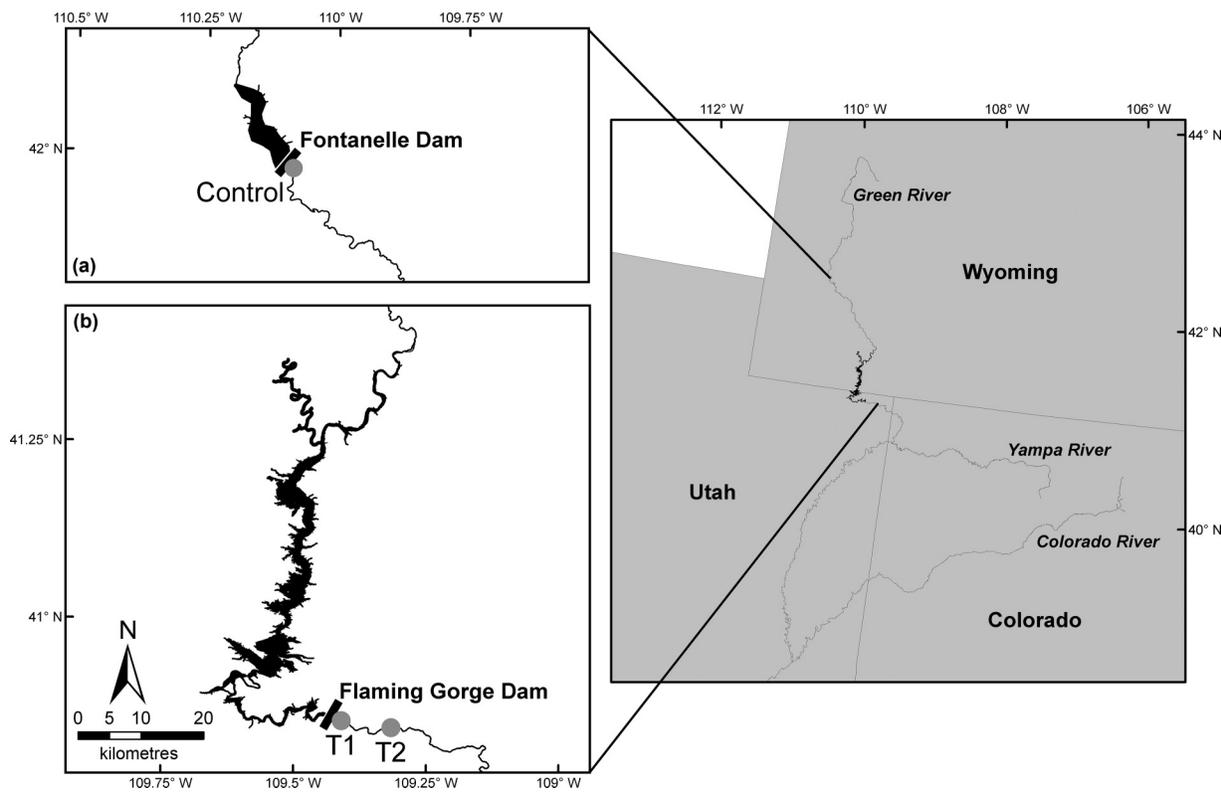
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**Fig. 1.** Location of the Green River within Wyoming, Utah, and Colorado. Panel (a) shows the Control site located immediately downstream from Fontanelle Dam, approximately 200 km upstream from Flaming Gorge Dam (FGD). Panel (b) shows the double-peaking study sites (impact), located immediately (T1) and 10 km (T2) downstream of FGD.



frequency, magnitude, and duration to accurately parameterize models of fish performance under different discharge scenarios.

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 concentration 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). Disparities in the direction and magnitude of responses among studies likely result from variability in the rate, frequency, duration, and (or) magnitude of discharge increases (Irvine and Henriques 1984; Shannon et al. 1996; Imbert and Perry 2000), but researchers 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. Meanwhile, the consequences of altering macroinvertebrate drift concentration and composition for drift-feeding fishes remains largely unknown; we know of only one study attempting to link hydropeaking-induced changes in food resource availability to fish foraging behavior (Lagarrigue et al. 2002).

In this study, we utilized both 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 hourly and monthly time scales. Specifically, we asked the following: (i) Do double-peak release patterns significantly alter macroinvertebrate drift concentration, biomass, and composition at both

hourly and monthly time scales? (ii) How does macroinvertebrate drift concentration and biomass respond to peaks of varying magnitude? (iii) Does hydropeaking affect benthic macroinvertebrate assemblages? and (iv) Does fish prey resource utilization differ between base and peak flows?

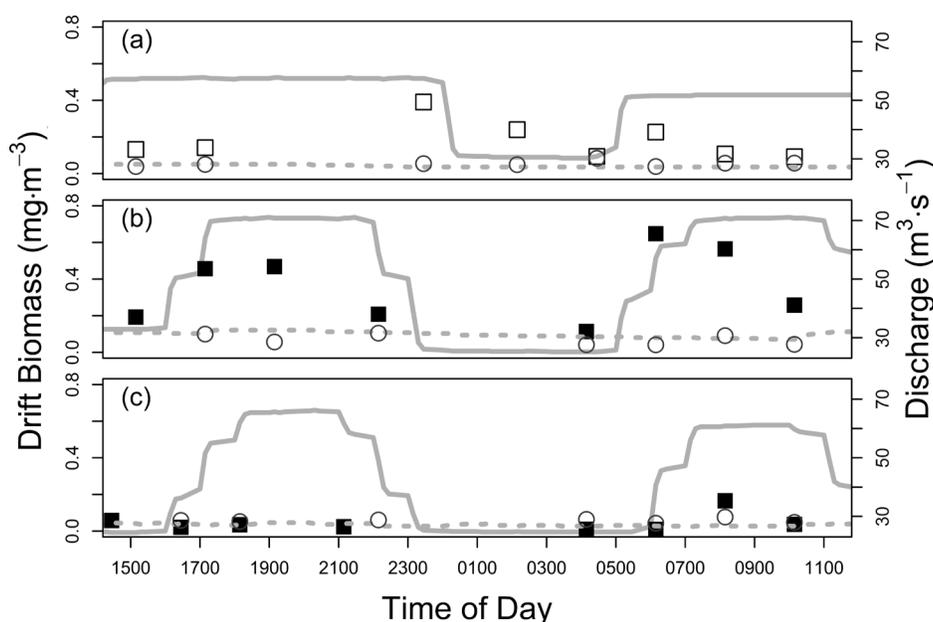
## Materials and methods

### Study area

Our study focused on the Green River, a large (115 800 km<sup>2</sup>) snowmelt-driven system that flows through the high desert plains of Wyoming, Colorado, and Utah (Fig. 1). The Green River alternates between low-gradient, broad alluvial valleys and higher-gradient, confined canyons before joining the Colorado River (Schmidt and Grams 1999). The hydrologic regime of the Green River is altered by two major dams, Flaming Gorge Dam (FGD) and Fontanelle. Fontanelle Dam is located approximately 200 stream kilometres upstream from FGD and primarily functions to store water for both downstream power production and irrigated agriculture and therefore has relatively constant discharge rates (Fig. 2). FGD is located in northwestern Utah, approximately 85 km upstream of the confluence with the Yampa River, and was completed in 1963 for hydroelectric power generation and water storage. FGD imparts the largest single effect on the hydrology of the Green River, with an annual storage capacity of  $4.67 \times 10^9$  cubic metres relative to a mean annual flow of 52 cubic metres per second (m<sup>3</sup>·s<sup>-1</sup>).

Double-peak release patterns from FGD were common throughout the 1970s and 1980s as a way to more efficiently meet daily electrical demand. However, concerns over impacts to native fishes and decadal drought promoted daily single-peak or steady daily flows 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

**Fig. 2.** Daily patterns of drift biomass (symbols) and discharge (lines) at Control (circles, dotted line) and T1 (squares, solid line) during pre-double-peak (a), 1 week (b), and 2 months (c) into double-peak release patterns.



2006, double-peak release patterns were implemented from October through March, pending water availability, and consisted of two hydroelectric generation peaks per day, morning and evening, with baseflows averaging  $28 \text{ m}^3\cdot\text{s}^{-1}$  or less and peaks exceeding  $75 \text{ m}^3\cdot\text{s}^{-1}$  for a sustained period of 2 to 4 h (Fig. 2). Ramp rates are constrained such that differences in mean daily flow between consecutive days cannot exceed 3%, and stage height at USGS gage 09261000 cannot change by more than 0.1 m (Muth et al. 2000).

The construction and management of FGD has substantially 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). For example, dam operations are associated with the local extirpation of greater than 20 macroinvertebrate genera (Vinson 2001) and the endangerment of four native fishes (VanSteeter and Pitlick 1998). The tail water below FGD now supports a non-native trout fishery of brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout that experiences thousands of angler hours per year, but is sustained by a relatively narrow prey base of less than five drifting macroinvertebrate genera (Filbert and Hawkins 1995).

### Study 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 impact sites sampled on multiple occasions both before and during double-peaking (Fig. 1). The control site was located immediately downstream of Fontanelle Dam and used to characterize natural daily and seasonal fluctuations in macroinvertebrate drift where macroinvertebrate assemblages have been altered by dam construction, but flows exhibit nominal diel and seasonal fluctuations (Fig. 2). Downstream of FGD two impact sites were selected to represent the two dominant channel morphologies: laterally constrained canyons (T1) and broad alluvial valleys (T2). Specifically, T1 was located <1 km downstream of FGD and is a higher-gradient (0.002%), constrained canyon with a mean wetted width of 45 m and a relatively coarse bed that is heavily armored (Vinson 2001). In contrast, T2 is a lower-gradient reach (0.0008%) located approximately 10 km downstream from FGD that has a mean wetted width of 63 m and finer bed material consisting of coarse gravel, cobble, and boulders.

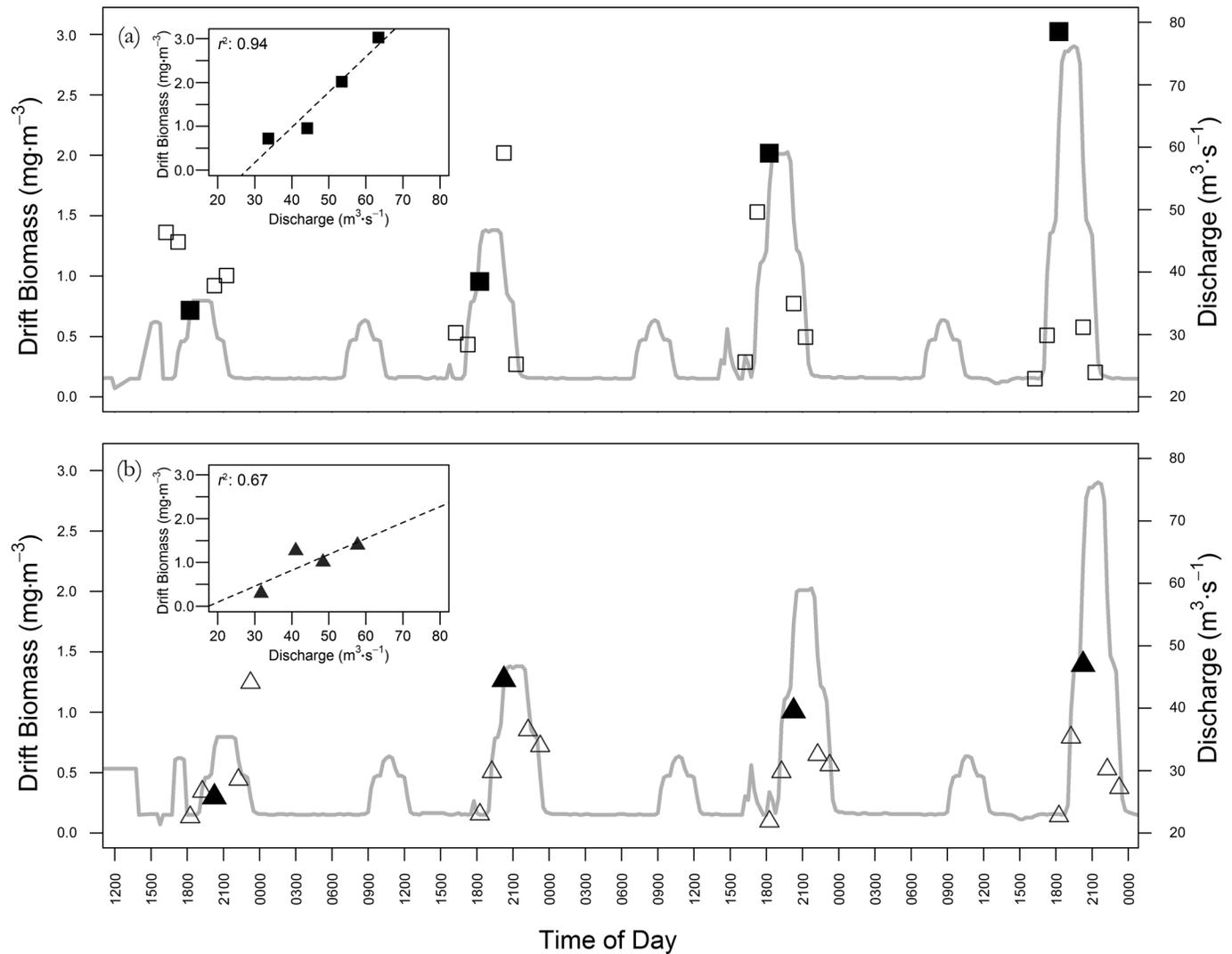
All three sites, one control and two impact, were sampled during two dates before and five dates after impact for a total of seven sample events between October and March of the 2010 water year. During each sample event, six to eight drift samples and a single composite benthic sample were collected over a 24 h time period coinciding with different hydrologic stages of single- and double-peaking (e.g., base flow, rising limb, peak flow; Fig. 2). All drift samples collected during a 24 h sampling event were kept separate and used as replicates for calculating daily means and 95% confidence intervals. In total, 147 drift samples and 21 benthic samples were collected (see the Macroinvertebrate sampling section below for details). Discharge was monitored using data from USGS gages 09211200 (Control) and 09234500 (T1), while flows at T2 were estimated based on a 2 h time of concentration for discharge from T1.

In addition to monitoring macroinvertebrates before and during double-peak releases, we requested experimental flow releases from dam operators to better understand how drift concentration and biomass increase as a function of peak magnitude. Specifically, during the first days of double-peak releases in November of 2011, we requested experimental releases in which the magnitude of the evening peak was gradually increased by  $14 \text{ m}^3\cdot\text{s}^{-1}\cdot\text{day}^{-1}$ , culminating in a peak daily discharge of  $75 \text{ m}^3\cdot\text{s}^{-1}$  (Fig. 3). Sampling occurred at impact sites (T1 and T2) and targeted baseflows, as well as the ascending, peak, and descending limbs of the hydrograph during each day of the 4-day experiment. In total, five drift samples were collected per day for a total of 20 drift samples per site over the duration of the experiment.

### Macroinvertebrate sampling

For each of the six to eight independent drift samples collected per 24 h sampling event, macroinvertebrate drift was quantified using seven drifts nets (45 cm × 20 cm, 500  $\mu\text{m}$  mesh) located in the bottom third of a single representative riffle per site. The only exception was at T1, where high flows impeded safe access, and four nets were deployed during the peak flow sample (i.e., one sample out of the six to eight samples per sampling event). The contents of all seven drift nets were composited into a single sample for processing to generate a single estimate of drift abundance at each hydrologic stage over the 24 h sampling event. Drift

**Fig. 3.** Within- and among-day responses of drift biomass to experimental increases in the magnitude of afternoon peak discharge for both T1 (a, squares) and T2 (b, triangles). Inset shows the relationship between peak discharge and drift biomass at the initiation of peak discharge (main and inset: solid symbols) for both T1 and T2.



nets were placed 10 cm off the stream bottom and deployed for 40 min intervals. At the start and end of each deployment, we measured velocity with a digital flow meter at the vertical midpoint of each drift net (20 cm from the stream bottom) and computed the mean velocity among all nets. The contents from all seven nets for a given collection time, including vegetation and other debris, were combined into a single sample and preserved in 95% ethanol. Mean drift concentration and biomass were used as the response variables, with replication obtained from the six to eight drift samples collected per 24 h sampling event. Drift concentration and biomass were computed as the number and biomass of individuals per cubic metre of water, respectively (Smock 2007).

To assess the impacts of double-peaking on benthic assemblages and to model macroinvertebrate drift responses, we utilized two separate datasets: a long-term dataset of January and April benthic samples collected at both T1 and T2 since 1995 and benthic samples collected at each of the control and impact sites once during each 24 h sampling event, respectively. The long-term benthic macroinvertebrate samples were collected on a single day in January and April of each year using a Hess sampler (0.08 m<sup>2</sup>, 250  $\mu$ m mesh), while a Surber sampler (0.09 m<sup>2</sup>, 500  $\mu$ m mesh) was used for the benthic samples collected during each of the

seven sample events associated with double-peaking during the 2010 water year. For both Hess and Surber samples, eight randomly located samples from riffle habitats were collected below the 30 m<sup>3</sup>·s<sup>-1</sup> discharge level, when possible, and were composited (0.64 and 0.72 m<sup>2</sup>, respectively) into a single sample and preserved in 95% ethanol. Similar to drift samples, multiple benthic samples collected at a single point in time were composited to increase the accuracy and precision of our benthic macroinvertebrate estimates (Vinson and Hawkins 1996; Li et al. 2001).

Benthic and drift samples were processed using a subsampling procedure where a minimum of 500 or 200 organisms, respectively, were randomly extracted from all samples (Caton 1991; Vinson and Hawkins 1996). We identified macroinvertebrates to genus; however, Chironomidae were identified to subfamily, and 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 the genus level.

The dry mass of drifting macroinvertebrates was determined at the order level because of low within-order richness (mean of 3 OTUs per order) and high numerical dominance (>90% of one or two morphologically similar OTUs per order). All individuals within a particular order were pooled, oven dried at 100 °C for

48 h, and weighed to the nearest tenth of a milligram. Finally, the blotted wet mass of all vegetative biomass captured in individual drift samples was also obtained.

### Fish sampling

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 impact sites. Specifically, fishes at T2 were sampled during baseflow ( $23.5 \text{ m}^3 \cdot \text{s}^{-1}$ ) on 15 November 2010 at 0800 following a 16 h hiatus from hydropeaking and at 1300 following a 4 h peak flow event ( $60.8 \text{ m}^3 \cdot \text{s}^{-1}$ ). Similarly, T1 baseflow fish diets were sampled the next day at 1100 following a 24 h hiatus from hydropeaking and at 1500 following a 3 h peak flow event. Disparate sampling times between sites and dates were required to account for the difference in time of concentration between sites ( $\sim 2$  h), maximize the baseflow period prior to diet sampling, and complete fieldwork during daylight hours. During each sampling event, fish were collected using a combination of backpack and boat-mounted electroshockers, with a target of 15 replicates per species in the 250–400 mm size class, the dominant size class of rainbow and brown trout below FGD (Filbert and Hawkins 1995; R. Mosley personal communication). 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 millimetre (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  $250 \mu\text{m}$  sieve, and the stomach reweighed 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. Relative gut fullness ( $\text{mg} \cdot \text{g}^{-1}$ ) was determined as the total macroinvertebrate biomass (mg) standardized to the emptied gut mass (grams) of each fish.

### Analyses

To compare the magnitude of within-day hydrologic variability between double-peak and non-double-peak water years, we used a two-sample *t* test. The response variable was the mean daily coefficient of variation (CV) for discharge, which was computed from hourly discharge values from USGS gage 09234500 (T1) for the period of 1 October to 31 March of each water year from 1995 to 2011 ( $n = 17$ ).

To quantify the effects of double-peaking on drift macroinvertebrate biomass, we tested whether control and impact sites responded differently between the periods before and after double-peak release using a BACI design (Stewart-Oaten et al. 1986). A separate analysis of each impact site (T1 and T2) with the control site was conducted. The statistical model was an analysis of variance (ANOVA) of a two-way factorial in a completely randomized design, assuming that sampling event (coded one through seven) and site class (control and impact) were fixed effects factors and that the six to eight drift samples per 24 h sampling event were random replicates. Biomass was transformed prior to analysis as  $\log_e(x)$  to better meet assumptions of normality and homogeneity of variances. Because we did not anticipate a persistent threshold response for the duration of double-peak releases, we computed contrasts to compare the difference (impact minus control) between the mean of the two prerelease sampling events and each of the postrelease sampling events. Though we recognize that the probability of finding significant results by chance increases as more tests are conducted, we chose to reduce the chance of ignoring ecologically meaningful results by reporting unadjusted tests (Moran 2003). Data computations were made using the GLIMMIX procedure in SAS/STAT for Windows Release 9.3.

To analyze relationships of daily drift patterns with discharge, as well as temporal patterns during experimental releases, we relied on both graphical analyses and simple linear regression. For the experimental increases in peak magnitude, we regressed

total drift biomass at the initiation of peak flows against peak discharge for a given date. We chose to analyze drift at the initiation of peaks flows (i.e., onset of afternoon peak discharge per daily experimental hydrograph) because of the observed hysteresis for macroinvertebrate drift within a given double-peak event and the consistent peak in drift biomass at this point in the hydrograph (e.g., Fig. 2).

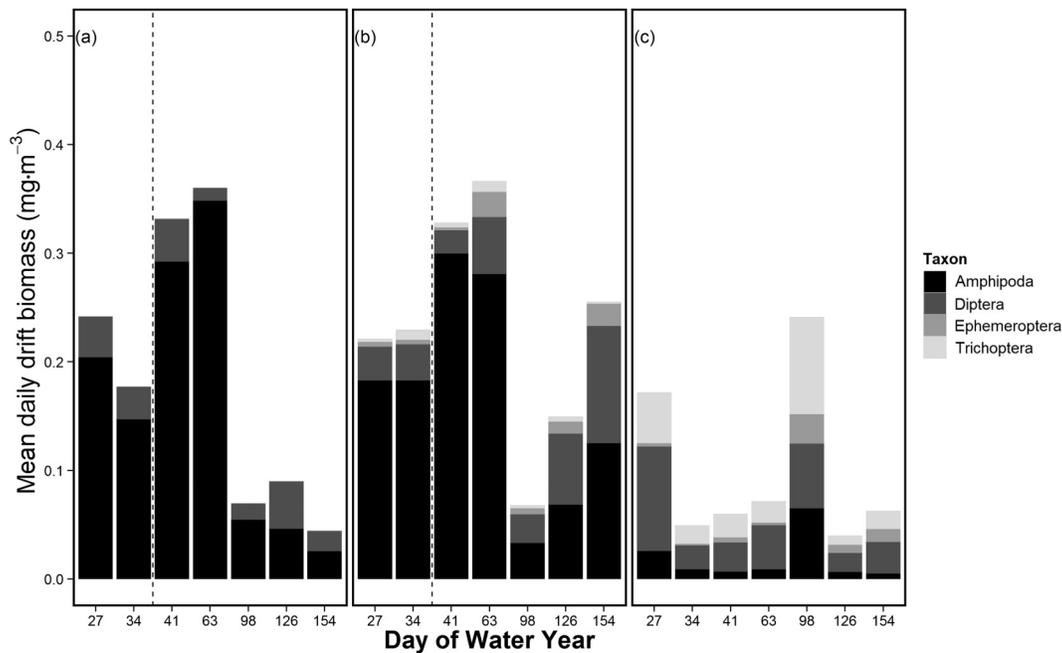
We used random forest (RF) regression models (Breiman 2001; Liaw and Wiener 2002) to identify potential drivers of daily and monthly variation in macroinvertebrate drift for each individual site, where biomass from individual drift samples was used as the response variable. RF models were used over traditional simple linear regression because of the prevalence of nonlinear responses, complex interactions among predictors, and to reduce the potential of over-fitting models because of the high number of predictor variables relative to sample size ( $n = 49$  per site). The predictor variables included time of day, day of water year, instantaneous discharge at the time of drift sample collection, the change in discharge occurring 2 h prior to sample collection, Froude number (computed from mean velocity and depth following Statzner et al. (1988)), vegetative biomass from drift samples, and benthic densities collected once during each 24 h sample event.

Random forest is a tree-based tool that uses bootstrap sampling to fit hundreds of classification or regression trees to a dataset where each split is based on a subset of predictors randomly chosen at each node (Breiman 2001). The algorithm is robust to outliers, prevents over-fitting, can handle a large number of categorical and continuous variables, and frequently generates more stable and accurate model results than traditional modeling approaches (Breiman 2001; Cutler et al. 2007; Siroky 2009). We used the randomForest package within program R in regression mode, with model results averaged across 500 trees. Model performance was assessed using a cross-validated  $R^2$  computed by applying the final model to data withheld from the bootstrap sample (Pang et al. 2006). Individual variable importance was assessed by computing increases in the mean squared error when the validation data for an individual variable was permuted (Goodwin et al. 2008). Final relationships were visually assessed using partial dependency plots, which plot the marginal effect of an individual predictor variable when all other predictor variables are held constant.

To test for relationships between the magnitude of daily hydrologic variability and macroinvertebrate density and richness at both T1 and T2, we utilized a 17-year record (1995–2011 water years) of macroinvertebrate benthic samples collected during January and April of each year. Specifically, we used hourly discharge measurements to compute the annual mean daily CV for each year for two time periods coinciding with double-peaking and the timing of benthic macroinvertebrate sampling: 1 October – 31 December and 1 January – 31 March. Relationships between macroinvertebrate benthic densities and richness with the mean daily CV for 17 years were quantified using simple linear regression ( $n = 17$  per impact site).

Lastly, absolute and compositional differences in relative fish gut fullness between base and peak flows were quantified using both univariate and multivariate analyses. Specifically, differences in gut fullness between flow levels (base versus peak flows), fish species (rainbow and brown trout), and the flow by species interaction were assessed using a two-way factorial design in a generalized linear model (GLM) with  $\log_{10}(x + 1)$ -transformed gut fullness data. Compositional diet differences (relative invertebrate composition as biomass standardized by gut mass) 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 in assemblage composition among two or more groups. A *p* value assesses the

**Fig. 4.** Change in mean daily drift biomass and composition through time for both T1 (a), T2 (b), and Control (c) for the 2010 water year (i.e., 1 September – 31 October). The dashed line separates before and after the initiation of double-peak samples, with no double-peaking at the Control.



**Table 1.** Comparisons of each postrelease sampling event to the mean of two prerelease sampling events for the difference in drift biomass ( $\log_e$  scale) between impact and control sites at the two impact sites (T1 and T2).

Contrast	T1			T2		
	Estimate	$t_{84}$	$p$ value	Estimate	$t_{84}$	$p$ value
Sampling event 3 – prerelease mean	1.031	2.28	0.03	0.412	0.94	0.35
Sampling event 4 – prerelease mean	1.139	2.52	0.01	0.658	1.49	0.14
Sampling event 5 – prerelease mean	-1.955	-4.33	<0.01	-2.031	-4.61	<0.01
Sampling event 6 – prerelease mean	-0.176	-0.39	0.70	0.008	0.02	0.99
Sampling event 7 – prerelease mean	-1.289	-2.85	0.01	0.189	0.43	0.67

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

### Hydrologic alterations

Daily hydrologic variability below FGD differed significantly between single- and double-peak flow years from 1995 and 2011 ( $t_{15} = 6.1$ ;  $p$  value < 0.001). The mean daily CV during periods of double-peaking was 30% on average compared with less than 10% during single- or nonhydropeaking years. During the 2010 water year, pre-double-peak release patterns consisted of relatively high, steady flows (50 and 60  $\text{m}^3 \cdot \text{s}^{-1}$ ), which were lowered to 30  $\text{m}^3 \cdot \text{s}^{-1}$  between 0100 and 0600 each day (Fig. 2a). Starting in October and continuing through March, double-peaking consisted of two daily peaks of equal magnitude (60 to 70  $\text{m}^3 \cdot \text{s}^{-1}$ ) and ramp rate (10.5 to 13  $\text{m}^3 \cdot \text{h}^{-1}$ ), but of disparate durations between the morning (3.5 h) and evening (5 h) peaks (Figs. 2b, 2c).

### Drift responses to double-peak release patterns: daily to monthly time scales

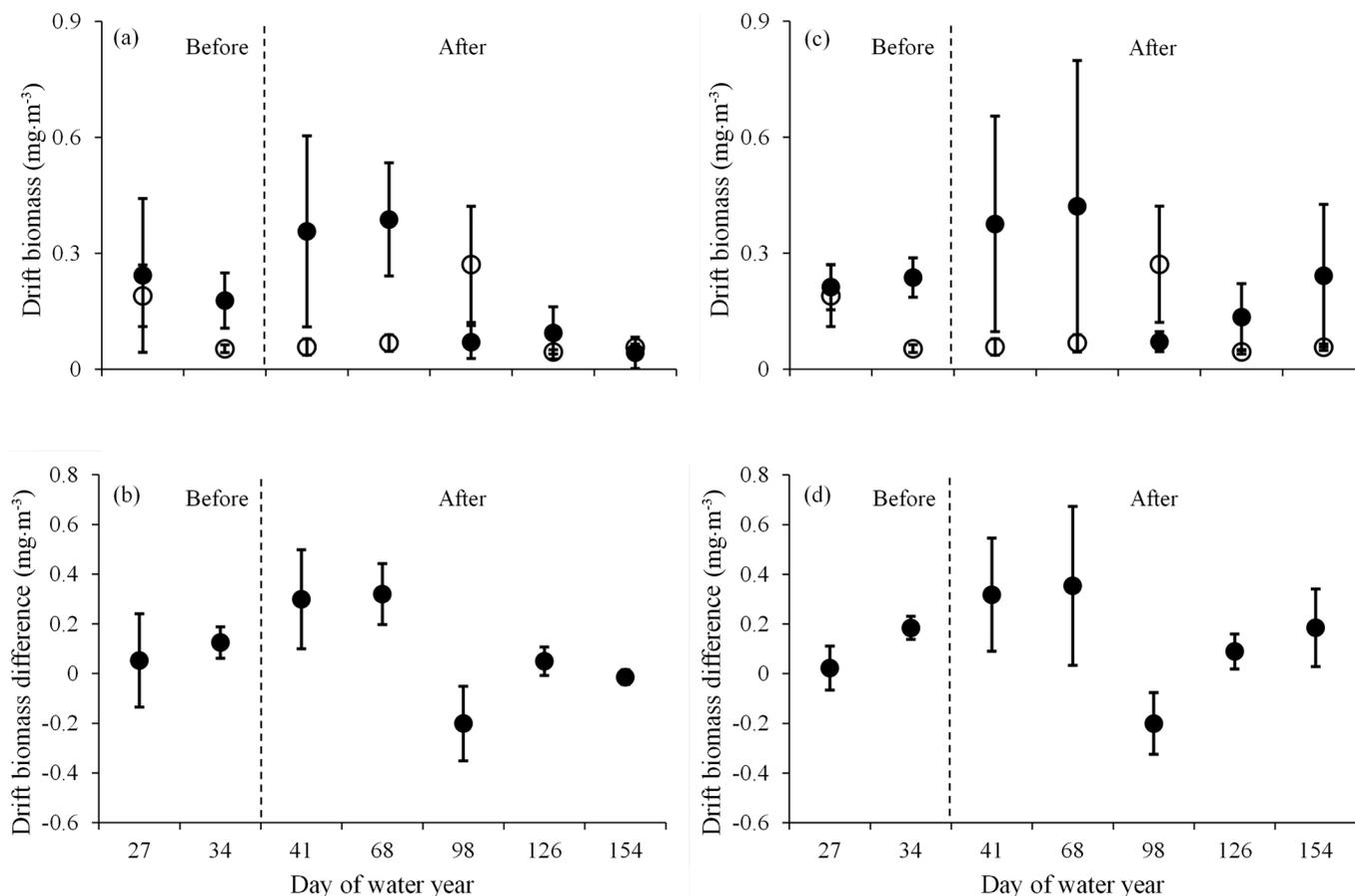
Total and mean richness among all drift samples was lowest at T1 (16 OTUs total, five per sample on average) followed by T2 (25 OTUs, eight per sample) and the control (24 OTUs, 11 per sample)

(Table S1<sup>1</sup>). On average, four orders comprised 98% of macroinvertebrate drift biomass among all sites (e.g., Fig. 4): Amphipoda (48%), Diptera (34%), Trichoptera (11%), and Ephemeroptera (5.3%). At the two impact sites (T1 and T2) Amphipoda, specifically *Hyallela*, comprised the majority of drift biomass (~85%) and Diptera, primarily Chironomidae and some Simuliidae, made up an additional 10%. In contrast, the control site had higher levels of Diptera (60.8%), moderate levels of Ephemeroptera and Trichoptera (~28%), and low but consistent drift biomass of Amphipoda (5.2%).

We observed a significant site class by sampling event interaction for both impact sites (ANOVA, T1:  $F_{[6,84]} = 10.3$ ,  $p$  value < 0.01; T2:  $F_{[6,84]} = 7.2$ ,  $p$  value < 0.01), indicating that differences between the control and impact sites were not the same for all sampling events (Table 1). At T1, drift biomass significantly increased for the first two sampling events during double-peaking, with drift biomass exceeding 0.38  $\text{mg} \cdot \text{m}^{-3}$  on average, an increase of more than 300% in the difference between the impact and control site relative to before double-peak samples (Figs. 5a, 5b). Thereafter, drift biomass at T1 decreased to below or near control levels, suggesting that drift increases only persisted for 30–60 days (i.e., through sampling events three and four). Drift biomass at T2 exhibited similar temporal patterns, but postrelease differences between the control and T2 differed from prerelease differences only during sampling event five, when drift biomass significantly in-

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0562>.

**Fig. 5.** Comparisons of mean daily macroinvertebrate drift biomass ( $\pm 95\%$  CI) between impact (solid symbols) and control (open symbols) sites (a and c) and the difference ( $\pm 95\%$  CI) between impact and control sites (b and d) for the two sample dates before and five sample dates after the initiation of double-peak for both T1 (a and b) and T2 (c and d). All sampling was conducted during the 2010 water year (i.e., 1 September – 31 October).



creased at the control site (Table 1; Figs. 5c, 5d). For both impact sites, it is important to note the presence of divergent patterns from the control site prior to the intervention; drift biomass at the control site declined, while biomass remained relatively constant at both impact sites.

#### Drift responses to double-peak release patterns: hourly time scales

Drift at the control site was relatively constant and did not exhibit strong diel fluctuations (Fig. 2). In contrast, drift at the impact sites appeared to respond to daily discharge fluctuations. For example, daily drift increases appeared greatest during double-peak events, with increases in drift biomass during the rising limb of the hydrograph or at the onset of peak flows constituting the greatest contributions to mean daily drift biomass (e.g., Fig. 2b). However, after approximately 2 h of peak flows, we observed hysteresis, in which elevated drift biomass was not sustained despite persistently high discharge exceeding  $60 \text{ m}^3 \cdot \text{s}^{-1}$ .

#### Responses of macroinvertebrate drift to peak magnitude and other environmental factors

During the experimental increase in peak magnitude, we observed proportional increases in maximum drift biomass that exceeded  $3.02 \text{ mg} \cdot \text{m}^{-3}$  ( $49.7 \text{ individuals} \cdot \text{m}^{-3}$ ), an increase of over 400% relative to pre-experimental conditions (Fig. 3). At T1, drift biomass at the initiation of peak discharge was strongly related to peak discharge ( $R^2 = 0.94$ ), and for every increase of  $10 \text{ m}^3 \cdot \text{s}^{-1}$ , biomass was predicted to increase by  $0.81 \text{ mg}$  ( $y = 0.081x - 2.25$ ).

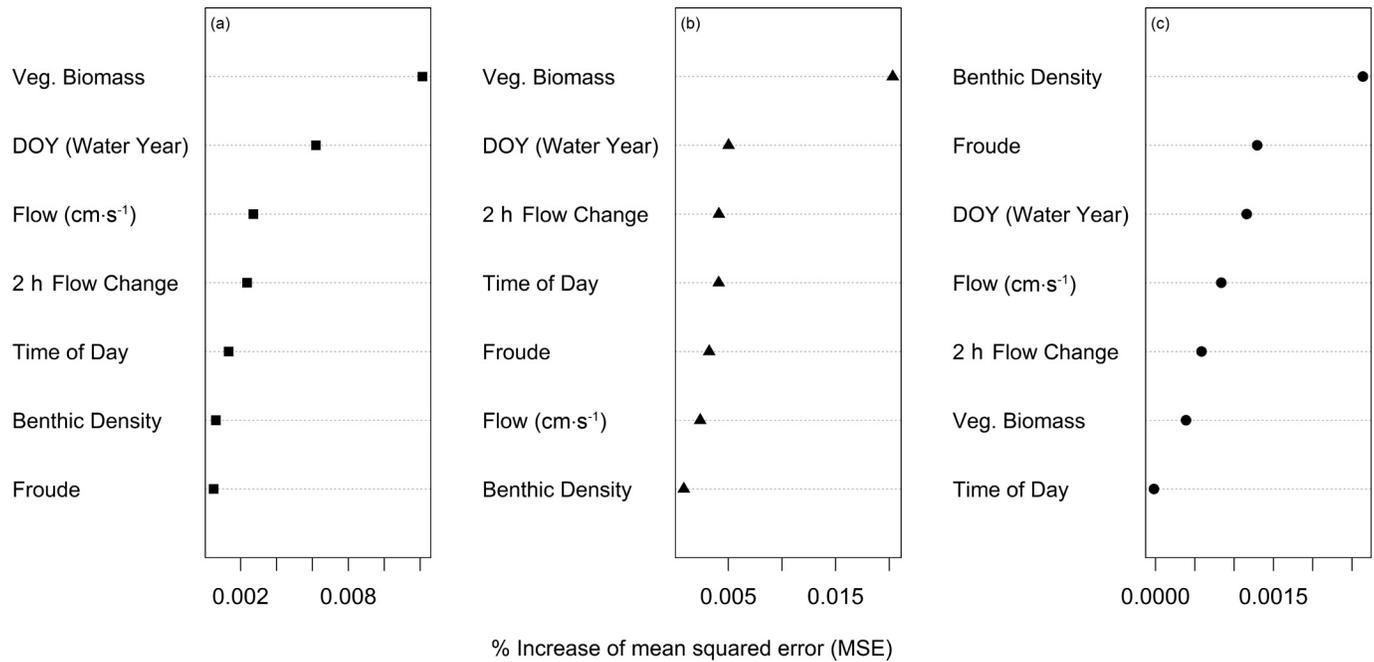
Responses at T2 were similar but more variable ( $R^2 = 0.67$ ) and muted ( $y = 0.036x - 0.63$ ), with a maximum drift biomass of  $1.39 \text{ mg} \cdot \text{m}^{-3}$ .

Model performance for variation in drift biomass differed among sites, with T1 having the highest model precision ( $R^2 = 43.4\%$ ) followed by T2 ( $R^2 = 35.2\%$ ) and the control ( $R^2 = 30.4\%$ ). Drift biomass at the control was most sensitive (i.e., greatest percent increase in mean square error) to densities of benthic macroinvertebrates and to a lesser extent Froude number and day of year (Fig. 6c). In contrast, vegetative biomass was the single best predictor for both of the impact sites (Figs. 6a, 6b), with drift biomass exhibiting a threshold response to vegetative drift (Figs. 7a, 7d); however, the range of observed values and subsequent thresholds differed by an order of magnitude between sites. Subsequent predictors of importance for both impact sites were day of year and measures of discharge or hydraulics. Specifically, drift biomass increased when discharge levels exceeded  $60 \text{ m}^3 \cdot \text{s}^{-1}$  or discharge increased by more than  $20 \text{ m}^3 \cdot \text{s}^{-1}$  prior to drift sampling (Figs. 7c, 7f); however, drift increases were sustained only for a minimum of 30 days from the start of double-peaking (Figs. 7b, 7e).

#### Hydropeaking effects on benthic macroinvertebrate assemblages

We observed relatively weak and variable responses of benthic macroinvertebrates to the degree of daily discharge variability across the 17-year period of record (Table 2). Taxa richness exhibited the only consistent response, with richness inversely related

**Fig. 6.** Variable importance plots for the random forest models developed to explain among- and within-day variation in drift biomass for T1 (a), T2 (b), and the Control (c) during the 2010 water year. 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 permuted. Predictor variable abbreviations include vegetative (Veg.) biomass and 2 h flow change.



to the mean daily coefficient of discharge variation for both the January and April samples at T1, while T2 exhibited no discernible patterns. Benthic densities were not strongly correlated with increasing daily CVs, except over the short term at T1 in the January samples.

#### Fish foraging responses to hydropeaking

The stomach contents of 166 fishes were analyzed across T1 and T2, with between 14 and 30 fish processed per site, species, and flow level combination. The mean length and mass of captured fish was 414 g and 335 mm, respectively. Relative gut fullness was significantly greater following peak versus base flows at both T1 and T2 (ANOVA, T1:  $F = 7.9$ ,  $p$  value = 0.006; T2:  $F = 11.2$ ,  $p$  value = 0.001). On average, gut fullness increased by 2.88 mg·g<sup>-1</sup> following peak flows for both sites and species, an average increase of more than 75%. 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 and  $p$  values < 0.05).

#### Discussion

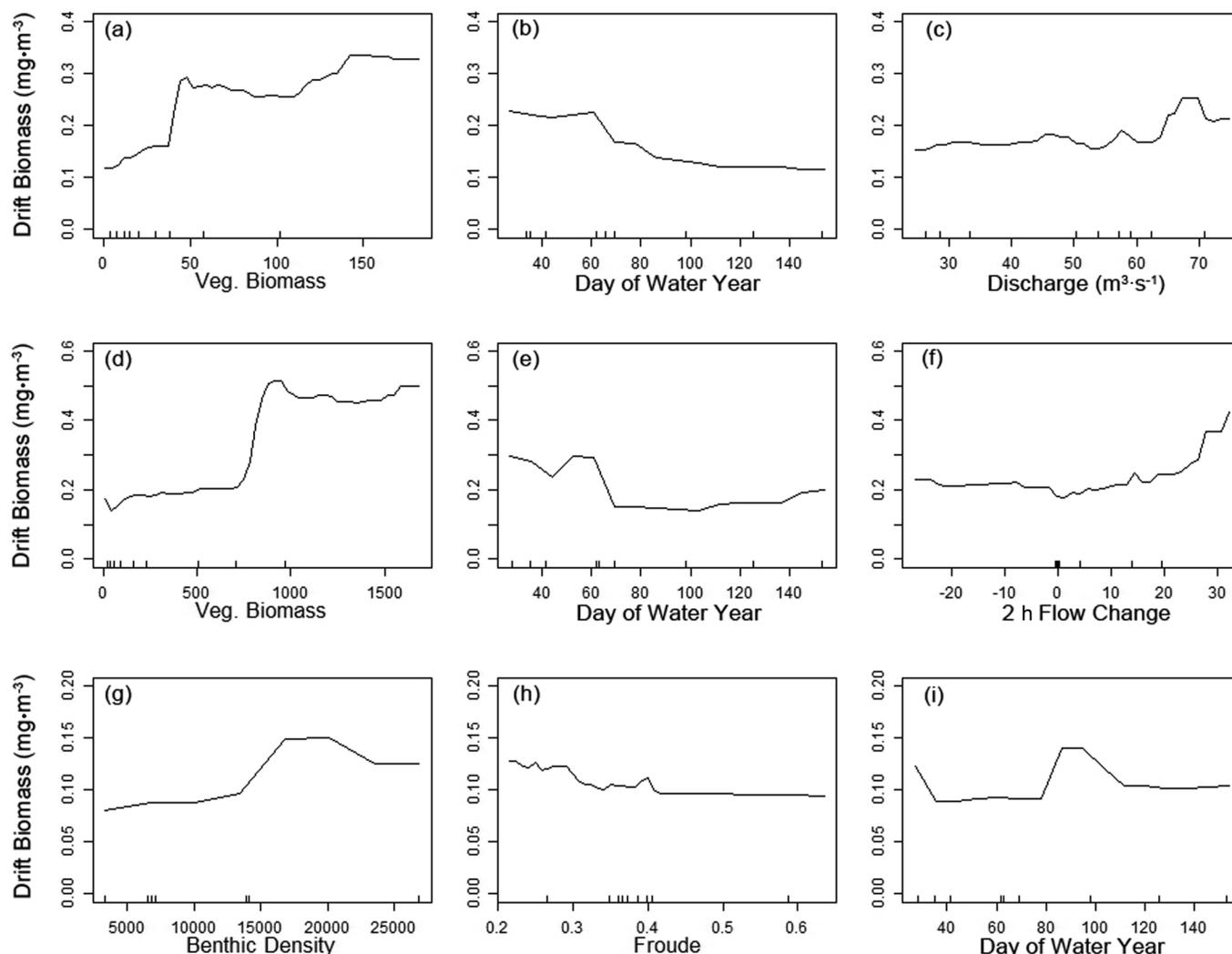
##### Drift responses to double-peak release patterns: daily to monthly time scales

Similar to other studies, we found that double-peaking significantly increased the degree of daily hydrologic variability (Cushman 1985; Gore et al. 1989, 1994), which increased average drift biomass by more than 50% for a period of 30 to 60 days. Despite the sustained high flows typical of single-peaking, we believe mean daily drift biomass increased during periods of double-peaking because invertebrates were responding to the more frequent, rapid rises in discharge. For example, drift increases were almost exclusively observed during the ascending limb of the hydrograph, and the change in flow was a moderate predictor of drift biomass (e.g., Figs. 2, 6). Increases in drift con-

centration and biomass 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; 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 and (or) vegetative substrates are dislodged from the benthos (Allan 1995). Given the relatively coarse substrate and heavy armoring immediately below FGD (Andrews 1986; Vinson 2001), double-peak discharges likely resulted in non-bed mobilizing flows. Thus, drift increases likely resulted from the dislodgement of individual invertebrates and (or) the mechanical shearing of the thick algal and bryophyte mats, which blanket much of the river and serve as substrate for benthic organisms (Vinson 2001).

Despite the observed drift responses, we found that drift increases were sustained only for 30–60 days. Decreases in mean daily drift biomass 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; Callisto and Goulart 2005), redistribution of benthic assemblages to instream 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 1985; Shannon et al. 1996; Tockner and Waringer 1997). Our modeling results suggest that both drift increases and the ephemeral nature of these increases were related to patterns in vegetative export and not changes in the density or distribution of benthic macroinvertebrates. Specifically, we failed to detect reductions in benthic densities, and with benthic densities exceeding 50 000 individuals per square metre, it is unlikely that adequate refugia existed to accommodate the redistribution of all individuals. Rather, the dominant taxa at impact sites, *Hyallela* and Chironmiidae midges, are commonly found at high densities in *Cladophora glomerata* and *Amblystegium riparium* mats (Power 1990; Shannon

**Fig. 7.** Partial dependency plots for the top predictors from random forest models for T1 (a–c), T2 (d–f), and the Control (g–i). Note that the y axis (partial dependence) is scaled within, but not among, sites. Rug plots (vertical lines extending upward from the x axes) indicate deciles of data contributing to the modeled response as a function of the x axis for each predictor variable.



**Table 2.** Relationships between macroinvertebrate density and richness and the mean daily coefficient of discharge variation (CV) compared between the two impact sites (T1 and T2) for the January and April benthic sampling events: 1995–2011.

	Density				Richness			
	T1		T2		T1		T2	
	January	April	January	April	January	April	January	April
R <sup>2</sup>	17	2	0	5	25	30	0	1
Slope	-239.5	81	-0.49	-91.8	-0.08	-0.06	-0.01	-0.02
p value	0.1	0.62	1	0.38	0.04	0.02	0.82	0.71

et al. 1996), the main filamentous algae and bryophyte within the Green River, both of which can be subject to considerable shear and export during frequent discharge fluctuations.

Hydropeaking has been shown to increase benthic organic matter export, with the rate of macroinvertebrate drift strongly correlated with the timing and magnitude of organic matter export (Irvine 1985; Shannon et al. 1996; Tockner and Waringer 1997). In our study, drift increases and the ephemeral nature of these increases were correlated with the biomass of drifting vegetation and its interaction with day of year (seasonal accrual and senescence of benthic algae). We observed rapid increases in drifting

vegetation following the initiation of double-peaking, which subsequently declined after 30–60 days (data not shown). The rate of vegetative export likely declined through time because of natural seasonal senescing initiated by decreased light levels and cooler temperatures at the onset of double-peaking in October (reviewed in Allan 1995), which combined with frequent wetting and drying cycles and high ramp rates that temporarily increased scour and export rates. Similarly, during a 1-month summer experiment, Blinn et al. (1995) observed biomass reductions exceeding 45% for *Cladophora glomerata* in varial zones experiencing 12 h exposure periods followed by scouring flows below Glen Canyon Dam.

Across broader time scales, Shannon et al. (1996) observed peak algal export in September followed by lowest observed levels in March despite persistent discharge fluctuations (Shannon et al. 1996), thus suggesting a similar seasonal signature to vegetative export under hydropeaking scenarios.

Alternatively, water temperature was highly correlated with day of year ( $r = -0.96$ ) and was not included in the random forest models because data were not available for the control and T2 sample sites. When included in the T1 model, temperature was one of the top predictors, with drift precipitously declining below 7 °C (data not shown). 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 Eikeland 1988; Allan 1995). However, across longer time scales, temperature is frequently a poor predictor of seasonal drift patterns as compared with discharge and benthic densities (Stoneburner et al. 1979; Allan 1987; Hieber et al. 2003). Thus, we believe temperature is unlikely to be the proximate cause, but rather a correlate of light availability and algal senescence.

#### Drift patterns during double-peaking: hourly time scales

Similar to results from other studies, drift increases were associated with the rising limb of the hydrograph and 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 similar mechanisms are operating to explain cyclical macroinvertebrate drift patterns. Hysteresis in macroinvertebrate drift is typically attributed to either reductions in benthic densities, similar to supply limitation for sediment and organic matter, 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 limiting factor, but rather the supply or shearing of vegetative biomass. We found vegetative export to be the top predictor of drift rates at daily and monthly time scales, which exhibited concordant patterns of daily hysteresis with invertebrate drift. Similarly, Irvine and Henriques (1984) observed that organic matter export was highly correlated ( $>0.83$ ) with short-term increases in macroinvertebrate drift. Alternatively, behavioral adaptations, specifically the redistribution of *Hyalloella* 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, mayflies, caddisflies, 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 and bryophyte mats, which were subject to considerable shear and transport.

#### Responses of macroinvertebrate drift to peak magnitude and other environmental factors

We utilized experimental flows from FGD to evaluate changes in drift biomass as a function of the magnitude of peak discharge. Our results suggest that drift increases in proportion to the magnitude of peak flows, although it was difficult to discern proportional from exponential increases with only four data points. 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 reductions during double-peaking, source populations appeared adequate to sustain increased drift densities over the course of the 4-day experiment. More extensive experiments over a greater range of discharges would be required to determine whether drift increases are initiated only above some threshold or absolute change in discharge (Imbert and Perry 2000; Robinson et al. 2004; Mochizuki et al. 2006) and whether drift plateaus or is otherwise unsustainable above certain magnitudes or varied ramp rates. Results from our random forest modeling suggest significant increases in drift biomass occur above 60  $\text{m}^3\cdot\text{s}^{-1}$  and following flow changes exceeding 10  $\text{m}^3\cdot\text{s}^{-1}$  (Fig. 7). However, discharge thresholds varied between sites and are likely artificially low because of persistent drift increases for approximately 2 h, during which no change in flow occurred (e.g., Fig. 2). 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 mean daily drift biomass exceeding 50% of pre-double-peak levels, we failed to detect significant decreases in benthic densities over a 17-year period of record encompassing a large range of daily hydrologic variability (CV: 0.6%–38%). This finding contrasts those of other studies finding reductions in benthic densities in response to both flood (Grimm and Fisher 1989; Shannon et al. 2001; Robinson et al. 2004) and hydropeaking events (Blinn et al. 1995; Cereghino and Lavandier 1998). The resistance of benthic densities to double-peaking below FGD is likely a result of non-bed mobilizing flows and the extremely high benthic biomass relative to observed drift rates; drift biomass never exceeded 1% of benthic biomass when scaled to mean daily drift biomass, following Elliott (1967). Furthermore, benthic assemblages below FGD are dominated by *Hyalloella*, Chironomidae midges, and a small proportion Baetidae mayflies, all of which are highly productive and disturbance-adapted organisms (Vinson 2001). Alternatively, given the lack of replication and subsequent error estimates for our benthic samples, the paucity of significant results may result from low statistical power, which was unknown. In contrast with responses of benthic densities, taxa richness significantly declined in response to increased hydrologic variability; however, the magnitude of species loss was low and responses were limited to T1. Although the densities of the 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.

#### Differential site responses of benthic and drifting macroinvertebrates to double-peaking

Responses of both drifting and benthic macroinvertebrates to double-peaking were consistently of greater magnitude and consistency for the T1 as compared with the T2 impact site. We believe the increases in drift biomass to both natural and experimental hydropeaking were greater and taxa richness reductions more significant for T1 than T2 because of considerable valley confinement, which results in increased stranding potential and more significant hydraulic changes between base and peak flows because of greater stage height and velocity changes. For example, during double-peaking, velocity increased by an average of 0.16  $\text{m}\cdot\text{s}^{-1}$  at T2 compared with 0.38  $\text{m}\cdot\text{s}^{-1}$  at T1. Such velocity increases are likely to result in greater algal export at T1, but not result in significant bed transport for either site. Furthermore, the partial dependency plots from the random forest modeling suggest that drift biomass increases at an order of magnitude lower algal export biomass, as compared with T2 (Figs. 7a, 7d). This likely re-

flects the elevated benthic densities at T1, which are frequently 1.5 times those found at T2.

### Fish foraging responses to hydropeaking

The impacts of hydropeaking on trout populations have been widely studied in terms of alterations to physical habitat, while a paucity of studies have addressed how altered prey resource availability affects foraging behaviors and subsequent fitness (but see Lagarrigue et al. 2002). It has been suggested that trout do not utilize the increased drift abundance 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). In contrast, we observed significant increases in gut fullness following peak flows that exceeded base flow levels by 75%. Our results are similar to those of Lagarrigue et al. (2002), who observed significant increases in brown trout gut fullness 2–4 h 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 2 h. Lagarrigue et al. (2002) sampled at 4 h 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. It appears that trout were able to utilize high flow refugia and increase feeding rates during peaking events in our study; however, we must acknowledge that increases in gut fullness could have resulted from natural temporal periodicity in feeding patterns, since the different flow stages (base versus peak flow) were confounded by time of day. 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 important 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.

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). Our results suggest that double-peak releases can significantly increase macroinvertebrate drift at both daily and weekly time scales; however, the magnitude and duration of drift responses were contingent upon several biotic and abiotic factors. Drift increases were strongly related to the magnitude and frequency of peak flows, suggesting that different flow release scenarios can result in markedly different responses of drifting macroinvertebrates. Furthermore, the differential response between sites highlights the potential for interactions among flow alteration and local geomorphology to influence the magnitude of biological responses. Finally, underlying all macroinvertebrate drift responses were strong relationships with algal shearing during elevated velocities associated with double-peaking. Despite a paucity

of studies highlighting this mechanism by which invertebrates are recruited into the drift, it is likely to be quite common below hypolimnetic dams, where the relatively stable, clear water promotes high primary production (Baxter 1977; Blinn et al. 1998). The associations of macroinvertebrate drift responses with peak magnitude, local geomorphology, and algal scour highlight some of the context dependencies that must be considered when trying to model macroinvertebrate response to hydropeaking. We demonstrate for two sites below a hypolimnetic dam that the effects of food resource availability on trout fitness cannot be considered independent of discharge fluctuations at both daily and monthly time scales. The extent to which the effects of double-peaking on macroinvertebrates can propagate through tail-water food webs has yet to be determined, as additional work is needed to determine the net benefit of increased consumptions given the potential increased energetic costs of foraging at higher velocities.

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