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The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river

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SUMMARY

1. Invertebrate drift is a fundamental process in streams and rivers. Studies from laboratory experiments and small streams have identified numerous extrinsic (e.g. discharge, light intensity, water quality) and intrinsic factors (invertebrate life stage, benthic density, behaviour) that govern invertebrate drift concentrations (# m^{-3}), but the factors that govern invertebrate drift in larger rivers remain poorly understood. For example, while large increases or decreases in discharge can lead to large increases in invertebrate drift, the role of smaller, incremental changes in discharge is poorly described. In addition, while we might expect invertebrate drift concentrations to be proportional to benthic densities (# m^{-2}), the benthic–drift relation has not been rigorously evaluated.

2. Here, we develop a framework for modelling invertebrate drift that is derived from sediment transport studies. We use this framework to guide the analysis of high-resolution data sets of benthic density and drift concentration for four important invertebrate taxa from the Colorado River downstream of Glen Canyon Dam (mean daily discharge 325 $m^3\ s^{-1}$) that were collected over 18 months and include multiple observations within days. Ramping of regulated flows on this river segment provides an experimental treatment that is repeated daily and allowed us to describe the functional relations between invertebrate drift and two primary controls, discharge and benthic densities.

3. Twofold daily variation in discharge resulted in a >10-fold increase in drift concentrations of benthic invertebrates associated with pools and detritus (i.e. *Gammarus lacustris* and *Potamopyrgus antipodarum*). In contrast, drift concentrations of sessile blackfly larvae (*Simuliium arcticum*), which are associated with high-velocity cobble microhabitats, decreased by over 80% as discharge doubled. Drift concentrations of Chironomidae increased proportional to discharge.

4. Drift of all four taxa was positively related to benthic density. Drift concentrations of *Gammarus*, *Potamopyrgus* and Chironomidae were proportional to benthic density. Drift concentrations of *Simulium* were positively related to benthic density, but the benthic–drift relation was less than proportional (i.e. a doubling of benthic density only led to a 40% increase in drift concentrations).

5. Our study demonstrates that invertebrate drift concentrations in the Colorado River are jointly controlled by discharge and benthic densities, but these controls operate at different timescales. Twofold daily variation in discharge associated with hydropeaking was the primary control on within-day variation in invertebrate drift concentrations. In contrast, benthic density, which varied 10- to 1000-fold among sampling dates, depending on the taxa, was the primary control on invertebrate drift concentrations over longer timescales (weeks to months).

Keywords: algal drift, benthic invertebrate, density-dependent, invertebrate drift, regulated river

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Introduction

Invertebrate drift is a fundamental process in streams and rivers, because it is both critical to maintenance of benthic invertebrate populations (Brittain & Eikeland, 1988; Hart & Finelli, 1999) and provides a key mechanism of resource delivery to drift-feeding fishes (Allan, 1978; Rader, 1997). Early studies describing nocturnal periodicity in invertebrate drift concentrations (Tanaka, 1960; Waters, 1962; Muller, 1963) captured the attention of ecologists and evolutionary biologists and motivated decades of research on the various extrinsic (e.g. light intensity, discharge, water velocity, water quality and presence of fish) and intrinsic factors (e.g. invertebrate life stage and benthic density) that govern invertebrate drift (see review by Brittain & Eikeland, 1988).

Discharge is a key extrinsic factor that governs invertebrate drift in streams and rivers by affecting accidental (passive) and intentional (behavioural) drift entry of invertebrates (Brittain & Eikeland, 1988; Hart & Finelli, 1999). Numerous studies have demonstrated that natural and artificial floods cause large increases in drift concentrations (Anderson & Lehmkuhl, 1968; O'Hop & Wallace, 1983; Perry & Perry, 1986; Poff & Ward, 1991), in part because of greater accidental drift entry associated with benthic scour and stream bed mobilisation (Gibbins, Vericat & Batalla, 2007); however, increases in drift concentrations that occur with floods are not entirely due to increases in the amount of accidental drift entry, because discharge-driven increases in drift concentrations for some taxa only occur with the onset of nightfall (Scullion & Sinton, 1983); that is, invertebrates may delay intentional drift entry to minimise the predation risk associated with entering the drift (Flecker, 1992). Large decreases in discharge can also cause increases in drift concentrations, because invertebrates intentionally enter the drift to avoid stranding (Perry & Perry, 1986; Poff & Ward, 1991; James, Dewson & Death, 2008). These examples highlight the strong role that discharge plays in governing both accidental and intentional drift of invertebrates, but these examples also represent the extreme endpoints of the discharge–drift relation. In contrast, the role that smaller, incremental changes in discharge play in controlling invertebrate drift concentrations is not well understood, particularly in large rivers.

In addition to uncertainty related to effects of discharge on drift, little is known about how drift varies as a function of benthic invertebrate density. Invertebrate drift concentrations should increase proportional to benthic density, because drifting invertebrates are derived from the benthos (i.e. the benthic–drift hypothesis; Hildebrand, 1974). Support for this hypothesis comes from both laboratory and field studies (Hildebrand, 1974; Humphries, 2002; Shearer *et al.*, 2003; Tonkin & Death, 2013). Yet, many studies that have evaluated the discharge–drift relation have been inconclusive regarding the benthic–drift relation (Pearson & Franklin, 1968; Perry & Perry, 1986; Poff & Ward, 1991; Shannon *et al.*, 1996). These equivocal results regarding a key intrinsic control of invertebrate drift (i.e. benthic density) make it difficult to generalise from past discharge–drift studies and generate predictions specific to a different stream or river.

Regulated rivers are an ideal setting for testing the role that discharge and benthic densities play in governing invertebrate drift. Ramping of discharge associated with hydroelectric power generation (hereafter, hydropeaking) provides an experimental treatment that is repeated daily and can be used to help parse out extrinsic versus intrinsic controls. Further, discharge variation in most regulated rivers is highly predictable, which allows careful development of study design and systematic allocation of sampling. Analysing and modelling drift data from regulated rivers is also relatively straightforward, because invertebrate assemblages are typically dominated by a small number of species or taxa compared to unregulated rivers (Bunn & Arthington, 2002).

Here, we develop a conceptual framework for modelling invertebrate drift by drawing upon the sediment transport literature. We then modify this framework and develop a suite of statistical models specific to both nonliving organic matter and invertebrates. We test these models using high-resolution data sets of filamentous algal drift, invertebrate drift concentrations and benthic invertebrate densities from the Colorado River downstream from the hydropeaking Glen Canyon Dam. We determine the best statistical models and corresponding parameter estimates for each of four taxa that either dominate benthic biomass and production in this river segment (*Gammarus lacustris* and *Potamopyrgus antipodarum*) or contribute disproportionately to fuelling rainbow trout (*Oncorhynchus mykiss*) production (i.e. Chironomidae and *Simulium arcticum*; see Cross *et al.*, 2011).

Methods

Conceptual framework

There are many similarities between the physical processes that regulate sediment and invertebrate drift concentrations in rivers. While the sediment entrainment and transport literature has a rich theoretical background that has been empirically tested in hundreds of rivers (Garcia, 2008), the additional complexity introduced by invertebrate behaviour, which is not captured in models based solely on physical principles, has frustrated attempts to reach general conclusions concerning invertebrate drift (Hart & Finelli, 1999). Our approach here is not to suggest a simple model to explain all invertebrate drift, but rather to treat expectations based on physical principles as null hypotheses for different species. To begin, we briefly review general expectations from sediment transport studies.

The rate of entrainment of sediment into suspension depends on the stress exerted by the water on the sediment grains, the settling velocity of the sediment grains and the relative abundance of sediment of a given grain size on the bed (Parker & Anderson, 1977; Garcia & Parker, 1991). Empirical relations for suspended sediment concentration commonly take the form:

$$C_s \propto \mu_*^m D_b^{-n} A_s \tag{1}$$

where C_s is the depth-averaged concentration of sediment in suspension, μ_* is shear velocity (related to flow strength; units = Pa = kg m^{-1} s^{-2}), D_b is the median grain size of the bed sediment that is available for entrainment into suspension (a measure of particle settling velocity; units = mm) and A_s is a proportional measure of the amount of the suspendable sediment covering the bed (a measure of benthic supply; range from 0 to 1). Thus, for a given sediment grain size and bed sediment supply, suspended sediment concentration is a simple power function of shear velocity. Because shear velocity can be locally variable and difficult to measure, discharge (Q) is often used as a site-specific proxy. For example, sediment transport at various locations in the Grand Canyon can be well approximated by a power-law relation with discharge, where the power is in the range of 3–4 (Wright *et al.*, 2010).

Here, we also assume that sediment supply (A_s) is constant over a sufficient length of channel such that C_s is the concentration achieved when the suspension is in equilibrium with the bed. The length of upstream channel that supplies suspended sediment to a drift measurement location downstream will depend on the transport distances of the sediment grains. Given average depth (4 m) and water velocity (0.6 m s^{-1}) of the Colorado River in Glen Canyon, fine sand (0.063–0.12 mm) will travel between 600 and 1800 m before settling. This example highlights the critical importance of characterising benthic invertebrate density throughout the reach upstream of the drift sampling location when attempting to characterise controls on invertebrate drift in large rivers, because invertebrate drift distances may exceed thousands of metres in large rivers.

Hypotheses

Our principal goal in modelling invertebrate drift was to test several hypotheses concerning the relation between invertebrate drift and two primary controls, discharge and benthic densities. A secondary goal of our modelling was to estimate daily invertebrate export from the Glen Canyon segment to evaluate whether negative feedbacks on benthic density might be occurring because of high export associated with hydropeaking. We had three main hypotheses:

Hypothesis 1: Invertebrate drift concentrations increase nonlinearly with discharge, as has been observed for fine sediment (i.e. the power in a relation with discharge should be $\gg$1).

Hypothesis 2: The value of the discharge exponent for invertebrate drift models will be similar to the value of the discharge exponent for the algal model, because algal shearing is a primary mechanism of accidental drift entry for invertebrates.

Hypothesis 3: Invertebrate drift concentrations vary proportional to benthic density.

General form of statistical models

The essential characteristics of eqn (1) that are expected to also apply to algal and invertebrate drift are (a) the nonlinear relation between drift concentration (# m^{-3}) and shear velocity (and by extension, discharge) and (b) a proportional relation between drift concentration and benthic supply (i.e. density, or #·m^{-2}). A relation analogous to eqn (1), but specific to invertebrate drift, might therefore take the form:

$$C \propto B^f Q^g \tag{2}$$

where B is benthic density (# m^{-2}) and Q is discharge (m^{-3} s^{-1}). We do not incorporate grain size into our model, because invertebrate size is a function of life stage, which could drive intentional drift entry (Brittain & Eikeland, 1988). *A priori*, we hypothesised that these size-mediated behavioural effects would overwhelm any effects that invertebrate size might have on settling velocity. In addition, while many studies of invertebrate drift analyse concentrations in units of mass per volume (e.g. mg m^{-3}), we analysed benthic and drift in terms of individuals per area or volume (i.e. # m^{-2} and # m^{-3}, respectively), because this analytical strategy allowed us to describe the critical state change, drift entry from the benthos, on a *per capita* basis (Wells & O'Hara, 2012).

The proportional eqn (2) can be converted to an exact equation by adding an intercept (e):

$$\frac{N_i}{V_i} = eB_i^f Q_i^g \tag{3}$$

where N_i is the count of the focal taxon in sample i and V_i is the volume of sample i. Linking eqn (3) to data, while also allowing for behavioural variation, can be accomplished by fitting a generalised linear mixed effect model with a Poisson error distribution:

$$\log(N_i) = \beta + \log(V_i) + f * \log(B_i) + g * \log(Q_i) + \eta_{month_i} \tag{4}$$

where η_{month_i} represents variation in the amount of drift between sampling events that is not explained by benthic density or discharge. We used different versions of the general model described in eqn (4) to test hypotheses related to controls of invertebrate drift. We additionally modified a version of eqn (4) to test hypotheses about the relation between discharge and concentrations of filamentous algal drift (C_i):

$$\log(C_i) = \beta + g * \log(Q_i) + \eta_{month_i} + \varepsilon \tag{5}$$

Equation (5) differs from our invertebrate drift model in the following ways: (i) benthic algal biomass is not included, because it was not measured during our study, (ii) biomass concentration (mg ash-free dry mass m^{-3}) was used as the response variable rather than individuals per volume (# m^{-3}), and (iii) we assumed a normal distribution for errors rather than a Poisson distribution, because our algal data was biomass and not counts.

Testing hypotheses with models

We were not interested in the relation between algal drift concentrations and discharge *per se*. However, modelling of the discharge–algal drift relation provided a null expectation for the exponent of the discharge–invertebrate drift relation. This null expectation allowed us to quantitatively evaluate whether the primary mechanism of accidental invertebrate drift entry is via algal shearing and entrainment. We compared models with and without discharge as a fixed effect to test whether relations between algal drift concentrations and discharge were statistically significant. We also modelled the discharge–algal drift relation to test whether confounding of time of day and discharge was a potential concern relative to modelling invertebrate drift. Confounding of time of day and discharge could complicate analysis of invertebrate drift data given patterns of water release from Glen Canyon Dam; that is, small discharges occur in the morning and large discharges occur in the afternoon and evening. Time of day can strongly affect invertebrate behaviour and intentional drift entry (Brittain & Eikeland, 1988), but it should not affect algal drift. Subdaily variation in algal drift concentrations should be related to variation in discharge alone. Thus, *a priori*, we predicted that algal concentrations would not vary with time of day. Time of day was a categorical, fixed effect in these models with two different levels: night (<0.5 h before sunset or after sunrise) and day (>0.5 h after sunrise or before sunset). We used times of sunset and sunrise from Page, AZ for these calculations (15 km from the study reach; http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

We tested hypotheses by fitting and comparing models that followed the general form of eqn (4), but which were constrained according to the hypothesis being tested. We fit generalised linear mixed models using the 'lmer' function in R package 'arm' (R version 2.15.0) and compared models using Bayesian information criterion (BIC). BIC is a measure of model fit that includes a penalty for complexity, which limits overfitting of models. Smaller BIC values indicate a better model.

To test our hypotheses for invertebrate taxa, we developed a series of mixed models (Table 1), all of which included date as a random effect, the number of individuals in the drift sample as the independent variable, the log of the sample volume as an offset, a Poisson error distribution and a log-link (Crawley, 2007). We evaluated Hypothesis 1 (a power-law relation between drift concentrations and discharge, where the power $\gg$1) by comparing the BIC for models that included the log of discharge as a fixed effect to models that did not include the log of discharge. To evaluate Hypothesis 2 (power on discharge for invertebrate drift is no different than power on discharge for algal drift), we considered models in which the log of discharge was multiplied by the estimated algal drift power, and this quantity was included as an offset. For each of the above models, we considered versions that included the log of benthic density (B) as an offset (i.e. exponent on benthic density = 1, Hypothesis 3), a power for benthic density was estimated or benthic density was excluded altogether. We also considered versions of the above models that did or did not include time of day as a fixed effect.

Table 1 Bayesian information criteria (BIC) values for the different algal and invertebrate drift models that were evaluated, where smaller BIC indicates a better performing model. The lowest BIC score for each taxa, which is standardised to zero for all taxa, is in bold font

Model	Algal	Chironomidae	*Gammarus lacustris*	*Simulium arcticum*	*Potamopyrgus antipodarum*	H1	H2	H3
α	54.3	154.7	309.5	339.6	4066.3	O		O
α_{tod}	59.0	157.5	202.1	287.4	3146.9	O		O
αB	NA	140.0	288.0	341.7	4050.3	O		X
$\alpha_{tod}B$	NA	142.9	182.1	291.5	3130.4	O		X
αB^f	NA	144.2	292.2	331.5	4052.7	O		X
$\alpha_{tod}B^f$	NA	147.1	186.4	280.6	3132.3	O		X
αQ^g	**0.0**	13.8	86.9	33.6	155.4	X	O	O
$\alpha_{tod}Q^g$	12.5	16.2	9.9	7.7	12.3	X	O	O
αBQ^g	NA	**0.0**	77.0	32.6	143.5	X	O	X
$\alpha_{tod}BQ^g$	NA	2.5	**0.0**	8.4	**0.0**	X	O	X
αB^fQ^g	NA	4.3	80.9	24.9	147.6	X	O	X
$\alpha_{tod}B^fQ^g$	NA	6.8	3.1	**0.0**	4.0	X	O	X
$\alpha Q^{g_{al}}$	NA	206.2	145.4	883.7	1060.0		X	O
$\alpha_{tod}Q^{g_{al}}$	NA	207.6	45.8	838.8	713.1		X	O
$\alpha BQ^{g_{al}}$	NA	193.7	128.8	887.8	1045.8		X	X
$\alpha_{tod}BQ^{g_{al}}$	NA	195.2	30.9	884.8	698.5		X	X
$\alpha B^fQ^{g_{al}}$	NA	198.1	133.2	877.0	1049.3		X	X
$\alpha_{tod}B^fQ^{g_{al}}$	NA	199.6	34.6	833.3	701.7		X	X

α – coefficient constant; α_{tod} – coefficient varies according to time of day; B – benthic density; f – power on benthic relation (assumed = 1 in models not designated with f); Q – discharge; g – power on discharge relation; g_{al} – power set at algal value (2.1; see Table 2). The three columns on the right of the table labelled H1–H3 represent contrasts in BIC values that were used to evaluate the three core hypotheses: H1 – drift concentrations vary with discharge raised to a power; H2 – the power on Q for invertebrate models is no different than the power on Q for the algal model; H3 – drift concentrations increase proportional to benthic density.

After identifying the best model using BIC, we also calculated multilevel R^2 for the best model and submodels where one predictor was removed. Multilevel R^2 can be interpreted similar to more traditional R^2 and allows users of multilevel, or hierarchical, models to estimate how well models are fitting data at different levels (Gelman & Pardoe, 2006). Importantly, the addition of a covariate may occasionally lead to a decreased R^2 at one level, or even a negative R^2, and an increased R^2 at another level (e.g. Yackulic *et al*., 2011). In the models we evaluated, there were two levels, sample and month. Thus, multilevel R^2 allowed us to estimate the amount of variation in invertebrate drift between samples taken within a month that was explained by the covariates time of day and discharge, relative to the amount of variation in invertebrate drift between months that was explained by the covariates benthic density and mean discharge. In other words, we defined the variance explained at the sample level as:

$$\text{pseudo-}R^2_{sample} = 1 - \frac{E\left(Var_{j=1}^{j=N_{sample}}\left(y_j - \exp\left(\log(V_j) + \beta X_j + \eta_{month_j}\right)\right)\right)}{E\left(Var_{j=1}^{j=N_{sample}}(y_j)\right)}$$

where N_{sample} is the number of samples, E is the expected value, Var is the variance, y_j and V_j are the count and sample volume of the jth sample, η_{month_j} is the random effect for the month associated with the jth sample, X_j is the matrix of covariates and β is the vector of estimated fixed effects. We refer to our R^2 values as pseudo-R^2 because we do not use the traditional formula associated with linear regression, rather we use a slightly modified definition that is more appropriate for log-Poisson regression. This modification is separate from multilevel modifications and is common for generalized linear models. The proportion of variance explained at the month level was defined as:

$$\text{pseudo-}R^2_{month} = 1 - \frac{E\left(Var_{k=1}^{k=N_{month}}(\eta_k)\right)}{E\left(Var_{k=1}^{k=N_{month}}(\eta_k + \beta\bar{X}_k)\right)}$$

where N_{month} is the number of months sampled, η_k is the random effect associated with the kth month and $\bar{X}_k$ is the matrix of mean values of covariates in the kth month.

We estimated total drift export (# d^{-1}) from the Glen Canyon segment on the days when drift and benthic sampling occurred using the parameter estimates (benthic density, time of day and discharge) and random effects from the best performing model for each taxon (Table 2). We estimated invertebrate population abundance by multiplying the mean habitat-weighted benthic

Table 2 Estimated drift concentrations based on time of day (day versus night) and parameter values (f and g) from the best performing model for algae and four invertebrate taxa (see Table 1). Parameters were estimated by fitting invertebrate drift concentrations (C, # m^{-3}), benthic densities (B, # m^{-2}) and discharge (Q, m^3 s^{-1}) collected from the Colorado River downstream of Glen Canyon Dam to the following equation: $C \propto B^f Q^g$. Values in parentheses represent the confidence interval of the estimate based on two standard errors. In cases where model selection indicated the value of f is 1 (all taxa except *Simulium*), we do not have an associated confidence interval because benthic density was an offset in these models. We were unable to estimate the parameter f for algae because we did not estimate benthic algal biomass during our study. Drift concentrations for day and night for each taxon were estimated using the parameter estimates from each of the best performing models at the mean discharge of our drift sampling events (317 m^3 s^{-1}) and at a standard benthic density for all taxa (3000 m^{-2}). Note that estimated drift concentrations for Chironomidae do not vary with time of day, because the best performing models did not include a time of day parameter

Taxa	Day (# m^{-3})	Night (# m^{-3})	f (Benthic density)	g (Discharge)
Filamentous algae	NA	NA	NA	2.1 (CI: 1.9, 2.3)
Gammarus lacustris	0.06	0.16	1.0	3.9 (CI: 3.3, 4.5)
Potamopyrgus antipodarum	0.89	0.59	1.0	4.1 (CI: 3.9, 4.3)
Simulium Arcticum	0.25	0.39	0.48 (CI: 0.36, 0.60)	−2.9 (CI: −3.2, −2.6)
Chironomidae	1.3	1.3	1.0	0.96 (CI: 0.88, 1.04)

density estimate (# m^{-2}) for that sampling day by the area of the segment between our drift sampling location and Glen Canyon Dam (length = 2.54×10^4 m, width = 1.28×10^2 m, area = 3.25×10^6 m^2). We express drift export as a percentage of total benthic invertebrate abundance in the Glen Canyon segment. Although mean invertebrate drift distances are almost certainly shorter than the 25.4-km segment for which we estimated export, estimating export over a shorter segment would have required estimates of invertebrate drift concentrations at the upstream end of the segment; estimates of invertebrate drift concentrations immediately downstream of Glen Canyon Dam were not necessary to estimate export for the entire Glen Canyon segment, because this location represents a boundary condition where drift concentrations are zero.

Study area

We characterised benthic invertebrate density, and algal and invertebrate drift, in the 25.4-km tailwater downstream of Glen Canyon Dam (Fig. 1). We sampled benthic invertebrates over an 8-km reach in the downstream half of the tailwater (Fig. 1). We estimated algal and invertebrate drift at the downstream end of this reach, near Lees Ferry and proximate to a US Geological Survey gaging station (see Fig. 1). River discharge originates from the hypolimnion of Lake Powell reservoir, and water temperature at the downstream end of the reach is relatively cold throughout the year (mean daily: 10.4 °C; based on November 2006–June 2009) with low diel fluctuation (0.5–1 °C; http://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09380000). Because there are no perennial tributaries in the entire tailwater, the water is clear for all but a few days of the year. River width and thalweg depth average *c.* 129 and 4 m, respectively, at the mean annual discharge of 325 m^3 s^{-1} (Grams, Schmidt & Topping, 2007). Bed substratum consists of cobble–gravel bars, variably-sized talus, cliff faces and deep pools (>10 m depth). Cobble–gravel bars are heavily armoured and immobile except during unusually high dam releases (Grams *et al.*, 2007). Pools and other sandy habitats support rooted vascular macrophytes (e.g. *Potamogeton* spp., *Chara* spp.), whereas filamentous algae, predominantly *Cladophora glomerata*, dominates cobble–gravel bars throughout most of the year (Angradi & Kubly, 1993). Based on underwater video transects, habitat proportions in the Glen Canyon segment are 52% sandy substratum, 27% cobble–gravel bars and 21% cliff and talus (see Cross *et al.*, 2010 for details). Because hydropeaking has occurred more or less continuously since closure of Glen Canyon Dam in 1963 (Topping, Schmidt & Vierra, 2003), invertebrate populations may be adapted to daily flow variation.

During our 2.5-yr study, two flow experiments were conducted: (i) a controlled flood was released from Glen Canyon Dam from 5–9 March 2008, and (ii) steady flows without hydropeaking were released in September and October 2008 (see Fig. 2). Both flow treatments were conducted as part of an ongoing adaptive management experimentation (http://www.gcdamp.gov/). Discharge during the controlled flood was sustained at 1207 m^3 s^{-1} for 60 h, and large portions of the benthos including sand and smaller gravels were mobilised (Melis, Korman & Kennedy, 2012). The controlled flood reduced benthic macrophyte and periphyton biomass (Rosi-Marshall *et al.*, 2010) and led to large changes in benthic invertebrate composition and assemblage structure (Cross *et al.*, 2011). Although we collected invertebrate drift measurements during the controlled

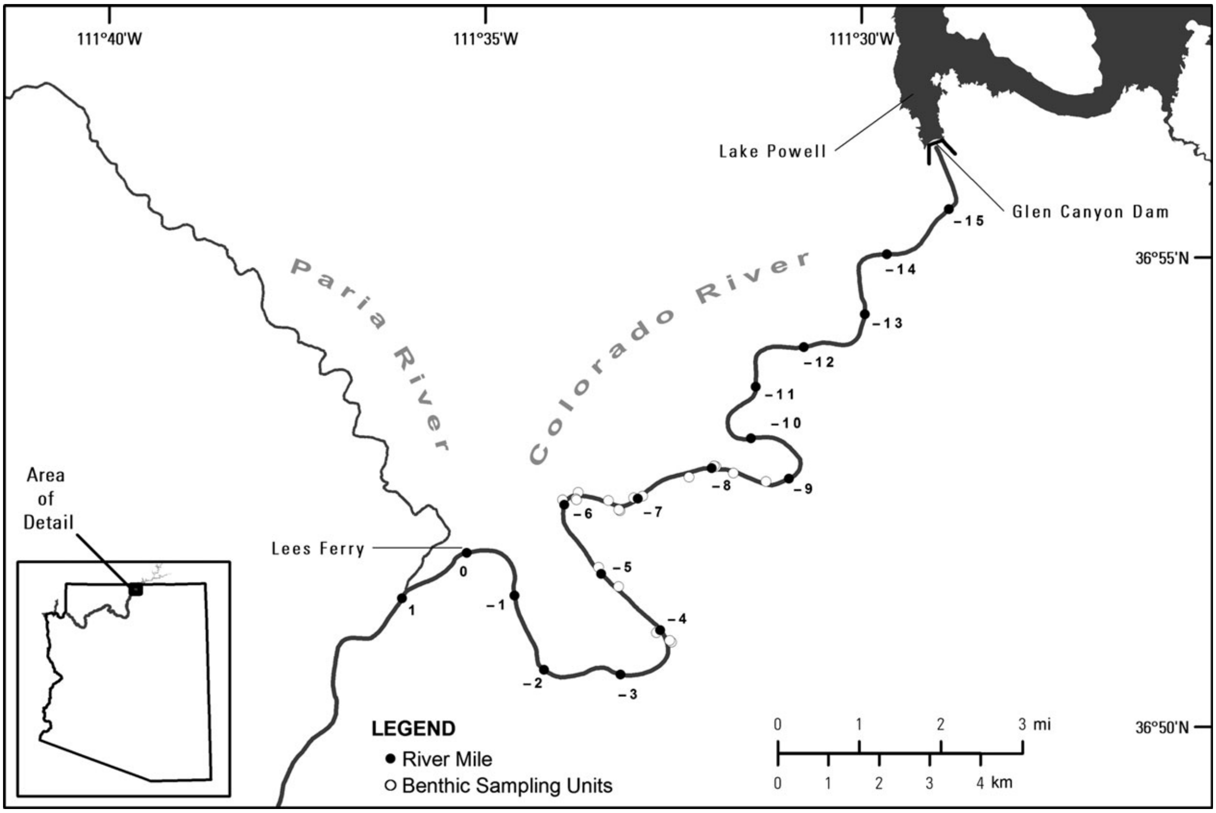

Fig. 1 Map showing the tailwater downstream of Glen Canyon Dam including the 20 benthic sampling units that were upstream of the drift sampling location. By convention, river mile zero is at Lees Ferry and river miles decrease upstream towards Glen Canyon Dam. Drift sampling occurred at river mile zero and proximate to a US Geological Survey gaging station (http://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09380000).

flood, we do not include those data in our modelling of discharge–drift relations because bed mobilisation occurred during these high dam releases. Further, it was not safe to measure benthic invertebrate density during the controlled flood, which made it impossible to evaluate possible mechanisms (i.e. changes in behaviour versus reductions in benthic supply) underlying hysteresis in these data. We do, however, include data from the September and October 2008 steady flow experiment in our analysis, because the underlying processes governing invertebrate drift were expected to be the same as during normal hydropeaking operations that occurred for the majority of our 2.5-year study (Fig. 2).

Drift and benthic sampling

We quantified algal drift monthly from November 2006–September 2007 based on the methods described by McKinney, Ayers & Rogers (1999). We collected drift samples in the channel centre from a boat tied to a navigation buoy. Each drift sampling event consisted of 3–5 individual collections that were each 5 min in duration. We conducted 3–7 sampling events from early morning to early evening to capture the full range of discharges occurring on that day. We focused our sampling on the daily increases in discharge that occur from early morning through evening in the reach, because accidental drift entry is most likely to occur on the ascending limb of the daily hydrograph as flow strength is increasing. We used a coarse mesh drift net (1-mm mesh, circular net with a 51-cm-diameter opening, 3 : 1 ratio of opening diameter to length) to quantify algal drift, because initial sampling indicated that the finer mesh nets needed to characterise drift of small benthic invertebrates also captured an abundance of zooplankton. Zooplankton in the reach are derived from Lake Powell and are not from the benthos. Further, zooplankton biomass can exceed drifting algal biomass during the winter, coincident with destratification of Lake Powell (Vernieu, Hueftle & Gloss, 2005).

We collected depth-integrated drift samples by slowly raising and lowering the drift net throughout the water column using a hand-powered winch (A-reel, Rickly Hydrological Company, Columbus, Ohio; http://www.rickly.com/). We attached a 1-m-long stainless steel

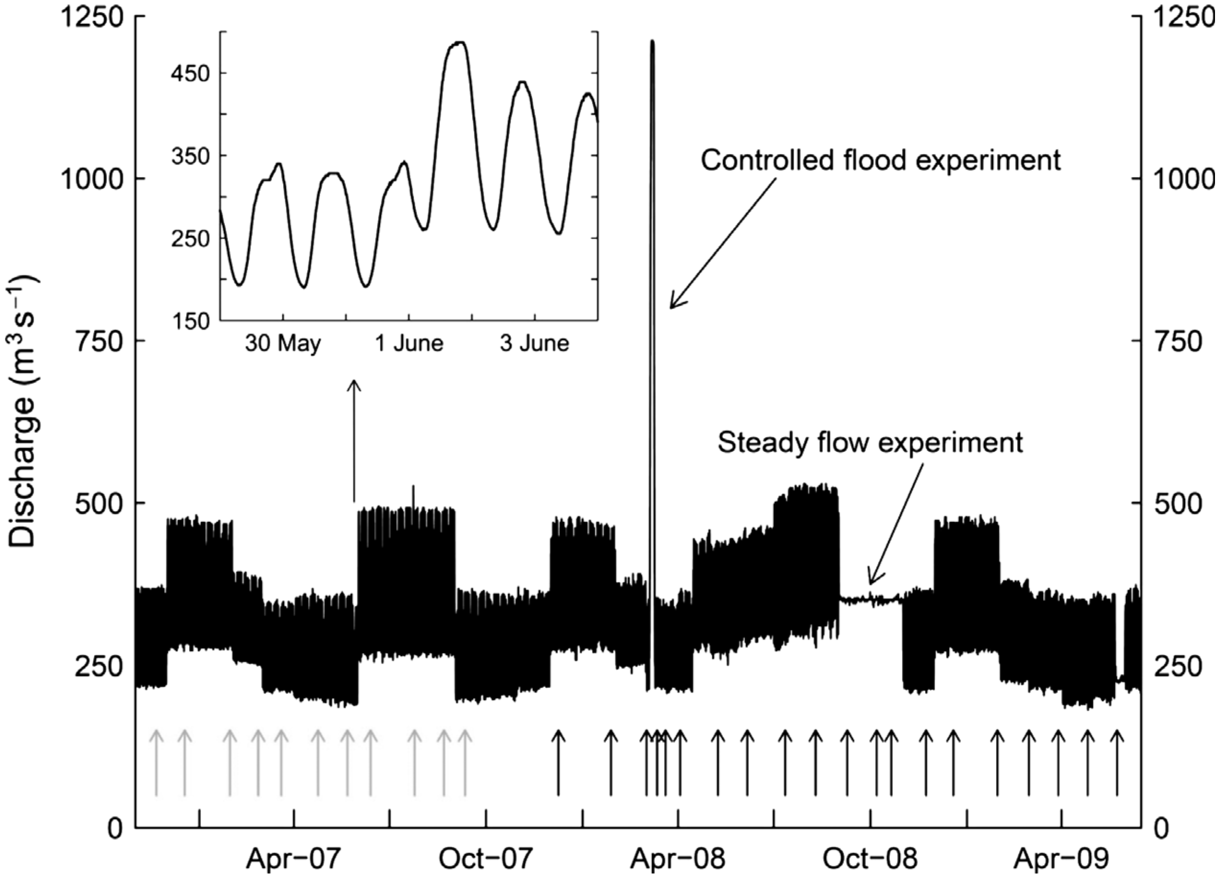

Fig. 2 Instantaneous discharge for the Colorado River downstream from Glen Canyon Dam. Subdaily variation in discharge associated with hydropower production, also known as hydropeaking, occurred for the majority of our 2.5-year study and caused the banding in this graph; inset panel shows daily flow variation associated with hydropeaking and the large changes in discharge that can occur across months. Two adaptive management flow experiments also occurred during our study: (i) a controlled flood was released from 5–9 March 2008 and (ii) steady flows without hydropeaking occurred from September through October of 2008. Grey arrows near the *x*-axis mark the 11 dates when algal drift sampling occurred, while black arrows mark the 20 dates when measurements of benthic and invertebrate drift occurred.

chain to the end of the winch cable, as well as a 40-kg lead sounding weight to the end of the chain to prevent nets from being swept downstream by the current. We clipped the net halfway down the chain (0.5 m above the sounding weight), and we kept the sounding weight 0.5 m above the bed to ensure that benthic material did not become disturbed by the weight and captured by the net. We estimated the volume of water sampled by the net using a flow meter positioned at the mouth of the net (model 2030R, General Oceanics, Miami, Florida; http://www.generaloceanics.com/). Discharge at the time of each drift collection was that measured at the nearby gaging station (http://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09380000). We kept samples on ice until they were processed in the laboratory (<48 h). In the laboratory, we placed entire samples into pre-weighed and pre-ashed aluminium pie tins and determined ash-free dry mass by combustion at 550 °C. Samples were not rinsed prior to processing.

We quantified invertebrate drift approximately monthly from December 2007 to May 2009 (i.e. 20 sampling days over 18 months). Collection methods were identical to algal methods, except we used a 0.25-mm mesh net to capture small invertebrates such as Chironomidae. Additionally, invertebrate drift nets had a 5 : 1 ratio of length to opening diameter to prevent clogging and backpressure associated with the smaller mesh size. We collected triplicate drift samples 3–5 different times throughout the day to encompass a wide range of discharges associated with hydropeaking. Sample collection was limited to 5 min, because initial sampling demonstrated that these fine mesh nets begin clogging after approximately 10 min of sampling. We preserved samples in the field using 95% ethanol. Because catches for even the dominant taxa were sometimes low to zero in an individual sample, we aggregated these triplicate samples in our analyses by summing both the counts and the volume sampled. As a result, sample sizes for the aggregated samples were relatively small for night-time (i.e. $n = 11$ versus 75 for daytime).

We measured benthic invertebrate density in the reach upstream from drift collections and concurrent with monthly drift collections. We estimated benthic invertebrate densities in the Glen Canyon reach by collecting samples from all dominant habitat types in the reach, proportional to their relative bed areas (i.e. $n = 10$ samples per month for sand, $n = 5$ for talus/cliff and $n = 5$ for cobble; see Cross *et al.*, 2011). We used three different devices to sample these different habitats (i.e. dredge for sand, suction sampler for talus and cliff and Hess sampler for cobble), and all samplers had the same diameter mesh as our invertebrate drift net (0.25 mm). Samples from hard substrata (i.e. talus, cliff and cobble) were collected in wadeable nearshore environments, because early investigations using SCUBA revealed that invertebrate densities did not vary strongly with depth. We conducted benthic sampling in the early morning hours when discharge was at a daily minimum to ensure samples were collected from the permanently wetted zone (Blinn *et al.*, 1995). We preserved samples in the field using 95% ethanol.

In the laboratory, invertebrate drift and benthic samples were processed similarly. We rinsed each sample onto nested sieves (pore sizes 1 and 0.25 mm), and the material retained on each sieve was elutriated to separate organic from inorganic material. We counted all invertebrates from the large fraction (>1 mm) at 10× magnification. The large fraction from prohibitively large benthic samples was subsampled using a device modelled after the Folsom Plankton Splitter (Wildlife Supply Company, Yulee, Florida; http://www.wildco.com/). To subsample the small fraction of benthic samples, we put the organic material (i.e. <1 and >0.25 mm) into a known volume of water, suspended it in a modified Imhoff cone (Ward's Science, Rochester, New York; https://wardsci.com/) with forced air and then subsampled the suspension with a 60-mL plastic syringe. We removed invertebrates from samples or subsamples at 15× magnification and counted all invertebrates. The number of invertebrates in drift samples was smaller than benthic samples, and thus, drift samples were never subsampled. We used the mean habitat-weighted benthic density estimate for each sampling day in our analyses (see Cross *et al.*, 2011).

Results

Algal drift

As anticipated, the algal model that included discharge alone was the highest performing model considered (Table 1). Including discharge as a fixed effect reduced the BIC relative to models that did not include discharge (i.e. BIC decreased by *c.* 54–59; see Table 1). Including time of day decreased the performance of algal models. Specifically, the algal model that included time of day as the only fixed effect performed more poorly than the model that just estimated a random effect for each sampling date (Table 1).

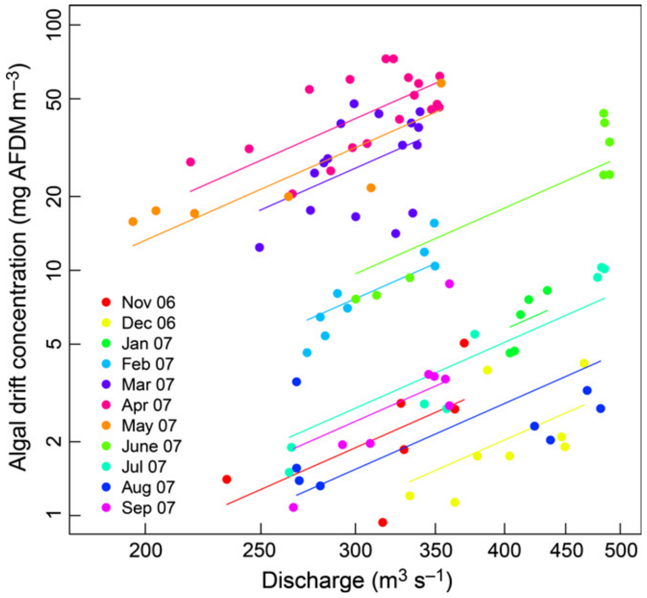

Fig. 3 Log–log plot showing the relation between discharge (m^3 s^{-1}) and algal drift concentrations (>1 mm, mg AFDM m^{-3}) for the Colorado River downstream of Glen Canyon Dam. Each point represents an individual drift collection, and lines represent the predicted relation between discharge and algal drift based on fitting of these data to a power-law relation using mixed effects models, where discharge was a fixed effect and sampling date was a random effect. Drift of coarse particulate organic matter varies proportional to discharge raised to the second power (2.1, confidence interval of 1.9–2.3).

Algal concentrations were proportional to discharge raised to the second power (2.1, standard error of 0.23; Fig. 3). There was substantial variation in algal concentrations among dates, with the largest values occurring in spring (mean from March and April = 38.6 mg AFDM m^{-3}) and the smallest values occurring in the autumn and winter (mean from November and December = 2.2 mg AFDM m^{-3}).

Benthic densities and drift concentrations

Potamopyrgus dominated benthic substrata during our study, with median habitat-weighted densities of 26 000 m^{-2} (See Figure S1 of Supporting Information). Benthic density of *Gammarus* and *Simulium* was more than an order of magnitude smaller, with median values of 1500 and 570 m^{-2}, respectively, while benthic density of Chironomidae was intermediate (median of 7400 m^{-2}).

There was substantial variation in habitat-weighted benthic densities among sampling dates. Benthic densities of *Simulium* varied by a factor of 1000 among dates (minimum and maximum of 2.2 and 3012 m^{-2}, respectively). Variation in benthic densities for the other three taxa was more modest, but still spanned one to two orders of magnitude (i.e. 10- to 100-fold variation; Figure S1).

Chironomidae had the largest average drift concentrations of any taxon during our study (median and mean of 0.51 and 3.2 m^{-3}, respectively). Drift concentrations for *Potamopyrgus* were also relatively large (median and mean of 0.28 and 2.3, respectively). Drift concentrations for *Gammarus* were the smallest for any taxa and more than an order of magnitude less than Chironomidae (median and mean of 0.043 and 0.11 m^{-3}, respectively). Drift concentrations for *Simulium* were intermediate (median and mean of 0.16 and 0.30 m^{-3}, respectively).

Testing hypotheses

The best performing model for each taxon included a fixed effect for discharge and benthic densities as either an offset (i.e. with exponents equal to 1) or with an estimated exponent (see Hypotheses 1 and 3; Table 1). The change in BIC for models that included discharge relative to models that did not include discharge was substantial; BIC decreased by 100 –1000s when discharge was included, depending on the taxa (Table 1). Model selection also indicated that the empirical relation between discharge and invertebrate drift was fundamentally different than for discharge and algal drift (Hypothesis 2). Specifically, the BIC for invertebrate models that fixed the power on discharge at 2.1, which was the power on discharge for the algal relation, was larger relative to the BIC for comparable models where the power on discharge was estimated (BIC increased by 100–1000s for all taxa except *Gammarus*, which had a more modest increase of 31 BIC; Table 1).

The relation between discharge and drift varied strongly among invertebrate taxa (Table 2; Figs 4a and S2). Two taxa, *Gammarus* and *Potamopyrgus*, had estimated powers that were much greater than one (Hypothesis 1) and similar to estimates for sediment in this river (3.9 and 4.1, respectively; see Table 2 and Fig. 4a). Another taxon, Chironomidae, had a power that was 1, suggesting a linear relation between drift concentrations and discharge (Table 2 and Fig. 4a). The fourth taxon, *Simulium*, had a power much <0 (−2.9; Table 2), indicating that drift concentrations actually decreased as a function of discharge (Figs 4a and S2).

The best performing models for three taxa (Chironomidae, *Gammarus* and *Potamopyrgus*) indicated that drift concentrations increased proportional to benthic density

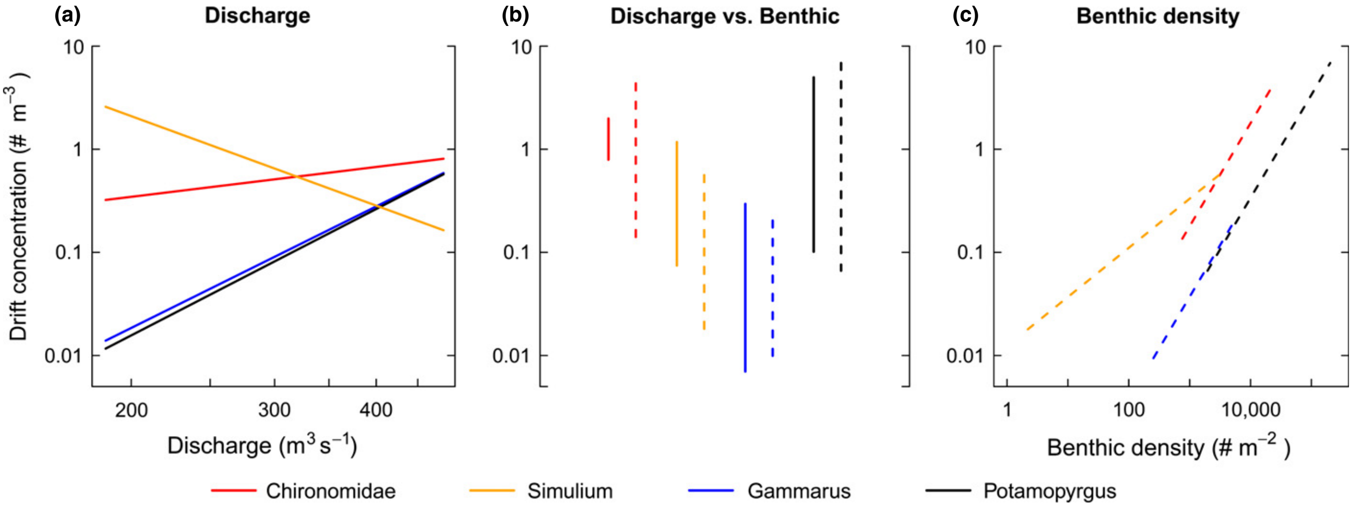

Fig. 4 Graphs showing predicted drift concentrations for four different taxa in the Colorado River downstream from Glen Canyon Dam, AZ. Panel *a* shows predicted drift concentrations at a standard benthic density for all taxa (3000 m^{-2}) across the range of discharges observed in our study (180–486 m^3 s^{-1}). Panel *c* shows predicted drift concentrations across the range of observed benthic densities for each taxon, and at the average discharge (317 m^3 s^{-1}), during the study. Panel *b* shows the total variation in drift concentrations observed during this study that can be attributed to variation in discharge (solid lines) versus benthic density (dashed lines). Note the log *y*-axis for all plots, and the log *x*-axis for panels *a* and *c*.

Table 3 Results of multilevel pseudo-R^2 analysis. Individual fixed effects were removed from the best performing model for each taxon to identify how much of the variation in drift concentrations that different fixed effects were explaining among samples versus among dates. Bold values indicate the fixed effect that, when removed, leads to the largest reduction in pseudo-R^2 among samples or among dates. Removing discharge from models had the greatest effect on pseudo-R^2 at the among-sample level for all taxa except Chironomidae. In contrast, removing benthic density from models had the greatest effect on pseudo-R^2 at the among-date level for all taxa

Taxa	Variation among	Pseudo-R^2 value from best model	Pseudo-R^2 value from model without: Discharge	Benthic density	Time of day
Chironomidae	Samples	0.77	0.77	0.77	NA
	Dates	0.51	0.52	**0.02**	NA
Simulium	Samples	0.80	**0.50**	0.80	0.75
	Dates	0.35	0.42	**−0.15**	0.36
Potamopyrgus	Samples	0.89	**0.65**	0.89	0.88
	Dates	0.46	0.56	**−0.04**	0.47
Gammarus	Samples	0.87	**0.63**	0.87	0.76
	Dates	0.64	0.76	**0.30**	0.53

(Hypothesis 3), whereas the best performing model for *Simulium* estimated an exponent less than one for the benthic–drift relation (0.48; Table 2 and Fig. 4c). The baseline of the benthic–drift relation for *Simulium* and Chironomidae was much larger than for *Gammarus* and *Potamopyrgus* (Fig. 4c). This means that for a given benthic density (e.g. 3000 m^{-2}; Fig. 4c), drift concentrations of Chironomidae and *Simulium* were considerably larger than for *Gammarus* and *Potamopyrgus*.

Including time of day as a fixed effect improved model fits for *Gammarus, Simulium* and *Potamopyrgus* (Tables 1 and 2). Drift concentrations for *Gammarus* and *Simulium* were largest during the night, whereas drift concentrations for *Potamopyrgus* were largest during the day (Table 2). In contrast, drift concentrations of Chironomidae did not vary as a function of daylight.

For all taxa but Chironomidae, the powers associated with discharge and benthic densities suggested both were responsible for similar variation in drift concentration over the range of observed variation in these controls (Fig. 4b). Multilevel pseudo-R^2 indicated that discharge was the primary control of among-sample variation in drift concentrations, while benthic density was the primary control of among-date variation in drift concentrations (Table 3). Specifically, pseudo-R^2 values for among-sample variation were smaller when discharge was eliminated from models, whereas pseudo-R^2 values for among-date variation were smaller when benthic density was eliminated from models. Benthic density, an intrinsic factor, varied 10- to 1000-fold among sampling dates during our study, depending on the taxa. This variation in the supply of benthic invertebrates controls the baseline drift concentrations (Fig. 4b,c). Although discharge only varied by a factor of two within days, and a factor of three among sampling events, the large power on the discharge–drift relations for individual taxa (−2.8, 1, 3.9, 4.1) offsets

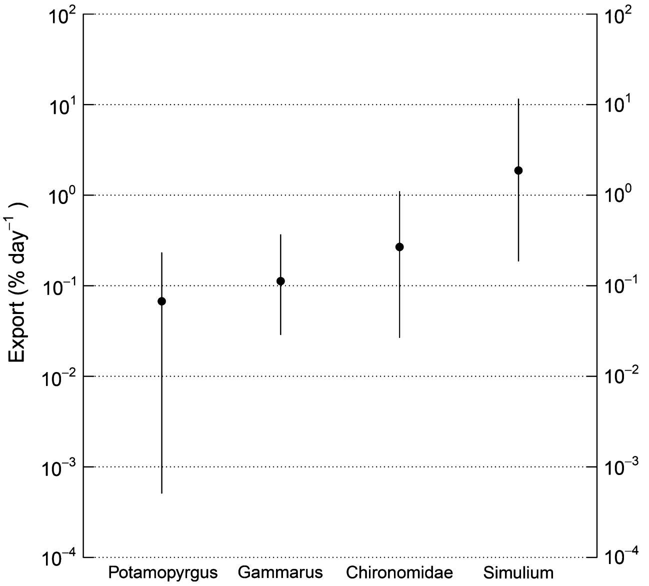

Fig. 5 Graph showing the mean (black circle) and range (lines) of daily drift rates (# d^{-1}) for four invertebrate taxa, expressed as a percentage of invertebrate population abundance in the Glen Canyon tailwater segment on that day (n = 20 different daily estimates). Total drift export from the tailwater segment was estimated on the days when drift sampling occurred using the instantaneous discharge record measured at the Lees Ferry gage on that day (15-minute sampling interval; US Geological Survey gage 09380000), times of sunrise and sunset from nearby Page, AZ, and the parameter estimates (benthic density, time of day and discharge) and random effects from the best performing model for each taxon (see Table 2). Invertebrate population abundance between our drift sampling location and Glen Canyon Dam was estimated by multiplying the habitat-weighted benthic density estimate (# m^{-2}) for that sampling event by the area of this segment (3.25 10^6 m^2).

the smaller amount of variation observed in this extrinsic control, relative to the much larger amount of variation observed in benthic density.

Daily export of Chironomidae and *Simulium* was relatively high (Fig. 5), particularly during summer 2008, when hydropeaking and discharge were at a maximum. Specifically, we estimated in 2008 that 1.1% d^{-1} of benthic Chironomidae in the upstream segment were exported in June, 1.0% d^{-1} were exported in July and 0.55% d^{-1} were exported in August. Thus, during this 3-month period, over 80% of benthic Chironomidae in the entire Glen Canyon segment were exported, assuming that there was no reproduction offsetting this export. Export estimates for *Simulium* (mean and median of 1.9 and 0.71% d^{-1}, respectively) were considerably larger than for Chironomidae (mean and median of 0.27 and 0.15% d^{-1}, respectively; Fig. 5). One of the *Simulium* export estimates was implausibly high (150% d^{-1}) and excluded from our analyses; this high estimate for *Simulium* was associated with the lowest benthic density estimate during the study (2.2 m^{-2}, on 29 March 2009). Benthic export for *Gammarus* (mean and median of 0.11 and 0.10% d^{-1}, respectively) and *Potamopyrgus* (mean and median of 0.067 and 0.052% d^{-1}, respectively) on a given day was generally less than for Chironomidae and *Simulium*, and the maximum export for *Gammarus* and *Potamopyrgus* was 0.37 and 0.23% d^{-1}, respectively (Fig. 5).

Discussion

Our study demonstrates that the concentration of drifting invertebrates in the Colorado River downstream of Glen Canyon Dam is jointly controlled by the magnitude of the discharge and by the density of invertebrates on the bed upstream from the site where drift is measured. Algal drift increased proportional to discharge raised to the second power. However, the functional relation between discharge and drift concentrations of four common invertebrate taxa was fundamentally different, suggesting that algal shearing was not the primary mechanism by which accidental drift of invertebrates occurred. Whereas daily variation in discharge associated with hydropeaking led to proportional changes in the drift of Chironomidae, the concentration of *Gammarus* and *Potamopyrgus* was more strongly affected, with a doubling of discharge leading to a roughly 16-fold increase in drift concentrations. Drift concentrations for these three taxa, all of which are mobile collector-gatherers, were proportional to benthic density, which supports the inference that the positive discharge–drift relation we documented occurred because of an increase in accidental drift entry associated with increases in benthic scour. Drift concentrations of *Simulium* were also positively related to benthic density, but the power was less than one. This may reflect a tendency to drift during certain life stages when benthic densities are not high. Drift concentrations for *Simulium* also decreased as a function of discharge, which supports the inference that drift of sessile taxa like *Simulium* that are adapted to high-velocity habitats is less likely to occur because of accidental entrainment and more likely to occur because of behavioural processes.

Conceptual framework and hypotheses

The conceptual framework we developed for modelling invertebrate drift was derived from studies of sediment transport and represents a passive entrainment model (Hart & Finelli, 1999). From this passive entrainment model, we developed three core hypotheses specific to invertebrate drift. Using model selection and high-resolution data sets of benthic density and drift concentrations from the Colorado River, we found support for two of these passive entrainment hypotheses. Specifically, model selection indicated that drift concentrations for two taxa (*Gammarus* and *Potamopyrgus*) were related to discharge taken to a power much >1 (Hypothesis 1), and drift concentrations for three taxa (*Gammarus*, *Potamopyrgus* and Chironomidae) increased proportional to benthic density (Hypothesis 3). Thus, passive entrainment models are a useful starting point for developing models of invertebrate drift, particularly in large rivers where flow strength is high, and a large proportion of invertebrate drift may therefore be accidental.

Algal shearing does not appear to be a primary mechanism of accidental drift entry for any of the four invertebrate taxa we modelled (Hypothesis 2). We found that algal drift varied with discharge raised to the second power, but the functional relation between discharge and drift concentrations for four important invertebrate taxa was fundamentally different (i.e. discharge raised to −2.8, 1, 3.9 and 4.1). It is worth noting that our test of the algal shearing hypothesis implicitly assumes that benthic invertebrate numbers are linearly proportional to benthic algal mass, which is a reasonable assumption in Glen Canyon, but may not hold in other rivers. Specifically, based on habitat choice experiments conducted in this river segment (Shannon, Blinn & Stevens, 1994), we reasoned that benthic invertebrate densities would be proportional to benthic algal surface area. Further, because increases in *Cladophora* spp. mass occur due to more and/or longer filaments, as opposed to increases in the diameter of filaments, algal surface area will increase proportional to algal mass. However, if the dominant vegetation in a river changes shape or geometry as it grows, then surface area will not increase proportional to mass, and it would be necessary to change expectations accordingly.

Our conceptual framework and modelling approach also allowed us to parse out the relative influence that discharge and benthic densities have on invertebrate drift concentrations in this river segment. Although functional relations between these two controls and invertebrate drift concentrations did not always match predictions, we suggest these deviations arose because the predictions were based on purely physical principals; that is, invertebrate behaviour and life-history strategy, particularly in the case of *Simulium*, created novel functional relations (i.e. a nonlinear benthic–drift relation, negative power on discharge–drift relation) that could not have been predicted based on passive entrainment models. Thus, we believe our conceptual framework and modelling approach are appropriate for use in future studies of invertebrate drift, even though they are derived from studies of sediment transport.

Empirical relations

The empirical relation between discharge and algal drift matched our predictions for entrainment and transport of relatively passive benthic material. Specifically, algal drift varied with discharge raised to the second power, and this power-law relation is similar to that observed in studies of sediment transport (Garcia & Parker, 1991). Including time of day in the algal model actually reduced its performance. Thus, potential confounding of discharge with time of day downstream from Glen Canyon Dam does not appear to be a concern relative to describing empirical relations between discharge and benthic material.

The empirical relation between discharge and invertebrate drift varied strongly among the four taxa we evaluated. Drift concentrations of *Gammarus* and *Potamopyrgus* increased with discharge raised to the fourth power, which is consistent with a passive entrainment model and empirical relations between discharge and suspended sediment for the Colorado River (Wright *et al.*, 2010). Drift concentrations of Chironomidae increased linearly with discharge, which is also consistent with a passive entrainment model, but the rate of increase (linear) differs from empirical relations between discharge and suspended sediment for this river segment. In contrast, drift of *Simulium* varied with discharge raised to a negative power (-2.8), and this negative relation between flow strength and drift concentration differs from any predictions one might make based on passive entrainment models or purely physical principles. *Simulium* larvae are unlikely to accidentally enter the drift because of increases in flow strength. Rather, *Simulium* larvae are more likely to intentionally enter the drift as flow strength decreases, because smaller discharges represent a decrease in food delivery rates and habitat quality for these filter-feeding invertebrates (Fonseca & Hart, 1996). Thus, discharge is an important control on drift concentrations of invertebrates in the Colorado River, but invertebrate behaviour and life-history strategy (e.g. sessile filter-feeder versus mobile collector-gatherer) play a role in determining the functional nature (i.e. negative or positive) of the discharge–drift relation.

Drift concentrations for all four taxa were positively related to benthic density upstream of the site where drift was measured, but, similar to discharge, the benthic–drift relation for *Simulium* did match predictions. Drift concentrations of Chironomidae, *Gammarus* and *Potamopyrgus* increased proportional to benthic densities, which is consistent with a passive entrainment model and empirical relations between bed sediment supply and suspended sediment concentration (Garcia & Parker, 1991). In contrast, drift concentrations of *Simulium* increased with benthic density at a rate that was <1 : 1; that is, drift of *Simulium* at the time of our study appeared to be density dependent. In a laboratory study, Fonseca & Hart (1996) came to similar conclusions – drift of *S. vittatum* was density dependent and inversely related to water velocity. The ability of *Simulium* to intentionally vary drift entry rates in response to both extrinsic (e.g. discharge, water velocity, time of day) and intrinsic factors (e.g. population density) can create relatively novel empirical relations that have only rarely been documented in field studies of invertebrate drift (Brittain & Eikeland, 1988; Hart & Finelli, 1999).

Discharge and benthic densities are primary controls on invertebrate drift in the Colorado River, but these controls operate at different timescales. Twofold daily flow variation associated with hydropeaking causes linear increases (Chironomidae), exponential increases (*Gammarus* and *Potamopyrgus*) and exponential decreases (*Simulium*) in drift concentrations. Thus, discharge is the primary control on invertebrate drift concentrations over short timescales (hours to days). In contrast, benthic density controls drift concentrations over longer timescales (weeks to months), because drift concentrations for all taxa were positively related to benthic densities, and there was 10- to 1000-fold variation in benthic densities among sampling dates. Simply put, if benthic invertebrate density is small, invertebrate drift concentrations will also be small, irrespective of the flow regime.

Management implications

Natural and artificial floods can cause short- (McMullen & Lytle, 2012) and long-term changes (Cross *et al.*, 2011; Robinson, 2012) in the structure and composition of invertebrate assemblages. Specifically, pulsed and recurring disturbances often lead to invertebrate assemblages dominated by fast-growing taxa such as Chironomidae and Simuliidae, with reductions in slower-growing taxa such as gastropods and amphipod crustaceans (Cross *et al.*, 2011; Robinson, 2012). For example, the 60-hour controlled flood released from Glen Canyon Dam in 2008 led to significant decreases in the abundance and biomass of *Potamopyrgus* and *Gammarus* and significant increases in the abundance and biomass of Chironomidae and *Simulium* (Cross *et al.*, 2011). Our study demonstrates that these types of flood-mediated changes could have large and persistent effects on food availability for drift-feeding fishes, because invertebrate assemblages shift towards dominance by taxa that are more prone to drifting.

Although there are a variety of mechanisms or causal pathways whereby hydropeaking can affect invertebrate populations (Olden & Naiman, 2010), negative feedbacks on benthic populations associated with accidental drift entry are among the most obvious and direct mechanisms (Hart & Finelli, 1999). Negative feedbacks can occur if a positive relation exists between benthic and drifting invertebrates. We documented a positive relation between benthic densities and drift concentrations for all four taxa we evaluated. Export for two of these taxa, *Simulium* and Chironomidae, was high, sometimes exceeding 1% d^{-1}, particularly during the summer of 2008 when discharge and hydropeaking were at a maximum. Because Glen Canyon Dam imposes an upstream boundary condition, all losses of benthic invertebrates from Glen Canyon are necessarily produced in this reach. Thus, growth and reproduction would need to be extremely high to completely offset these daily losses and, indeed, benthic densities and drift concentrations for both Chironomidae and *Simulium* declined during the summer 2008, concomitant with these high estimates of export (data not shown). However, identifying whether negative feedbacks were occurring was not possible in this study, because we lacked estimates of other important losses (i.e. trout consumption and emergence) and renewals (i.e. egg deposition and recolonisation following emergence, upstream movements by adults and larvae).

Although drift concentrations of *Gammarus* and *Potamopyrgus* increased with discharge raised to the fourth power, the small absolute value of the benthic–drift relation for these taxa suggests they will be less susceptible to negative feedbacks associated with high rates of export relative to Chironomidae and *Simulium*. Amphipod crustaceans such as *Gammarus*, and *Potamopyrgus*, the New Zealand mudsnail, dominate benthic habitats in tailwaters globally (Alonso & Castro-Diez, 2008). Our study demonstrates that the ability of these non-native invertebrates to minimise drift entry is one causal mechanism underlying their dominance in systems with highly altered flow regimes.

Simulium and Chironomidae, the only two insect taxa present in the Glen Canyon Dam tailwater, had high baseline drift concentrations and are therefore readily available to drift-feeding fishes (Rader, 1997; Cross *et al.*, 2011). High baseline drift concentrations for these insects also mean they will be susceptible to high rates of export from tailwaters, even in the absence of unusually large dam releases such as controlled floods. Aquatic insects are generally more abundant in the drift than non-insect taxa (Rader, 1997), because drift is a fundamental aspect of insects' overall life history; drift allows for rapid recolonisation of benthic substrata by larvae following emergence and egg deposition by adults. *Simulium* and Chironomidae often have high growth rates and short generation times (Huryn & Wallace, 2000), which may allow these taxa to recover rapidly following periods of high fish predation or downstream export from a tailwater. Insect taxa that readily drift (i.e. Ephemeroptera; Rader, 1997) are often extirpated from regulated rivers (Brittain & Saltveit, 1989; Vinson, 2001), and Ephemeroptera (mayflies) are conspicuously absent from the Colorado River downstream of Glen Canyon Dam (Cross *et al.*, 2013). Although thermal alteration has played a major role in driving structural changes in invertebrate assemblages of regulated rivers (Brittain & Saltveit, 1989; Olden & Naiman, 2010), large structural changes including the local extirpation of Ephemeroptera have been documented in regulated rivers that have minimally altered (Brittain & Saltveit, 1989) or partially restored thermal regimes (Vinson, 2001). Our study demonstrates that the propensity for insect taxa to drift, and for non-insect taxa to avoid drifting, may be an important causal mechanism underlying structural changes in the invertebrate assemblages of rivers that have experienced a high degree of flow alteration.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Graph showing the relation between drift concentration and benthic density.

Figure S2. Graphs showing drift concentrations as a function of discharge.

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