

Species traits and channel architecture mediate flow disturbance impacts on invertebrate drift

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SUMMARY

1. Pulsed flow disturbances strongly influence invertebrate drift in lotic ecosystems. However, drift-flow relationships are often context dependent and non-intuitive, suggesting that local abiotic and biotic conditions mediate the impacts of flow on the physical and behavioural drivers of drift entry. Two factors may be particularly important: physical channel architecture, which modulates how flow influences velocity and habitat area; and species traits, which determine behavioural responses to flow and susceptibility to passive entrainment.

2. We examined how channel architecture and species traits (e.g. mobility, body size, and dislodgement susceptibility) mediated the effects of flow on bulk drift abundance and taxa-specific per capita drift rates (the rate of emigration from the benthos). In complementary experiments, we reduced and increased flows in stream mesocosms with contrasting cross-sectional channel profiles: concave channels, where habitat area contracted and expanded with altered flow but velocity remained relatively constant; and flat channels, which maintained constant habitat area but experienced greater changes in velocity.

3. Total drift concentration increased following flow reductions and decreased following flow increases whereas drift flux (the total number drifting) showed the opposite pattern. Channel architecture did not influence drift during flow reductions, but during flow increases drift flux and concentration were amplified in flat channels that experienced larger increases in velocity and shear stress.

4. Contrasting responses among individual taxa to flow manipulation were explained by variation in mobility (swimming and crawling ability) and body shape (susceptibility to drag). Per capita drift rates for the most mobile taxa increased *c.* 10% under flow reduction, indicating a behavioural response, whereas drift of other taxa declined. Per capita drift increased for all taxa following elevated flow but by the largest magnitude in taxa with body shapes that experience more drag, suggesting passive dislodgement.

5. Our results imply that: (i) stream channel architecture can modify the impacts of flow increases on stream invertebrates; and (ii) invertebrate taxa vary in their vulnerability and behavioural responses to flow disturbance. Together these inferences clarify some of the previously unexplained context-dependent responses of drift to flow disturbances.

Keywords: invertebrate drift, habitat, disturbance, context dependence, traits, channel profile

Introduction

Disturbances induced by physical forces (e.g. wind, waves, and running water) characterise many ecosystems

(Sousa, 1984; Pickett & White, 1985). Establishing connections between these physical disturbances and biological processes is of great interest but often complicated by context dependency (e.g. Cardinale, Nelson & Palmer,

2000; Agrawal *et al.*, 2007), whereby the magnitude and direction of responses to a given disturbance intensity are modified by proximate factors that may include both abiotic (e.g. habitat characteristics), and biotic (e.g. behavioural or morphological species traits) components (Sousa, 1984; Haddad *et al.*, 2008). These mediating factors are often poorly understood, even in systems where disturbance is well-studied. In lotic ecosystems, for instance, the ecological impacts of pulsed flow disturbance (e.g. spates and droughts) have received enormous attention (e.g. Resh *et al.*, 1988; Lake, 2000) yet results often lack generality (e.g. Poff & Ward, 1989; Dewson *et al.* 2007b).

A case in point is the relationship between flow disturbance and invertebrate drift, the downstream transport of benthic invertebrates in suspension (Müller, 1954). While flow impacts on drift are well studied given the important functions of drift as mode of patch movement for invertebrates and a trophic flux to fish (Naman, Rosenfeld & Richardson, 2016), results are strongly context dependent. For example, while abrupt increases in flow often lead to elevated drift as invertebrates are physically dislodged from substrate ('passive drift'; Anderson & Lemkuhl, 1968), the magnitude that drift changes for a given flow increase ranges widely (Allan & Castillo, 2007). In addition, decreases in flow may also lead to elevated drift (Minshall & Winger, 1968; James, Dewson & Death, 2008), a counterintuitive response that highlights the importance of behavioural drift entry ('active drift') as flows decline. However, like the effects of increasing flow, this response is inconsistent among studies and varies among taxa (Poff & Ward, 1991; Dewson *et al.*, 2007b; Kennedy *et al.*, 2014).

The factors generating context-dependent flow-drift relationships are poorly resolved but may be related to physical habitat structure. Flow influences drift, in part, through changes in velocity and wetted streambed area. Rising velocity and hydraulic stress as flows increase results in a higher likelihood of passive drift through dislodgment (Gibbins, Vericat & Batalla, 2007), while shrinking bed area as flows decline result in a higher likelihood of active drift due to density-dependence and desiccation risk (Carrarino & Brusven, 1983; Boulton, 2003; Dewson, James & Death, 2007a). The rate that velocity and benthic habitat area change during high and low flow disturbances can be strongly mediated by channel architecture, specifically cross-sectional bank profile (e.g. Gippel & Stewardson, 1998). When flows decline, the area of benthic habitat for invertebrates will shrink most rapidly in channels with moderately sloping banks (hereafter 'concave' channels) relative to those

with steeper, more vertical banks and flat bottoms (hereafter 'flat' channels; Ferguson, 2003; see Figure S1). In contrast when flows increase, velocity will rise more rapidly in flat channels where flow is confined by steep banks relative to concave channels, where rising discharge can be accommodated by an increase in wetted width. Consequently, the effects of flow increases on drift rates may be amplified in flat channels as rising velocity triggers passive drift, and effects of flow decreases may be amplified in concave channels as shrinking habitat area triggers active drift.

Flow effects on drift may be further modified by trait variation among invertebrate taxa. For instance, the relative susceptibility to dislodgement from increased flow may be higher in taxa with body morphologies that experience more drag forces, and lower mobility that limits the capacity to find refuge from hydraulic stress (reviewed in Rader, 1997). Similarly, when flows decline, the relative tendency for active drift may increase with mobility (e.g. swimming ability). These traits vary considerably among taxa but also within taxa; for instance, individuals with larger body sizes can have enhanced mobility (Poff *et al.*, 1991) but may also experience more drag forces (Statzner, 1987). In addition, unlike passive drift that responds rapidly to flow increases (Gibbins & Batalla, 2010), active drift may exhibit delayed responses if invertebrates drift nocturnally to minimise predation risk from fish during daylight (Bishop, 1969; Flecker, 1992).

Habitat and trait-mediated effects on drift induction may also influence the short-term (i.e. within-generation) impacts of disturbance on benthic populations and communities. At small scales, stream invertebrate populations are composed of spatially distinct patches (e.g. Townsend, 1989; Winemiller, Flecker & Hoenighaus, 2010) within which variation in emigration and immigration through drift may affect population size and persistence (Englund, 2005). If flow impacts on drift differ among habitat patches (e.g. Lancaster & Hildrew, 1993; Robson 1996), spatial structure in net loss or gain of individuals among patches may result. Likewise, community composition may be altered if predisposition to drift varies among taxa. For instance, during flow reductions only the most mobile taxa may drift out of a given patch (Kohler, 1985; Poff & Ward, 1991; Hammock & Wetzel, 2013), while during flow increases drift entry may increase for a wide range of taxa (e.g. Gibbins *et al.*, 2007).

Our goal is to clarify how channel architecture and species traits modify the impacts of flow disturbance on drift. In two complementary experiments, we

manipulated flows in concave and flat stream mesocosms. This approach allowed us to explicitly test the influence of channel architecture while keeping other factors (e.g. substrate) constant, which is not possible in natural streams. In the first experiment, we reduced flows and concave channels lost 30% more wetted area than flat channels. In the second experiment, we increased flows and flat channels increased in velocity *c.* 25% more than concave channels. Following each manipulation, we quantified invertebrate drift in terms of both gross community-wide fluxes, and taxon-specific per capita rates incorporating concurrently measured benthic abundance. We then inferred potential impacts to the benthos by examining how flow treatments impacted per capita rates of emigration through drift relative to immigration into mesocosms.

We made several predictions based on the hypothesis that channel structure and trait variation mediate drift responses to flow manipulations. Specifically, we predicted that: (i) drift responses to reduced flow would be stronger in concave channels due to shrinking habitat area, whereas responses to increased flow would be stronger in flat channels due to higher velocities; (ii) elevated drift from flow reductions should occur in more mobile taxa that drift actively, whereas elevated drift from flow increases should occur across all taxa, but by more for those vulnerable to dislodgement (e.g. less mobile, higher drag); (iii) drift should be higher at night during flow reductions as drift entry would be a primarily active process, while day/night differences should be reduced during flow increases as drift would be primarily passive; and (iv) the community structure of the drift should diverge from the benthos during flow reductions as only the more mobile component of the benthic assemblage drifts actively, while community structure should converge between the drift and benthos following flow increases as a larger portion of the benthic community would enter the drift passively through physical dislodgement (e.g. Gibbins *et al.*, 2007).

Methods

Experiment logistics

We carried out our experiments in the University of British Columbia's Malcolm Knapp Research Forest (49°35'N, 123°50'W), which is described in detail in Richardson (1991). We constructed 24 gravity-fed stream mesocosm channels (6.8 m long \times 0.15 m wide) with water piped in from Mayfly Creek, an adjacent 3-m wide oligotrophic stream (Figure S2). Two header boxes

distributed flow into 12 outflow spigots, each of which split flow into one concave and one flat channel through a three-way splitter with a closed plastic ball valve in the middle arm (Figure S3). We constructed concave channels from 6-inch diameter PVC pipe cut lengthwise and flat channels from 6-inch width plastic-lined aluminium gutters. In order to maintain consistency in channel geometry and bed roughness within and between treatments, we used a combination of natural gravel from Mayfly Creek (10–40 mm diameter) alternating with one inch square unglazed ceramic tiles as substrate. Other physical and abiotic features such as gradient (slope 0.08 m m⁻¹), light and temperature (12–14 °C) were consistent among channels. We allowed channels to naturally colonise with invertebrates for 6 weeks prior to starting experiments. Discharge into the channels during this period averaged 0.30 m³ s⁻¹, typifying summer base-flow conditions in nearby streams. Immigration rates averaged 30 (\pm 19.2) individuals day⁻¹ and did not differ systematically among channels. Initial benthic densities and composition were qualitatively similar to previous experiments in Mayfly creek (Richardson, 1991; Rowe & Richardson, 2001).

In both experiments, we used a 2 \times 2 before-after-control-impact design in which we measured response variables before and after flow manipulations in randomly assigned flow treatment and control outflows corresponding to paired concave and flat channels ($n = 6$ per treatment combination). Starting on 13 August 2013, we ran each experiment over 4 days and staged flow manipulations over 2 h starting at 09:00 hours on the third day. To decrease flows in treatment channels, we opened the middle ball valve of the three-way splitter, which diverted water (*c.* 0.2 m³ s⁻¹) outside of each channel pair and lowered the discharge by 75% on average in treatment channels while control channels remained relatively constant at *c.* 0.25–0.3 m³ s⁻¹. The magnitude of this change (along with the flow increase described below) was comparable to natural late summer discharge fluctuations in nearby streams (Moore *et al.*, 2005).

We began the second experiment 3 days after concluding the first. To increase flows, we completely closed outflows corresponding to the 12 treatment channels from the previous experiment and simultaneously opened the middle valves in 6 of the 12 remaining outflows (the control channels from the previous experiment). This maintained constant flow in control channels and increased the flow in treatment channels ($n = 6$) by 75%. Note that this also reduced sample size for the flow increase experiment from 24 to 12 channels (i.e. six

replicates for each treatment combination in the flow reduction experiment, three replicates for the flow increase experiment). Carry-over effects of the flow reduction experiment on the flow increase experiment are unlikely as treatment channels did not overlap (i.e. no channel was subjected to both decreased and increased flow) and initial benthic densities and composition were not different between the two experiments (density: *t*-test, $t = -0.36$, $P = 0.77$; composition: PERMANOVA, $F_{1,21} = 0.96$, $P = 0.45$).

We collected invertebrate drift during each experiment by placing a 250- μm mesh net at the end of each channel, which filtered 100% of the discharge and captured drifting invertebrates (Elliott, 1970). To quantify diurnal periodicity, we collected separate drift samples during the day and at night. Each sampling period lasted *c.* 12 h, with dawn and dusk included in night samples. We quantified immigration into channels at each flow level by placing a 250- μm net over each inflow pipe. In order to estimate immigration during experiments without influencing drift and benthic populations, we collected two replicate immigration samples of 30 min each in both the day and night at each flow level during transition periods when downstream drift nets were being processed (i.e. drift was not being sampled). Because 30 min samples captured few individuals, we collected additional 12 h immigration samples ($n = 2$ per channel) after the experiments concluded. We estimated benthic densities before and after each flow manipulation (total of four collections) by collecting nine ceramic tiles at three random locations in each channel with a customised 250- μm metal framed net placed directly downstream of each sampling location to capture any dislodged invertebrates as tiles were removed. We scraped invertebrates and biofilm from tiles with a metal brush, and then returned the tiles to their exact place of origin. For all drift and benthic samples, we sieved all contents through 250- μm mesh and stored invertebrates in 95% ethanol for subsequent identification in the laboratory.

To determine flow-related changes in habitat conditions, we measured cross-sectional transects of depth and wetted width at 10 cm longitudinal intervals in each channel and flow level, and measured discharge by the time required to fill a 4 L bucket at the downstream end of each channel. We measured velocity at the deepest point in each cross section, using a Marsh-McBirney® Flow Mate 2000 (Hach Company, Loveland). Shallow depths (<5 cm) precluded the direct measurement of velocity at reduced flow levels, so instead we inferred velocity using the formula $Q = AV$, where Q is the

discharge, V is the velocity, and A is the cross-sectional area (the product of measured depth and wetted width) at each transect. To corroborate physical dislodgement as the primary mechanism of drift entry following flow increases, we calculated the shear stress before and after flow increases in each channel (see Appendix S1 for details on calculation).

We sorted and identified all aquatic invertebrates to the lowest possible taxonomic level (usually genus) under a dissecting microscope using dichotomous keys (Merritt & Cummins, 1996). To estimate individual body mass, we staged and photographed each individual, using a microscope camera (Leica® DMC4500, Leica Camera AG, Wetzlar), estimated total body length using ImageJ® photo imaging software (U.S. National Institute of Health, Bethesda), then used allometric relationships (Benke *et al.*, 1999; S. M. Naman, unpubl. data) to convert body length to mass. Equations are of the form $Y = aX^b$, where Y is mass (mg), X is body length (mm), and a and b are scaling constants fitted for specific taxa.

Statistical analysis

We quantified several complementary measurements of drift for our analysis. First, we calculated gross drift flux as the total number or mass of invertebrates drifting per sampling period (12 h), and drift concentration as the total flux standardised by the volume of water filtered. These metrics describe aggregate drift responses to flow manipulation; however, they give little insight into the underlying mechanisms causing drift or its consequences for the benthos (Naman *et al.*, 2016). To make further inferences into these processes, we calculated per capita drift rates as the proportion of the total benthic population in a channel drifting per unit time. We estimated benthic population size by multiplying the average benthic density by the total area of substrate in each channel less the area sampled from each preceding interval, to account for the depletion of benthic populations during sampling. To validate density estimates, we counted all the invertebrates present in two of the control channels at the end of the experiment. Estimates from the two methods were qualitatively similar, suggesting our sampling approximated true population sizes in the channels. For the per capita analysis, we focus on six taxa that comprised the dominant portions of the drift and benthic assemblage (Table 1). These taxa included Chironomidae larvae (*Brillia retifinis*, *Corynoneura* spp., and *Tanytarsini* spp.), the mayfly *Baetis* spp., the nemourid stonefly *Zapada* spp., and the brachycentrid caddisfly *Micrasema* sp. They differ in both their

Table 1 Mean (\pm SE) benthic densities and trait characteristics of taxa used for trait analysis and per capita analysis (in bold) ranked by % frequency of total drift abundance. Mobility and drag index scores are based off of Rader (1997) and are on a scale from 0 to 9. Note that despite high abundance in drift, we did not include pupal life stages of chironomids in the per capita analysis due to potentially confounding effects of emergence.

Taxon	% Drift frequency	Benthic density ($n\ m^{-2}$) Mean (\pm SE)	Traits Feeding mode	Mobility	Drag Index
<i>B. retifinis</i>	33	2027.3 (172.8)	Shredder	1	1
<i>Baetis</i> spp.	13.7	1386.8 (118.7)	Scraper	9	4.7
Chironomid pupae	13.5	753.7 (69.7)	N/A	0	5
<i>Corynoneura</i> spp.	9.9	1381.3 (112.7)	Collector gatherer	1	1
Tanytarsini spp.	6.9	1510.2 (121.9)	Filtering collector	1	1
<i>Micrasema</i> sp.	5.6	236.2 (24.8)	Omnivore	1	9
<i>Zapada</i> spp.	3.4	1532.2 (143.6)	Shredder	3	5.4
<i>Parapsyche</i> spp.	2.5	163.6 (20.8)	Scraper	0	0.7
Simuliidae	2	146.1 (35.8)	Filtering collector	6	5.4
Tanytopodinae spp.	1.7	433.2 (48)	Predator	1	1
Elmidae larvae	1.1	162.7 (23.3)	Omnivore	3	5
<i>Dixa</i> spp.	1	151.5 (44.6)	Filtering collector	3	2
<i>Epeorus</i> spp.	0.8	174.7 (15.3)	Scraper	1	5.9

tendency for behavioural drift and susceptibility to scour (Table 1), thus we expected variation in their responses to flow manipulations.

For each experiment, we used an information theoretic approach and multi-model inference to evaluate the main and interactive treatment effects of flow, habitat (flat versus concave) and time (day or night) on total drift flux, concentration, and per capita drift rates of the six dominant taxa. All response variables were computed as the difference between pre- and post-flow manipulation within a channel (with the two pre-flow manipulation samples averaged). We constructed sets of linear mixed effects models, using the R package *lme4* (Bates *et al.*, 2015), including all combinations of flow, channel type, time, and their two-way interactions as fixed effects, and a random intercept term grouped by channel to account for the non-independence of repeated measurements (i.e. day and night measurements from the same channel). In order to compare interactions and main effects, we standardised fixed predictors to a mean of 0 and a difference of 1, using the *Standardise* function within R package *arm* (Gelman *et al.*, 2009; Schielzeth, 2010) and assessed normality with residual plots. To select the best approximating model for each response, we used Akaike's Information Criteria corrected for small sample sizes (AIC_c). AIC_c selects the most parsimonious models within a candidate model set with more plausible models receiving lower AIC_c scores (Burnham & Anderson, 2002). We considered a model to have substantial support if the difference between a given model and the best fitting model (ΔAIC_c) was under four (Burnham & Anderson, 2002). We also

calculated AIC weights (W_i), which represent a probability a given model is the best fitting model within a given set. To further evaluate the fit of top ranked models, we computed a marginal and conditional R^2 following the methods of Nakagawa & Schielzeth (2013). The marginal R^2 indicates the proportion of variance accounted for by only the fixed effects in a model while the conditional R^2 accounts for the proportion of variance accounted for by both the fixed and random effects. We estimated standardised model averaged slope coefficients and associated 95% confidence intervals for each fixed effect using the *MuMin* package in R (Bartón, 2009).

To further explore which specific traits may drive differential drift responses among taxa, we analysed per capita drift rates across a wider range of fourteen taxa (Table 1). In this analysis, the change in per capita drift rate for each taxon was combined into a single response variable (i.e. an observation represents a unique combination of taxa, stream, and time; $n = 286$ for reduction, $n = 142$ for increase). We modelled change in per capita drift rate (before/after flow intervention) as a function of flow, channel, and time as fixed effects and taxon identity as a random intercept term nested within the random effect of channel. To test relationships between ecological attributes and propensity to drift, we included three integrated ecological trait scores as fixed continuous variables based on Rader (1997): *mobility*, which incorporates morphological and behavioural attributes of taxa that influence the tendency for active drift (Rader, 1997); *drag index*, based on the ratio of organism width to height (Wilzbach, Cummins & Knapp, 1988), approximates (in the absence of more precise hydraulic

measurements; see Statzner, 1987) the amount of drag an organism experiences in moving water and its likelihood of dislodgment; and the mean *body size* of each taxa relative to its benthic source population (hereafter 'residual body size') based on the rationale that larger individuals have more behavioural control over drift entry but may also be more susceptible to drag (Wilzbach *et al.*, 1988; Poff *et al.*, 1991). In this analysis, candidate model sets included only two-way interactions between each predictor and flow. To compare effects between continuous and categorical predictors, we standardised continuous variables by subtracting the mean and dividing by two standard deviations (Schielzeth, 2010). Model selection and model averaging were conducted in the same manner as described for taxa-specific responses.

To assess the short-term impacts of flow-induced drift on benthic populations, we calculated the net population impact of flow treatments as the difference between the per capita rates of emigration and immigration (day and night combined) in each channel. In essence, this value reflects a per capita colonisation rate (Richardson, 1991); negative values (emigration > immigration) indicate a net loss of individuals from the benthic population, positive values (immigration > emigration) imply net gains, and a value of zero suggests no change in benthic population accrual rate. Because we found weak effects of channel type for all individual taxa except *Baetis* spp. (see Results) we aggregated channel treatments for this analysis. In addition to drift, emergence to terrestrial life stages may have been another source of emigration in response to flow manipulation (Boulton, 2003). While we did not measure emergence directly, we suspect it had minimal influence on our results given the timing (i.e. many individuals were in early instar life stages), relatively short channel lengths, and short duration of the experiments. However, we cannot rule out the possibility that some drifting individuals emerged before being captured in our drift nets, thus our estimates of total emigration may be conservative.

At the community level, we used multivariate analyses to examine compositional changes in drift and benthos due to flow manipulations. First, we used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with the *adonis* function in the R package *vegan* (Oksanen *et al.*, 2013). PERMANOVA fits linear models to Euclidean distance matrices, then uses a permutation test with pseudo *F* ratios to partition variation and calculates exact *P*-values based on 999 permutations to test the null hypothesis of no difference in composition within versus among groups.

Because PERMANOVA is sensitive to differences in dispersion, we tested for multivariate homogeneity of variance among groups using the *betadisper* function in *vegan*, which computes the mean Euclidean distance to the centroid of each group. Group differences in community composition and associated axes of maximum variation were then visualised with non-metric multidimensional scaling plots. We then used similarity percentage analysis (SIMPER; Clarke, 1993) to determine the mean dissimilarity between drift and benthos and treatment and controls for flow level.

Results

Habitat characteristics

Changes in habitat area and velocity agreed with expectations based on hydraulic geometry (Table 2). Following flow reductions, habitat area declined by 28% on average in concave channels while flat channels did not change. Velocity in both habitat treatments also declined relative to controls when we reduced flows, but by 25% more on average in flat channels. In the second experiment with enhanced flows, mean velocity increased by 64% in flat channels and 38% in concave channels relative to their respective controls. Increased flow also resulted in a 12% increase in wetted habitat area in concave channels. High flows did not induce bed movement; however, shear stress increased *c.* 10× in flat channels (from 0.7 to 8.2 dynes cm⁻²) and by *c.* 6× in concave channels (from 0.7 to 5 dynes cm⁻²) following elevated flows.

Total drift flux and concentration

Total drift flux and concentration responded differently to changes in flow. Flow reductions had no apparent impacts on total drift flux (Fig. 1a, b) and flow was not included in the top ranked models for either numeric or biomass flux (Table S1). In contrast, numerical and biomass drift concentration increased nearly threefold after flow reduction (Fig. 1c, d). There was a lag associated with this response such that concentration did not increase until nightfall, at which point flow treatment channels were *c.* 4× higher than controls (Fig. 1c, d). Statistical support for a delayed drift concentration response to flow reduction was evident in the retention of a flow × time interaction (Table S1), and 95% CIs did not overlap zero for numeric (increase of 3–9.6 individuals m⁻³) or biomass (increase of 0.04–0.99 g m⁻³) concentration. Contrary to predictions, there were no

Table 2 Mean values (\pm SE in parenthesis) of discharge, velocity and wetted habitat area in each channel type ($n = 12$ each of flow reduction; $n = 6$ each for flow increase) before and after flow manipulations.

Channel architecture	Discharge ($\text{m}^3 \text{s}^{-1}$)		Velocity (m s^{-1})		Wetted area (m^2)	
	Before	After	Before	After	Before	After
Flow reduction						
Concave						
Control	0.32 (0.01)	0.21 (0.01)	0.2 (0.02)	0.13 (0.01)	0.79 (0.02)	0.81 (0.02)
Reduced	0.35 (0.01)	0.06 (0)	0.22 (0.02)	0.08 (0.01)	0.79 (0.02)	0.58 (0.01)
Flat						
Control	0.32 (0.02)	0.26 (0.01)	0.17 (0.01)	0.11 (0)	0.76 (0)	0.75 (0)
Reduced	0.31 (0.02)	0.05 (0)	0.19 (0.01)	0.06 (0.01)	0.76 (0)	0.75 (0)
Flow increase						
Concave						
Control	0.21 (0.01)	0.19 (0.01)	0.13 (0.01)	0.13 (0.01)	0.81 (0.02)	0.63 (0.02)
Increased	0.22 (0.01)	0.78 (0.01)	0.13 (0.01)	0.22 (0.01)	0.8 (0.02)	0.92 (0)
Flat						
Control	0.26 (0.01)	0.17 (0.01)	0.11 (0)	0.11 (0.01)	0.75 (0)	0.75 (0)
Increased	0.24 (0.01)	0.79 (0.01)	0.12 (0)	0.28 (0.02)	0.75 (0)	0.75 (0)

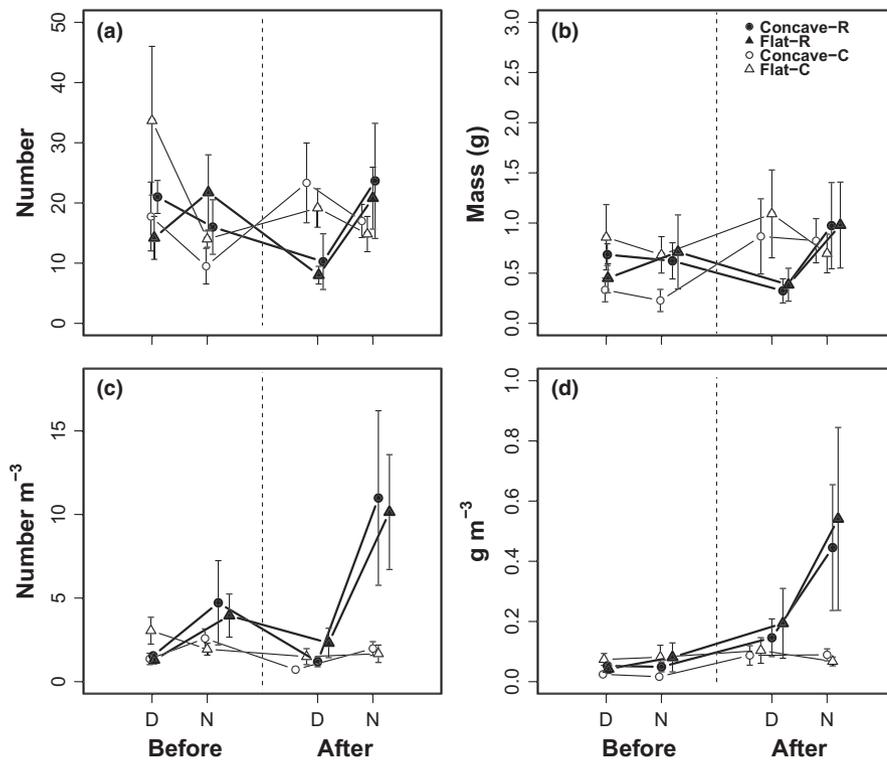


Fig. 1 Mean (\pm SE) of the total numeric (a) and biomass (b) drift flux, and numeric (c) and biomass (d) drift concentration before and after flow reduction during the day and at night ($n = 6$ per treatment combination). Flow treatment (R) channels have bolded lines relative to controls (C). Points are slightly jittered to ease interpretability.

differences between channel treatments for any bulk drift responses following flow reduction.

In the flow increase experiment, total flux increased rapidly by fourfold following the flow manipulation in both channel types (Fig. 2a, b). Interestingly, the trajectories of the two habitat treatments diverged at night as drift flux continued to increase out of flat channels by an additional 10% relative to daytime, while drift flux from concave channels decreased by *c.* 40% relative to daytime, despite remaining 2–3 \times higher than controls.

In contrast, drift concentration decreased in response to increased flow although drift concentration in flat channels at night remained *c.* 2 \times greater than control and concave treatment channels (Fig. 2c, d).

Per capita drift rates

Flow effects on per capita drift varied among the six focal taxa. Following flow reductions, *Baetis* spp. was the only of the six taxa to increase per capita drift rates.

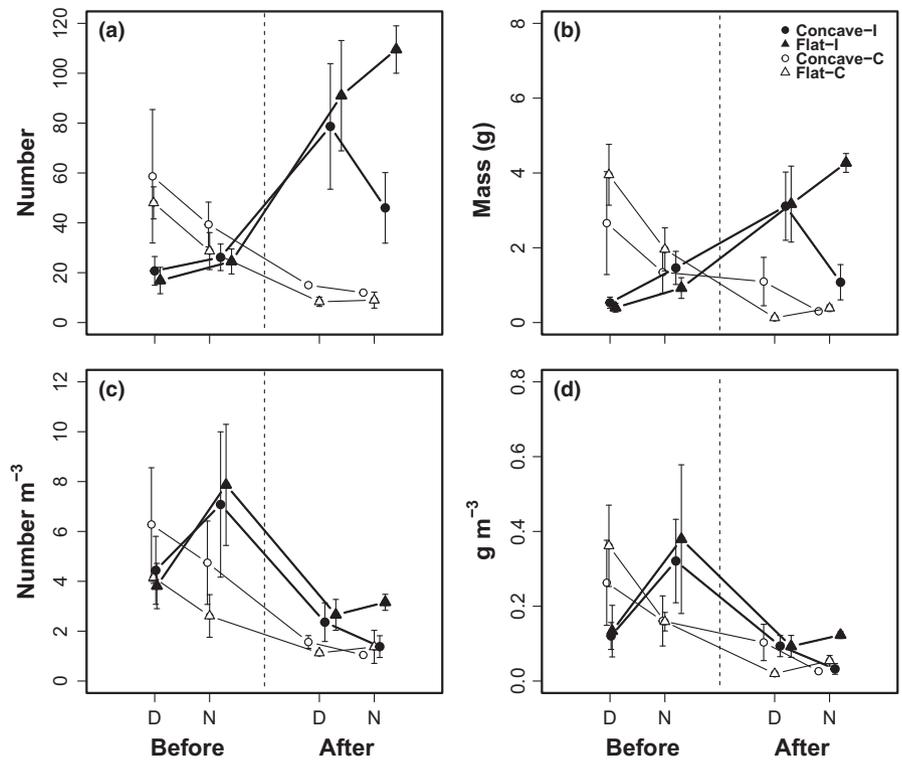


Fig. 2 Mean (\pm SE) of the total numeric (a) and biomass (b) drift flux, and numeric (c) and biomass (d) drift concentration before and after flow increases during the day and at night ($n = 3$ per treatment combination). Flow treatment channels (I) have bolded lines relative to controls. Symbols are consistent with Fig. 1.

Model selection identified flow, time of day, and their interaction as the most important variables to explain *Baetis* spp. drift (Table S2). The top ranked model included a flow \times time interaction term, suggesting that per capita drift of *Baetis* spp. increased by 8% (95% CI: 2–13%) when flows were reduced at night (Fig. 3). In contrast, per capita drift declined for *Zapada* spp. by 1.6% (–3 to –0.3%) and *Corynoneura* spp. by 2.4% (–4 to –0.5%). For *B. retifinis*, *Tanytarsini* spp., and *Micrasema* sp., flow reduction had no apparent effects on drift rates. In these cases, flow was not included in the top ranked model and 95% CIs for all terms overlapped zero. In concordance with aggregate flux and concentration results, there was no support for channel architecture effects on per capita drift responses for any taxa.

When flows were increased, per capita drift was consistently elevated and flow was included in the top ranked model for every taxa (Table S2). However, the magnitude of this response varied considerably (Fig. 4). Per capita drift increased for *Zapada* spp. by 3.5% (1.1–5.8%) and *Corynoneura* spp. by 6.4% (1.5–11.6%) in flow treatment channels, while most other taxa experienced more substantial flow-induced increases in per capita drift, as high as 30% (11–50%) for *Micrasema* sp. Consistent with predictions, time of day had minimal support for most taxa, providing no evidence for a behavioural lag in drift induction with elevated flows. An exception to this was

B. retifinis, where a flow \times time interaction had substantial support, suggesting per capita drift of *B. retifinis* declined by 14% (–23 to –7%) in flow treatment channels at night, opposite to what would be expected based on behaviourally-induced predator avoidance. Predictions that habitat would mediate drift responses had mixed support. Channel type was not an important predictor for any taxa except *Baetis* spp., where a flow \times channel interaction term was included in the top ranked model. Consistent with predictions, *Baetis* spp. drift was elevated 12% (1–23%, 95% CIs) in flat channels, which experienced greater increases in velocity.

Trait-based analysis of per capita drift rates

Mobility and drag index both had support to explain variable per capita responses to changing flow among taxa. Mobility appeared to influence whether a given taxa increased drift in response to reduced flow (Fig. 5 top panel). While per capita drift of all taxa declined by 3.4% on average with flow reduction, drift increased with higher mobility index values. In addition, diurnal periodicity was also significant under reduced flow, as a flow \times time interaction was included in the best approximating model (Table S3), and nocturnal per capita drift rates increased by 4.2% (1.4–6.9%) on average following flow reduction.

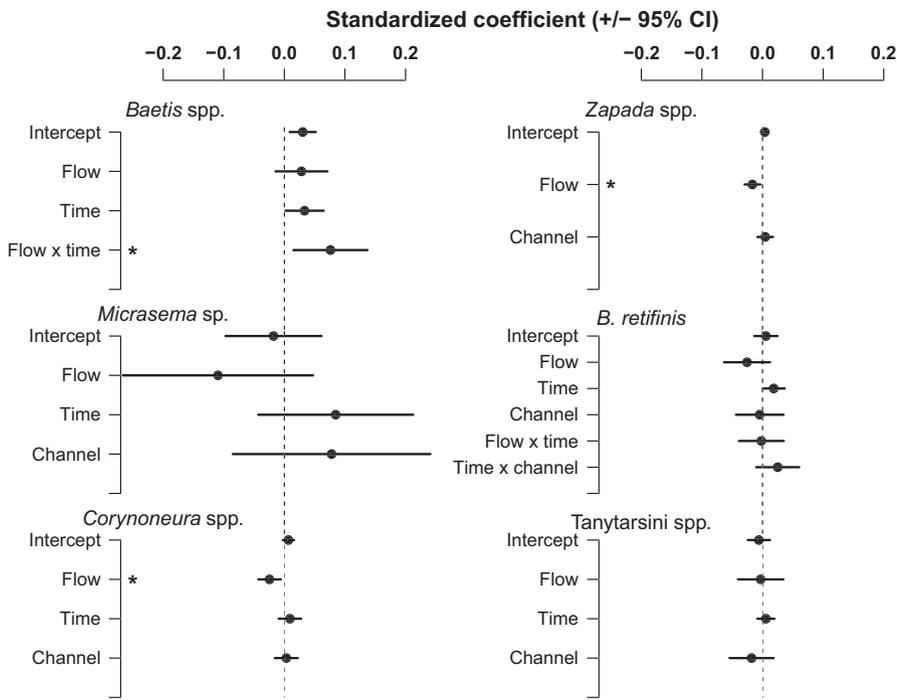


Fig. 3 Standardised model averaged slope coefficients ($\pm 95\%$ CIs) from top ranked models ($\Delta AIC < 4$) explaining the change in per capita drift rates for the six focal taxa from before to after flow reduction. *Flow* represents channels where flow was reduced relative to controls, *Channel* represents flat relative to concave habitat treatments, and *Time* represents night relative to day. Asterisks represent cases where 95% CIs do not overlap zero.

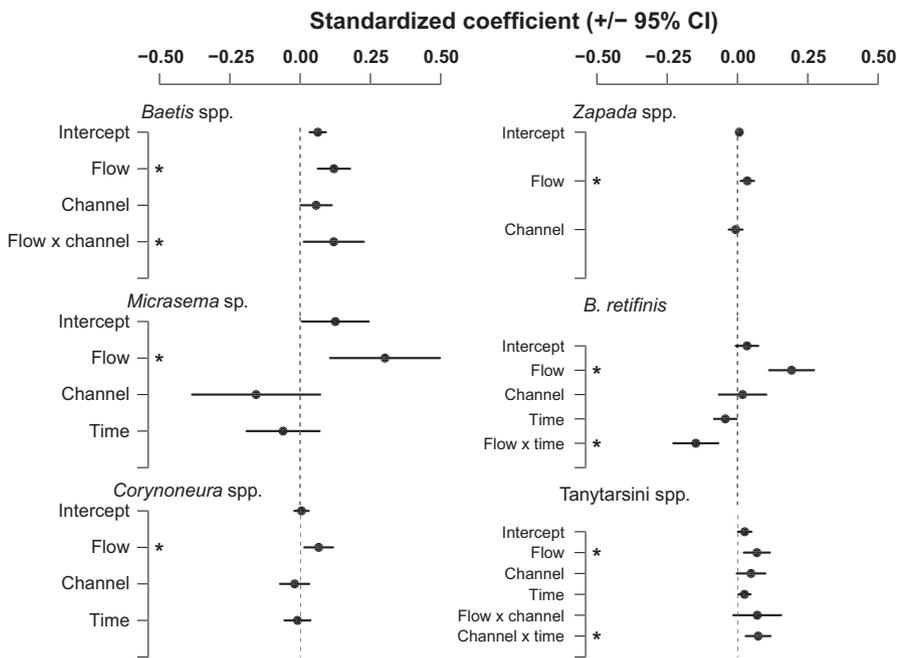


Fig. 4 Standardised model averaged slope coefficients ($\pm 95\%$ CIs) based on models explaining the change in per capita drift rate for the six focal taxa from before to after flow increase. Notation is the same as Fig. 3

Under elevated flows, per capita drift increased by 14% on average across all taxa. Consistent with flow reduction, mobility modified responses to flow increase, but the direction of the effect was reversed such that per capita drift rates declined on average for more mobile taxa when flows were increased (Fig. 5 bottom panel; Table S3). As expected, susceptibility to scour (drag index) emerged as another important trait during flow increases. Taxa with high drag index values experienced

higher overall per capita drift rates and responded more strongly on average when flows were elevated as evidenced by a flow \times drag index interaction term that was well supported statistically (Table S3).

Potential impacts of drift to the benthos

The potential impacts of flow-induced drift on benthic population size varied among taxa (Fig. 6). Generally,

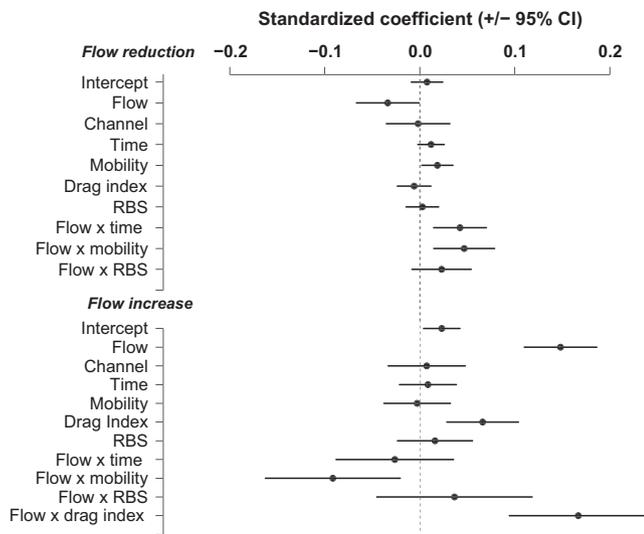


Fig. 5 Standardised model averaged slope coefficients and 95% confidence intervals for models predicting change in per capita drift across 15 taxa in flow reduction (top panel) and flow increase (bottom panel) experiment. Notation for *Flow*, *Channel* and *Time* are consistent with Figs 3 & 4. *RBS* represents the mean residual body size for drifting taxa relative to their source benthic population.

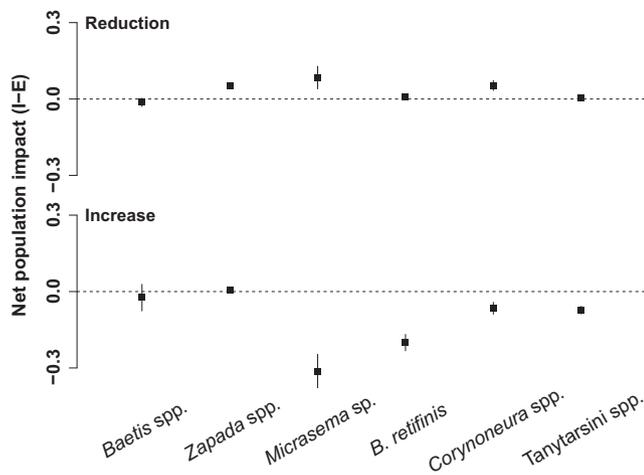


Fig. 6 Net population impact (\pm SE) of flow reductions (top panel) and increases (bottom panel) on the six focal taxa. Population impact is defined as the difference between per capita emigration rates (number day⁻¹) relative to per capita immigration rates. Negative values indicate net losses of individuals from the benthic population.

impacts were strongest where per capita drift changed significantly. Flow reductions resulted in net gains of individuals (emigration < immigration) for three of six taxa [*Zapada* spp. (0.04 ± 0.005 individuals day⁻¹), *Micrasema* sp. (0.08 ± 0.04), and *Corynoneura* spp. (0.05 ± 0.01)]. In contrast, flow increases resulted in substantial net losses of individuals for four of six taxa [*Micrasema* sp. (0.31 ± 0.06), *B. retifinis* (0.2 ± 0.03),

Table 3 Average pairwise proportional dissimilarities, based on SIMPER analysis, between drift in flow treatment channels compared with benthos and drift from control channels before and after flow manipulations.

Treatment – Interval	Dissimilarity	
	Benthos	Control
Flow reduction		
Reduced – Before	0.51	0.44
Reduced – After	0.58	0.52
Control – Before	0.52	–
Control – After	0.51	–
Flow increase		
Reduced – Before	0.51	0.43
Reduced – After	0.33	0.57
Control – Before	0.49	–
Control – After	0.58	–

Corynoneura spp. (0.06 ± 0.02) and *Tanytarsini* spp. (0.07 ± 0.03)]. *Baetis* spp., despite increasing per capita drift *c.* 10% following both increased and decreased flow, did not experience changes to its relative rates of immigration and emigration.

Our multivariate analyses indicated that drift community structure diverged from benthic community structure following flow reduction, and converged (became more similar) following flow increases (Table 3). During flow reductions, greater proportions of *Baetis* spp. and Simuliidae spp. in the drift in treatment channels relative to control channels and the benthos appeared to drive compositional divergence (Fig. 7 top row). In contrast, during flow increases, greater proportions of *Micrasema* sp. and several chironomid taxa in the drift in treatment channels appeared to drive the compositional convergence with the benthos (Fig. 7 bottom row). The PERMANOVA model testing the interaction of flow and sampling interval on drift composition was significant for flow reductions ($F = 2.65$, $P = 0.008$) although the proportion of explained variation was low ($R^2 = 0.03$). The same model was also significant for flow increases ($F = 5.43$, $P = 0.001$, $R^2 = 0.11$); however, this difference was likely driven by treatment effects on multivariate dispersion, as drift became more variable in composition when flows were elevated (*betadisper*, $F = 3.55$, $P = 0.02$). Effects of flow manipulations did not extend to the benthos, as composition was not statistically different before to after flow reduction (PERMANOVA, $F = 0.42$, $P = 0.97$) or increase ($F = 0.85$, $P = 0.56$).

Discussion

Consistent with many of our *a priori* predictions, our results suggest that species traits, and to some extent

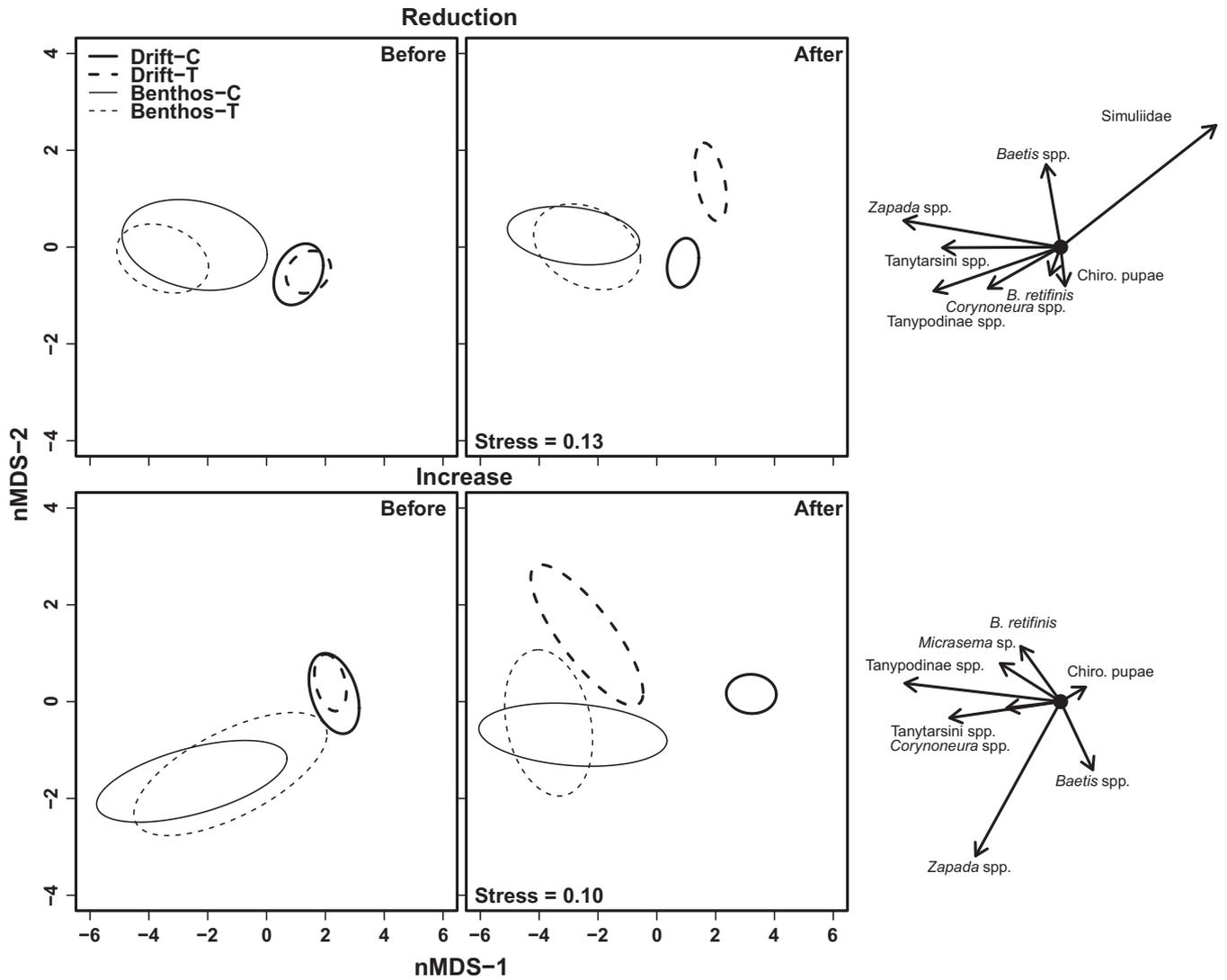


Fig. 7 Non-metric multidimensional scaling plots showing compositional differences between drift (bolded) and benthos (non-bolded) for flow treatment (T) and controls (C) before and after flow reduction (top panel) and increase (bottom panel). Ellipses represent bivariate 95% confidence regions around the data in multivariate space. Spatial differences in ellipse positions indicate compositional differences among groups. Taxa significantly correlated with the axes are shown for each ordination to the right. Arrows indicate direction of increasing relative abundance.

channel architecture, mediated invertebrate drift responses to flow disturbances. Following flow reductions, drift increased only for the most mobile taxa, with additional evidence that this response was behavioural. First, increased drift occurred primarily at night, indicating invertebrates likely waited *c.* 12 h from the initial manipulation before responding, although increased night-time drift distances may have played a role (Statzner & Mogel, 1985). Second, the divergent community composition between drift and benthos following flow reduction suggests a smaller component of the benthic assemblage drifted at low flows. The taxa driving this compositional difference, *Baetis* spp. and Simuliidae, are

well known to drift behaviourally (Poff *et al.*, 1991; Fonseca & Hart, 1996).

Drift responses to increased flow were also in general agreement with predictions as elevated flows increased total drift flux as well as per capita drift rates across all taxa. The rapid response of drift to flow increases, apparent compositional convergence between drift and benthos, and increased dispersion of drift in treatment channels suggests that a larger and more variable component of the benthic assemblage entered the water column through passive drift. This inference is consistent with previous studies that have found drift and benthic composition to converge as flows increased (Imbert & Perry,

2000; Gibbins *et al.*, 2007). The taxa driving convergence in our study, including *Micrasema* sp. and several chironomid species, are generally more susceptible to scour and are not known to drift behaviourally (Poff *et al.*, 2006).

While we expected shrinking habitat area in concave channels to be the primary driver of drift during flow reductions, this prediction was not supported. The influence of habitat area on drift induction during flow declines has also differed among previous studies. For example, Corrarino & Brusven (1983) observed increased drift following flow reductions only after habitat area contracted by 30%, while James *et al.* (2008) found that flow reduction induced a 10-fold increase in drift despite no change in habitat area. While unmeasured abiotic factors associated with low flows can trigger drift (e.g. oxygen), many did not likely change in the short duration of our experiments. Increased drift is most likely related to reduced velocity, which has been shown to elicit active drift of filter feeding taxa (generally low in abundance in our study) through decreased particulate food inputs (James *et al.*, 2008). However, for mobile grazing taxa like *Baetis* spp., the mechanisms linking reduced velocity to drift are less clear. Biotic factors associated with reduced velocity, such as elevated benthic predation risk (Wellnitz, 2014) or biofilm depletion (Hintz & Wellnitz, 2013), may have played a role, but we are unable to distinguish among them.

For the flow increase experiment, there was mixed support for our prediction that flow effects on drift would be amplified in flat channels. *Baetis* spp. experienced a larger increase in per capita drift in flat relative to concave channels as predicted, but other supporting evidence was less definitive. For instance, flat versus concave channels displayed contrasting nocturnal responses in total drift flux following flow increases, with reduced night drift in the concave channels. The interpretation of this result is less clear given that the response was not immediate, such that physical dislodgement alone is an insufficient explanation. Possible explanatory mechanisms include active drift associated with larger velocity increases in flat channels and refugia created by expanding habitat area in concave channels, which may have promoted faster recovery from high flows (e.g. Lancaster, 2000). Apart from *Baetis* spp., channel architecture was not an important modifier of flow effects on per capita drift rates of any focal taxa, suggesting that velocity increases in concave channels may have been sufficient to induce passive drift for many taxa. However, shear stress values in our concave channels (*c.* 5 dynes cm⁻²) were below the threshold of passive drift entry (9 dynes cm⁻²) demonstrated in

Gibbins *et al.* (2007). This may indicate an active drift response to increased flow or from differences (e.g. interstitial refugia, rate of flow increase) between our study and Gibbins *et al.* (2007) such that thresholds of passive drift initiation may not be fully transferable.

Caveats and implications

While many aspects of our experiment were in the range of natural conditions (e.g. velocity, discharge, benthic densities), substrate and bed topography were considerably simplified to maintain consistency in channel morphology within treatments. In natural streams, variation in substrate and bed roughness will further modify the relationships among habitat area, velocity and cross-sectional geometry (e.g. Nikora *et al.*, 2004). In addition, spatial variation in scour is considerable in natural streams (Beisel *et al.*, 1998), whereas our channels were relatively homogenous. Further, while interstitial spaces were available in our channels, hyporheic refugia (Boulton *et al.*, 1998) was largely absent, which may have exacerbated responses (Stubbington, 2012). While these issues should not confound our overall interpretations, extrapolating absolute relationships from our study (e.g. how much drift concentration changes for a given flow increase) may not be appropriate.

With these qualifications in mind, our study still provides several important insights into the abiotic and biotic factors mediating drift responses to flow disturbance. The larger effects of flow increases on aggregate drift flux and per capita *Baetis* drift in flat channels supports the notion that channel architecture can mediate the flow-induced changes in velocity and hydraulic stress an organism will experience. Specifically, channel architecture permitting wetted width to increase with rising flow may buffer invertebrates against the risk of passive entrainment from high velocities. This inference is in line with Robson (1996) who found that more complex riffle architecture reduced the impacts of high flow events on benthic invertebrates, and numerous other studies that demonstrated the importance of hydraulic refugia at smaller scales during high flow disturbance (e.g. Lancaster & Hildrew, 1993; Lancaster, 2000). Taken together, these results highlight the need to consider the physical context when predicting biotic responses to flow alteration, a critical task given the ever more difficult balancing act between maintaining freshwater ecosystems and human water demand.

Our trait-based analyses also provide insights into the possible mechanisms driving the contrasting responses to flow disturbance among taxa. During flow reductions,

increased drift was strongly related to mobility – the capacity of invertebrates to control their own movements in the drift and on the benthos; however, as mentioned previously, the ultimate motivation for drifting (i.e. habitat preferences, predation risk) for mobile taxa is not clear. In contrast, drift of less mobile taxa either decreased or showed no response to flow reduction, suggesting these taxa drift primarily passively or in relation to flow independent factors. During flow increases, the large effect of drag index intuitively suggests that the response of a taxa to high flow disturbance depends on their vulnerability to physical dislodgement from the substrate. Body shape is the specific trait influencing drag index; however, there are numerous other adaptations (e.g. hooks, claws and adhesions) that influence dislodgement probability (Lancaster & Belyea, 1997) that we did not account for in our study. Interestingly, mobility also appeared to be an important trait during flow increases, exhibiting a negative interaction with flow. While this may be a statistical artefact of a larger number of taxa with low mobility values, it could also suggest that more mobile taxa suppress drift at high flows due to habitat preferences for high velocities (Fonseca & Hart, 1996; Fenoglio *et al.*, 2013) or enhanced ability to locate refugia (Lancaster, 2000).

Our net population impact analysis revealed additional contrasts in the strategies used by invertebrates to cope with flow disturbance. For instance, the magnitude per capita drift rates responded to flow disturbances and the short-term impacts to their benthic populations were not necessarily congruent. Specifically, the change in emigration relative to immigration was twofold higher in *Micrasema* sp. relative to the *B. retifinis* following increased flow, despite similar increases in per capita drift following flow manipulation. We cannot fully resolve the mechanisms responsible for this result, but given that chironomids are known to be rapid colonisers (Milner, 1994) and that *B. retifinis* were more abundant in the drift, we speculate that this taxon mitigated high flow-induced emigration with fast colonisation rates. In contrast, *Micrasema* sp. may rely on within-habitat refugia from high flow (Lancaster & Belyea, 1997; Lancaster, 2000) that was largely absent in our study.

Because we integrated multiple measurements of drift, our results are also useful to examine the interrelationships among drift concentration, flux, and per capita drift rates, and their responses to changing flows. One important implication from our results is that relatively small changes in per capita drift rates from the benthos resulted in disproportionately large changes in drift concentration and flux. For instance, the total flux of *Zapada* spp.

increased *c.* 25% when flows were raised, despite an average per capita drift rate increase of only 3% on average. Thus, because benthic standing stock far exceeds drift abundance, even minimal spatiotemporal variation in per capita drift entry rates from the benthos can result in substantial variation in drift concentration or flux.

Interpreting drift concentration requires additional consideration of flow-related changes in water volume, which can complicate inferences into drift-flow relationships given that it is a component of both the predictor (discharge) and the response (organism number or mass per m^{-3}). While altered concentration in response to flow variation is often attributed to changes in drift entry, it can also result from increased or reduced water volume under constant drift entry (Hayes *et al.*, 2016), in essence a dilution or reverse dilution effect. Dilution effects were evident in our study as drift concentration declined following elevated flow despite a threefold increase in total flux and substantial increases in per capita drift rates in most taxa. Because concentration is often the common standard for measuring drift (references in Dewson *et al.* 2007), another implication from our study is the need to carefully consider dilution effects when interpreting drift-flow relationships (Hayes *et al.*, 2016; Wooster, Miller & DeBano, 2016).

Finally, extending inferences from our work beyond streams, there are numerous examples of more complex habitats either dampening the direct impact of disturbance on local abiotic conditions (e.g. Sousa, 1979) or providing refugia after the disturbance has occurred (e.g. Lancaster & Hildrew, 1993; Syms & Jones, 2000). Similarly, contrasting responses to disturbance associated with behavioural (e.g. Beale, 2007) and morphological (e.g. Demes *et al.*, 2013) trait variation both among and within species is widely evident. These factors can be considered as hierarchical filters within the two-stage disturbance framework proposed by Lake (2000). During the application of a physical disturbance, local habitat structure can modulate both the direct magnitude and the effects of disturbance on proximate abiotic conditions. Then, once a disturbance of a given magnitude is applied, the traits among both the species and individuals mediate the behavioural or numerical response from the biota. This approach may be useful as a starting point in future work aimed at understanding how context-dependent disturbance impacts arise.

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Supporting Information

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

Figure S1. Conceptual representation of the rationale behind the habitat treatments used in the experiments.

Figure S2. Photograph of drift sampling of all 24 stream mesocosms.

Figure S3. Photograph of outflow spigots feeding a concave and flat channel before (top) and after (bottom) flow reduction.

Figure S4. Photographs showing fine inorganic and organic matter on substrate before and after (from left to right) flow increases in flat (top row) and concave (bottom row) channels.

Appendix S1. Shear stress calculations.

Table S1. AIC_c scores for models explaining variation in the change in aggregate drift measures from before to after flow manipulations.

Table S2. Top ranked candidate models explaining variation in per capita drift rates for the six focal taxa.

Table S3. Top ranked candidate models explaining variation in mean per capita drift rates across 15 taxa.

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