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**Habitat-specific production of aquatic and terrestrial
invertebrate drift in small forest streams: implications for
drift-feeding fish**

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Complete List of Authors:	Naman, Sean; University of British Columbia, Zoology Rosenfeld, Jordan; British Columbia Ministry of the Environment, Third, Laura; University of British Columbia, Forest and Conservation Sciences Richardson, John; University of British Columbia,
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Sean M. Naman^{1*}, Jordan S. Rosenfeld², Laura C. Third³, John S. Richardson³

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1. Department of Zoology, University of British Columbia,
4200-6270 University Blvd. Vancouver, B.C. Canada V6T 1Z4
* Corresponding author: naman@zoology.ubc.ca, 604-619-4274

2. Fisheries Science Section, British Columbia Ministry of the Environment
2202 Main Mall, University of British Columbia, Vancouver, Canada V6T 1Z4
Jordan.Rosenfeld@gov.bc.ca

3. Department of Forest and Conservation Sciences, University of British Columbia
2424 Main Mall, Vancouver, BC V6T 1Z4
laura.third20@gmail.com
John.Richardson@ubc.ca

Abstract

The influence of stream channel structure on the production of prey for drift-feeding fish is not well understood. We quantified drift production, the entry rate per streambed area, and drift flux, the total export rate per channel unit, in three second-order, forested streams in southwest British Columbia, Canada. We tested whether: (1) drift production was higher in riffles than pools; (2) drift flux increased with riffle length; and (3) prey body size was larger from riffles relative to pools and from terrestrial drop relative to aquatic drift. Total and aquatic-derived drift production ($\text{mg}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) was ~ 3.5 times higher in riffles relative to pools; however, terrestrial drift did not differ between channel types. Total drift flux ($\text{mg}\cdot\text{h}^{-1}$) was positively related to riffle length. Terrestrial invertebrates were ~ 3 times larger than aquatics, and invertebrates from riffles were ~ 3 times larger on average than those from pools. These results suggest that channel structure directly affects prey availability and prey quality for drift-feeding fish and that long riffles may be key areas of prey generation.

Introduction

Invertebrate drift, the downstream transport of suspended macroinvertebrates, is a primary source of prey for many stream fishes including salmon and trout (Salmonidae). Together, drift abundance and habitat conditions (e.g., depth, velocity, and temperature) determine the energetic profitability (prey intake) relative to costs (e.g., from swimming) at a given location (Fausch 1984, Hughes and Dill 1990), and ultimately the distribution of usable habitat and potential fish production across a landscape (Chapman 1966, Poff and Huryn 1998, Rosenfeld and Taylor 2009).

The physical environment (e.g., depth, velocity, substrate) differs markedly across constituent channel units within stream reaches; for instance, between shallow, high-velocity riffles and deep, lower-velocity pools (Jowett 1993, Montgomery and Buffington 1997). While pool-riffle channel structure has well-documented effects on individual- and population-level performance attributes of fish (e.g., Bisson 1988; Rosenfeld and Boss 2001; Sharma & Hilborn 2001), how this variation in channel form influences drifting prey is less well understood. This knowledge gap is surprising given the large body of work on drift (reviewed in Brittain & Eikeland 1988; Naman et al. 2016), and that spatial variation in benthic invertebrate abundance is well described (e.g., Downes et al., 1993).

The abundance of drift, generally measured as a concentration (e.g., number or mass of animals per volume), is determined by the relative rates of invertebrate entrainment into suspension from the benthos (hereafter “drift production”), and exit from suspension through settlement, predation, or emergence (hereafter “depletion”). Because of the well-known influence of hydraulics on both entrainment and settlement, some have posited a source-sink model in which drift abundance (hereafter used synonymously with concentration) increases in

riffles and decreases in pools (Poff and Huryn 1998, Rosenfeld and Raeburn 2009). While conceptually intuitive, support for this hypothesis is surprisingly mixed (Naman et al. 2016). One source of ambiguity is that drift production is rarely measured directly; instead, drift concentration is used as a surrogate (e.g., Leung et al. 2009). Thus, it is conceivable that drift production is spatially homogenous and that it is actually differences in depletion rates that drive spatial variation in abundance (Lancaster et al. 1996, Oldmeadow et al. 2010).

A related issue is that concentration does not provide a clear indication of where drift originates. Consequently, spatial mismatches between where drift is measured and where it was produced may occur (Naman et al. 2016), so that habitat effects on drift production (i.e., differences between channel unit types) may be obscured if drift is homogenized over short channel units (e.g., Leung et al. 2009). Fully resolving source-sink vs. spatially constant drift therefore requires measuring drift production directly in pools and riffles, which has not been attempted in the field.

Regardless of whether drift production exhibits source-sink or spatially constant patterns, riffles in small streams serve a key function of prey refuge and regeneration because of hydraulically harsh conditions that minimize drift-foraging by fish (Rosenfeld and Boss 2001, Harvey et al. 2006). For a given discharge, the total drift produced and exported from a riffle (hereafter “drift flux”) will influence both the individual growth potential and total capacity of fish occupying suitable habitats downstream (Hayes et al. 2007, Weber et al. 2014). Assuming production and depletion are in equilibrium, drift flux should be a product of the drift production rate and the distance that drift is suspended (Larkin and McKone 1985, Elliott 2002). This leads to the prediction that drift abundance should increase longitudinally within a riffle and that longer riffles should export more drift on average (Rosenfeld and Raeburn 2009). However, drift

distances can be short in small streams (e.g., Elliott 1971) such that riffle length effects on drift flux and concentration may be non-linear, with an asymptote corresponding to the average drift distance. This simple model has some empirical support (Hansen and Closs 2007) but has not been rigorously tested.

Terrestrial invertebrate inputs are also an important source of prey for drift-feeding fish, in some cases contributing more to annual fish production than *in situ* resources (Kawaguchi and Nakano 2001, Sweka and Hartman 2008). While many studies have addressed temporal patterns in terrestrial inputs (e.g., Edwards and Huryn 1995, Rundio and Lindley 2008), or spatial variation across stream sizes (Wipfli and Baxter 2010, Syrjanen et al. 2011) and vegetation types (Wipfli 1997, Allan et al. 2003), spatial patterns of terrestrial inputs within forested streams remain poorly understood. In principle, terrestrial drift should be governed by processes unrelated to pool-riffle channel structure. Consequently, source-sink drift patterns may be reduced if terrestrial inputs compose a large portion of total drift. Still, assuming spatially homogenous input rates, terrestrial drift flux should increase with upstream riffle length and surface area.

In addition to total abundance and biomass, the body size distribution of drifting invertebrates is an important determinant of the availability and quality of prey to salmonids (Hayes et al. 2000, Esteban and Marchetti 2004, Dodrill et al. 2016). Larger bodied prey are more easily captured (Wankowski 1981, Bannon and Ringler 1986), provide greater energetic benefits, and influence the distribution of resources among conspecifics (Nielsen 1992). There is some evidence that terrestrial prey are larger than aquatic prey (Nielsen 1992, Li et al. 2016) but there may also be size differences between aquatic invertebrates drifting from pools and riffles due to differences in benthic community structure (Robinson and Minshall 1986), or hydraulic

entrainment thresholds (Statzner 1987, Wilzbach et al. 1988) that select for entry of larger bodied individuals into the drift.

To better understand how stream channel structure influences invertebrate drift and prey availability for drift-feeding fish, we used a novel method to estimate production of aquatic and terrestrial drift in riffles and pools across three small, forested streams. Specifically, we predicted that: (1) drift production would exhibit source-sink patterns leading to greater production in riffles than pools; (2) when examined separately, terrestrial drift would be unrelated to pool-riffle channel structure; (3) drift flux and concentration would increase with riffle length with a possible asymptote corresponding to the average drift distance; and (4) body sizes of terrestrial drift would be larger on average than aquatic drift and body sizes of aquatic drift would be larger on average from riffles than pools.

Methods

Between July 14th and 21st, 2014 we sampled three coastal forest streams in the Sunshine Coast region of southwest British Columbia, Canada, 50 km north of the city of Vancouver, Canada. Streams drained separate catchments composed primarily of second-growth forest dominated by western red cedar *Thuja plicata*, Douglas-fir *Pseudotsuga menziesii*, bigleaf maple *Acer macrophyllum*, and red alder *Alnus rubra*, and had similar physical characteristics including channel gradient, width, and discharge (Table 1). In each stream, we selected channel units with the goal of sampling representative pools and a gradient of riffle lengths. To quantify physical habitat characteristics in each channel unit, we measured 3-6 lateral transects of depth and velocity at 20 cm intervals using a Marsh McBirney[®] flow metre (Hach Company, Loveland, CA), visually estimated substrate composition in each transect, and estimated canopy cover using a densiometer.

Measuring the drift produced in each channel unit necessitated blocking incoming drift from adjacent upstream habitat. To this end, we constructed wide drift nets consisting of 250 μ m Nitex mesh attached to wooden rectangular frames that were customized to span the channel width at the upstream and downstream end of each habitat unit. Each frame was designed to fit into a wooden sill, which we attached to a flat board to function at the upstream and downstream end of each channel unit. Three days prior to drift sampling, we semi-buried the slotted sills in the substrate perpendicular to flow across the upstream and downstream end of each unit, taking care to create minimal disturbance to the benthos (Fig. 1a). To ensure that sills were sealed to the benthos, we attached 10 cm strips of pond liner to the wooden sills and buried the liner flush with in the substrate. We avoided structurally complex channel units (e.g., those with wood or undercut banks) because of the difficulty installing block nets with minimal disturbance.

Drift sampling was initiated by carefully sliding the upstream net into the slotted sill from the stream bank (Fig. 1b), then repeating this procedure 15 minutes later for the downstream net to allow any disturbance from installing the upper net to subside. Nets remained in place for 2-4 hours between 1100 and 1600 after which we collected the contents of downstream nets. Captured material was stored in 70% ethanol for subsequent identification. To ensure that sampling introduced minimal benthic disturbance, we compared depth and velocity transects (3-6 per habitat) measured 3 days prior to sampling to measurements directly after the downstream nets were removed. We rejected samples where depth or velocity changed more than 10%. While we originally intended to sample 8 pools and 8 riffles in each stream, these screening criteria reduced sample size to 5 riffles in three streams and 3 pools in two streams (Coho Creek and Cook Creek).

Coastal cutthroat trout *Oncorhynchus clarkii clarkii* and coho salmon *O. kisutch* were present in all study streams and could potentially influence results if drift consumption was substantial (e.g., Leung et al. 2009). To minimize this source of bias, we chased fish out of pools from the stream bank using long-handled dip nets prior to installing downstream drift nets, taking care not to disturb the benthos. We then snorkelled through each pool after drift sampling to account for any remaining fish. Across all pools, only 3 trout (all < 50 mm fork length) were present, suggesting drift predation had minimal influence on our results. To avoid benthic disturbance, we did not attempt to remove fish from riffles, but assume that predation was negligible given shallow depths and high velocities that likely minimized fish foraging.

We identified all invertebrates to the lowest practical taxonomic level (usually genus for aquatic invertebrates, family or order for terrestrials) and enumerated all individuals in each sample. To estimate biomass, we measured body lengths of a random subset of individuals (up to 30 for each taxon and sample) using an ocular micrometer, then used published equations to convert length to mass (Hodar 1996, Benke et al. 1999, Sabo et al. 2002). We then categorized each taxon as aquatic larvae (hereafter “aquatic”), adult aquatic, or terrestrial, distinguishing adult aquatic and terrestrial invertebrates based on whether a taxon has an aquatic juvenile life stage. We did not include adult aquatic insects in the habitat-specific estimates of drift production because we could not determine with certainty if they originated in the same channel units they were captured in. However, adult aquatics were included in analyses of total drift flux and concentration.

Drift flux was computed as the total number or biomass of drift exported per hour (e.g., Wooster et al. 2016, Naman et al. 2017). To account for size differences among streams, we divided drift flux measurements by the wetted width of each habitat unit to generate a

standardized specific flux rate per metre width of channel (number or $\text{mg}\cdot\text{h}^{-1}\cdot\text{m}^{-1}$). Within streams, variation in wetted width was low (i.e., less than 0.3 metres) such that this standardization did not influence relative fluxes among riffles. We also computed drift concentration at the outlet of each riffle as the number or mass of invertebrates per volume of water filtered through each drift net. Drift production was computed as the quotient of drift flux and the area of habitat over which it was sampled (i.e., drift entry rates $\text{m}^{-2}\cdot\text{h}^{-1}$). Because variation in wetted width among habitats was small relative to variation in length, these estimates also approximated production expressed as drift flux per length of stream channel. Note that our drift production measurements are a net production rate and include both drift entry and resettlement within channel units.

Data Analysis

Drift production in pools and riffles

We used two-way analysis of variance (ANOVA) to test for differences in drift production (number or biomass $\text{m}^{-2}\text{h}^{-1}$) between pools and riffles. Stream was treated as a two-level factor variable (note that pools were only sampled in two of the three study streams). We used Levene's test to validate assumptions of homogenous variances and $\log+1$ transformed any cases that deviated from normality. Because the design was unbalanced ($n = 10$ riffles and 6 pools), we computed F -statistics using Type 3 sum of squares with the *car* package (Fox and Weisberg 2010) in R version 3.2.2 (R Core Team 2013). To quantify uncertainty around drift production estimates for pools and riffles, we computed 95% confidence intervals using a nonparametric bootstrapping procedure ("basic method"; Puth et al., 2015). We did not incorporate the different streams into the bootstrap resampling because we found no differences in drift production between them (see *Results* Table 2).

Drift flux and riffle lengths

We used an information theoretic approach with linear mixed effects models to examine how drift flux and concentration varied across a gradient of riffle lengths. Response variables included total drift flux (number or biomass $\text{h}^{-1} \text{ m channel width}^{-1}$) and fluxes of aquatic and terrestrial prey categories separately. Because concentration (number and mg m^{-3}) exhibited responses that were similar to drift flux, we only report results for total concentration to reduce redundancy. For each response we formulated a set of models including riffle length as a fixed effect and stream as a random intercept ($n = 5$ riffles per stream in three streams). We included canopy cover as an additional fixed covariate in models for all responses, and mean velocity (m sec^{-1}) and depth (m) as additional fixed covariates for total and aquatic drift flux. Substrate was similar across all riffles so was not included in the analysis. To address the hypothesis of an asymptotic relationship corresponding to riffle length exceeding average drift distances, some candidate models for each response included $\log(+0.5)$ transformed (hereafter “pseudo threshold”) riffle length as a predictor (Franklin et al. 2000). Each candidate set (3-5 models) also included a null model, which included only a random intercept.

We evaluated candidate models using Akaike’s Information Criteria corrected for small sample sizes (AIC_c), with more parsimonious models getting lower AIC_c scores (Burnham and Anderson 2002). We considered a model to have strong support if the deviation of its AIC_c score from that of lowest scoring model in the set (ΔAIC_c) was less than 2 (Burnham and Anderson 2002). We also calculated AIC weights (W_i), which represent the probability a given model is the best fitting model in the candidate model set. For models with strong support, we evaluated fixed effects by examining whether 95% confidence intervals around the slope estimates overlapped

zero and overall model fits by computing marginal and conditional R^2 , which represent the variance explained by the fixed and fixed plus random effects, respectively (Nakagawa and Schielzeth 2013). We conducted all analyses in R using the *lme4* (Bates et al. 2015) and *MuMin* packages in R (Bartón 2009).

Many aquatic taxa have behavioural adaptations to shorten or prolong their time in drift (e.g., Elliott, 2002), and variation in drift distances among taxa could obscure community-level longitudinal drift patterns. To explore this possibility, we examined the relationship between drift flux and riffle length for four abundant taxa presenting a range of behavioural control over drift distance. Baetidae and Simuliidae both have substantial behavioural control over drift entry and settlement (Allan and Feifarek 1989, Fingerut et al. 2006), thus we predicted a weaker relationship with riffle length. In contrast, Dixidae and Chironomidae are frequent drifters but lack sophisticated behavioural and morphological adaptations to exit drift once entrained (Rader 1997). Therefore we predicted the flux of these taxa to show stronger positive relationships with riffle length. For each taxa, we used the same model selection approach described above.

Individual body size and community structure

To describe the size structure of drifting invertebrates we compared several attributes of the body mass-frequency distribution between aquatic and terrestrial drift and between aquatic drift in riffles and pools. For mean individual body mass, we first performed two-sample *t*-tests on group means, and then used non-parametric bootstrapping to generate 95% confidence intervals. To examine differences in median body mass, we used a two-way permutation test (10,000 iterations) for group medians following the procedure outlined in Good (2013) and nonparametric bootstrapping to estimate 95% CIs. We were also interested in the skewness of

the size distribution, which indicates the degree to which total biomass was driven by large individuals. We used the resampling procedure described above to create distributions based on group means and standard deviations, then used a two-way permutation test to compute exact P -values testing differences in skewness between groups. More positive skewness values indicate a more right-tailed distribution (i.e., skewed toward more small invertebrates; Groeneveld & Meedan, 1984).

To examine compositional differences in aquatic prey between riffles and pools we used a permutational analysis of variance (PERMANOVA) with the *adonis* function in the R package *vegan* (Oksanen et al. 2013). PERMANOVA computes a pseudo F-statistic and P values based on stratified permutations of the data ($n = 999$) to test the null hypothesis that the taxonomic composition is more similar within vs. among groups (Anderson 2001). Channel type (pool or riffle) was treated as a fixed effect in our model and stream identity served as strata.

Results

Across all drift samples, aquatic taxa were four times more abundant than terrestrials. The dominant taxa were larval and adult Chironomidae, Baetidae, Dixidae, and Simuliidae, together comprising over 62% of the total abundance. The three most abundant terrestrial taxa were adult Psocoptera, Collembola, and Araneae, comprising 12% of the total abundance. Despite these large differences in abundance, total biomass was similar between aquatic (total 281 mg dry mass for all samples combined) and terrestrials (261 mg dry mass for all samples). In terms of biomass, the dominant taxa were adult Chironomidae (24%), adult Psocoptera (13%), and Araneae (5%). Larval Baetidae, Simuliidae, and chironomids comprised a combined 11% of total

biomass. Contrary to expectations, there was no evidence for distinct drift community structures between pools and riffles (PERMANOVA, $F_{1,14} = 0.83$, $P = 0.62$).

Differences in drift production between pools and riffles

Total drift production (biomass and number $\text{m}^{-2} \text{h}^{-1}$) and aquatic drift production (biomass $\text{m}^{-2} \text{h}^{-1}$) were significantly greater in riffles than pools (Table 2). Riffles produced 3.5-3.6 times more drift per area of streambed (Fig. 2), supporting the source-sink hypothesis. As predicted, terrestrial drift production did not differ significantly between habitat types (Table 2). Although the mean production of terrestrial drift biomass appears larger in riffles (Fig. 3), this was primarily driven by inputs of several anomalously large terrestrial Coleoptera larvae in one riffle in Cook Creek. Interestingly, despite differences in discharge, drift production did not vary significantly among streams (Table 2) even when production in riffles were compared separately with Snake Creek included (ANOVA, $F_{2,12} = 1.4$, $P = 0.28$).

Effects of riffle length on drift flux

As predicted, the total flux of drift out of riffles increased with riffle length (Fig. 3). For total numeric flux (number $\text{h}^{-1} \text{m}^{-1}$), the top-ranked model included a linear effect of riffle length ($W_i = 0.54$) and explained 37% of the variation. A non-linear (pseudo-threshold) model also had empirical support ($\Delta\text{AIC} = 0.37$; $W_i = 0.45$), and explained 25% of the variation (Table 3). For biomass flux, the top ranked model included a pseudo-threshold term ($W_i = 0.62$), which explained 27% of the variation. For both responses 95% confidence intervals around the slope estimates did not overlap zero (Table 3). When we analyzed the aquatic and terrestrial drift separately, there was only weak support for any of the fixed effects (Table 3) and top ranked

models explained less than 10% of the variation. Canopy cover, mean velocity, and depth had little support to explain drift flux and were not included in plausible models for any responses.

Drift fluxes of individual taxa differed in their response to riffle length. Fluxes of Baetidae and Simuliidae were weakly related to riffle lengths, as the top ranked models explained less than 10% of the variance and confidence intervals around slopes overlapped zero (Table 3). In contrast, models including pseudo-threshold terms had the most support explaining longitudinal increases in Chironomidae ($W_i = 0.73$) and Dixidae ($W_i = 0.79$) flux, and 95% CIs around slope estimates did not overlap zero (Table 3). Dixidae exhibited the strongest relationship, with riffle length explaining 48% of the variation in drift flux (Fig. 5).

Drift concentration was also positively related to riffle length (Fig. 4). For numeric concentration, a linear effect of riffle length had the most support ($W_i = 0.67$) and explained 83% of the variation. For biomass concentration, there was support for models including both nonlinear ($W_i = 0.39$) and linear terms ($\Delta AIC = 1.1$; $W_i = 0.22$) in addition to an intercept only model ($\Delta AIC = 0.1$; $W_i = 0.38$). 95% confidence intervals did not overlap zero for both numeric and biomass concentration (Table 3).

Aquatic and terrestrial invertebrate body size

Individual body mass of aquatic invertebrates drifting from riffles was ~5 times greater on average than those from pools (t -test = 3.15, $df = 493$, $P < 0.01$), and terrestrial body mass was 3.5 times greater on average than aquatic (t -test = 3.44, $df = 185$, $P < 0.01$). Chilopoda, Formicidae, and Hymenoptera were the largest terrestrials, while Gammaridae, Perlidae, and Hydropsychidae were the largest aquatics. Median body mass was also larger for aquatics from riffles relative to pools (Two-way permutation, exact $P = 0.005$), and for terrestrials relative to aquatics (two-way permutation test $P = 0.007$). Body mass-frequency distributions were right

tailed for all invertebrates but did not differ between riffles and pools ($P = 0.2$). In contrast, mass-frequency distributions differed between terrestrials and aquatics (Fig. 6). Skewness values were ~3 times lower in terrestrials (Table 5) indicating that rare, large individuals had a larger influence on overall terrestrial biomass than aquatics.

Discussion

Our observation of greater drift production in riffles than in pools supports source-sink dynamics and suggests that previously demonstrated differences in drift concentration between habitats (e.g., Leung et al. 2009) may be driven by spatial variation in drift production as well as drift depletion (i.e. settling or consumption in pools). Given that our study is observational, we cannot confirm the mechanisms that underlie this pattern. One possible explanation is that hydraulic stress and turbulent flows in riffles are more likely to dislodge invertebrates from the benthos as well as make it more difficult for settlement relative to pools, which are more hydraulically benign at low flows (Jowett 1993). In addition, benthic densities and productivity are often greater in riffles (Brown & Brussock 1991; Grubaugh et al. 1997; but see Halwas et al. 2005), which may lead to higher drift (Hammock and Wetzel 2013, Weber et al. 2014).

While pool-riffle differences in drift production could also be influenced by contrasting community structures, e.g., if riffles included more drift prone taxa (Scullion et al. 1982), we were surprised to find similar drift composition between the two channel unit types. Leung et al. (2009) also found similar community structure between drift in pools and riffles, which they attributed to drift being homogenized over short channel units. This is a less plausible explanation for our results given that we blocked drift from adjacent upstream channel units. While differences may have emerged with greater replication, another possibility is that the process of drift essentially selects for a consistent set of taxa from the benthos; for instance,

epibenthic taxa prone to dislodgement or behavioural drift entry (Rader 1997). Within this subset of taxa, riffle-pool differences in body size indicate more nuanced effects of habitat type on the physical and behavioural drivers of drift. For example, higher velocities and greater turbulence in riffles may have exceeded entrainment thresholds for larger bodied individuals or reduced their settling rates (Statzner 1987), or larger individuals in pools may have suppressed their tendency to drift as a tactic to reduce predation risk (e.g., Poff et al. 1991, Peckarsky 1996).

Our prediction of greater drift fluxes out of longer riffles was generally supported as the total number and mass of exported drift increased with riffle length. Upstream riffle length was also a significant predictor of total drift concentration, which increased over 10 fold across the gradient of sampled riffle lengths. There was some evidence for a saturating relationship; however, drift flux and concentration were both still increasing across the range of riffle lengths we sampled, suggesting that the average distance for total aggregate drift likely exceeds the length of our longest riffle (~10 m). This is not surprising given that total drift flux and concentration integrated all taxa, including terrestrial and adult aquatic invertebrates that lack the capacity to exit the drift once entrained. For small forest streams with typically short channel units (e.g., Montgomery et al. 1995), this suggests that long riffles may be key areas of drift generation and that adjacent downstream habitats may have particularly high capacity to support drift-feeding fish.

Interestingly, riffle length was a poor predictor of drift flux when categories (aquatic vs. terrestrial) were examined individually. For aquatic-derived drift, the lack of relationship likely results from the integration of multiple taxa with strong differences in ecology, behaviour, and life history. In a similar study in a small New Zealand stream, Hansen and Closs (2007) found that relationships between drift abundance and riffle length were less apparent for Baetid

mayflies compared to Trichoptera species, suggesting that behavioural influences on drift distances can obscure longitudinal patterns. Our results support this inference as Baetidae and Simuliidae, which have sophisticated control of resettlement from drift (Otto and Sjöström 1986, Fingerhut et al. 2006), were not influenced by riffle length. In contrast, Dixidae and Chironomidae, which have less control over resettlement (Rader 1997), exhibited positive saturating relationships where drift abundance continued to increase downstream.

For particularly drift-prone taxa like Baetidae, some estimates of drift distances at similar velocities to our study are less than 2 m (Elliott 1971, Townsend and Hildrew 1976), which we would not have been able to detect with the range of riffle lengths we sampled (i.e., Baetidae drift concentration may asymptote at a 2 m riffle length). Our overall regression model relating total drift flux to riffle length gives further insight into how short drift distances may have influenced our results. If we assume the true intercept of the relationship between riffle length and total numeric flux is zero (i.e., no invertebrates drift from a length of zero), the model predicts that ~30 individuals enter the drift within the first metre (Fig 3A). Considering that the model predicts drift flux will increase by only an additional 50 individuals over the next 9 metres, this suggests a highly skewed distribution of drift distances with many invertebrates drifting less than 1 metre. This is consistent with numerous studies that have used a negative exponential function to describe the number of invertebrates in suspension downstream from a known release point (McLay 1970, Larkin and McKone 1985, Elliott 2002).

Riffle length was a poor predictor of terrestrial drift flux, suggesting that input rates vary strongly over space. In our case, terrestrial drift seemed to vary haphazardly among habitats irrespective of canopy cover. In addition, despite being nearly equal to aquatic drift in terms of total biomass, the contribution of terrestrial invertebrates to drift appeared to be driven by

infrequent inputs of large-bodied individuals as evidenced by larger mean and median body sizes, and lower skewness relative to aquatics. While spatial patterns may have emerged with greater replication, other studies have also found substantial variability in terrestrial inputs over relatively small areas (Wipfli 1997, Rosenfeld and Raeburn 2009). Taken together, these results suggest drivers of terrestrial input rates (e.g., invertebrate activity levels, wind and rain; Baxter et al. 2005) are unrelated to pool-riffle channel structure and that this source of prey may not be spatially predictable within stream reaches. However, more work linking input rates to drivers of riparian arthropod abundance (e.g., vegetation composition, microclimates (Allan et al. 2003, Henshall et al. 2011) could clarify this issue.

While our work addresses a considerable knowledge gap about drift in small streams, we are cautious not to over interpret our results given the limited sample size and substantial unexplained variability. Further, inference should be restricted to daylight during summer low flow conditions as our study was not replicated seasonally and it is unclear as to whether the spatial patterns we observed are persistent. In a similar study, Hansen and Closs (2007) found that spatial patterns in drift were consistent over time. By contrast, others have observed smaller differences among habitat types at higher discharges (Leung et al. 2009, Gibbins et al. 2010, Barbero et al. 2013). It is also worth noting that we did not sample more structurally complex habitats (e.g., those with wood) due to logistic challenges installing block nets and removing fish. We suspect that structural complexity would have greater influence on transport and settling rates than production (e.g., Bond et al., 2000; Kiffney et al., 2014), although wood can enhance invertebrate production and drift in some cases (Benke and Wallace 2003, Gustafsson et al. 2014).

Given that so few studies have attempted to measure drift production (as opposed to drift concentration), there are limited published data for comparison. Romaniszyn et al. (2007) used a similar blocking technique over larger sections (~40 m) of Appalachian streams. Their hourly estimates of aquatic and terrestrial drift production ($0.15\text{--}3\text{ mg m}^{-2}\text{ h}^{-1}$) are similar to ours ($\sim 0.2\text{--}6\text{ mg m}^{-2}\text{ h}^{-1}$), although direct comparison is complicated by differences in methodology (e.g., mesh size, sampling area). Other studies have indirectly inferred spatial variation in drift production. For instance, Poff and Huryn (1998) proposed a 3.5:1 drift production ratio between riffles and pools based on measured pool-riffle differences in benthic production (Huryn and Wallace 1987, Grubaugh et al. 1997). The pool: riffle drift production ratio we observed (~ 3.5 for total drift) is remarkably similar to their estimate suggesting a possible link between benthic and drift production (Waters 1966). However, more data are clearly needed to determine if this result is generalizable.

It is surprising that research into the processes generating spatial heterogeneity in drift is so scarce given that spatial variation in benthic abundance is so well studied (e.g., Downes et al. 1993, Wiens 2002). In principle, spatial variation in drift abundance should occur through changes in the relative rates of production (drift entry) and depletion (Naman et al. 2016). For example, reduced drift abundance in hydraulic dead zones likely results from increased settlement without commensurate increases in production (Bond et al. 2000). In this sense, there may be spatially discrete “patches” of homogeneous drift concentration where production and depletion rates are in relative equilibrium. Our results, along with other work on drift transport (Lancaster et al. 1996, Wilcox et al. 2008) and concentration (Leung et al. 2009), suggests that hydraulic gradients across distinct channel units may contribute to this spatial structure. However, similar to benthic abundance, which differs strongly over microhabitat gradients

(Downes et al. 1993, Brooks et al. 2005), rates of drift production and depletion may also vary at small scales *within* channel units; for instance from turbulence (Blanckaert et al. 2013), and lateral settling at channel margins (Ciborowski 1983). In essence, the benthos and drift can be conceptualized as vertically layered patches linked by drift entry and settlement. Whether these patches are spatially congruent is largely an open question and depends on the spatial scale of variation in drift production and depletion and the corresponding extent of homogenous drift patches.

Implications for drift-feeding fish

A corollary of the source-sink drift production patterns demonstrated in our study is that reach-scale pool-riffle configuration is an important control of prey production for drift-feeding fish. This is a key insight into the functional roles of contrasting habitat types within lotic ecosystems and supports the perspective of Poff and Huryn (1998) who proposed a fundamental trade-off between trophic (riffle) and non-trophic (pool) habitats such that reach-scale fish production should be optimized at intermediate pool-riffle combinations. While this trade-off is generally supported (Bowlby and Roff 1986, Rosenfeld 2014), it remains poorly defined in a quantitative sense. Our results provide a starting point for future empirical and modelling work aimed at more clearly defining the influence of habitat configuration (e.g. relative areas, adjacency, and interspersions of pools and riffles) on trophic transfer and reach-scale fish production in small streams. This line of research, along with investigations into factors governing benthic production (e.g., light and nutrients; Kiffney et al. 2004), is fundamental to understanding the controls on productive capacity as well as optimizing channel design in restoration projects.

Quantifying source-sink drift patterns may also inform drift-foraging bioenergetics models, an increasingly common strategy to assess habitat capacity for fish (Piccolo et al. 2014,

Rosenfeld et al. 2014). Many applications of these models to date make simplifying assumptions that drift concentration is spatially uniform (Stark et al. 2002, Jenkins and Keeley 2010, Urabe et al. 2010). In addition to other factors (e.g., benthic foraging; Harvey and Railsback 2014), assuming spatial uniformity in drift may contribute to deviations between predicted and observed capacity estimates (Wall et al. 2016). In more complex models that include spatially explicit drift components (Hayes et al. 2007, 2016, Anderson et al. 2013), parameterizing drift entry rates is a crucial source of uncertainty. For small streams, our production estimates could be useful to validate modelled entry rates if the scale of interest is whole channel units. Alternatively, our predicted drift fluxes at short riffle lengths could provide reasonable estimates of instantaneous drift entry if smaller scales (e.g., foraging territories) are of interest.

Descriptive field data similar to those presented here are important for validating and refining drift transport and drift-foraging models (Hayes et al. 2016), and ultimately for integrating both food and space into the management and conservation of drift-feeding fish populations (Chapman 1966). This is an important task given the precipitous declines of many species of drift feeders and large and costly efforts directed at restoring habitat to increase their production.

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Tables

Table 1. Site characteristics of the three sampled streams. Depth and velocity are averaged across each habitat type and stream. Bankfull width and gradient are from Rosenfeld et al. (2000). We did not sample pools in Snake Creek.

Table 2. Results from two-way ANOVAs (type 3 SS) testing the effects of stream and habitat type on various drift production metrics. Significant P values (< 0.05) are in bold.

Table 3. Linear mixed effects models explaining variation in drift flux ranked by AIC_c scores. Abbreviations are as follows: L-L is the log likelihood; ΔAIC_c is the difference between the AIC_c score of a model and the best fitting model in the set; W_i is the probability model i is the best fitting model in the set; R^2_m represents the proportion of variation explained by fixed effects only, and R^2_c represents the amount of variation explained by fixed and random effects. Slopes of fixed effects (β_1) are included when 95% confidence intervals did not overlap zero; β_0 is the fixed intercept. Each model included stream as a random intercept term. The fixed components of the pseudo-threshold models are of the form: $\theta = \beta_0 + \beta_1 \log_e(x_1)$. Only models with ΔAIC_c values less than 2 are shown.

Table 4. Estimates of mean and median individual body sizes for drifting invertebrates. Numbers in parentheses are bootstrapped 95% confidence intervals.

Figures

Figure 1. Overview of drift sampling protocol. (A) Shows the slotted wooden sill positioned across the top of a riffle. (B) Shows the drift net slid into the slot to intercept drift entering the channel unit. Note that A is looking upstream while B is looking downstream.

Figure 2. Estimates of drift production in riffles (filled circles) and pools (open circles). Left panels are total drift and right panels are separated into aquatic and terrestrial. Error bars represent bootstrapped 95% confidence intervals.

Figure 3. Total drift flux in counts (a) and biomass (b) as a function of riffle length. Lines represent the top ranked linear mixed effects model fitted to the entire data set. Shaded areas represent 95% confidence regions. Symbols represent different streams: Coho (triangles), Cook (circles), and Snake (squares).

Figure 4. Total drift concentration in counts (a) and biomass (b) as a function of riffle length. Lines represent the top ranked linear mixed effects model fitted to the entire data set. Shaded areas represent 95% confidence regions. Symbols are the same as Figure 3.

Figure 5. Drift flux of Baetidae, Simuliidae, Dixidae, and Chironomidae as a function of riffle length. Lines represent the best fitting mixed effects model fitted to the entire dataset. Shaded area represents the 95% confidence region around the regression line. Regression lines are not shown for Baetidae and Simuliidae because 95% confidence intervals around the slope overlapped zero. Symbols are the same as Figures 3 and 4.

Figure 6. Probability density histograms for individual body sizes (mg) of aquatic and terrestrial invertebrates. Body sizes are sorted into 0.1 mg bins. The total area under the bars sums to 1.

838

839 **Table 1.**

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Table 2.

Factor	Type III SS	F _{1,13}	P value
<i>Total biomass (mg m⁻² h⁻¹)</i>			
Stream	0.09	0.01	0.92
Channel unit type	45.4	4.69	0.04
Residual	125.96		
<i>Total Count (num. m⁻² h⁻¹)</i>			
Stream	1.44	2.94	0.11
Channel unit type	2.62	4.47	0.05
Residual	6.32		
<i>Aquatic biomass (mg m⁻² h⁻¹)</i>			
Stream	2.02	3.28	0.09
Channel unit type	4.05	6.55	0.02
Residual			
<i>Aquatic count (num. m⁻² h⁻¹)</i>			
Stream	2.7	4.01	0.06
Channel unit type	2.1	3.55	0.08
Residual	7.12		
<i>Terrestrial Biomass (mg m⁻² h⁻¹)</i>			
Stream	8.69	1.19	0.3
Channel unit type	11.99	1.65	0.23
Residual	80.15		
<i>Terrestrial Count (num. m⁻² h⁻¹)</i>			
Stream	4.22	0.65	0.44
Channel unit type	18.26	2.87	0.12
Residual	71.53		

859 Table 3

Model	k	L-L	AIC _c	ΔAIC _c	W _i	R ² _m	R ² _c	β ₁ (95% CI)	β ₀
<u>Drift Flux</u>									
Total count (<i>n h⁻¹ m⁻¹</i>)									
Length	4	63.41	138.81	0	0.54	0.37	0.5	6.85 (2.06-11.6)	26.45
Log(length + 0.5)	4	63.59	139.18	0.37	0.45	0.25	0.36	19.56 (0.37-38.7)	31.97
Total mass (<i>mg h⁻¹ m⁻¹</i>)									
Log(length + 0.5)	4	43.42	98.83	0	0.62	0.27	0.27	4.96 (0.18-9.74)	1.04
Length	4	44.32	100.64	1.8	0.25	0.19	0.2	1.2 (0.26-2.13)	3.48
Aquatic Mass (<i>mg h⁻¹ m⁻¹</i>)									
Log(length + 0.5) + V	5	29.81	76.28	0	0.53	0.17	0.39	----	2.92
Terrestrial Mass (<i>mg h⁻¹ m⁻¹</i>)									
Intercept	3	18.53	45.23	0	0.93			----	1.45
Baetidae (<i>n h⁻¹ m⁻¹</i>)									
Log(length + 0.5)	4	44.53	101.05	0	0.48	0.01	0.49	----	10.25
Intercept	3	46.55	101.29	0.24	0.43				8.27
Simuliidae (<i>n h⁻¹ m⁻¹</i>)									
Log(length + 0.5)	4	40.98	93.96	0	0.57	0.09	0.09	----	8.96
Intercept	3	43.41	94.99	1.04	0.34				5.14
Dixidae (<i>num h⁻¹ m⁻¹</i>)									
Log(length + 0.5)	4	31.66	75.33	0	0.79	0.48	0.48	3.88 (1.50-6.26)	-0.62
Chironomidae (<i>n h⁻¹ m⁻¹</i>)									
Log(length + 0.5)	4	46.91	105.81	0	0.73	0.21	0.4	7.06 (0.27-13.8)	2.88
<u>Drift Concentration</u>									
Total count (<i>n m⁻³</i>)									
Length	4	6.76	-1.5	0	0.67	0.83	0.84	0.08 (0.06-0.11)	0.07
Log(length + 0.5)	4	6.04	-0.1	1.45	0.32	0.76	0.84	0.35 (0.23-0.46)	-0.03
Total mass (<i>mg m⁻³</i>)									
Log(length + 0.5)	4	24.66	-37.3	0	0.39	0.53	0.55	0.05 (0.02-0.07)	0
Intercept	3	22.73	-37.2	0.1	0.38			----	
Length	4	24.12	-36.2	1.1	0.22	0.53	0.58	0.012 (0-0.02)	0.02

Table 4

	Body Size (mg)		Skewness	<i>P</i> - value
	Mean	Median		
Aquatic	0.15 (0.11-0.19)	0.03 (0.02-0.04)	14.5	0.005
Terrestrial	0.57 (0.2-0.6)	0.15 (0.08-0.35)	5.3	
Riffles	0.18 (0.12-0.29)	0.04 (0.03-0.05)	12.6	0.20
Pools	0.05 (0.04-0.06)	0.02 (0.01-0.03)	8.1

Figure 1
81x60mm (300 x 300 DPI)