

Hydraulic and geomorphic effects on mayfly drift in high-gradient streams at moderate discharges

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ABSTRACT

We investigated relationships between geomorphic and hydraulic factors and invertebrate drift in high-gradient streams. We measured drift density of a highly mobile mayfly (*Baetis bicaudatus*) into and out of 12 stream reaches in western Colorado, as well as benthic density and abiotic variables within those reaches, during a time of moderate discharge. Multiple regression analysis indicated that drift propensity (drift density/benthic density), a measure of drift standardized by the benthic density of the source population, was significantly related to Reynolds number, a dimensionless ratio of fluid inertial forces to viscous forces, and Shields number, a dimensionless ratio of shear stress to submerged particle weight that quantifies flow competence. Drift propensity was positively correlated with Reynolds number, but counter to our hypothesis that stronger hydraulic forces would be associated with higher drift, mayflies in reaches with greater flow competence (Shields number) showed lower propensities to drift. Further, immigration ratio (drift in/drift out of each reach) increased significantly with Shields number, indicating that more individuals drifted into than out of reaches with higher flow competence. Although we hypothesized that more hydraulically rough stream reaches (i.e. those with greater flow resistance) would be more favourable to benthic invertebrates and would thus have lower drift, neither drift propensity nor immigration ratio were related to flow resistance. In high-gradient streams at discharges below the range of incipient motion of bed particles, mayfly drift behaviour may be influenced by hydraulic forces, but the relationships we observed are not indicative of passive, abiotically driven drift. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS drift; mayfly; ecogeomorphology; Reynolds number; Shields number; high-gradient streams; fluvial geomorphology; *Baetis*

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INTRODUCTION

Invertebrate drift, or the downstream movement of invertebrates in the water column, is likely influenced by some combination of biotic and abiotic factors whose relative importance varies spatially and temporally. Flow, associated hydraulic forces, channel morphology, and sediment transport are among the physical processes and properties that have been suggested to affect invertebrate drift (Waters, 1972; Hart and Finelli, 1999; Bond and Downes, 2003; Gibbins *et al.*, 2007).

Previous studies have linked increases in drift rates to increases in shear stress, velocity, and/or discharge. The clearest case of abiotically driven drift occurs in large floods, when the entire bed is mobilized and transport of bed sediments forces benthic organisms into the water column in what is sometimes referred to as catastrophic drift (Bond and Downes, 2003; Gibbins *et al.*, 2007). Under less extreme conditions, exceedence of bedload transport thresholds may produce marked increases in drift (Gibbins *et al.*, 2007). Even when the stream bed

is stable, increases in flow alone have been linked to increases in drift (Poff and Ward, 1991; Imbert and Perry, 2000; Bond and Downes, 2003; Mochizuki *et al.*, 2006). Maximum drift rates have been found to occur during the rising limb of flood hydrographs, with declines from this maximum occurring as the rising limb continues (Imbert and Perry, 2000; Robinson *et al.*, 2004; Mochizuki *et al.*, 2006), and with no correlation occurring between drift and peak flow magnitude or duration (Mochizuki *et al.*, 2006). Decreases in flow have also been linked to increased drift rates (Poff and Ward, 1991; Dewson *et al.*, 2007).

Relationships between invertebrate drift, hydraulics, and feeding conditions are often used to speculate about the mechanisms influencing entry of benthic organisms into the water column, i.e. whether drift is active (voluntary) or passive (involuntary) (Kohler, 1985; Fonseca and Hart, 1996; Lancaster, 1999). Furthermore, active drift mechanisms are often invoked to explain the observations that mayflies are more likely to drift nocturnally, when risk of predation by drift-feeding fish is lowest (Flecker, 1992; Douglas *et al.*, 1994; Huhta *et al.*, 2000; McIntosh *et al.*, 2002), or when benthic densities are highest (e.g. Hildebrand, 1974).

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Whereas drift is more likely to be abiotically driven under conditions of increasing or high hydraulic forces, studies of biotic factors affecting drift have primarily been carried out at low to moderate flows. However, the effect of abiotic processes on drift at stable, low to moderate discharges, below the threshold for mobilization and transport of bed materials, remains ambiguous.

Our study investigates how hydraulics and channel form affect mayfly drift in high-gradient streams under moderate flow conditions that are below the threshold for mobilization and transport of bed materials. We investigated the relationships between drift and abiotic conditions in both fish-bearing and fishless streams. We measured the drift of the highly mobile mayfly, *Baetis bicaudatus* Dodds, into and out of 12 study reaches (6 with fish and 6 fishless), mayfly densities within those study reaches, and geomorphic and hydraulic variables with potential relevance to invertebrate drift and abundance. From our field data, we have calculated a set of dimensionless variables describing flow hydraulics and channel form that are standard in fluid mechanics and fluvial geomorphology as a means of combining a large number of geomorphic and hydraulic variables into a smaller number of variables suitable for comparisons among streams at a range of scales. These dimensionless abiotic variables are used as explanatory variables in a multiple regression analysis of drift patterns.

We use the results of the multiple regression analysis to evaluate two general hypotheses about how hydraulics and channel morphology may influence drift in high-gradient streams. First, we hypothesize that even during periods of moderate flow, stronger hydraulic forces will be associated with higher drift, analogous to previously observed relationships between drift and velocity and/or shear stress under high-flow conditions. Second,

we hypothesize that more hydraulically rough stream reaches (i.e. those with greater flow resistance) will be more favourable to benthic invertebrates and will thus have lower drift. This hypothesis is based on the idea that in high-energy environments typical of mountain streams, the roughness and flow resistance generated by bed forms, channel banks, large particles, and woody debris (Bathurst, 1993; Curran and Wohl, 2003; Wilcox and Wohl, 2006) provide important habitat complexity and velocity refugia for aquatic organisms. This work builds on previous investigations in streams near the Rocky Mountain Biological Laboratory (RMBL) in the Colorado Rockies that have highlighted the effects of biotic controls, in particular, the presence or absence of drift-feeding fish, on mayfly drift, recruitment, size, and development rates (McIntosh *et al.*, 2002; Peckarsky *et al.*, 2001, 2002).

METHODS

Study area

We measured invertebrate drift, benthic density, and geomorphic and hydraulic variables in 45-m reaches of 12 streams in the upper East River basin, Colorado, near the RMBL (elevation ~ 2900 m) (Figure 1), in June/July 2003. The study streams have gradients ranging from 0.02 to 0.12 m/m; step-pool, cascade, step-riffle, or plane-bed morphology (using the Montgomery and Buffington, 1997 classification system); and drainage areas ranged from 0.05 to 45.9 km². Run-off in these streams is derived from snowmelt, groundwater, and convective rainstorms, with average peak discharges usually occurring in late spring to early summer (late May to early July).

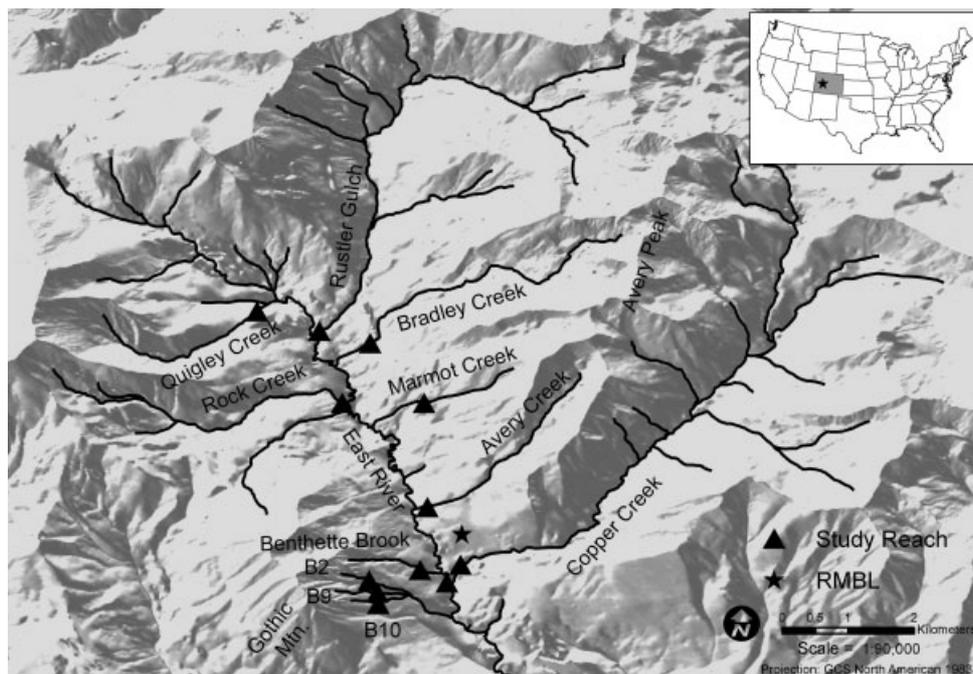


Figure 1. Study streams and digital elevation model of the upper East River basin, Colorado, USA (RMBL : Rocky Mountain Biological Laboratory).

The macroinvertebrate communities of the study streams are numerically dominated by mayflies, particularly *B. bicaudatus*, which are highly mobile and disperse downstream via drift (McIntosh *et al.*, 1999). Six of the stream reaches contain naturally reproducing populations of non-native brook trout, *Salvelinus fontinalis* (Mitchell). The remaining six study streams are fishless, generally as a result of the presence of natural barriers to fish migration (McIntosh *et al.*, 2002).

Invertebrate data collection and analysis

We estimated benthic densities in each reach by averaging six electrobug samples taken using a 0.09 m² sampler; this method employs electrofishing equipment to sample invertebrates without disturbing the substrate (Taylor *et al.*, 2001). We measured invertebrate drift one week after benthic samples were collected, within an 11-day period, on the falling limb of the annual snowmelt hydrograph. The number of *B. bicaudatus* larvae immigrating into and emigrating out of each reach was estimated by simultaneously blocking off the upstream and downstream ends of reaches with 200- μ m mesh Wildco (Wildlife Supply Company, Saginaw, MI, USA) drift nets just after dark, for 5–50 min. Sample lengths were determined on the basis of preliminary estimates of drift rates collected the previous year and were sufficient to collect large numbers of *Baetis*. Further, our previous experience in these streams indicates that drift does not change substantially over the course of one hour, suggesting that variations in sample length (i.e. between 5 and 50 min) are unlikely to have caused bias. Drift was normalized by dividing by stream discharge, producing drift density values (number drifting per m³ of water) into and out of each reach (immigration and emigration, respectively).

Discharge (Q) was calculated at each transect where drift was sampled by measuring wetted width (w), water depth (d), and flow velocity (v) using a Marsh-McBirney Model 201 (Frederick, MD, USA) electromagnetic current meter (ECM). The number of d and v measurements used to develop Q estimates (and used in other hydraulic calculations described below) varied with stream size, ranging from 3 per transect in the smallest streams up to 18 per transect in the East River. We estimated average discharge for each reach as the average of the discharges measured at the upstream and downstream ends of the study reaches. None of the reaches had tributary inflows between the upstream and downstream transects, and it is likely that the local geology limits flow gains or losses through the bed or banks within the study reaches. For the three largest streams (East, Copper, and Rustlers), available drift nets were not large enough to block the entire upstream and downstream widths of the study reaches. In those reaches, approximately 50% of the stream discharge was sampled with drift nets in an attempt to capture the largest possible number of drifting insects. Total immigration and emigration from the reaches was then estimated by extrapolating by the ratio of discharge sampled to the total discharge.

Next, the immigration-to-emigration ratio (drift in/drift out) of each study reach was calculated to determine whether reaches were gaining or losing individuals as a result of drift. Where the ratio of immigration to emigration >1, the reach was gaining individuals, and where the ratio was <1, the reach was losing individuals.

We also estimated the drift propensity of *Baetis* in each reach by dividing the drift density measured at the downstream transect by the benthic density in the study reach (McIntosh *et al.*, 2002). Drift propensity thereby provides a measure of drift standardized by the benthic density of the source population, assuming that the mean benthic density for the reach upstream of each drift net is representative of the benthic density in the areas where individual mayflies enter the water column. All biological parameters were estimated using total individuals of *Baetis*, which were primarily in late instars at the time of the study (Stage III: wing pads elongating and females developing eggs).

We tested for differences in drift density, drift propensity, benthic density (all log-transformed), and immigration ratio (square-root transformed) between the six fishless and six fish streams using MANOVA followed by univariate ANOVA when the MANOVA was significant. These tests were completed to gain insight into whether potential relationships between abiotic factors and drift, analysis of which is discussed below, may be confounded by fish effects on drift. For drift density, where we had data from transects at both the upstream and downstream ends of the study reaches, only data from the downstream transects (i.e. drift density out of study reaches) were used in the MANOVA for consistency with drift propensity and benthic density data.

Abiotic data collection and analysis

In addition to the width, depth, and velocity data collected at the time of drift measurements, we surveyed additional geomorphic and hydraulic characteristics (Table I) several weeks after completion of drift and benthic density measurements. We used a total station to survey longitudinal profiles, from which channel gradients were determined, and two to three cross-section profiles per reach. Cross-section data and the program WinXSPRO (Hardy *et al.*, 2005) were used to calculate the wetted perimeter (P), cross-sectional area (A), and hydraulic radius (R , where $R = A/P$) for conditions at the time of drift surveys.

Random-walk pebble counts of 100 particles (Wolman, 1954) were completed in each reach to measure bed-surface grain-size distribution, D_{50} (median grain size), and D_{84} , the size for which 84% of particles are finer, and a value that is typically considered representative of the 'dominant' grain size in terms of bed roughness and sediment transport calculations.

These data were used to calculate a series of dimensionless variables describing flow hydraulics and channel form. First, we calculated a dimensionless shear stress known as the Shields number (τ^*), which is a ratio of the

Table I. Summary of biotic and abiotic variables measured or calculated for 12 study streams in the East River basin, Colorado. Boldfaced variables are dimensionless and were included in multiple regression analysis of abiotic effects on drift.

Type of variable	Variable	Symbol/Formula	Units
<i>Biotic</i>	Drift density		(#/m ³)
	Benthic density		(#/m ²)
	Drift propensity	(drift density/ benthic density)	1/m
	Immigration ratio	(drift in/drift out)	—
<i>Abiotic</i>	Velocity (reach-average)	<i>U</i>	m/s
	Flow depth	<i>d</i>	m
	Wetted width	<i>w</i>	m
	Discharge	<i>Q</i>	m ³ /s
	Bed gradient	<i>S_o</i>	—
	Hydraulic radius	<i>R</i>	m
	Median grain size	<i>D₅₀</i>	m
	Grain size for which 84% of particles are finer	<i>D₈₄</i>	m
	Boundary shear stress	<i>τ_o</i>	N/m ²
	Shields number	<i>τ*</i>	—
	Reynolds number	<i>Re</i>	—
	Froude number	<i>Fr</i>	—
	Darcy-Weisbach friction factor	<i>ff</i>	—
	Relative submergence	<i>R/D₈₄</i>	—

boundary shear stress, or the force exerted by the flow per unit area averaged over the channel bed and banks, to the submerged weight of sediment grains per unit area (Church, 2006):

$$\tau^* = \frac{\tau_o}{[(\rho_s - \rho_w)]gD_x} \quad (1)$$

where τ_o is boundary shear stress, calculated as

$$\tau_o = \rho_w g R S \quad (2)$$

ρ_w is water density, g is gravitational acceleration, S is slope (channel gradient), ρ_s is sediment density, and D_x is representative grain diameter (here, set equal to D_{84}). The Shields number quantifies stream competence, or a stream flow's capacity to mobilize bed particles of a given size (Church, 2006), and is positively correlated with increased hydraulic forces and decreased stability of bed sediments.

Next, we calculated the Reynolds number, a dimensionless ratio of fluid inertial to viscous forces. Reynolds number distinguishes between laminar and turbulent flow regimes, is related to the scale of turbulent eddies (Roberston and Crowe, 1997), and is considered an important measure of hydraulic conditions affecting biota (Allan, 1995). Bulk flow Reynolds number, which represents a composite Reynolds number for a river channel, is

$$Re = \frac{UR}{\nu} \quad (3)$$

where R serves as the characteristic length scale in the Re calculation, U is reach-average velocity (i.e. the average

of velocities measured using the ECM at the upstream and downstream transects) and ν is the kinematic velocity (1.31×10^{-6} m²/s for freshwater at 10 °C).

Another dimensionless measure of hydraulic forces, the Froude number, represents the ratio of inertial forces to gravitational forces:

$$Fr = \frac{U}{(gd)^{0.5}} \quad (4)$$

where d is the flow depth. The Froude number distinguishes between supercritical ($Fr > 1$), critical ($Fr = 1$), and subcritical ($Fr < 1$) flow regimes and, by providing a measure of where flow lies on the spectrum from slow and deep ($Fr < 1$) to fast and shallow ($Fr > 1$), is sometimes used as an index of local habitat characteristics (Gordon *et al.*, 1992).

We also calculated the Darcy–Weisbach friction factor (ff), a dimensionless measure of flow resistance:

$$ff = \frac{8gRS}{U^2}. \quad (5)$$

The friction factor represents the total flow resistance generated by the channel bed, banks, bed-forms, woody debris, or other factors that counter the gravitational force of flow and create habitat complexity and velocity refugia.

Relative submergence of bed particles, R/D_{84} , quantifies the scale of cross-sectional flow in relation to dominant bed particle size, is central to calculations of the flow resistance associated with bed particles (i.e. grain resistance) (Keulegan, 1938; Einstein and Barbarossa, 1952), and distinguishes between scales of roughness in mountain streams, where for large-scale roughness $R/D_{84} < 1$, for intermediate-scale roughness $1 < R/D_{84} < 4$, and for small-scale roughness $R/D_{84} > 4$ (Bathurst, 1985). Most alluvial rivers have small-scale roughness, but in cases of large-scale roughness, as are common in steep channels, flow resistance is dominated by large particles, and velocity profiles are commonly non-logarithmic (Jarrett, 1984; Bathurst, 1993).

Relationships between abiotic factors and drift were tested using multiple regression analysis on two drift-related dependent variables: (1) drift propensity out of each study reach, which standardizes drift density by benthic density of the source reach and (2) immigration ratio (drift in/drift out of the study reach). Drift propensity and immigration ratio data were log-transformed and square-root transformed, respectively, to satisfy statistical assumptions. The five dimensionless abiotic variables described above (τ^* , Re , Fr , ff , R/D_{84}) were used as potential explanatory variables. Selection of the best model for describing each response variable (i.e. drift propensity and immigration ratio) was based on stepwise selection. In addition, using MANOVA, we tested for differences in the dimensionless abiotic variables between the fish and fishless streams.

RESULTS

Macroinvertebrate drift and density

The MANOVA evaluating differences in drift density, benthic density, drift propensity, and immigration ratio (data shown in Table II) between fish and fishless streams was significant (Wilk's Lambda = 0.27, $F_{4,7} = 4.9$, $p = 0.03$). Fish streams tended to have greater drift densities and lower benthic densities than fishless streams, but the differences were not significant (for drift density, $F_{1,10} = 3.2$, $p = 0.10$; for benthic density, $F_{1,10} = 4.2$, $p = 0.07$; Figure 2). Drift propensities were significantly higher in fish streams than in fishless reaches ($F_{1,10} = 6.0$, $p = 0.03$; Figure 2).

The median immigration ratio (drift in/drift out) among all 12 streams was approximately equal to 1 (0.94). Immigration ratios were not significantly different between fish and fishless streams ($F_{1,10} = 0.09$, $p = 0.76$; Figure 2). However, immigration ratios were positively correlated with benthic densities ($r^2 = 0.64$, $F_{1,10} = 17.4$, $p = 0.002$; Figure 3). Stream reaches with high benthic densities were typically gaining individuals (immigration

exceeded emigration), and those with low benthic densities were losing individuals (emigration exceeded immigration).

Morphology and hydraulics of study streams

Physical characteristics of the study streams are summarized in Table III. Median grain sizes ranged from 15 mm (fine gravel) to 130 mm (large cobble) (Table III), and most streams had consistent alluvial cover. Relative submergence was less than 1.3 in all streams, placing these channels in or close to the large-scale roughness regime (Bathurst, 1985) described above. Shields number, which scales shear stress to grain size and is typically positively correlated with sediment mobility, ranged from 0.01 to 0.064, with most values <0.045 (Table III). The extensive literature investigating the critical value of Shields number (τ_{cr}^*) for particle entrainment (reviewed in Buffington and Montgomery, 1997) suggests that τ_{cr}^* is approximately 0.045 in alluvial rivers (Buffington and Montgomery, 1997; Church, 2006), although greater values may characterize steep channels (Church, 2002). Most study streams were therefore well under the

Table II. *Baetis bicaudatus* data measured in 12 study streams in the East River basin, Colorado, including drift density, benthic density, drift propensity, and immigration ratio. The mean and standard errors shown for benthic densities are based on six electrobug samples in each study reach. Because drift measurements were completed once at each of the 24 measurement transects, standard errors of drift density, drift propensity, and immigration ratio in each reach are not available.

Stream	Fish ^a	Drift density ^b	Benthic density ^c	Drift propensity ^d	Immigration ratio ^e
Avery	F	3.92 (in) 0.88 (out)	798 ± 185	0.0011	4.4
Copper	F	17.8 (in) 17.5 (out)	172 ± 53	0.101	1.0
East	F	12.7 (in) 15.5 (out)	74 ± 24	0.209	0.8
Rock	F	2.95 (in) 3.46 (out)	113 ± 52	0.031	0.9
Quigley	F	0.24 (in) 0.88 (out)	52 ± 23	0.017	0.3
Rustlers	F	10.9 (in) 14.4 (out)	196 ± 34	0.073	0.8
B10	N	1.64 (in) 1.00 (out)	811 ± 93	0.0012	1.7
B2	N	1.19 (in) 1.46 (out)	420 ± 152	0.0035	0.8
B9	N	0.50 (in) 1.17 (out)	128 ± 18	0.0092	0.4
Benthette	N	1.74 (in) 0.91 (out)	639 ± 131	0.0014	1.9
Marmot	N	4.72 (in) 3.08 (out)	339 ± 55	0.0075	1.5
Bradley	N	5.1 (in) 2.88 (out)	409 ± 118	0.0070	1.8
Mean		5.27	346	0.039	1.4
SD		5.89	275	0.063	1.1

^a F=fish streams, N=fishless streams.

^b number of drifting *Baetis* per m^3 of water at the measurement transect; "in" and "out" refer to drift measurements at the upstream and downstream ends of each study reach, respectively.

^c individuals per m^2 .

^d drift density out of the study reach / benthic density in the study reach.

^e drift in/drift out

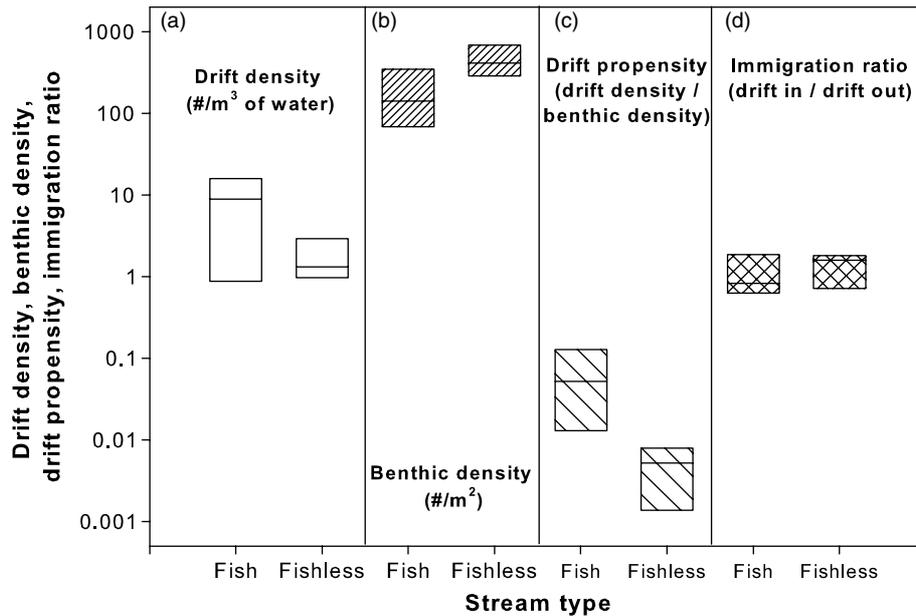


Figure 2. Box plots of data for *Baetis bicaudatus* from 12 study streams, including (a) drift densities out of the study reaches (individuals per m³ of water; left panel), (b) benthic densities (individuals per m²; centre-left panel), (c) drift propensities (drift density out of the study reach/benthic density in the study reach; centre-right panel), and (d) immigration ratio [drift in (immigration)/drift out (emigration); right panel]. Data include six fish and six fishless reaches. Boxes bound 25th and 75th percentiles, and solid lines in boxes illustrate medians; sample size is too small for illustration of whiskers. Differences between fish and fishless streams are significant for drift propensity ($p = 0.03$) and are not significant for drift density ($p = 0.10$), benthic density ($p = 0.07$), and immigration ratio ($p = 0.76$).

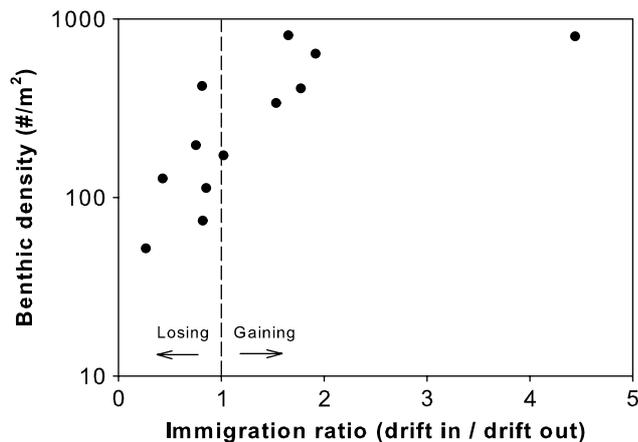


Figure 3. Immigration ratio (drift in/drift out) versus benthic density (individuals per m²) of *B. bicaudatus* in each of 12 study reaches. A significant relationship was observed between immigration ratio (square-root transformed) and benthic density (log-transformed) ($r^2 = 0.64$, $F_{1,10} = 17.4$, $p = 0.002$), such that losing streams (emigration > immigration) have lower benthic densities and gaining streams (emigration < immigration) have higher benthic densities.

entrainment threshold, and we did not observe bed material transport.

The MANOVA comparing the five dimensionless abiotic variables between fish and fishless streams indicated that the multivariate difference in physical characteristics between these sets of streams was not significant (Wilk's Lambda = 0.36, $F_{5,6} = 2.1$, $p = 0.20$).

Effects of abiotic factors on drift dynamics

Multiple linear regression analysis of dimensionless abiotic variables on log-transformed drift propensity, using stepwise model selection, produced a model containing

Reynolds number (Re) and Shields number (τ^*) (model $r^2 = 0.86$). Drift propensity was positively correlated with Re ($p = 0.001$, partial $r^2 = 0.61$; Figure 4(a)), and negatively correlated with τ^* ($p = 0.003$, partial $r^2 = 0.25$; Figure 4(b)). There was no correlation between Re and τ^* ($p = 0.34$; $r = -0.301$).

Multiple regression analysis of abiotic effects on immigration ratio (drift in/drift out) using stepwise model selection indicated that Shields number (τ^*) was significant (model $r^2 = 0.50$) and was positively correlated with the immigration ratio (Figure 4(b)) ($p = 0.01$). This result suggests that immigration exceeds emigration in reaches with higher Shields number values.

DISCUSSION

Linkages between abiotic variables and drift

In a set of high-gradient study streams, we investigated how hydraulic forces, flow resistance, and channel form influence mayfly drift, using drift propensity (drift density/benthic density) and immigration ratio (drift in/drift out) as our response variables. First, we hypothesized that stronger hydraulic forces would be associated with higher drift propensities and/or lower immigration ratios. This hypothesis is based on the premise that stronger hydraulic forces may induce either passive drift by dislodging organisms from the bed, or active drift by creating less favourable habitat conditions, thus promoting downstream dispersal of invertebrates.

We found that two measures of hydraulic forces, Reynolds number (Re) and Shields number (τ^*),

Table III. Summary of hydraulic and geomorphic characteristics of study streams in the East River basin, Colorado, at the time of drift surveys (June–July 2003) (see Table I for definitions of variables; variables for which no units are shown are dimensionless).

Stream	DA (km ²) ^a	S _o	Q (m ³ /s)	U (m/s)	d (m)	w (m)	R (m)	D ₅₀ (mm)	D ₈₄ (mm)	τ _o (N/m ²)	τ*	Re	Fr	ff	R/D ₈₄	Channel type ^b
Avery	1.8	0.11	0.09	0.5	0.10	1.7	0.09	50	130	100	0.047	37 300	0.5	2.8	0.7	s-p
Copper	24.3	0.03	1.6	0.9	0.27	6.2	0.21	97	176	64	0.022	150 000	0.6	0.6	1.2	p-b
East	45.9	0.02	2.6	0.9	0.29	10.1	0.27	130	280	47	0.010	179 000	0.5	0.5	0.9	p-b
Rock	3.6	0.04	0.22	0.5	0.19	2.3	0.14	81	135	58	0.027	51 300	0.4	1.9	1.0	p-b
Quigley	2.1	0.02	0.22	0.8	0.20	1.4	0.13	24	96	24	0.016	74 300	0.5	0.3	1.3	p-r
Rustlers	15.1	0.04	1.3	0.7	0.26	6.8	0.22	105	223	90	0.025	120 000	0.4	1.4	1.0	s-r
B10	0.11	0.11	0.007	0.3	0.05	0.5	0.06	15	90	63	0.043	13 700	0.4	5.6	0.7	s-r
B2	0.05	0.10	0.016	0.4	0.10	0.4	0.03	25	54	31	0.035	8 400	0.4	1.8	0.6	s-r; s-p
B9	0.11	0.11	0.004	0.2	0.04	0.6	0.04	57	135	48	0.022	5 400	0.2	14	0.3	s-r
Benthetie	0.34	0.08	0.09	0.5	0.12	1.5	0.09	37	102	69	0.042	32 000	0.5	2.3	0.8	s-p
Marmot	0.93	0.12	0.05	0.5	0.09	1.0	0.06	41	117	73	0.038	22 800	0.5	2.6	0.5	s-r; s-p
Bradley	3.8	0.11	0.28	1.1	0.22	1.1	0.15	70	150	156	0.064	126 000	0.7	1.0	1.0	cascade
Mean	8.2	0.07	0.53	0.6	0.16	2.8	0.12	61	141	69	0.03	68 412	0.5	2.9	0.8	
SD	14.0	0.04	0.84	0.3	0.09	3.1	0.08	36	62	35	0.02	60 508	0.1	3.9	0.3	

^a Drainage area was measured from 1:24 000-scale U.S. Geological Survey topographic maps using a digitizer and AutoCad, although accurate delineation of drainage divides was difficult for the smallest streams.
^b s-p, step-pool; p-b, plane-bed; p-r, pool-riffle; s-r, step-riffle.

significantly affected drift propensity. Reynolds number was positively correlated with drift propensity and explained 61% of the variance in drift propensity (Figure 4(a)). Reynolds number represents the ratio of fluid inertial forces to viscous forces and illustrates the turbulence of the flow regime and the scale of turbulent eddies (Roberson and Crowe, 1997). Turbulent fluctuations may dislodge benthic organisms, affect dispersal distance, and mediate the return of drifting invertebrates to the bed (McNair *et al.*, 1997). This suggests a potential mechanism for the positive correlation we observed between *Re* and drift propensity, although the *Re* we calculated represents a reach-averaged property of the bulk flow, and therefore, is not a direct measure of the intensity of small-scale turbulent fluctuations (the issue of reach-average versus local measures is elaborated upon below). Overall, this result was consistent with our first hypothesis that stronger hydraulic forces would be associated with higher drift. It is also consistent with previous research on abiotic effects on invertebrates that has documented relationships between Reynolds number and invertebrate distribution, abundance, and community composition (Quinn and Hickey, 1994; Merigoux and Doledec, 2004; Brooks *et al.*, 2005).

In contrast, Shields number (τ^*) was negatively correlated with drift propensity and positively correlated with immigration ratio (Figure 4(b)), which ran counter to our first hypothesis. Because τ^* combines data on boundary shear stress and dominant grain size, and thus serves as a measure of the flow's competence to mobilize the bed, we expected that streams with higher τ^* values (i.e. with greater flow strengths and particles closer to the threshold of incipient motion) would have higher drift rates. Under the moderate discharge conditions of our survey, however, when bed particles were below the threshold of motion, reaches with high τ^* values (i.e. with greater flow competence) had lower drift propensities. The lower drift propensities observed in streams more closely approaching thresholds of bed mobility may indicate active avoidance of stronger flows by invertebrates and/or selection of less competent flows when reattachment opportunities may be greater. The absence of a positive relationship between τ^* and drift in our study streams, combined with findings elsewhere that local *increases* in boundary shear stress are associated with increases in drift (Gibbins *et al.*, 2007), also suggest that the entry of benthic organisms into the water column may be more sensitive to rates of change than magnitude of shear stress. Analogously, patterns of invertebrate movement across an experimental substrate, below particle-entrainment thresholds, appear to reflect the relative, rather than absolute, hydraulic forces experienced by benthic organisms (Rice *et al.*, 2008).

The opposite relationships with drift observed for *Re* and τ^* may appear incongruous, but these two dimensionless variables represent different forces; *Re* describes how turbulent the bulk flow is, and τ^* measures the flow's competence to mobilize its bed. Although some

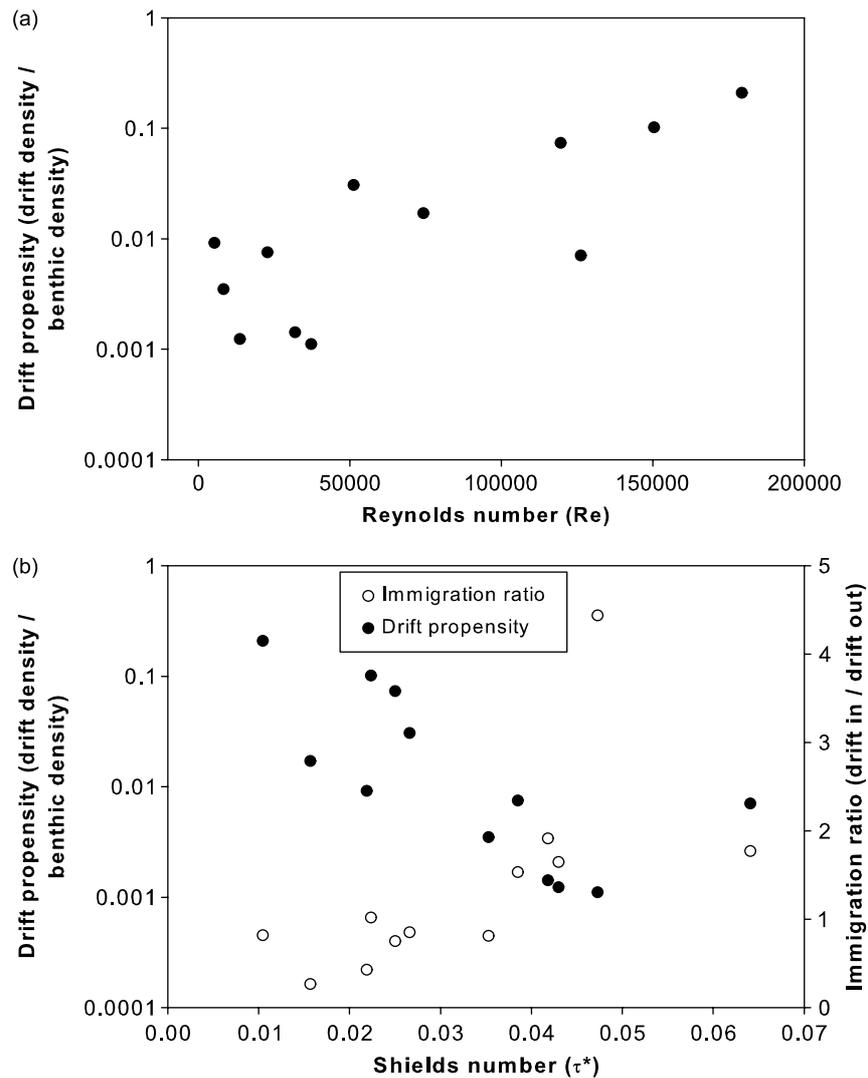


Figure 4. (a) Reynolds number (Re) versus drift propensity (drift density/benthic density); (b) Shields number (τ^*) versus drift propensity and immigration ratio (drift in/drift out). Multiple regression analysis of dimensionless abiotic variables against drift propensity (log-transformed) with stepwise model selection indicated that a model containing Re and τ^* explained approximately 86% of the variance in drift propensity; Re had the highest partial r^2 (0.61). A significant relationship was also found between τ^* and immigration ratio.

relationship between Re and τ^* may be expected, the reach-average values we calculated were uncorrelated.

Our second hypothesis was that more hydraulically rough stream reaches (i.e. those with greater flow resistance) would be more favourable to benthic invertebrates, and would thus have lower drift propensities, and/or would be gaining reaches in terms of immigration exceeding emigration. Our premise here was that reaches with greater flow resistance may provide more potential velocity, refugia, and relief from the strong hydraulic forces that characterize steep channels. Our data were not consistent with this hypothesis, however; neither the Darcy–Weisbach friction factor (ff) nor the relative submergence (R/D_{84}), the measures of channel roughness that we employed, was associated with either drift propensity or immigration ratio.

Channel roughness may be more biologically important at high flows, when sources of flow resistance such as woody debris and boulders can provide low-velocity refugia (Hax and Golladay, 1998; Church, 2002; Wilcox

and Wohl, 2006). Moreover, flow resistance values in our study reaches did not vary substantially among reaches and were relatively low (Table III) compared to values reported for steep channels elsewhere (Comiti *et al.*, 2007). The relatively low friction factor values we observed may be attributable to the absence of pools in many of our study streams. Streams with gradients of approximately 0.04–0.12 m/m (our study reaches ranged from 0.02 to 0.12 m/m; Table III) are typically organized into alternating sequences of steps and pools (Montgomery and Buffington, 1997; Chartrand and Whiting, 2000; Chin and Wohl, 2005) that exhibit high flow resistance as a result of tumbling flow into pools and associated spill resistance (MacFarlane and Wohl, 2003; Wilcox *et al.*, 2006). Although some of the study streams indeed displayed step-pool morphology, the paucity of pools in many reaches produced cascade, step-riffle, or plane-bed morphology.

Our results suggest that at the moderate discharges present at the time of this study (on the falling limb of

the annual snowmelt peak, below the range of incipient motion of bed particles), mayfly drift behaviour shows some association with abiotic factors. Overall, however, our results do not strongly support a passive entrainment model, whereby hydraulic forces cause invertebrates to involuntarily enter the water column, in agreement with previous flume results (Kohler, 1985; Fonseca and Hart, 1996). At higher discharges, however, as boundary shear stresses increase towards incipient motion of bed particles, invertebrates using those bed particles may sense the onset of motion and actively enter the water column before the bed sediments begin to roll, hop, or slide along the streambed in a manner that would likely be lethal for any organisms remaining attached to mobile sediments (Bond and Downes, 2003; Gibbins *et al.*, 2007). Alternatively, benthic invertebrates may take advantage of refugia created by stable and/or low-stress patches on the bed during high flows (Lancaster and Hildrew, 1993; Rice *et al.*, 2008) or, where sufficient alluvial cover over bedrock is present, may seek refuge from hydraulic forces by burrowing deep into the substrate (Williams and Hynes, 1984). Data collection over a broader range of flows in one or more streams could further illuminate the hypothesized relationships between abiotic factors and mayfly drift that were considered in our between-stream comparison, in which all biological data were collected within a narrow discharge range in each stream.

Variation in invertebrate drift

Drift propensity varied not only as a function of the abiotic variables indicated by the multiple regression analysis (Re and τ^*), but also between fish and fishless streams. The multivariate difference between fish and fishless streams observed for drift variables suggests that abiotic and biotic effects on drift may be confounded to some extent. The higher nocturnal drift propensity (drift density/benthic density in the source reach) observed in fish versus fishless streams (Figure 2) is consistent with previous field studies (Flecker, 1992; Douglas *et al.*, 1994; McIntosh *et al.*, 2002). The nocturnal drift differences between fish and fishless streams are not likely to be explained by abiotic factors, given that daytime drift of mayflies is very low in fish streams compared to fishless streams (McIntosh *et al.*, 2002).

Challenges for future study

Identifying and measuring the geomorphic and hydraulic variables that directly and indirectly affect biota, quantifying the effects of spatial and temporal variability in physical habitat, and separating geomorphic and hydraulic effects from biological, chemical, and other factors affecting invertebrate dispersal dynamics are important challenges in river science.

The spatial scale of measurements is a fundamental issue in studies of ecohydraulic linkages. For example, reach-average and/or vertically averaged velocities, as are typically reported in field studies (including this one), may be poor descriptors of the conditions on the channel

boundary and thus of limited relevance to benthic biota (Nowell and Jumars, 1984). Many hydraulic properties likely to affect organisms, such as near-bed Reynolds stresses and turbulent kinetic energy (Clifford and French, 1993), are meaningful at local (i.e. over a point in the bed) rather than reach scales. In hydraulically complex mountain streams, velocities and turbulence intensities vary substantially longitudinally, laterally, vertically, and temporally (Wilcox and Wohl, 2007), complicating the identification and accurate measurement of biologically relevant hydraulic properties. Studies of the behaviour of individual organisms may entail biological data collection at an analogous local scale (e.g. Rice *et al.*, 2008), but many ecosystem processes and properties, such as those considered in our study, fundamentally operate at the reach scale. We suggest that the use of reach-average abiotic measures to gain insight into reach-scale biological properties (e.g. immigration ratio) is appropriate.

Nevertheless, further development of mechanistic relationships between abiotic and biotic processes will benefit from local-scale hydraulics measurements. High-frequency, multidimensional, near-bed-velocity measurements are needed to better quantify both the forces to which benthic biota are exposed (e.g. the local Reynolds stresses), and the related turbulent fluctuations that may cause involuntary drift. Technologies such as acoustic Doppler velocimeters facilitate such measurements and have been applied to biological (Bouckaert and Davis, 1998; Merigoux and Doledec, 2004) and geomorphic (Lamarre and Roy, 2005; Legleiter *et al.*, 2007) studies of lower-gradient rivers and ecohydraulic studies in flumes (Rice *et al.*, 2008). Field application of such methods, however, remains extremely difficult in steep channels such as those investigated here, where rough beds complicate near-bed measurements and highly aerated flows interfere with acoustic methods (Wilcox and Wohl, 2007).

Advances in understanding of physical–ecological linkages in streams will also benefit from more innovative and interdisciplinary field methods. For example, stream ecologists commonly measure physical variables such as mid-water column velocity, width, and depth, but measurements of bed gradient, hydraulic radius, and grain-size distribution are less standard. These variables are not difficult to measure and are needed to calculate measures of hydraulic forces such as boundary shear stress, dimensionless shear stress, or friction factor. Further, whereas geomorphologists typically consider features like grain size in terms of basic parameters such as D_{50} and D_{84} , other descriptors of bed particles (e.g. spatial arrangement, heterogeneity, and shape) may be more biologically important (Cardinale *et al.*, 2002; Encalada and Peckarsky, 2006). Continued collaboration among geomorphologists or other physical scientists and ecologists, as suggested by others (e.g. Hart and Finelli, 1999; Benda *et al.*, 2002; Nilsson *et al.*, 2003; Urban and Daniels, 2006; Rice *et al.*, 2008), is needed to address the many important questions at the intersection of disciplines in aquatic sciences.

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REFERENCES

- Allan JD. 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall: London; 388.
- Bathurst JC. 1985. Flow resistance estimation in mountain rivers. *Journal of Hydraulic Engineering-ASCE* **111**: 625–643.
- Bathurst JC. 1993. Flow resistance through the channel network. In *Channel Network Hydrology*, K Beven, Kirkby MJ (eds). Wiley: Chichester; 69–98.
- Benda LE, Poff NL, Tague C, Palmer MA, Pizzuto J, Cooper S, Stanley E, Moglen G. 2002. How to avoid train wrecks when using science in environmental problem solving. *Bioscience* **52**: 1127–1136.
- Bond NR, Downes BJ. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* **48**: 455–465.
- Bouckaert FW, Davis J. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology* **40**: 77–86.
- Brooks AJ, Haeusler T, Reinfelds I, Williams S. 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology* **50**: 331–344.
- Buffington JM, Montgomery DR. 1997. A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. *Water Resources Research* **33**: 1993–2029.
- Cardinale BJ, Palmer MA, Swan CM, Brooks S, Poff NL. 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* **83**: 412–422.
- Chartrand SM, Whiting PJ. 2000. Alluvial architecture in headwater streams with special emphasis on step-pool topography. *Earth Surface Processes and Landforms* **25**: 583–600.
- Chin A, Wohl E. 2005. Toward a theory for step pools in stream channels. *Progress in Physical Geography* **29**: 275–296.
- Church M. 2002. Geomorphic thresholds in riverine landscapes. *Freshwater Biology* **47**: 541–557.
- Church M. 2006. Bed material transport and the morphology of alluvial river channels. *Annual Review of Earth and Planetary Sciences* **34**: 325–354.
- Clifford NJ, French JR. 1993. Monitoring and modelling turbulent flow: historical and contemporary perspectives. In *Turbulence: Perspectives on Flow and Sediment Transport*, Clifford NJ, French JR, Hardisty J (eds). Wiley: Chichester; 1–34.
- Comiti F, Mao L, Wilcox A, Wohl EE, Lenzi MA. 2007. Field-derived relationships for flow velocity and resistance in step-pool streams. *Journal of Hydrology* **340**: 48–62.
- Curran JH, Wohl EE. 2003. Large woody debris and flow resistance in step-pool channels, Cascade Range, Washington. *Geomorphology* **51**: 141–157.
- Dewson ZS, James ABW, Death RG. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* **26**: 401–415.
- Douglas PL, Forrester GE, Cooper SD. 1994. Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia* **98**: 48–56.
- Einstein HA, Barbarossa NL. 1952. River channel roughness. *ASCE Transactions* **117**: 1121–1146.
- Encalada AC, Peckarsky BL. 2006. Selective oviposition of the mayfly *Baetis bicaudatus*. *Oecologia* **148**: 526–537.
- Flecker AS. 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology* **73**: 438–448.
- Fonseca DM, Hart DD. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**: 49–58.
- Gibbins C, Vericat D, Batalla RJ. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* **52**: 2369–2384. DOI:10.1111/j.1365-2427.2007.01858.x.
- Gordon ND, McMahon TA, Finlayson BL. 1992. *Stream Hydrology: An Introduction for Ecologists*. Wiley: Chichester; 526.
- Hardy T, Palavi P, Mathias D. 2005. WinXSPRO, a channel cross section analyzer, user's manual, USDA Forest Service RMRS-GTR 147, Fort Collins.
- Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* **30**: 363–395.
- Hax CL, Golladay SW. 1998. Flow disturbance of macroinvertebrates inhabiting sediments and woody debris in a prairie stream. *American Midland Naturalist* **139**: 210–223.
- Hildebrand SG. 1974. The relation of drift to benthos density and food level in an artificial stream. *Limnology and Oceanography* **19**: 951–957.
- Huhta A, Muotka T, Tikkanen P. 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology* **45**: 33–42.
- Imbert JB, Perry JA. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* **436**: 191–208.
- Jarrett RD. 1984. Hydraulics of high-gradient streams. *Journal of Hydraulic Engineering-ASCE* **110**: 1519–1539.
- Keulegan GH. 1938. Laws of turbulent flow in open channels. *Journal of Research of the National Bureau of Standards* **21**: 707–741.
- Kohler SN. 1985. Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* **66**: 1749–1761.
- Lamarre H, Roy AG. 2005. Reach scale variability of turbulent flow characteristics in a gravel-bed river. *Geomorphology* **68**: 95–113.
- Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology* **41**: 605–619.
- Lancaster J, Hildrew AG. 1993. Characterizing in-stream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1663–1675.
- Legleiter CJ, Phelps TL, Wohl EE. 2007. Geostatistical analysis of the effects of stage and roughness on reach-scale spatial patterns of velocity and turbulence intensity. *Geomorphology* **83**: 322–345.
- MacFarlane WA, Wohl E. 2003. Influence of step composition on step geometry and flow resistance in step-pool streams of the Washington Cascades. *Water Resources Research* **39**: 1037. DOI:10.1029/2001WR001238.
- McIntosh AR, Peckarsky BL, Taylor BW. 1999. Rapid size-specific changes in mayfly drift caused by alterations in fish odour. *Oecologia* **118**: 256–264.
- McIntosh AR, Peckarsky BL, Taylor BW. 2002. The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biology* **47**: 1497–1513.
- McNair JN, Newbold JD, Hart DD. 1997. Turbulent transport of suspended particles and dispersing benthic organisms: How long to hit bottom? *Journal of Theoretical Biology* **188**: 29–52.
- Merigoux S, Doledec S. 2004. Hydraulic requirements of stream communities: a case study on invertebrates. *Freshwater Biology* **49**: 600–613.
- Mochizuki S, Kayaba Y, Tanida K. 2006. Drift patterns of particulate matter and organisms during artificial high flows in a large experimental channel. *Limnology* **7**: 93–102.
- Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* **109**: 596–611.
- Nilsson C, Pizzuto JE, Moglen GE, Palmer MA, Stanley EH, Bockstael NE, Thompson LC. 2003. Ecological forecasting and the urbanization of stream ecosystems: challenges for economists, hydrologists, geomorphologists, and ecologists. *Ecosystems* **6**: 659–674.
- Nowell ARM, Jumars PA. 1984. Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics* **15**: 303–328.

- Peckarsky BL, McIntosh AR, Taylor BW, Dahl J. 2002. Predator chemicals induce changes in mayfly life history traits: a whole-stream manipulation. *Ecology* **83**: 612–618.
- Peckarsky BL, Taylor BW, McIntosh AR, McPeck MA, Lytle DA. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. *Ecology* **82**: 740–757.
- Poff NL, Ward JV. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 1926–1936.
- Quinn JM, Hickey CW. 1994. Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. *Freshwater Biology* **32**: 489–500.
- Rice SP, Buffin-Belanger T, Lancaster J, Reid I. 2008. Movements of a macroinvertebrate (*Potamophylax latipennis*) across a gravel-bed substrate: effects of local hydraulics and micro-topography under increasing discharge. In *Gravel-Bed Rivers VI: From Process Understanding to River Restoration*, Habersack H, Piegay H, Rinaldi M (eds). Elsevier; 637–660.
- Roberson JA, Crowe CT. 1997. *Engineering Fluid Mechanics*. Wiley: New York.
- Robinson CT, Uehlinger U, Monaghan MT. 2004. Stream ecosystem response to multiple experimental floods from a reservoir. *River Research and Applications* **20**: 359–377.
- Taylor BW, McIntosh AR, Peckarsky BL. 2001. Sampling stream invertebrates using electroshocking techniques: implications for basic and applied research. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 437–445.
- Urban MA, Daniels M. 2006. Introduction: exploring the links between geomorphology and ecology. *Geomorphology* **77**: 203–206.
- Waters TF. 1972. The drift of stream insects. *Annual Review of Entomology* **17**: 253–272.
- Wilcox AC, Nelson JM, Wohl EE. 2006. Flow resistance dynamics in step-pool channels: 2. Partitioning between grain, spill, and woody debris resistance. *Water Resources Research* **42**: W05419, DOI:10.1029/2005WR004278.
- Wilcox AC, Wohl EE. 2006. Flow resistance dynamics in step-pool channels: 1. Large woody debris and controls on total resistance. *Water Resources Research* **42**: W05418, DOI:10.1029/2005WR004277.
- Wilcox AC, Wohl EE. 2007. Field measurements of three-dimensional hydraulics in a step-pool channel. *Geomorphology* **83**: 215–231.
- Williams DD, Hynes HBN. 1984. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology* **4**: 233–256.
- Wolman MG. 1954. A method of sampling coarse river-bed material. *EOS, Transactions-American Geophysical Union* **35**: 951–956.