

# Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes

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**Abstract:** Invertebrate drift, the downstream transport of aquatic invertebrates, is a fundamental ecological process in streams with important management implications for drift-feeding fishes. Despite long-standing interest, many aspects of drift remain poorly understood mechanistically, thereby limiting broader food web applications (e.g., bioenergetics-based habitat models for fish). Here, we review and synthesize drift-related processes, focusing on their underlying causes, consequences for invertebrate populations and broader trophic dynamics, and recent advances in predictive modelling of drift. Improving predictive models requires further resolving the environmental contexts where drift is driven by hydraulics (passive drift) versus behaviour (active drift). We posit this can be qualitatively inferred by hydraulic conditions, diurnal periodicity, and taxa-specific traits. For invertebrate populations, while the paradox of population persistence in the context of downstream loss has been generally resolved with theory, there are still many unanswered questions surrounding the consequences of drift for population dynamics. In a food web context, there is a need to better understand drift-foraging consumer-resource dynamics and to improve modelling of drift fluxes to more realistically assess habitat capacity for drift-feeding fishes.

**Résumé :** La dérive d'invertébrés, soit le transport vers l'aval d'invertébrés aquatiques, est un processus écologique fondamental dans les cours d'eau qui a d'importantes conséquences pour les poissons qui se nourrissent d'aliments à la dérive. Malgré un intérêt de longue date, de nombreux aspects de la dérive demeurent mal compris d'un point de vue mécaniste, ce qui limite les applications plus larges des réseaux trophiques (p. ex. les modèles d'habitat reposant sur la bioénergétique pour les poissons). Nous passons en revue et résumons les processus associés à la dérive, en mettant l'accent sur leurs causes sous-jacentes, les conséquences pour les populations d'invertébrés et la dynamique trophique plus large, ainsi que les avancées récentes en modélisation prédictive de la dérive. L'amélioration des modèles prédictifs nécessite une meilleure résolution des milieux dans lesquels la dérive est mue, d'une part, par l'hydraulique (dérive passive) ou, d'autre part, par le comportement (dérive active). Nous postulons que cela peut être inféré de manière qualitative à partir des conditions hydrauliques, de la périodicité diurne et de caractères propres aux taxons. Pour les populations d'invertébrés, si le paradoxe de la persistance des populations dans le contexte de perte en aval a généralement été résolu en faisant appel à la théorie, de nombreuses questions demeurent quant aux conséquences de la dérive pour la dynamique des populations. Dans un contexte de réseaux trophiques, il est nécessaire de mieux comprendre la dynamique dérive-consommateur s'alimentant-résource et d'améliorer la modélisation des flux de dérive pour évaluer de manière plus réaliste la capacité des habitats pour les poissons se nourrissant de la dérive. [Traduit par la Rédaction]

## Introduction

Invertebrate drift, the downstream transport of stream invertebrates, is a defining feature of running water systems at multiple levels of organization. For individuals, drifting may be a mode of patch selection for invertebrates balancing resource acquisition and predation risk (e.g., Kohler and McPeck 1989). At the population level, drift can influence spatial population structure by linking populations through dispersal (Townsend and Hildrew 1976; Mackay 1992) and may also represent a form of density-independent emigration or density-dependent self-thinning (Waters 1965). In a broader ecosystem context, drift constitutes a key trophic pathway in streams, providing the prey base for a diverse guild of fishes adopting a specialized central place drift-foraging strategy (Grossman 2014). The total energy flux available as drift is therefore a key determinant of the productive capacity of habitats to support populations

of drift feeders, including iconic species such as salmon and trout (Salmonidae; Waters 1969; Poff and Huryn 1998).

Given its importance to the function and productivity of lotic ecosystems, drift has been the focus of considerable research (for earlier reviews see Keupp 1988; Brittain and Eikeland 1988; Malmqvist 2002). Studies have generally fallen into two categories: theoretically driven studies focused on the ecology and mechanisms of why animals drift and descriptive studies aimed at explaining spatial and temporal patterns in drift dynamics. The underlying motivation differs between these two approaches. Theoretically focused studies have been primarily concerned with both the proximate causes of drift and understanding the consequences of drift to taxon-specific populations and their resources, particularly the role of drift in the density-dependent regulation of benthic populations (e.g., Waters 1966; Turner and Williams 2000; Humphries 2002). In contrast, descriptive empirical studies have primarily focused on

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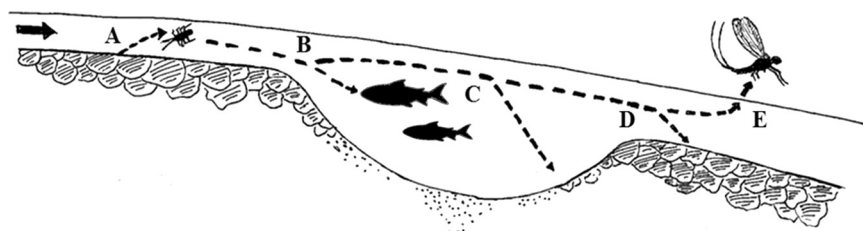
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**Fig. 1.** Schematic outlining the processes involved in drift. Drift entry is shown at A as an invertebrate departs the substrate and becomes entrained in the water column. Invertebrates exit drift through one of several processes, including predation (B), passive settlement in hydraulic dead zones (C), active settlement into new patches (D), or emergence (E). Drift transport is the total distance an organism travels in the drift and is represented by vectors AB, AC, AD, and AE.



describing bulk community fluxes of drift (e.g., Elliott 1967a; McLay 1970; Shearer et al. 2003), often with specific reference to predicting availability of prey for fish (e.g., Hayes et al. 2000; Weber et al. 2014).

Despite these parallel approaches, a general process-based understanding of invertebrate drift remains elusive. This may be due to the many context-dependent drivers of drift dynamics, for which the domains of importance of causative mechanisms remain poorly resolved. For empirical applications, predictive models of drift flux have lagged behind taxon-specific mechanistic studies, limiting the ability to quantitatively study the role of drift in an ecosystem context and to effectively account for variation in prey abundance when managing populations of drift-feeding fishes. In this review, we attempt to reconcile these contrasting mechanistic versus descriptive approaches. Our goal is not to exhaustively review the topic of drift, as this has been done elsewhere (e.g., Brittain and Eikeland 1988). Rather, we aim to synthesize processes related to drift in both theoretical and empirical contexts with the hope that our work leads to stronger linkages between these two lines of inquiry. We specifically address (1) the processes generating drift and the domains over which they operate; (2) the spatial and temporal dynamics of drift; (3) the importance of drift for benthic invertebrate populations and trophic fluxes to fish; and (4) progress in the formulation of predictive models of drift dynamics and community drift fluxes. We close by highlighting several key areas of uncertainty that should be resolved if robust predictions of invertebrate drift are to be achieved. First we define the primary components of invertebrate drift.

### Component processes of invertebrate drift

Invertebrate drift is composed of three distinct processes (Ciborowski 1987): the departure of an organism from the substrate and entrainment in the water column (henceforth drift entry); hydraulic transport downstream (drift transport); and removal from the drift (drift exit), which may occur through settlement back to the substrate, predation, or emergence to the terrestrial life stage (Fig. 1).

#### Drift entry

Multiple drivers of drift entry have been identified and have led to various categorization schemes (reviewed in Brittain and Eikeland 1988). At a broad level, drift entry (number per area per time) can be partitioned into “passive drift”, where organisms accidentally lose purchase from the substrate due to hydraulic stress, and “active drift”, where organisms deliberately leave the substrate to enter the water column (Table 1).

Passive drift occurs via mechanical dislodgement from the substrate because of near-bed shear stress and often results from increases in discharge or turbulence, which may be associated with substrate mobilization (Gibbins et al. 2007b). “Catastrophic drift” or “mass drift”, defined as a rapid increase in passive drift (Anderson and Lehmkuhl 1968; Gibbins et al. 2007a), may result from several flow-related thresholds. First, the critical level of shear stress where organic matter becomes entrained increases the passive drift of animals using detritus or algal mats as substrate (Vinson 2001). A second threshold is reached as saltation of sand and fine organic matter

scour exposed benthic invertebrates (Gibbins et al. 2007a), followed by a third threshold at bed-mobilizing flows as surface and near-surface invertebrates are entrained during mobilization of all particles on the stream bed (Anderson and Lehmkuhl 1968). However, substrate mobilization may not be a crucial condition for mass drift if the critical shear stress for substrate entrainment exceeds that for invertebrates. In this case, catastrophic drift may be frequently initiated by high discharge events not considered disturbances in geomorphic terms (Statzner et al. 1984; Gibbins et al. 2007a).

Passive drift below critical entrainment thresholds has been termed “constant drift” (Brittain and Eikeland 1988). Unlike catastrophic drift, relationships between hydraulics and constant drift are less clearly defined, with multiple studies demonstrating incongruence between observed drift entry thresholds and those predicted based on hydraulic particle-transport relationships, which link entrainment and settling thresholds to particle size, density, and hydraulic stress (Ciborowski 1987; Wilcox et al. 2008; Oldmeadow et al. 2010). Constant drift may relate to factors independent of velocity, such as accidental loss of footing on the substrate during periods of increased activity, as well as variation in shear stress associated with turbulent flow. Turbulent flow associated with rough bed surfaces creates substantial variation in velocity (Davis and Barmuta 1989; Hart and Finelli 1999), and pulses of accelerating velocity (turbulent sweeps) may cyclically exceed critical shear stress for entrainment, resulting in elevated passive drift (Blanckaert et al. 2013).

Active drift, in contrast, results from deliberate behaviours, including benthic predator avoidance (Peckarsky 1980; Malmqvist and Sjöström 1987; Kratz 1996; Huhta et al. 2000), active patch selection while foraging (Hildebrand 1974; Kohler 1985), or escape from unfavourable abiotic conditions (Lauridsen and Friberg 2005; Gibbins et al. 2007b; James et al. 2009; Larsen and Ormerod 2010). Density dependence may also increase drift entry owing to increased competition for space (Corkum 1978; Hildrew and Townsend 1980; Kohler 1992) or resource limitation (Dimond 1967; Richardson 1991; Fonseca and Hart 1996; Rowe and Richardson 2001; Siler et al. 2001). While mostly studied in isolation, these factors interact to influence active drift. For instance, given the conflicting demands on benthic invertebrates to maximize foraging intake and minimize predation risk (Gilliam and Fraser 1987; Lima and Dill 1990), active drift is likely a joint response to both predation risk and local per capita resource availability. This trade-off between maximizing energy intake and minimizing mortality is exemplified by strong nocturnal peaks in drift (Bishop 1969), which are usually attributed to invertebrates searching for new foraging patches while avoiding predation from visually foraging, drift-feeding fishes (Allan 1978; Flecker 1992). In this case, invertebrates drift at night to minimize predation risk from drift-feeding fishes, but the ultimate motivation for moving among habitats is likely resource limitation, although escape from nocturnally foraging benthic predators may also play a role (Hammock et al. 2012).

**Table 1.** A summary of different active and passive mechanisms of drift entry and relevant references.

Mechanism of drift entry	Example references
<b>Passive</b>	
Accidental dislodgment at noncatastrophic flows	Corkum 1978; Humphries 2002; Elliott 2003
Catastrophic dislodgment due to mobilization of organic substrate and detritus	Vinson 2001
Catastrophic dislodgment due to mobilization of inorganic substrate	Anderson and Lehmkuhl 1968; Gibbins et al. 2007a
<b>Active</b>	
Predator avoidance	Peckarsky 1980; Malmqvist and Sjöström 1987; Huhta et al. 2000; Hammock et al. 2012
Active foraging without density dependence	Hildebrand 1974; Shearer et al. 2003; Hammock and Wetzel 2013
Escape from unfavourable abiotic conditions	Gibbins et al. 2007b; Larsen and Ormerod 2010
Density dependence — space limitation	Fonseca and Hart 1996
Density dependence — food limitation	Köhler 1985; Richardson 1991; Siler et al. 2001; Hammock and Wetzel 2013
Density dependence — predator avoidance	Kratz 1996

### Drift transport

The transport of drifting invertebrates has been treated similarly to suspended inert particles, where variation in water velocity and hydraulic heterogeneity (e.g., turbulence) imposed by physical habitat structure controls particle movement (Ciborowski 1983). However, multiple lines of evidence indicate an important behavioural component to drift transport, with invertebrates actively controlling their time in the drift. First, hydraulic particle–transport relationships adequately explain observed transport dynamics for only a limited subset of taxa (Lancaster et al. 1996); second, multiple studies have found disparities in drift transport between living and dead organisms (Townsend and Hildrew 1976; Ciborowski et al. 1977; Allan and Feifarek 1989); and third, a number of taxa possess behavioural and morphological adaptations to facilitate either settlement or prolonged drifting. These include the adhesive silk filaments of black fly larvae (Simuliidae) or swimming behaviour by mayflies (Ephemeroptera) (Fingerut et al. 2006), both of which allow rapid exit from the drift. As a result, there is a wide variation among empirical estimates of transport distances (typically measured when animals were released or disturbed from the streambed at fixed locations; McLay 1970; Elliott 1971; Ciborowski 1983; Larkin and McKone 1985). In general, however, despite some extreme distance estimates of over 100 m (see references in Brittain and Eikeland 1988), drift distances for given conditions (e.g., velocity, stream size) appear to be conserved for drift-prone taxa and are relatively short (e.g., around 2–10 m on average; Elliott 1971, 2002, 2003; Townsend and Hildrew 1976).

### Drift exit

The exit of animals from the drift can occur through three discrete pathways: settlement back to the substrate (e.g., Fonseca 1999), predation (e.g., Wilzbach et al. 1986), or emergence to terrestrial adult life stages, which occurs in short temporal pulses specific to the phenology of individual taxa (Reisen and Prins 1972). Settlement can occur passively, such as in hydraulic “dead zones” (depositional areas; e.g., Downes 1990; Lancaster et al. 1996), or actively through behaviours or morphological adaptations that increase settlement probability. The ability of drifting individuals to settle may also be contingent on hydraulic conditions imposed by local geomorphology (Holomuzki and Van Loan 2002; Oldmeadow et al. 2010). For example, Oldmeadow et al. (2010) found settling abilities differed between two species of mayfly in plane bed versus turbulent environments in experimental flumes, suggesting that hydraulic constraints on drift settlement may have important consequences for the ability of some taxa to access otherwise suitable habitats or to exit the drift in a timely manner once entrained. In a more general sense, abiotic or biotic constraints on drift settlement have the potential to affect distributional patterns and densities of benthic in-

vertebrates (Fonseca and Hart 2001; Downes and Lancaster 2010; Oldmeadow et al. 2010).

In fish-bearing streams, the proportion of drift lost to predation may be substantial, but will depend on the total energetic demand of the drift-foraging assemblage, which is a function of fish density, size distribution, and ambient temperature (Smith and Li 1983). Depletion will be further affected by the efficiency of prey capture, which is contingent on multiple factors, including water velocity (Hill and Grossman 1993; Piccolo et al. 2008), turbidity (Harvey et al. 2009), canopy cover (Wilzbach et al. 1986), seasonal light levels (Fraser and Metcalfe 1997), the size composition of drift (Wankowski 1981; Dunbrack and Dill 1983; Wilzbach et al. 1986), and the availability of suitable foraging habitat, which determines the proportion of stream discharge that drift-feeders can scan to intercept drifting prey (Hughes and Dill 1990; Rosenfeld and Ptolemy 2012).

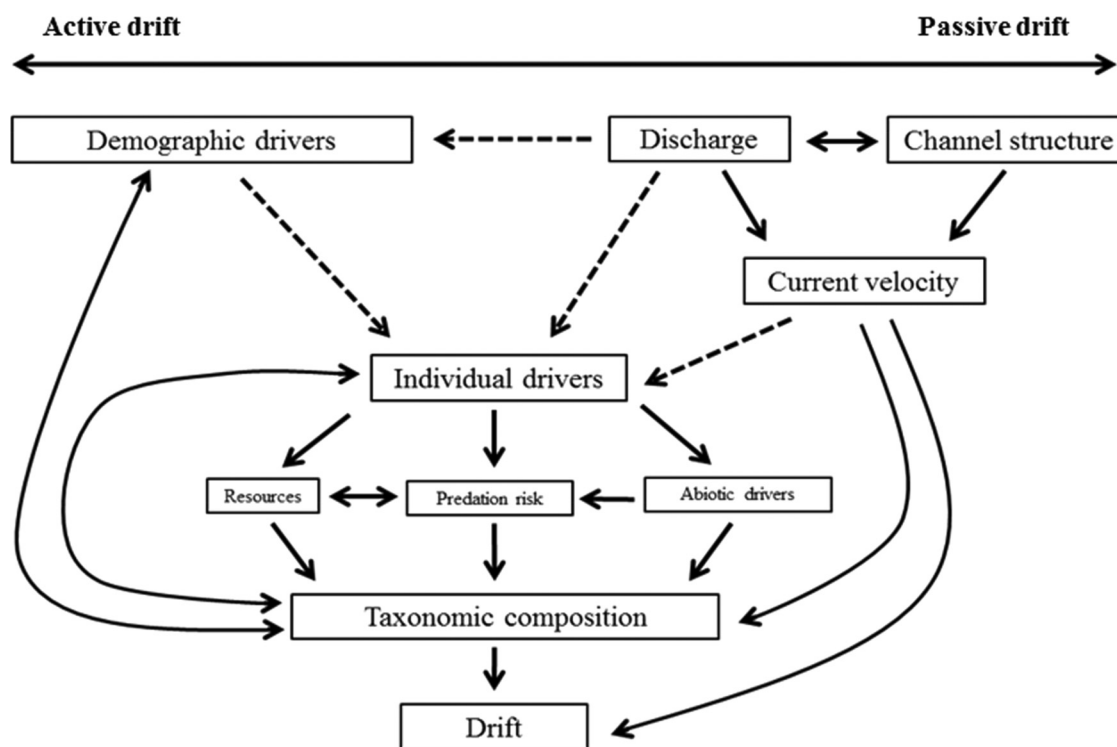
Direct empirical estimates of drift depletion through fish predation in small streams have ranged widely but may be substantial. For instance, McLaughlin et al. (2000) estimated that less than 42% of available drifting prey was consumed by juvenile brook trout (*Salvelinus fontinalis*), while Wilzbach et al. (1986) estimated up to an 80% reduction in drift by cutthroat trout (*Oncorhynchus clarkii*). Leung et al. (2009) used a simple bioenergetics approach to estimate drift consumption by young-of-the-year and 1-year-old cutthroat trout feeding in pools at 25% and 50% of their maximum daily consumption and concluded that 36%–71% of drift could be lost to fish predation in a small trout stream. While these estimates suggest predation on drift may be a large component of daytime drift depletion, foraging efficiency and activity are generally much lower at night (Allan 1978; Sagar and Glova 1988; but see Elliott 2011) when drift abundances generally peak in fish-bearing streams (Bishop 1969). Therefore, while fish may deplete a major portion of diurnal drift in smaller streams, overall losses due to predation may be a negligible fraction of the total drift flux. Similarly, the fraction of drift consumed likely declines in larger rivers, where a much smaller proportion of physical habitat may be available to drift-foraging fishes of a given size (Rosenfeld et al. 2007).

### Domains of passive versus active drift dynamics

The relative contributions of active versus passive processes to drift are highly context-specific and often correlated (Fig. 2). For example, hydraulic stress influences passive drift but may also influence behaviour (e.g., Hoover and Richardson 2009). However, the general domains in which drift is primarily active or passive can be inferred in a qualitative sense, based on hydraulic conditions, diurnal periodicity, and taxonomic attributes.



**Fig. 2.** Conceptual diagram illustrating the potential interactions and hierarchical relationships among causal drivers of invertebrate drift. In this model, larger-scale biotic (population level) and abiotic (discharge, channel structure) drivers influence local active and passive individual-level drivers of drift. Many of these factors ultimately depend on the specific attributes of taxonomic groups. Dashed lines indicate that factors are not always interdependent or interact indirectly. For example, drift induced through predator avoidance occurs independent of discharge, although changes in discharge can mediate predator foraging efficiency or frequency of encounter through changes in habitat area.



### Taxonomic specificity and drift flux

Taxa and life stages differ greatly in their tendency to drift, often resulting in striking differences in community and size structure between the drift and benthos (O'Hop and Wallace 1983; Shearer et al. 2003). Predisposition to drift will vary among taxa depending on behavioural, ecological, and morphological traits (Wilzbach et al. 1988; Rader 1997; Elliott 2003). For instance, differences in body morphology and habitat use may influence the susceptibility of taxa to scouring flows. Rader (1997) used 12 behavioural and morphological traits to develop a classification index to rank invertebrates by their drift propensity. This trait-based classification approach has been integrated into broader functional classifications (e.g., Poff et al. 2006) and may provide a mechanistic basis for anticipating taxa-specific drift responses to environmental disturbance (e.g., Lancaster 2000). For example, taxa with high behavioural drift tendency may be predicted to increase drift relative to less mobile taxa following the addition of an abiotic stressor. Similarly, passive drift could be inferred if the drift composition is dominated by taxa with a high drag potential (i.e., more susceptible to scour). Currently, the main limitation of trait-based approaches is that the detailed natural history information required to generate the criteria for ranking drift propensity are unavailable for many taxa. Additionally, interspecific studies within the family Baetidae suggest that drift behaviour may differ substantially even at fine taxonomic levels (Peckarsky 1980, 1996), such that aggregating taxa into broader groups may generate misleading predictions.

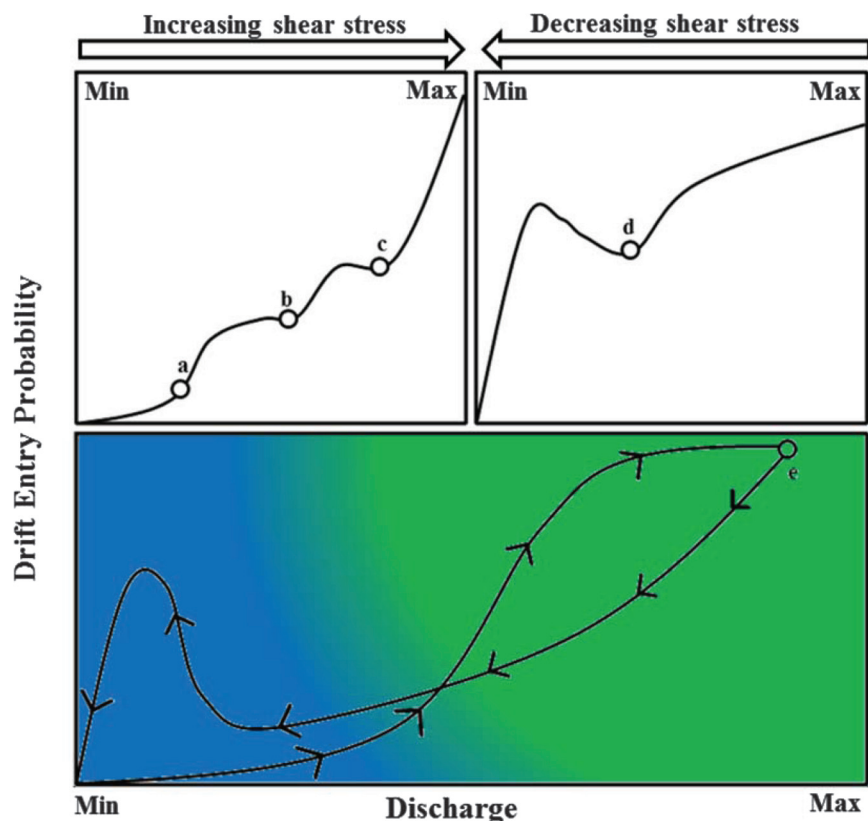
### Hydraulic effects on drift flux

The underlying dynamics of drift entry, transport, and exit are highly specific to local hydraulic conditions (e.g., Wilcox et al. 2008; Oldmeadow et al. 2010). Catastrophic drift is the most obvious case where hydraulic forces cause involuntary entrainment and transport of both invertebrates and bed particles. For example, (Gibbins et al.

2007a) found a clear threshold of shear stress at which catastrophic drift entry was initiated, where catastrophic drift was defined as rapid increases in suspended invertebrate abundance and a compositional shift in drifting taxa to resemble that of the benthos. Identifying a causal mechanism for drift at flows below a catastrophic threshold is more difficult and requires careful experimentation. For example, Hammock and Wetzel (2013) demonstrated that herbivore drift changed eightfold at stable flows when predators and food levels were manipulated relative to controls, suggesting that drift may be a predominantly active process during noncatastrophic flow. Much more work is needed, however, to fully resolve the context dependencies of active versus passive drift at stable flows.

During flow reductions, behavioural drivers generally dominate drift dynamics. Despite a more hydraulically benign environment as flows decline (i.e., lower turbulence and shear stress), multiple studies have observed increases in drift following rapid experimental flow reductions (e.g., Minshall and Winger 1968; Poff and Ward 1991; Dewson et al. 2007; James et al. 2009). Increased behavioural drift associated with declining flows likely results from several concurrent processes that influence fitness, including reduced habitat area and decreased water velocities. Shrinking wetted habitat area increases benthic densities, competition for resources, and potentially predator encounter rates (Dewson et al. 2007). Declining velocities reduce suspended and benthic particulate food transport and may shift abiotic conditions (e.g., depth, dissolved oxygen; James et al. 2009) beyond the suitable range for any particular taxon (Anderson et al. 2006b). Shrinking habitat area and reduced velocities on a declining hydrograph are confounded, but both appear to be important triggers of drift. James et al. (2008) reduced flows and observed short-term increases in drift with no change in habitat area, implying a reduction in area or quality of suitable microhabitats for drifting taxa despite constant wetted area, whereas Corrarino and

**Fig. 3.** Conceptual figure illustrating the relationship between flow and the probability an invertebrate will drift. The top panels show hypothetical flow-related thresholds in drift entry. When flow is increasing (top left panel), there are several potential sequential entrainment thresholds that would initiate mass drift: (a) scouring of organic detritus, which is initiated at the lowest shear stress; (b) scouring of attached algal mats; and (c) scouring of inorganic substrates. When flow is decreasing (top right panel), drift decreases with flow reduction either because of acclimation to high flow conditions or depletion of benthos (i.e., fewer potential drifters). With continued decreasing flows, behavioural thresholds are reached (d) because of changing abiotic (e.g., velocity) or biotic (e.g., competition or predation) conditions, causing an increase in drift entry. The overall response of drift to flow variation — shown in the bottom panel — can therefore take on two trajectories from the minimum (the origin in the bottom panel) or the maximum (e) flow depending on whether flow is increasing or decreasing. The colours in the bottom panel represent the domains where drift is primarily active (blue, left side) and passive (green, right side). [Colour online.]



Brusven (1983) found drift to increase only after 30% of habitat area was dewatered following flow reduction.

There are several important exceptions to drift increases at low flows. First, the time scale over which flow is reduced may be a critical determinant of whether behavioural drift increases. For instance, several studies have observed decreased drift flux and concentration across natural declines in flow (Leeseberg and Keeley 2014) or experimental declines over multiple weeks (Harvey et al. 2006; Wooster et al. 2016). Second, there is some evidence that taxa may respond in different directions to flow declines (James et al. 2009; Kennedy et al. 2014). Taken together, these results suggest that increased drift following reduced flows may be a temporary response over short time scales and varies across taxa.

Overall, we conceptualize a transition of domains from increasingly behaviourally dominated drift along a declining hydrograph to primarily passive drift on an increasing hydrograph (Fig. 3). This represents an example of hysteresis (Gunderson 2000), where the response of a system depends on prior conditions (i.e., drift magnitude for a given flow differs between the rising and falling limbs of the hydrograph). A key consequence of this conceptual model is that the absolute magnitude of hydraulic stress may be less important than its direction and rate of change in determining the response of invertebrate drift to flow variation (Imbert and Perry 2000). Empirical support for this model comes from drift observations during hydropeaking in regulated rivers, where differences in drift concentration between ascending and descending points along a

hydrograph are regularly observed (Perry and Perry 1986; Patterson and Smokorowski 2011; Miller and Judson 2014).

#### Diurnal versus nocturnal effects on drift

Behavioural drift can be envisioned as a form of active patch selection under predation risk. Foraging theory generally predicts that animals will balance conflicting demands for energy acquisition and predator avoidance by minimizing the ratio of mortality risk to foraging opportunity (Sih 1980; Werner and Gilliam 1984; Fraser and Huntingford 1986; Gilliam and Fraser 1987; Lima and Dill 1990). In fish-bearing streams, invertebrates face predation risk from both benthic and drift-feeding predators while foraging in a spatially and temporally patchy environment. The fish avoidance hypothesis (Allan 1978) posits that nocturnal peaks in drift are a result of invertebrates optimizing foraging opportunities while minimizing mortality risk from visually feeding fish. There are multiple lines of evidence indicating strong effects of fish on invertebrate drift behaviour (reviewed in Allan and Castillo 2007), most notably that drift is generally aperiodic in fishless streams (Flecker 1992). Several studies have also demonstrated changes in the magnitude of photoperiodicity in response to manipulations of fish presence (e.g., Flecker 1992; McIntosh and Peckarsky 1996) and light levels (Perkin et al. 2014), suggesting that diurnal periodicity is a plastic behavioural adaptation to avoid fish predation.

If invertebrates actively minimize mortality relative to foraging gains, then drifting (searching for a new foraging patch) should occur

under conditions where local resource abundance is low, benthic predation risk is high, and drift predation risk is low. Nocturnal drifting appears to satisfy these conditions; drift-feeding fish are less active and efficient at night (Allan and Feifarek 1989), within-patch foraging opportunities may be reduced if algal resources are depleted during the day, and benthic predators are more active at night (Hammock et al. 2012). The importance of active versus passive drift entry mechanisms may therefore be dependent on photoperiod, and it has been suggested that diurnal drift is entirely passive while volitional behavioural mechanisms dominate nocturnal drift entry (Huhta et al. 2000; Humphries 2002; Hammock et al. 2012).

Invertebrates can also use indicators of predation risk other than light levels to adjust their drift behaviour (e.g., Fraser and Huntingford 1986), in particular the presence of waterborne chemical cues from predators (Douglas et al. 1994; McIntosh and Peckarsky 1996; Crespo 2011). For instance, McIntosh and Peckarsky (2004) demonstrated that the mayfly *Baetis bicaudatus* adjusted its drift behaviour proportionally to the risk imposed by the odours of different fish predators. Studies have also shown *Baetis* to adjust its drift behaviour along gradients of fish density (Flecker 1992) and in response to simultaneous manipulations of predation and resources (Culp et al. 1991; Scrimgeour and Culp 1994a, 1994b; Hoover and Richardson 2009). These results indicate that *Baetis*, a highly drift-prone taxa, has a moderately sophisticated response to balance foraging opportunities and predator avoidance using multiple environmental cues. The levels of behavioural sophistication among other taxa are unclear, but likely comparable.

## Spatial and temporal drift dynamics

### Habitat effects on drift

Although streams are hydraulically diverse, spatial variation in drift dynamics across physical habitat gradients remains poorly understood. One reason for this is that drift is typically measured in the field as a concentration (the number or biomass of animals per volume of water; Allan and Russek 1985). Drift concentration is a measure of standing crop and an emergent property of drift entry, transport, and exit rates. Consequently, spatial relationships are potentially confounded because multiple combinations of entry, transport, and exit rates can generate the same drift concentration. In addition, because of the nature of downstream transport in running water, drift concentration will exhibit a spatial lag of unknown distance between the discrete location in which it was measured and the upstream patch where it was produced, resulting in a spatial mismatch between drift concentration at a given location and the habitat features to which it is causally linked. A more informative approach for characterizing drift–habitat relationships is to directly measure rates of entry, transport, and exit in the field. However, because of logistic challenges, empirical measurements of these rates are rare.

Small streams show striking gradients in depth, velocity, and substrate among discrete habitat types such as pools, riffles, runs, and glides (Montgomery and Buffington 1997). Invertebrates using these habitats are subjected to different biotic conditions and hydraulic forces (Peterson and Rabeni 2001; Walters et al. 2003) that can be expected to influence the dynamics of drift entry, transport, and exit. At one extreme, drift entry and transport may be highest in riffles, erosional habitats with greater turbulence and shear stress and often greater benthic densities (Scullion et al. 1982; Grubaugh et al. 1997; Grossman 2014). Alternatively, drift entry and transport would be expected to be low, while exit through settlement and predation would be high, in pools, low-velocity depositional habitats. With these predictions in mind, streams can be envisioned as a continuous source–sink matrix composed of habitats where drift is produced and those where drift is depleted owing to settlement and predation by drift-feeding fishes (Rosenfeld and Raeburn 2009).

A corollary of the source–sink framework is the inference that spatial variation in velocity is a primary driver of drift entry, transport, and exit (Ciborowski 1983, 1987; Bond et al. 2000). However, empirical support for this assumption is mixed. In one of the only studies to directly measure drift distances in situ across different habitat configurations, Lancaster et al. (1996) found that reach-scale drift increased with mean velocity and decreased with the number of depositional microhabitats. Similarly, some studies have found drift to be consistently higher in riffles than other habitat types (Leung et al. 2009) and to increase with riffle length and area (Hansen and Closs 2007). Pools as drift sinks, however, have received less support. While several studies have found reduced drift concentration at the downstream end of pools (Waters 1965; Martin and Knight 1989), others have found no change or even increased drift concentration below pools (Elliott 1971; Kovalak 1978). Moreover, in contrast with Lancaster et al. (1996), there does not appear to be a consistent relationship between drift concentration and velocity within habitat types. Some studies have found significant correlations (Keeley and Grant 1997; Nislow et al. 1998; Hayes et al. 2012), while others have not (Hansen and Closs 2007; Leung et al. 2009).

Other aspects of habitat complexity may also modify the spatial dynamics of drift. In-stream wood can reduce drift concentration through direct entrapment (i.e., reducing transport; Bilby 1981) by increasing settlement through creation of hydraulic dead zones (Lancaster et al. 1996; Bond et al. 2000) or by increasing depletion through predation if fish densities are higher in complex habitats (e.g., Roni and Quinn 2001). Kiffney et al. (2014) found reduced drift concentration in experimental stream channels augmented with wood as well as decreased drift in reaches with higher wood abundance in a fourth-order stream. They also observed a positive relationship between wood abundance and local density of drift-feeding coho salmon (*Oncorhynchus kisutch*), providing support for drift concentration reduction through both physical entrapment and predation. In contrast, Gustafsson et al. (2014) found increased drift following experimental wood additions, suggesting that enhanced benthic production on wood (Benke et al. 1984; Benke and Wallace 2003) may increase drift entry. In addition to wood, channel sinuosity, substrate heterogeneity, and surface roughness may also influence the source–sink dynamics of drift but have received limited attention.

Ultimately, understanding spatial dynamics of drift requires characterizing the habitat dependency of each of the components of drift (entry, transport, and exit rates) and the parameter space combination that generates observed drift concentrations. For instance, it is conceivable that drift production is relatively uniform among habitat types and spatial variation in concentration is primarily driven by heterogeneity in transport and exit dynamics (e.g., Anderson et al. 2013). Empirically, flume experiments and a small number of field observations have given limited insights into transport and exit rates (e.g., Lancaster et al. 1996). In contrast, field measurements of drift entry — expressed as a production rate per bed area — are virtually nonexistent (but see Romanisyn et al. 2007). Drift entry is a fundamental production parameter, the measurement of which will likely generate key insights into physical controls underlying spatial variation in drift flux and concentration. While field measurements of drift entry, transport, and exit rates are logistically challenging, their quantification should be a goal of future drift research.

### Seasonal dynamics

While short-term drift dynamics are dominated by nocturnal peaks, drift shows important seasonal trends over longer temporal scales (Waters 1965; Keeley and Grant 1997; Jenkins and Keeley 2010). However, the direction and magnitude of seasonal trends varies among studies. For temperate streams, drift abundance appears to peak in spring and decline through the summer and fall (O'Hop and Wallace 1983; Hieber et al. 2003; Leeseberg and Keeley 2014), although fall (Stoneburner and Smock 1979) and summer (Hayes



et al. 2000) peaks have been observed. In contrast, tropical streams show generally less consistent seasonal patterns (Ramirez and Pringle 2001). This difference may be a result of biotic processes unique to tropical streams (i.e., continuous benthic invertebrate reproduction associated with reduced seasonality and precipitation-induced flood events), but also may reflect the deficit of studies in the tropics relative to temperate systems.

Seasonal trends in drift may reflect seasonal changes in discharge, suspended sediment (O'Hop and Wallace 1983), temperature (Dudgeon 1990), and photoperiod. Alternatively, seasonal variation in drift may be largely driven by temporal succession in benthic community structure (Elliott 1967b). Not surprisingly, a close match between the seasonal abundance and composition of drift and the benthos supports close linkages among invertebrate life history phenology, adult emergence, and seasonal drift patterns (O'Hop and Wallace 1983; Rincón and Lobon-Cervia 1997). However, given their seasonal covariation, teasing apart abiotic constraints and phenology as drivers of seasonal drift patterns will require manipulative experiments that, to our knowledge, have yet to be performed.

## Relevance of drift to invertebrate populations and energy flow to higher trophic levels

### Benthic density and drift

Empirically relating drift to benthic abundance is critical for understanding the consequences of drift to benthic population dynamics. Drift may be directly proportional to benthic abundance (i.e., if it is passive) or density-dependent (if it is related to per capita resource abundance). Many studies have considered the role of density dependence in benthic invertebrate population dynamics, either to test for general properties of population limitation or generalizable predictors of drift abundance (Shearer et al. 2003; Tonkin and Death 2013; Weber et al. 2014). Results to date have been equivocal. Density dependence has been inferred directly in some studies (Dimond 1967; Fonseca and Hart 1996) based on a curvilinear relationship between drift concentration or flux and benthic abundance (Chang and Sell 1984). Moreover, ancillary evidence showing that drifting individuals are often smaller (Poff and Ward 1991; Richardson 1991) and exhibit higher frequency of injury and lower gut fullness than those in the benthos (Williams and Levens 1988; Turner and Williams 2000) is consistent with density-dependent self-thinning. In contrast, other studies have found drift to be either proportional or unrelated to benthic densities (Corkum 1978; Statzner et al. 1987; Humphries 2002; Shearer et al. 2003; Elliott 2003; Weber et al. 2014) and demonstrated no differences in individual condition between drifting and benthic individuals (Ploskey and Brown 1980; Wilzbach 1990). Based on these variable results, broadly generalizable, quantitative relationships between drift and benthic density appear unlikely (e.g., Shearer et al. 2003).

These incongruent findings may reflect issues with sampling designs (e.g., inappropriate ranges of benthic densities), innate environmental or taxonomic specificity of density dependence (e.g., Kerans et al. 2000), or a poor quantitative understanding of how environmental correlates, such as resource abundance, mediate the effects of benthic density on drift. For instance, benthic per capita resource intake depends on both consumer density and resource (e.g., algal and detrital) abundance. Because of variation in resource abundance, density per se will only be a coarse indicator of per capita resource availability. Consequently, density-dependent thresholds that are demonstrable experimentally are inevitably context-specific and therefore likely to be poorly transferrable between streams or lack consistency in synoptic surveys. Studies that manipulated food resources directly have more consistently identified density-dependent thresholds, generally finding decreased drift entry following increases in resources (Hildebrand 1974; Kohler 1985; Richardson 1991; Siler et al. 2001; Hammock and Wetzel 2013). Likewise, experimental increases of herbivore densities leading to

depleted periphyton also elevated drift (Hillebrand 2005). These findings provide evidence that density-dependent resource competition can be an important driver of drift, which would not have been obvious without explicit manipulation of resource levels.

Spatial scale further complicates interpretation of drift–benthos relationships. Given that the upstream spatial integration of a typical drift sample is unknown (see section on Spatial and temporal drift dynamics), the appropriate scale at which benthic abundance and drift should be measured is poorly defined. This is a key methodological issue that is rarely considered. Density-dependent drift at different scales may also reflect different underlying processes. For example, density dependence at small scales (e.g., within a riffle) likely reflects within-patch aggregation dynamics (e.g., resource competition), whereas density dependence at larger scales may imply regional dispersal processes (e.g., recruitment limitation) more relevant to population dynamics (Anderson et al. 2006a). Spatial scale should therefore be given careful consideration when interpreting both descriptive and experimental studies of density-dependent drift (Englund and Cooper 2003; Melbourne and Chesson 2005).

### Implications of drift for invertebrate population dynamics

Historically, research has focused on benthic population persistence in the face of constant unidirectional losses of individuals through drift (i.e., the “drift paradox”; Müller 1954, 1982; Waters 1965; Humphries and Ruxton 2002). The core debate concerned whether compensatory upstream movement was necessary for population persistence or, alternatively, if drift represented surplus production in excess of carrying capacity. This debate appears to have been resolved theoretically, as several studies have demonstrated population persistence in advective environments through the processes of density dependence, random directional benthic dispersal (e.g., through crawling), and high benthic productivity (Anholt 1995; Speirs and Gurney 2001; Lutscher et al. 2010). More recent work concerns the role of drift-mediated dispersal as a determinant of spatial variation in abundance within streams.

Given the large number of animals often found in drift, population dynamics of stream invertebrates have been traditionally thought to be dominated by emigration and immigration, and drift was seen as a key dispersal agent linking spatially discrete population patches (Townsend 1989; Palmer et al. 1996; Winemiller et al. 2010). More recent work has posed an alternative view that widespread dispersal of freshwater invertebrates is not as pervasive as was assumed (Bohonak and Jenkins 2003; Downes and Lancaster 2010; Lancaster et al. 2011). This shift in thinking has led to the idea that small-scale movements (i.e., within-patch aggregation) dominate local dynamics, but larger-scale population processes primarily result from environmental variability in birth and death rates (Anderson et al. 2005). This viewpoint implies that drift, while important for individual habitat selection and distribution, may have minimal consequences to larger-scale population dynamics of stream invertebrates.

We offer a more nuanced perspective and suggest that drift may still be essential to spatial population dynamics, but the extent of its contribution depends on the broader life history adaptations of specific taxa (reviewed in Verberk et al. 2008) and whether a taxa is recruitment-limited (at low densities below the capacity of the habitat). For taxa whose life history strategy is selected against strong nymphal dispersal, drift may be rare and have little consequence to population dynamics unless it is of sufficient magnitude to reduce a population below carrying capacity (e.g., catastrophic drift). Examples would include taxa like *Emephmerella ignita* that widely disperse their eggs when they broadcast oviposit in the stream water column (Lancaster et al. 2011). For these taxa, dispersal effectively happens during oviposition. For taxa that are limited to ovipositing in a limited subset of habitat types that may be rare or patchily distributed (e.g., *Baetis rhodani* restricted to ovipositing on emergent rocks in riffles; Lancaster et al. 2011), dispersal will have to take place at either

an adult or a nymphal life history stage (e.g., through drift or benthic movement), where it may be density-dependent (Fonseca and Hart 1996; but see Lancaster et al. 2011).

While this perspective has a theoretical basis (further discussed in the section on Population-level drift models), the role of drift relative to other movement strategies based on empirical work is ambiguous. Numerous studies have quantified the relative contributions of contrasting movement strategies to dispersal and spatial distribution of benthic populations (reviewed in Mackay 1992; Bilton et al. 2001; Malmqvist 2002); however, they have been primarily taxa-specific (e.g., Downes and Lancaster 2010). Generalizing the extent to which life history traits mediate the effect of drift on invertebrate populations will require a thorough review and synthesis of the relative dispersal modes and their attendant fitness consequences for taxa across a gradient of life history characteristics, for example, taxa that vary in drift frequency, oviposition behaviour, or adult dispersal distance (e.g., Elliott 2003).

Broadening the context of drift dispersal to the whole life cycle of stream invertebrates will also require integrating drift measurements over the whole nymphal life stage of an organism (Anderson et al. 2005). While most estimates of drift distances have been measured over single drift events (e.g., Larkin and McKone 1985), lifetime drift distance provides a more meaningful measure of dispersal given that individuals may drift many times throughout their aquatic life stage (Humphries and Ruxton 2003). Similarly, drift-associated mortality risk is rarely assessed over time scales longer than single drift events. While logistical challenges to these measurements are steep, some researchers have managed to overcome them using a diversity of approaches. For example, lifetime dispersal has been directly estimated using mark-recapture to track movements over multiple dispersal events (Jackson et al. 1999; Elliott 2003). Others have used indirect correlative approaches, where dispersal distances or mortality risk is inferred from drift and (or) settlement measured at different locations. For example, Lancaster et al. (2011) measured drift at downstream and upstream ends of adjacent riffles and estimated that few individuals drifting out of a riffle reached the next riffle downstream. This observation, coupled with a positive correlation between benthic densities of *Baetis* neonates and egg masses, led them to conclude that long-distance drift dispersal of this taxon was minimal on average, and spatial distribution was primarily driven by aerial dispersal of adults.

### Consequences of drift variation for energy flux to fish

Drift-foraging predators are a large guild of riverine fishes that are particularly abundant in temperate zones (Grossman 2014). Although drift-foraging fish may have considerable dependence on terrestrial invertebrates (e.g., Wipfli 1997), drift of benthic origin constitutes the primary prey source for many, such as stream-rearing salmonids (e.g., Nielsen 1992), which are often food-limited (Boss and Richardson 2002; McCarthy et al. 2009; Wipfli and Baxter 2010). Drift availability is therefore of great importance to drift-feeding fish production, and the magnitude of drift flux to fishes has been directly linked to increased growth (Keeley 2001; Kiffney et al. 2014; Weber et al. 2014), abundance (Fausch et al. 1991), survival (Rosenfeld et al. 2005), and movement patterns (Hansen and Closs 2009). Drift is therefore an important determinant of fish habitat quality and consequently is a key parameter in drift-foraging bioenergetic models (e.g., Hughes and Dill 1990), which are emerging as an increasingly common approach for assessing habitat capacity for drift-feeding fishes (Rosenfeld et al. 2014).

In this applied trophic dynamics context, fish biologists have focused on bulk drift concentration or total prey flux — rather than taxon-specific drift rates — because bulk drift metrics are more easily linked to fish consumption (Hansen and Closs 2009; Weber et al. 2014). While drift-foraging models have been successful in terms of exploring the energetic trade-offs involved in foraging position choices and behavioural strategies of drift-feeding fishes (Fausch 1984; Nielsen 1992; Hughes 1998; Piccolo et al. 2014),

absolute predictions are very sensitive to estimated drift abundance as an input parameter (e.g., Rosenfeld and Taylor 2009). Uncertainty in how drift varies spatially and temporally complicates attempts to quantitatively predict drift concentration (see above section on Spatial and temporal drift dynamics) and consequently also reduces confidence in predictions from drift-foraging models. As a result, most empirical applications have treated drift as a constant or fitted parameter when modelling habitat quality over a range of physical conditions or locations (Railsback et al. 2003; Urabe et al. 2010; Rosenfeld and Ptolemy 2012). Improved empirical predictions of fish biomass and production using drift-foraging models will require a much better understanding of the spatial and temporal drivers of variation in drift abundance.

Potential feedbacks between drift predation and drift production also remain poorly resolved. While it is known that predation may have localized effects on drift concentration (i.e., causes depletion immediately downstream of a fishes focal point; Hughes 1992; Hayes et al. 2007), an implicit assumption of most drift-foraging models is that there are no active feedbacks from predation on drifting invertebrate behaviour or populations (i.e., drift-feeding is assumed to be donor-controlled). Several studies have failed to detect an effect of drift-feeding fish on the benthos (Allan 1982; Dahl and Greenberg 1996); however, there is some evidence that predation on drift may have top-down effects (Forrester 1994; Diehl et al. 2000; Meissner and Muotka 2006), and the ability of trout to consume a significant fraction of benthic production is well documented (e.g., Huryn 1996). Incorporating a major feedback between predation and drift production (entry rates) could substantially alter current drift-foraging modelling approaches. Overall, the controls on drift-foraging consumer-resource coupling remains a fundamental gap in our understanding of trophic dynamics in streams, as well as the ability to accurately assess trophic interactions and habitat quality using drift-foraging models.

### Predictive modelling of drift dynamics

Models describing drift dynamics generally fall into three categories: behavioural-based mechanistic or theoretical models rooted in individual decisions related to balancing predation risk and foraging opportunities; population-level models, generally focused on population persistence or spatial population distribution; and models of bulk community drift aimed at estimating the flux of invertebrate prey to drift-feeding fish. Individual and population models have been conceptually focused and less concerned with empirical prediction (but see Anderson et al. 2013), while bulk community models have generally ignored underlying biotic processes and focused on empirical prediction of drift concentration. Given this disparity in underlying motivation and minimal examples of model validation against field data, quantitative comparison among modelling frameworks is impractical. Instead, we provide an objective overview of each approach and discuss the potential for integrated approaches in the future.

#### Individual behavioural models

Behaviourally induced drift has been modelled as a form of active patch selection and builds on the trade-off animals make between increasing energy intake and elevating predation risk while foraging (Werner and Gilliam 1984; Gilliam and Fraser 1987; Sih and McCarthy 2002). For example, Ruetz and Stephens (2003) formulated a predictive behavioural drift model using a probabilistic, discrete-time approach that envisions streams as a random configuration of patches varying in food availability and benthic predation risk. A transition matrix then describes the likelihood of animals shifting states (i.e., entering the drift or returning to the substrate). Given the assumption that invertebrates optimize foraging gain relative to predation risk, the model intuitively predicts that invertebrates should drift when benthic predation risk is high and when food availability and predation risk while drifting are low.



This type of individual drift model offers a promising avenue to generate and test hypotheses of behavioural drift dynamics, especially in an experimental context where both food and predation risk can be manipulated (e.g., Kohler and McPeck 1989; Scrimgeour and Culp 1994a; Hammock and Wetzel 2013). The main appeal of this approach is that it allows for multiple factors (foraging opportunities, benthic predation risk, and predation risk while in the drift) to be simultaneously considered in a quantitative framework. While the approach of Ruetz and Stephens (2003) makes several simplifying assumptions, including constant individual traits and environmental conditions, there are opportunities within this framework to incorporate additional realism.

The utility of behaviour-based modelling approaches in an empirical, predictive context may be limited, however. Given that models are generated under the assumption that drifting is the primary antipredator behaviour, predictions are extremely sensitive to other avoidance behaviours that modify predation risk, such as burrowing (e.g., Peckarsky 1996). Addressing this assumption to correctly parameterize predation models requires detailed behavioural information that is absent for most taxa and thereby precludes most predictive applications.

### Population-level drift models

Population-level models have generally focused on the influence of drift on population persistence (Pachepsky et al. 2005; Lutscher et al. 2010) or spatial population distribution (Diehl et al. 2008). Persistence-focused approaches primarily describe drift with dispersal kernels, a temporally explicit probability distribution of an organism moving a given distance, which can be derived empirically (Humphries and Ruxton 2003) or through mechanistic movement models (Speirs and Gurney 2001; Lutscher et al. 2010). Conditions for population persistence are then derived by simulating population dynamics over a range of demographic (e.g., birth and death rates) and dispersal parameters. Spatially focused population models are aimed at understanding the dynamics of populations in heterogeneous environments linked by movements. Specifically of interest is the transition of spatial domains in which local population dynamics dominated by drift-mediated dispersal shift to regional dynamics driven by birth and death rates (Anderson et al. 2005; Melbourne and Chesson 2005). Dispersal through drift is a key model parameter that has been either fitted from field data (Melbourne and Chesson 2006; Diehl et al. 2008) or modelled from an exponential distribution (discussed in the following section; Anderson et al. 2005).

### Modelling bulk community drift

In contrast with individual and population models, bulk community drift modelling applications have broadly ignored individual behavioural decisions and population dynamics and have focused on predicting total drift concentration with the goal of understanding both turbulent transport processes (McNair and Newbold 2001) and prey availability for drift-feeding fishes (e.g., Hayes et al. 2007). Empirical estimates of invertebrate transport and settling rates have been used to parameterize drift transport models (McLay 1970; Elliott 1971; Larkin and McKone 1985), which ultimately predict drift concentration and the total flux of drift to fish (Hayes et al. 2007). One general approach has been to model the proportion of released individuals remaining in suspension as a negative exponential function of distance below the release site (i.e., location of drift entry). This framework, originally described by McLay (1970), takes the following form:

$$N_x = N_0 e^{-Rx}$$

where  $N_x$  is the number of animals in the drift at  $X$  distance from their point of entry,  $N_0$  is the initial density of animals, and  $R$  is the rate of settlement.  $R$  can be parameterized for different species based on empirical observations (Elliott 1971) or hydraulic settling

relationships derived for inert particles (see references in Anderson et al. 2013; Kennedy et al. 2014). While exponential settling models have generally been well supported empirically (Larkin and McKone 1985), McNair and Newbold (2012) argue that this approach inaccurately predicts near-field (i.e., close to the entry site) settling dynamics and advocate an alternative local exchange model based on advection–diffusion fluid mechanics. The key advancement of the local exchange model is that it considers both longitudinal and vertical dimensions (as opposed to only longitudinal), resulting in the prediction that an exponential settling distribution will hold for far-field but not near-field settling. This was supported by a meta-analysis of empirical data, where McNair and Newbold (2012) concluded that exponential settling time and distance distributions were suitable for predicting far-field drift but not accurate for describing drift dynamics close to release points, suggesting that local exchange modelling is a more accurate approach.

In addition to exponential and local exchange models, predictive drift models have also been developed based on Markov processes describing lateral and downstream dispersion in turbulent environments. This approach was pioneered by Ciborowski (1983), with the goal of predicting mayfly redistribution from drift. More recently, the framework was extended by Hayes et al. (2007) as a component of a drift-foraging bioenergetics model. Using site-level entry and settling rates and upstream drift concentration as inputs, their model makes spatially explicit predictions of drift concentration through a given area of stream (for more extensive review see Rosenfeld et al. 2014).

For both mechanistic dispersion-based and exponential or local exchange-based models, the parameterization of drift entry rate is a crucial source of uncertainty and limits their application and transferability. Drift entry rates are usually adjusted as part of the model-fitting process; using settling rates as fixed parameters from the literature, entry rates are adjusted to generate observed drift concentrations (e.g., Hayes et al. 2007; Anderson et al. 2013; Railsback et al. 2003, 2009). Other applications have either assumed constant drift concentration (Rosenfeld and Taylor 2009) or that entry is directly proportional to benthic density (Kennedy et al. 2014). The predictive power of bulk community drift models may be contingent on the relative contribution of active versus passive processes to drift dynamics. For example, community models may have high predictive power in large rivers, where drift may behave similarly to passive particles (i.e., accidental drift may dominate, with transport primarily controlled by discharge; Kennedy et al. 2014). Similar models, however, may be less applicable in smaller streams where entry and transport may have stronger behavioural controls and there may be substantial depletion through predation (Leung et al. 2009).

### Comparison and integration of approaches

As with any modelling endeavor in ecology, there are trade-offs between the predictive ability of a model and its computational complexity and information requirements. For modelling drift flux, a key question moving forward is the extent to which prediction would be improved by incorporating taxon-specific behavioural and population-level processes (e.g., predator avoidance or density dependence). It is currently unclear whether individual- and population-based approaches should remain conceptual exercises or be integrated into a common framework with bulk hydraulic-based drift flux models. To date, Anderson et al. (2013) is the only example we are aware of that combines benthic population dynamics with hydraulic and particle tracking models. However, the predictive power gained from this added complexity is unclear given this model has yet to be tested against field data.

### Conclusions

Invertebrate drift is a key process in running waters that affects benthic production, community structure, and energy flow to higher trophic levels. An improved process-based knowledge of drift is fundamental to our basic understanding of stream ecosystem dynamics,

**Table 2.** A summary of some key areas of invertebrate drift deserving further study.

	Description	Example references
Individual	Determine relative influence of active and passive causes of drift Predation risk assessment ability across taxa	Hammock and Wetzel 2013 McIntosh and Peckarsky 2004
Population	Lifetime drift distances and mortality risk Importance of rare long-distance drift events Population-level consequences of within-patch drift dynamics The effects of selective drift on intraspecific population variation	Humphries and Ruxton 2003; Elliott 2003
Spatial and temporal variation in drift	Field measurements of drift entry, transport, and exit  The effects of habitat complexity on drift rates The relative effects of discharge and phenology on seasonal changes in drift	Romaniszyn et al. 2007; Lancaster et al. 1996; Elliott 2002 Kiffney et al. 2014; Gustafsson et al. 2014
Trophic dynamics	What determines whether drift is donor controlled?	
Predictive drift modelling	Integrating individual- and population-level processes within bulk community models Parameterization of drift entry rates	Humphries and Ruxton 2003; Anderson et al. 2013 Hayes et al. 2007

Note: References shown represent examples of approaches that may be appropriate to address each issue.

as well as the management and conservation of drift-feeding fishes. Like most developing fields in ecology, the challenge lies in moving beyond qualitative descriptions of processes to quantitative models that allow concrete predictions of rates, fluxes, and their associated consequences for populations and communities (Table 2). Four broad themes emerge as priority research gaps: (i) *quantitatively determining the relative influence of passive versus active causes of drift and the domains where they operate*; this is fundamental to both theoretical and descriptive applications and will require controlled experiments with multiple causal factors; (ii) *linking drift to broader population demographics*; creative experimental and field-based approaches should aim to measure drift at spatial and temporal scales relevant to regional population processes to resolve the role of drift in benthic population dynamics; (iii) *characterizing how explicit components of drift (entry, transport, and exit) vary spatially and temporally*; and (iv) *synthesizing descriptive, experimental, and theoretical approaches for developing predictive models of drift, ranging from strictly empirical models to process models incorporating individual-, population-, and community-level processes*.

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