

**THE INFLUENCE OF PHYSICAL HABITAT STRUCTURE ON INVERTEBRATE
DRIFT AND PACIFIC SALMON PRODUCTION IN FOREST STREAMS**

by

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Abstract

Untangling the mechanisms linking the physical world to ecological processes is paramount for effectively conserving and restoring habitat for threatened species. Pacific salmon rearing in small streams have been particularly well studied in this regard given that physical habitat features (e.g., velocity) strongly influence their performance and that habitat alteration is a major cause of their decline in many areas. However, despite strong evidence that stream salmonids are food limited, we lack commensurate understanding of how habitat influences their food supply - suspended invertebrates drifting downstream (invertebrate drift). Consequently, the mechanisms linking physical habitat structure to salmonid production remain unclear. My dissertation attempts to address this issue. First, in Chapter 2, I review and synthesize the mechanisms underlying invertebrate drift, discuss potential caveats in methodology, and identify key knowledge gaps. I particularly highlight how the physical and behavioural processes governing drift entry are highly dependent on context-specific abiotic and biotic attributes (e.g., hydraulics, individual condition). In Chapter 3, I use flow manipulation experiments to show that some of this context dependency can be explained by considering behavioural and morphological traits of invertebrate taxa, which underlie their tendencies to drift behaviourally or passively; for instance, body shape predicted the magnitude of responses to increased flows. In Chapter 4, I show that aggregate community-level drift rates vary spatially in streams over scales relevant to individual drift-feeding salmonids. Specifically, I measured spatially explicit rates of drift production, demonstrating that shallow high velocity riffles and deep low velocity pools form distinct sources and sinks of drift within stream networks. In Chapter 5 I build on this result to show that drift generation in riffles coupled with strong preferences for low velocity pools by salmonids

leads to maximum fish production occurring in habitats with intermediate ratios of pool-riffle areas; in essence, a trade-off between increasing space but declining food as pool area increases. I extend these results with bioenergetic simulations to show that the shape of this trade-off is sensitive to alternative modes of prey delivery (e.g., aerial inputs of terrestrial invertebrates), which may be decoupled from in-stream habitat conditions.

Lay Summary

Small streams provide critical rearing habitat for juvenile Pacific salmon yet experience widespread alteration of their physical character. Predicting the effects of these alterations is a critical research area, which has led to a large body of work relating physical conditions (depth, water velocity) to fish abundance. However, considering fish abundance in the context of physical habitat alone misses out on potentially important effects habitat change on food availability. Here, I consider the influence of stream habitat on salmon food supply – suspended invertebrates drifting downstream (“invertebrate drift”). I found that invertebrate drift varies systematically across distinct habitat types in streams; specifically that high velocity areas act as sources of prey, while low velocity areas act as sinks. This variation lead to complex effects of habitat structure on salmon production due to the conflicting demand for low velocity areas preferable for fish occupancy and high velocity habitats that generate food.

Preface

Chapter 2: A version of this chapter is published in a peer reviewed journal with the following citation: Naman SM, Rosenfeld JS, and Richardson JS. 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes.

Canadian Journal of Fisheries and Aquatic Sciences. 73 (8): 1292-1305. I conducted the literature review and wrote the manuscript with edits and input from Jordan Rosenfeld (hereafter JR) and John Richardson (hereafter JSR).

Chapter 3: A version of this chapter is published in a peer reviewed journal with the following citation: Naman SM, Rosenfeld JS, Richardson JS, and Way JL. 2017. Species traits and channel architecture mediate flow disturbance impacts on invertebrate drift. *Freshwater Biology*. 62(2): 340-345 I designed the study with input from JR and JSR; I constructed the mesocosms, performed the experiment, and conducted the lab work with help from JW. I analyzed the data and wrote the paper with input from all co-authors.

Chapter 4: A version of this chapter is published in a peer reviewed journal with the following citation: Naman SM, Rosenfeld JS, Third LC, and Richardson JS. 2017. Habitat-specific production of aquatic and terrestrial invertebrate drift in small forest streams: implications for drift feeding fish. *Canadian Journal of Fisheries and Aquatic Sciences*. 74: 1208-1217. I designed the study with help from JR; LC and I performed the fieldwork, and processed the samples; I analyzed the data and wrote the paper with input from all authors.

Chapter 5: A version of this chapter is in preparation for a peer reviewed journal. I conceived the study design with help from JR, JSR, and P. Kiffney (PK). I performed the experiment with help from JR and PK; I conducted the lab work, analyzed the data, and wrote the paper with input from all authors.

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Chapter 1 General introduction

The physical world profoundly shapes the ecology of living organisms. The performance of individuals, the dynamics of populations, and the nature of species interactions are all directly linked to abiotic conditions imposed by physical habitat (Hutchinson 1958, Pulliam 1988). Physical habitat conditions are also strongly heterogeneous at multiple spatial and temporal scales across nearly every ecosystem on the planet (Persson et al. 1996, Kovalenko et al. 2011). Consequently, understanding the implications of physical habitat heterogeneity for biotic processes has been a longstanding goal in ecology, forming the premise of a large body of theory (McCoy and Bell 1991, Dunning et al. 1992, Rooney et al. 2008) and empirical study (Huffaker 1958, Crowder and Cooper 1982, Grabowski 2004).

The influence of physical heterogeneity spans multiple levels of ecological organization (Addicott et al. 1987). For instance, if the performance (e.g., growth, survival) of individuals in spatially heterogeneous habitats often differs among patches with contrasting abiotic conditions (Menge and Lubchenco 1981), population demographics may be strongly affected by the availability and configuration of suitable and unsuitable habitat patches (Pulliam 1988, Dunning et al. 1992). Similarly strong effects of habitat heterogeneity are evident on predator-prey interactions. For instance, habitat patches where predators have reduced foraging efficiency can function as refuge for prey and prevent consumers from accessing the full population of their resources (Hassell 1978). This spatial separation of predators from prey strongly impacts interaction strengths (Gause 1934, Grabowski 2004), and in turn patterns of energy flow through food webs (Tunney et al. 2012, Bellmore et al. 2015).

The ecological impacts of habitat heterogeneity are especially evident in lotic ecosystems, where the unidirectional flow of water governs the physical environment and its biotic inhabitants (Vogel 1994). In particular, hydraulic forces associated with flow (e.g., drag) exert a constant and pervasive influence on the ecology of stream organisms (Power et al. 1988, Hart and Finelli 1999, Trinci et al. 2017). These hydraulic forces and associated structural conditions (e.g., substrate size) are strikingly variable in space and time; for instance, between seasonal floods and droughts or among distinct erosional and depositional areas. A particularly notable example occurs in many single-channel alluvial streams where alternating bathymetric highs and lows form characteristic sequences of shallow, high velocity riffles and deep, low velocity pools (Milne 1982, Bisson et al. 2006). Pools and riffles are fundamental units of alluvial rivers that are often used for descriptions of habitat use given that they occur at scales relevant to many stream organisms (Jowett 1993).

Many biotic attributes in streams ranging from body morphology to whole ecosystem function are tightly coupled to the hydraulic environment (Townsend and Hildrew 1994, Cardinale et al. 2010). The ecological traits of stream organisms have evolved for life in flowing water; hence there are numerous examples of animals exploiting water movement to assist processes necessary for survival, including predator avoidance (Peckarsky 1980), dispersal (Fonseca 1999), and resource acquisition (Cummins and Klug 1979). A wide array of stream animals have adopted relatively stationary feeding strategies to intercept food in transport downstream; perhaps the most iconic example are drift-feeding stream fishes, which defend fixed central-place territories and harvest invertebrate drift, suspended aquatic and terrestrial invertebrates drifting through their reactive field (reviewed in Piccolo et al. 2014). Drift-feeding has been observed in a diverse array of stream fishes around the world (Closs 1994, Herder and

Freyhof 2006, Grossman 2014), the most well-known of which may be Pacific salmon (family Salmonidae: salmon, trout, and char), an ecologically, economically, and culturally important taxon throughout its range (Gresh et al. 2000, Schindler et al. 2003).

Many salmonid species spend all or significant portions of their life cycle rearing in small streams (Quinn 2011), during which time they often experience strong density dependent population regulation due to inter- and intra-specific competition for both drifting prey and habitat suitable for growth and survival (Chapman 1966, Steingrimsson and Grant 1999, Keeley 2001). While regulation of salmonid populations by food and physical habitat were historically studied independently, there is now an abundance of evidence highlighting the importance of their interaction (Piccolo et al. 2014). Foundational studies by Fausch (1984) and Hughes and Dill (1990) first described drift-foraging as essentially an energy optimization trade-off where, as velocity increases, fish can scan a larger volume of water for drift but will expend more energy and capture prey less efficiently (Hughes 1992, Piccolo et al. 2008). Consequently, fish can only achieve positive energy balance where swimming costs can be more than offset by energy intake. In hydraulically heterogeneous streams, only a subset of habitats may meet these conditions (Rosenfeld and Boss 2001, Harvey et al. 2005), and these individual-level foraging constraints can lead to habitat-mediated population bottlenecks (Nislow et al. 1999, Kennedy et al. 2008).

Drift-foraging salmonids are an attractive system to study population regulation in relation to individual foraging behaviour and habitat use. Relative to other taxa with more complex foraging behaviours, the remarkable simplicity of drift foraging allows the energetic costs and benefits of habitat use to be explicitly quantified in the field (Gowan and Fausch 2002, Kennedy et al. 2008). In addition, drift-foraging lends itself well to predictive modelling and a growing body of theory and predictive models have been developed rooted in optimal foraging

and energetics (reviewed in Fausch 2013, Piccolo et al. 2014). These drift-foraging models range from optimization models describing individual habitat selection (Fausch 1984, Hughes and Dill 1990) to watershed-scale models predicting population capacity (Wall et al. 2016b, McHugh et al. 2017). Part of the appeal of drift-foraging models is that they mechanistically integrate constraints associated with both prey abundance (i.e. invertebrate drift) and physical habitat (i.e. velocity and depth effects on prey flux and capture success).

The use of drift-foraging models has been of increasing interest in an applied context given the declines of many salmonid populations across their range (Gresh et al. 2000, Ruckelshaus et al. 2002). Along with overharvest, migration barriers, and poor hatchery practices, physical habitat alteration is implicated as a key driver of these declines (Nehlsen et al. 1991) and enormous resources are invested in restoring physical habitat conditions (Beechie et al. 2009). Evaluating stream habitat conditions for salmonids historically involved developing correlative relationships between fish density and specific habitat features (Rosenfeld 2003); however these relationships are often limited in transferability (Garshelis 2000). Drift-foraging models have emerged as a promising tool for habitat evaluations insofar as they capture the fundamental mechanisms linking fish to their environment and use an energetic currency with a clear biological interpretation (Rosenfeld et al. 2014). Studies have used drift-foraging models both as post hoc evaluations of habitat quality (Urabe et al. 2010), and as predictive tools to explore optimal restoration designs (Railsback et al. 2013, Wall et al. 2016a) or future climate and land use scenarios (McHugh et al. 2017).

While empirical study and subsequent modelling of drift foraging behaviour is increasing in sophistication (Neuswanger et al. 2014, Hayes et al. 2016, McHugh et al. 2017), a commensurate understanding of invertebrate drift dynamics is lacking. Consequently,

uncertainty about spatiotemporal variation in prey abundance has limited our basic understanding of how physical habitat structure mediates energy flow and biomass production of drift-foraging stream fishes. In addition, realistic quantification of prey availability is often a lingering source of uncertainty in habitat evaluations and predictive modelling in applied contexts (Rosenfeld et al. 2014, Weber et al. 2017).

The fact that drift as a food resource for fish is not well understood is surprising given that food limitation of stream fish is well recognized (e.g., Boss and Richardson 2002, Romaniszyn et al. 2007), and that the process of invertebrate drift has drawn considerable attention from stream ecologists (Brittain and Eikeland 1988, Baxter et al. 2017). Perhaps the primary reason for this knowledge gap is the complexity of underlying mechanisms causing drift. On one hand, drift is an inevitable consequence of the constant action of hydraulic forces on stream organisms; epibenthic invertebrates frequently lose their purchase in turbulent conditions or are scoured from the substrate during high flow events in a similar manner to non-living particles (Gibbins et al. 2007a, Wilcox et al. 2008). However, invertebrates also drift behaviourally to avoid predators (Peckarsky 1980, Hammock and Wetzel 2013), unfavourable abiotic conditions (James et al. 2009) or low food availability (Kohler 1985). The tendency to drift through passive versus active processes varies considerably among taxa according to morphological, behavioural, and life history traits (Rader 1997, Poff et al. 2006). As a result, drift is strongly context dependent and exhibits inconsistent patterns (Naman et al. 2016). For example, drift often responds counterintuitively to flow manipulation, e.g., drift rates increasing after flow reduction due to active drift entry (Dewson et al. 2007b). Similarly, how drift varies spatially with habitat structure is often inconsistent among studies (Kovalak 1978, Martin and

Knight 1989); although it is less well studied than temporal flow variation (but see: Lancaster et al. 1996, Leung et al. 2009).

Terrestrial invertebrate inputs also complicate efforts to quantify spatial and temporal variation in salmonid prey availability. In addition to drifting aquatic invertebrates, terrestrial invertebrate inputs from riparian vegetation and flying insects ovipositing on the water surface are important sources of prey for stream salmonids (Edwards and Huryn 1995, Nakano and Murakami 2001). Input rates of terrestrial prey likely differ in their relationships to habitat structure given that they originate outside the aquatic environment. Consequently, unknown variation in these alternative modes of prey delivery can degrade predictions based on drift foraging theory that assumes prey abundance is either static or a simple function of velocity and depth (Gowan and Fausch 2002, Stark et al. 2002).

Mechanistically linking physical habitat structure to invertebrate drift, terrestrial inputs, and ultimately salmonid populations requires an integrative approach linking disparate disciplines and ecological scales. This thesis is my attempt to resolve several issues related to this enormous task and to improve our understanding of how invertebrate food resources for fish are influenced by physical habitat structure. Using a combination of observations, experiments, modelling, and literature synthesis, I address the following general questions: (1) what factors explain the context dependent effects of hydraulic forces on drift; (2) how drift varies spatially in streams among discrete hydraulic channel units; (3) how spatial variation in drift and abiotic constraints on foraging efficiency influence salmonid production; and (4) how the relationship between physical heterogeneity and salmonid production is influenced by terrestrial prey inputs. Ultimately, my goal is to use a mechanistic approach to extend our conceptual understanding of how food and space jointly regulate salmonid populations in forest streams.

1.1 Structure of this dissertation

This dissertation is broken into six chapters including these introductory remarks (Chapter 1). In Chapter 2, I review and synthesize the literature on invertebrate drift, focusing on the individual- and population-level mechanisms underlying drift, its role as a trophic flux to fish, and its relationship to habitat structure. Then in Chapter 3, I attempt to unpack the relationship between drift and flow by manipulating both discharge and habitat structure (cross sectional channel profile) in complementary mesocosm experiments to examine the drift responses of invertebrates spanning a wide diversity of behavioural and morphological traits.

In Chapter 4, I move to more natural systems to empirically address several fundamental assumptions of how drift and prey availability vary spatially with stream channel hydraulics; specifically, the hypothesis that drift should exhibit source-sink dynamics between habitat patches characteristic of forest streams: high velocity riffles where drift is generated and low velocity pools where it is depleted. Chapter 5 builds on these results to address how spatial heterogeneity in drift rates imposed by physical habitat interacts with physical constraints on drift-foraging to limit the biomass production of stream salmonids. I conducted a field experiment in a natural stream to test the hypothesis that a trade-off between riffles, where drift is generated, and pools, which are suitable for foraging, would cause a nonlinear relationship between salmonid production and pool-riffle habitat composition. I complemented this study with bioenergetic model simulations to further explore how this relationship may be affected by terrestrial invertebrate subsidies, which are unrelated to pool-riffle channel structure. Finally, I conclude in Chapter 6 by discussing the relevance of my work to the understanding invertebrate drift and energy flow patterns in streams, and broader interactions between habitat heterogeneity, cross-ecosystem subsidies, and predator-prey dynamics.

Chapter 2 Causes and consequences of invertebrate drift: from individuals to populations and trophic fluxes

*The current of the river swept over them, all young and old, rich and poor, good and evil, the current going its own way, knowing only its own crystal self.
Each creature in its own manner clung tightly to the twigs and rocks of the river bottom, for clinging was their way of life, and resisting the current what each had learned from birth. But one creature said at last, "I am tired of clinging. Though I cannot see it with my eyes, I trust the current knows where it is going. I shall let it take me where it will.
Clinging, I shall die of boredom."*

Excerpt from *Illusions* by Richard Bach (1977 Dell Publishing Co.)

2.1 Summary

Invertebrate drift, the downstream transport of aquatic invertebrates, is a fundamental ecological process in streams with important management implications for drift-feeding fishes. Despite longstanding 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) vs. 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 structure. In a food web context, there is a need to better understand drift-foraging consumer-resource dynamics and

to improve modeling of bulk drift fluxes to more realistically assess habitat capacity for drift-feeding fishes.

2.2 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 Mcpeek 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 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 continues to be 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 vs. 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 significance 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.

2.2.1 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 (Figure 2.1).

Drift Entry

Multiple underlying 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 2.1).

Passive drift occurs via mechanical dislodgement from the substrate due to near-bed shear stress and often results from increases in discharge or turbulence, which may, but not necessarily, be associated with substrate mobilization (Gibbins et al. 2007b). “Catastrophic drift” or “mass drift”, defined as a rapid increase in passive drift (Anderson and Lemkuhl 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 at the stream bed (Anderson and Lemkuhl 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 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 due to increased competition for space (Corkum 1978, Hildrew and Townsend 1980, Kohler 1992) or resource limitation (Dimand 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).

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 governs particle movement (Ciborowski 1983). However, multiple lines of evidence indicate a significant behavioural component to drift transport such that invertebrates actively control their time in the drift. First, hydraulic particle-transport relationships 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 transport distances are relatively short, e.g., around 2-10 m on average (Elliott 1971, 2002c, 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 vs. 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 ability have the potential to affect distributional patterns and densities of benthic invertebrates (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 (Rosenfeld and Taylor 2009).

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 clarki*). Leung et al. (2009) used a simple bioenergetics approach to estimate drift consumption by young-of-the-year and one 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 significant 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).

2.3 Domains of passive vs. active drift dynamics

The relative contributions of active vs. passive processes to drift are highly context-specific and often correlated (Figure 2.2). 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.

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 twelve 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, intra-specific studies in 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 eight-fold at stable flows when predators and food levels were manipulated relative to controls, suggesting that drift may be a predominantly active process during non-catastrophic flow. Much more work is needed, however, to fully resolve the context dependencies of active vs. 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. 2007b). 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 et al. (1983) found drift to increase only after 30% of habitat area was de-watered following flow reduction.

There are several important exceptions to drift increases at low flows. First, the timescale 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). 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 vary 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 (Figure 2.3). 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 on 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 vs. 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 vs. 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, 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.

2.4 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, due to 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, due to 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, and exit through settlement and predation 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 due 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 non-existent (but see Romaniszyn 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 et al. 1979) and summer (Hayes et al. 2000) peaks have been observed. In contrast, tropical streams show generally less consistent seasonal patterns (Pringle and Ramirez 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 the benthic community structure (Elliott 1967b). Not surprisingly, a close match between the seasonal abundance and composition of drift and the benthos supports close linkages between 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.

2.5 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 (Dimand 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), have 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 and 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 *Spatial Drift Dynamics* section), 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 population structure in 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 population structure, 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 *Emphmerella 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 theoretical basis (further discussed in *Population-Level Drift Models* section), 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 life history traits mediate the effect of drift on invertebrate populations will require thorough review and synthesis of the relative dispersal modes and their attendant fitness consequences for taxa representing a gradient of life history characteristics. For example, taxa which 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 timescales 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., Nielson 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 bioenergetics models (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), 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 *Spatial and Temporal Variation in Drift* section above), 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 significant feedback between predation and drift production (entry rates) could substantially alter current drift-foraging modeling approaches. Overall, the controls on drift-foraging consumer-resource coupling remain unclear and is an important gap in the fundamental understanding of trophic dynamics in streams as well as the ability to accurately assess trophic interactions and habitat quality using drift-foraging models.

2.6 Predictive modeling 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 structure; 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 unfeasible. 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 modeled 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 anti-predator 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 thereby preclude 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 structure (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 structure 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 which has been either fitted from field data (Melbourne and Chesson 2006, Diehl et al. 2008) or modelled from an exponential distribution (discussed in following section; Anderson *et al.* 2005).

Modelling Bulk Community Drift

In contrast to 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 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 make 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- and exponential/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 vs. 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 be high and 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 as to 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) the only example we are aware of to combine 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.

2.7 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 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. Four broad themes emerge as priority research gaps (Table 2.2): i) *quantitatively determining the relative influence of passive vs. 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*

2.8 Tables and figures

2.8.1 Tables

Table 2.1 Summary of different active and passive mechanisms of drift entry and relevant references.

Mechanism of drift entry	Example references
<i>Passive</i>	
Accidental dislodgment at non-catastrophic flows	Corkum (1978); Humphries (2000); Elliott (2003)
Catastrophic dislodgment due to mobilization of organic substrate and detritus	Allan (1995); Vinson (2001)
Catastrophic dislodgment due to mobilization of inorganic substrate	Anderson and Lemkuhl (1968); Allan (1995); Gibbins et al. (2007)
<i>Active</i>	
Predator avoidance	Peckarsky (1980); Malmvquist and Sjostrom (1987); Huhta 1999; Hammock et al. (2012)
Active foraging without density dependence	Hilenbrand (1974); Shearer et al. (2003); Wetzel et al. (2013)
Escape from unfavourable abiotic conditions	Gibbins et al. (2007); Larson and Ormerod (2010)
Density dependence - space limitation	Fonseca and Hart (1996)
Density dependence - food limitation	Kohler (1985); Richardson (1991); Siler et al. (2001); Hammock and Wetzel (2013)
Density dependence - predator avoidance	Kratz (1999)

Table 2.2 Summary of some key areas of invertebrate drift deserving further attention. References are examples of potential approaches to each issue

	Description	Example References
<i>Individual</i>	The relative influence of active and passive causes of drift	Hammock and Wetzel (2013)
	Predation risk assessment across taxa	McIntosh et al. (2004)
<i>Population</i>	Lifetime drift distances and mortality risk	Elliott (2003); Humphries and Ruxton (2003)
	Importance of rare long distance drift events	
	Population-level consequences of within-patch drift dynamics	Lancaster et al. (2011)
<i>Spatial and Temporal Variation</i>	Field measurements of drift entry, transport and exit	Lancaster et al. (1996); Elliott (2002); Romaniszyn et al. (2007)
	The effects of habitat complexity on drift rates	Gustafsson et al. (2014); Kiffney et al. (2014)
	Relative influences of discharge and phenology on seasonal patterns	
<i>Trophic Dynamics</i>	Determinants of whether drift is donor controlled	Muotka et al. (2006)
<i>Predictive Modelling</i>	Integrating individual and population-level processes within bulk community models	Humphries and Ruxton (2003); Anderson et al. (2013)
	Parameterization of drift entry rates	Hayes et al. (2007)

2.8.2 Figures

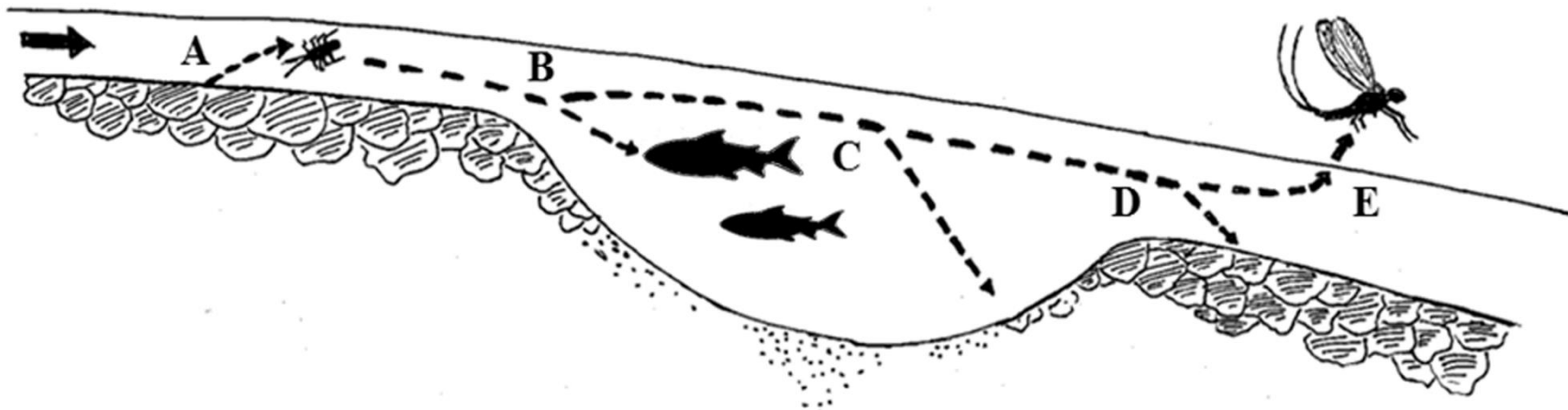


Figure 2.1 Schematic outlining the processes involved in drift. Drift entry is shown in A as an invertebrate departs the substrate and becomes entrained in the water column. Invertebrates exit drift through one of several processes including predation (B), passive settlement in hydraulic dead zones (C), 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.

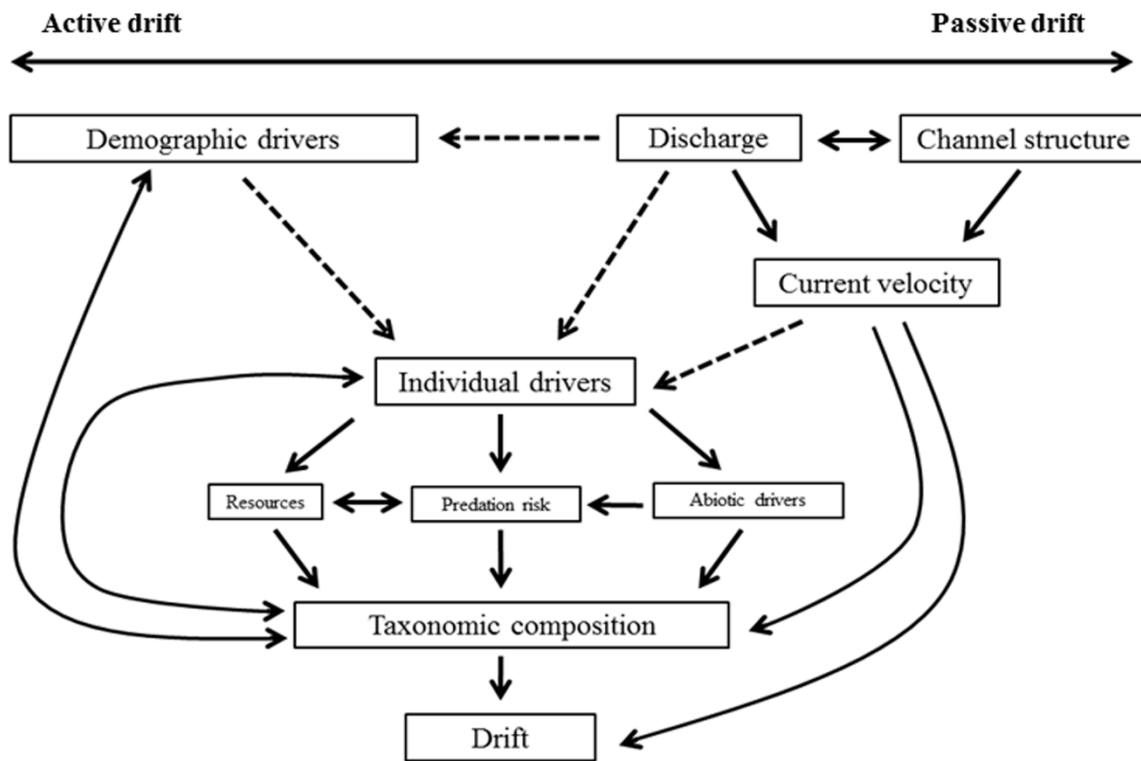


Figure 2.2 Conceptual diagram illustrating the potential interactions and hierarchical relationships among causal drivers of invertebrate drift. In this model, larger scale biotic (population level) and abiotic (discharge, channel structure) drivers influence local active and passive individual-level 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.

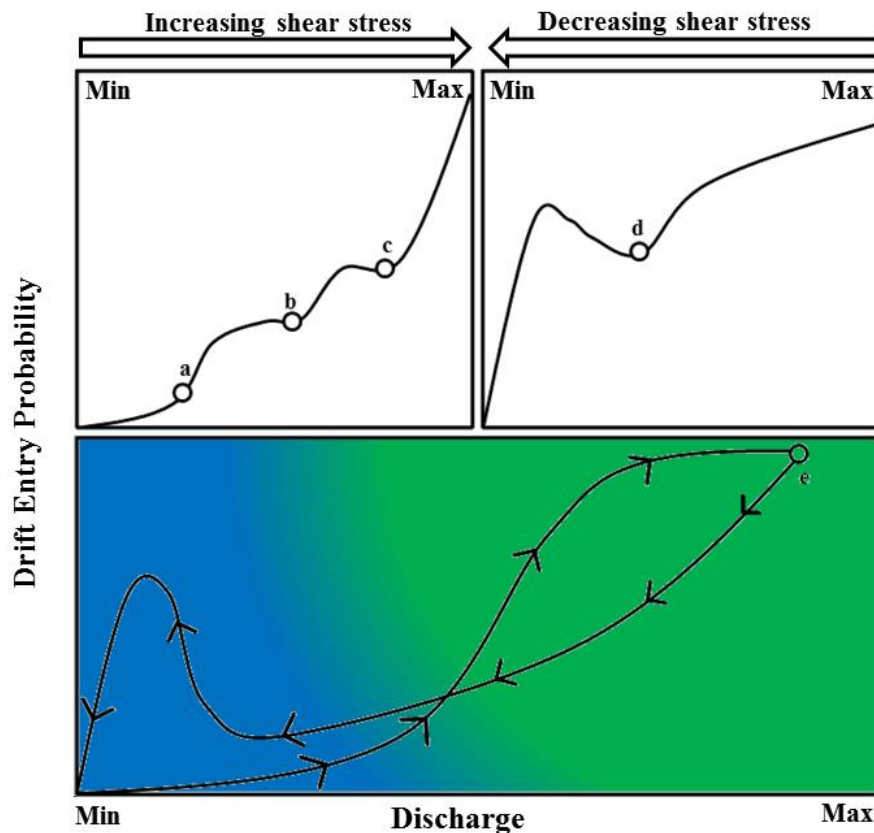


Figure 2.3 Conceptual figure illustrating the relationship between flow and the probability an invertebrate will drift. The top panels show hypothetical flow-related thresholds in drift entry. When flow is increasing (top left panel) there are several potential sequential entrainment thresholds that 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 due to acclimation to high flow conditions or depletion of benthos (i.e., fewer potential drifters). With continued decreasing flows, behavioural thresholds are reached (*d*) due to changing abiotic (e.g., velocity) or biotic conditions (e.g., competition or predation), 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) and passive (green).

Chapter 3 Species traits and channel architecture mediate flow disturbance impacts on invertebrate drift

3.1 Summary

Pulsed flow disturbances strongly influence invertebrate drift in lotic ecosystems. However, drift-flow relationships are often context dependent and non-intuitive, suggesting that local abiotic and biotic conditions mediate the impacts of flow on the physical and behavioural drivers of drift entry. Two factors may be particularly important: physical channel architecture, which modulates how flow influences velocity and habitat area; and species traits, which determine behavioural responses to flow and susceptibility to passive entrainment. We examined how channel architecture and species traits (e.g. mobility, body size, and dislodgement susceptibility) mediated the effects of flow on bulk drift abundance and taxa-specific per capita drift rates (the rate of emigration from the benthos). In complementary experiments, we reduced and increased flows in stream mesocosms with contrasting cross-sectional channel profiles: concave channels, where habitat area contracted and expanded with altered flow but velocity remained relatively constant; and flat channels, which maintained constant habitat area but experienced greater changes in velocity. Total drift concentration increased following flow reductions and decreased following flow increases whereas drift flux (the total number drifting) showed the opposite pattern. Channel architecture did not influence drift during flow reductions, but during flow increases drift flux and concentration were amplified in flat channels that experienced larger increases in velocity and shear stress. Contrasting responses among individual taxa to flow manipulation were explained by variation in mobility (swimming and crawling ability) and body shape (susceptibility to drag). Per capita drift rates for the most mobile taxa increased ~10%

under flow reduction, indicating a behavioural response, whereas drift of other taxa declined. Per capita drift increased for all taxa following elevated flow but by the largest magnitude in taxa with body shapes that experience more drag, suggesting passive dislodgement. Our results imply that: (1) stream channel architecture can modify the impacts of flow increases on stream invertebrates; and (2) invertebrate taxa vary in their vulnerability and behavioural responses to flow disturbance. Together these inferences clarify some of the previously unexplained context-dependent responses of drift to flow disturbances.

3.2 Introduction

Disturbances induced by physical forces (e.g. wind, waves, and running water) characterize many ecosystems (Sousa 1984, Pickett and White 1985). Establishing connections between these physical disturbances and biological processes is of great interest but often complicated by context dependency (e.g. Cardinale, Nelson and Palmer 2000; Agrawal et al. 2007), whereby the magnitude and direction of responses to a given disturbance intensity are modified by proximate factors that may include both abiotic (e.g. habitat characteristics), and biotic (e.g. behavioural or morphological species traits) components (Sousa 1984, Haddad et al. 2008). These mediating factors are often poorly understood, even in systems where disturbance is well-studied. In lotic ecosystems, for instance, the ecological impacts of pulsed flow disturbance (e.g. spates and droughts) have received enormous attention (e.g. Resh et al. 1988; Lake 2000) yet results often lack generality (e.g. Poff and Ward 1989; Dewson et al. 2007).

A case in point is the relationship between flow disturbance and invertebrate drift, the downstream transport of benthic invertebrates in suspension (Müller 1954). While flow impacts on drift are well studied given the important functions of drift as mode of patch movement for invertebrates and a trophic flux to fish (Naman et al. 2016), results are strongly context

dependent. For example, while abrupt increases in flow often lead to elevated drift as invertebrates are physically dislodged from substrate ("passive drift"; Anderson and Lemkuhl 1968), the magnitude that drift changes for a given flow increase ranges widely (Allan and Castillo 2007). In addition, decreases in flow may also lead to elevated drift (Minshall and Winger 1968, James et al. 2008), a counterintuitive response that highlights the importance of behavioural drift entry ("active drift") as flows decline. However, like the effects of increasing flow, this response is inconsistent among studies and varies among taxa (Poff and Ward 1991, Dewson et al. 2007b, Kennedy et al. 2014).

The factors generating context dependent flow-drift relationships are poorly resolved but may be related to physical habitat structure. Flow influences drift, in part, through changes in velocity and wetted streambed area. Rising velocity and hydraulic stress as flows increase results in a higher likelihood of passive drift through dislodgment (Gibbins et al. 2007a), while shrinking bed area as flows decline result in a higher likelihood of active drift due to density-dependence and desiccation risk (Corrarino and Brusven 1983, Boulton 2003, Dewson et al. 2007a). The rate that velocity and benthic habitat area change during high and low flow disturbances can be strongly mediated by channel architecture, specifically cross-sectional bank profile (e.g. Gippel and Stewardson 1998). When flows decline, the area of benthic habitat for invertebrates will shrink most rapidly in channels with moderately sloping banks (hereafter "concave" channels) relative to those with steeper, more vertical banks and flat bottoms (hereafter "flat" channels; Ferguson 2003; see Appendix A, Figure A1). In contrast when flows increase, velocity will rise more rapidly in flat channels where flow is confined by steep banks relative to concave channels, where rising discharge can be accommodated by an increase in wetted width. Consequently, the effects of flow increases on drift rates may be amplified in flat

channels as rising velocity triggers passive drift, and effects of flow decreases may be amplified in concave channels as shrinking habitat area triggers active drift.

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

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

and Wetzel 2013), while during flow increases drift entry may increase for a wide range of taxa (e.g. Gibbins et al. 2007).

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

We made several predictions based on the hypothesis that channel structure and trait variation mediate drift responses to flow manipulations. Specifically, we predicted that: (1) drift responses to reduced flow would be stronger in concave channels due to shrinking habitat area, whereas responses to increased flow would be stronger in flat channels due to higher velocities; (2) elevated drift from flow reductions should occur in more mobile taxa that drift actively whereas elevated drift from flow increases should occur across all taxa, but by more for those vulnerable to dislodgement (e.g., less mobile, higher drag); (3) drift should be higher at night during flow reductions as drift entry would be a primarily active process while day/night differences should be reduced during flow increases as drift would be primarily passive; and (4) the community structure of the drift should diverge from the benthos during flow reductions as

only the more mobile component of the benthic assemblage drifts actively, while community structure should converge between the drift and benthos following flow increases as a larger portion of the benthic community would enter the drift passively through physical dislodgment (e.g. Gibbins *et al.* 2007).

3.3 Methods

Experiment Logistics

We carried out our experiments in the University of British Columbia's Malcolm Knapp Research Forest (49°35'N, 123°50'W), which is described in detail in Richardson (1991). We constructed 24 gravity-fed stream mesocosm channels (6.8 m long x 0.15 m wide) with water piped in from Mayfly Creek, an adjacent 3 m wide oligotrophic stream (Appendix A, Figure A2). Two header boxes distributed flow into twelve outflow spigots, each of which split flow into one concave and one flat channel through a three-way splitter with a closed plastic ball valve in the middle arm (Appendix A, Figure A3). We constructed concave channels from 6-inch diameter PVC pipe cut lengthwise and flat channels from 6-inch width plastic-lined Aluminum gutters. In order to maintain consistency in channel geometry and bed roughness within and between treatments, we used a combination of natural gravel from Mayfly Creek (10-40 mm diameter) alternating with one inch square unglazed ceramic tiles as substrate. Other physical and abiotic features such as gradient (slope 0.08 m m⁻¹), light, and temperature (12-14 °C) were consistent among channels. We allowed channels to naturally colonize with invertebrates for six weeks prior to starting experiments. Discharge into the channels during this period averaged 0.30 m³ sec⁻¹, typifying summer base-flow conditions in nearby streams. Immigration rates averaged 30 (± 19.2) individuals day⁻¹ and did not differ systematically among channels and initial benthic

densities and composition were qualitatively similar to previous experiments in Mayfly creek (Richardson 1991, Rowe and Richardson 2001).

In both experiments, we used a 2 x 2 before-after-control-impact (BACI) design in which we measured response variables before and after flow manipulations in randomly assigned flow treatment and control outflows corresponding to paired concave and flat channels ($n = 6$ per treatment combination). Starting on August 13th, 2013, we ran each experiment over four days and staged flow manipulations over 2 h starting at 0900 on the third day. To decrease flows in treatment channels, we opened the middle ball valve of the three-way splitter, which diverted water ($\sim 0.2 \text{ m}^3 \text{ sec}^{-1}$) outside of each channel pair and lowered the discharge by 75% on average in treatment channels while control channels remained relatively constant at $\sim 0.25\text{-}0.3 \text{ m}^3 \text{ sec}^{-1}$. The magnitude of this change (along with the flow increase described below) was comparable to natural late summer discharge fluctuations in nearby streams (Moore et al. 2005).

We began the second experiment 3 days after concluding the first. To increase flows, we completely closed outflows corresponding to the 12 treatment channels from the previous experiment and simultaneously opened the middle valves in 6 of the 12 remaining outflows (the control channels from the previous experiment). This maintained constant flow in control channels and increased the flow in treatment channels ($n = 6$) by 75%. Note that this also reduced sample size for the flow increase experiment from 24 to 12 channels (i.e. six replicates for each treatment combination in the flow reduction experiment, three replicates for the flow increase experiment). Carry over effects of the flow reduction experiment on the flow increase experiment are unlikely as treatment channels did not overlap (i.e., no channel was subjected to both decreased and increased flow) and initial benthic densities and composition were not

different between the two experiments (density: t -test, $t = -0.36$, $P = 0.77$; composition: PERMANOVA, $F_{1, 21} = 0.96$, $P = 0.45$).

We collected invertebrate drift during each experiment by placing a 250 μm mesh net at the end of each channel, which filtered 100% of the discharge and captured drifting invertebrates (Elliott 1970). To quantify diurnal periodicity, we collected separate drift samples during the day and at night. Each sampling period lasted ~ 12 h, with dawn and dusk included in night samples. We quantified immigration into channels at each flow level by placing a 250 μm net over each inflow pipe. In order to estimate immigration during experiments without influencing drift and benthic populations, we collected two replicate immigration samples of 30 min each in both the day and night at each flow level during transition periods when downstream drift nets were being processed (i.e., drift was not being sampled). Because 30 min samples captured few individuals, we collected additional 12 h immigration samples ($n = 2$ per channel) after the experiments concluded. We estimated benthic densities before and after each flow manipulation (total of four collections) by collecting 9 ceramic tiles at three random locations in each channel with a customized 250 μm metal framed net placed directly downstream of each sampling location to capture any dislodged invertebrates as tiles were removed. We scraped invertebrates and biofilm from tiles with a metal brush, and then returned the tiles to their exact place of origin. For all drift and benthic samples, we sieved all contents through 250 μm mesh and stored invertebrates in 95% ethanol for subsequent identification in the laboratory.

To determine flow-related changes in habitat conditions, we measured cross sectional transects of depth and wetted width at 10 cm longitudinal intervals in each channel and flow level, and measured discharge by the time required to fill a 4 L bucket at the downstream end of each channel. We measured velocity at the deepest point in each cross section using a Marsh-

McBirney® Flow Mate 2000 (Hach Company, Loveland, CA). Shallow depths (< 5 cm) precluded the direct measurement of velocity at reduced flow levels, so instead we inferred velocity using the formula $Q=AV$, where Q is the discharge, V is the velocity, and A is the cross sectional area (the product of measured depth and wetted width) at each transect.

To support physical dislodgement as the primary mechanism of drift entry following flow increases, we estimated shear stress before and after flow increases in each channel using the method described in Gibbins et al. (2007) where:

$$\text{Shear stress } (\tau_b) = \rho(v_z k)^2 [\ln(10z/D_{84})]^{-2}$$

Here, ρ is the fluid density of water (kg m^{-3}) at 10°C ; v_z is the flow velocity at height z above the bed; k is von Karman's constant ($= 0.40$); and D_{84} is the size of the D_{84} sediment ($= 25.4 \text{ mm}$).

We used this measure of shear stress rather than others because it did not require a detailed vertical velocity profile and because Gibbins et al. (2007) demonstrated a clear threshold of shear stress where mass drift was initiated, providing a biological context to place our results.

Following Gibbins et al. (2007), we express shear stress in dynes cm^{-2} (where $1 \text{ dyne cm}^{-2} = 1 \text{ N m}^{-2}$). Note that we used the mean water column velocity as opposed to near bed velocity, which reduces the precision of our estimates.

In addition to calculating shear stress, we also qualitatively estimated the change in epibenthic organic matter in treatment channels following flow increases. Reductions in organic matter, in particular cases of chironomids, would suggest scour as a mechanism of drift entry.

We sorted and identified all aquatic invertebrates to the lowest possible taxonomic level (usually genus) under a dissecting microscope using dichotomous keys (Merritt and Cummins 1996). To estimate individual body mass, we staged and photographed each individual using a microscope camera (Leica® DMC4500), estimated total body length using ImageJ® photo

imaging software, then used allometric relationships (Benke *et al.* 1999; S.M. Naman Unpublished data) to convert body length to mass. Equations are of the form $Y = aX^b$, where Y is mass (mg), X is body length (mm), and a and b are scaling constants fitted for specific taxa.

Statistical Analysis

We quantified several complementary measurements of drift for our analysis. First, we calculated gross drift flux as the total number or mass of invertebrates drifting per sampling period (12 h), and drift concentration as the total flux standardized by the volume of water filtered. These metrics describe aggregate drift responses to flow manipulation; however, they give little insight into the underlying mechanisms causing drift or its consequences for the benthos (Naman *et al.* 2016). To make further inferences into these processes, we calculated per capita drift rates as the proportion of the total benthic population in a channel drifting per unit time. We estimated benthic population size by multiplying the average benthic density by the total area of substrate in each channel less the area sampled from each preceding interval, to account for the depletion of benthic populations during sampling. To validate density estimates, we counted all the invertebrates present in two of the control channels at the end of the experiment. Estimates from the two methods were qualitatively similar, suggesting our sampling approximated true population sizes in the channels. For the per capita analysis, we focus on six taxa that comprised the dominant portions of the drift and benthic assemblage (Table 3.1). These taxa included Chironomidae larvae (*Brillia retifinis*, *Corynoneura* spp., and *Tanytarsini* spp.), the mayfly *Baetis* spp., the stonefly *Zapada* spp., and the caddisfly *Micrasema* sp. These taxa differ in both their tendency for behavioural drift and susceptibility to scour (Table 3.1), thus we expected variation in their responses to flow manipulations.

For each experiment, we used an information theoretic approach and multi-model inference to evaluate the main and interactive treatment effects of flow, habitat (flat vs. concave) and time (day or night) on total drift flux, concentration, and per capita drift rates of the six dominant taxa. All response variables were computed as the difference between pre- and post- flow manipulation within a channel (with the two pre-flow manipulation samples averaged). We constructed sets of linear mixed effects models (LME) using the R package *lme4* (Bates et al. 2015) including all combinations of flow, channel type, time, and their two-way interactions as fixed effects, and a random intercept term grouped by channel to account for the non-independence of repeated measurements (i.e. day and night measurements from the same channel). In order to compare interactions and main effects, we standardized fixed predictors to a mean of 0 and a difference of 1 using the *Standardize* function within R package *arm* (Gelman et al. 2009, Schielzeth 2010) and assessed normality with residual plots. To select the best approximating model for each response, we used Akaike's Information Criteria corrected for small sample sizes (AIC_c). AIC_c selects the most parsimonious models within a candidate model set, with more plausible models receiving lower AIC_c scores (Burnham and Anderson 2002). We considered a model to have substantial support if the difference between a given model and the best fitting model (ΔAIC_c) was under 4 (Burnham and Anderson 2002). We also calculated AIC weights (W_i), which represent a probability a given model is the best fitting model within a given set. To further evaluate the fit of top ranked models, we computed a marginal and conditional R^2 following the methods of Nakagawa and Schielzeth (2013). The marginal R^2 indicates the proportion of variance accounted for by only the fixed effects in a model while the conditional R^2 accounts for the proportion of variance accounted for by both the fixed and random effects. We

estimated standardized model averaged slope coefficients and associated 95% confidence intervals for each fixed effect using the *MuMin* package in R (Bartón 2009).

To further explore which specific traits may drive differential drift responses among taxa, we analyzed per capita drift rates across a wider range of fourteen taxa (Table 3.1). In this analysis, the change in per capita drift rate for each taxon was combined into a single response variable (i.e. an observation represents a unique combination of taxa, stream, and time; $n = 286$ for reduction, $n = 142$ for increase). We modelled change in per capita drift rate (before/after flow intervention) as a function of flow, channel, and time as fixed effects and taxon identity as a random intercept term nested within the random effect of channel. To test relationships between ecological attributes and propensity to drift, we included three integrated ecological trait scores as fixed continuous variables based on Rader (1997): *mobility*, which incorporates morphological and behavioural attributes of taxa that influence the tendency for active drift (Rader 1997); *drag index*, based on the ratio of organism width to height (Wilzbach et al. 1988), approximates (in the absence of more precise hydraulic measurements; see Statzner 1987) the amount of drag an organism experiences in moving water and its likelihood of dislodgment; and the mean *body size* of each taxa relative to its benthic source population (hereafter “residual body size”) based on the rationale that larger individuals have more behavioral control over drift entry but may also be more susceptible to drag (Wilzbach et al. 1988, Poff et al. 1991). In this analysis, candidate model sets included only two-way interactions between each predictor and flow. In order to compare effects between continuous and categorical predictors, we standardized continuous variables by subtracting the mean and dividing by two standard deviations (Schielzeth 2010). Model selection and model averaging were conducted in the same manner as described for taxa-specific responses

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

At the community level, we used multivariate analyses to examine compositional changes in drift and benthos due to flow manipulations. First, we used a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) with the *adonis* function in the R package *vegan* (Oksanen et al. 2013). PERMANOVA fits linear models to Euclidean distance matrices, then uses a permutation test with pseudo *F* ratios to partition variation and calculates exact *P*-values based on 999 permutations to test the null hypothesis of no difference in composition within vs. among groups. Because PERMANOVA is sensitive to differences in dispersion, we tested for multivariate homogeneity of variance among groups using the *betadisper* function in *vegan*, which computes the mean Euclidian distance to the centroid of each group. Group differences in

community composition and associated axes of maximum variation were then visualized with non-metric multidimensional scaling plots (nMDS). We then used similarity percentage analysis (SIMPER; Clarke 1993) to determine the mean dissimilarity between drift and benthos and treatment and controls for flow level.

3.3 Results

Habitat Characteristics

Changes in habitat area and velocity agreed with expectations based on hydraulic geometry (Table 3.2). Following flow reductions, habitat area declined by 28% on average in concave channels while flat channels did not change. Velocity in both habitat treatments also declined relative to controls when we reduced flows, but by 25% more on average in flat channels. In the second experiment with enhanced flows, mean velocity increased by 64% in flat channels and 38% in concave channels relative to their respective controls. Increased flow also resulted in a 12% increase in wetted habitat area in concave channels. High flows did not induce bed movement; however, shear stress increased ~10X in flat channels (from 0.7 to 8.2 dynes cm⁻²) and by ~ 6X in concave channels (from 0.7 to 5 dynes cm⁻²) following elevated flows.

Qualitatively, organic matter was dramatically reduced on substrate surface following flow increases (Appendix A, Figure A4), suggesting that in our experimental arena, shear stress was sufficient to induce scour.

Total Drift Flux and Concentration

Total drift flux and concentration responded differently to changes in flow. Flow reductions had no apparent impacts on total drift flux (Figure 3.1a and b) and flow was not included in the top ranked models for either numeric or biomass flux (Appendix A, Table A1). In contrast, numerical and biomass drift concentration increased nearly three-fold after flow reduction

(Figure 3.1c and d). There was a lag associated with this response such that concentration did not increase until nightfall, at which point flow treatment channels were ~4X higher than controls (Figure 3.1c and d). Statistical support for a delayed drift concentration response to flow reduction was evident in the retention of a flow x time interaction (Appendix A, Table A1), and 95% CIs did not overlap zero for numeric (increase of 3 to 9.6 individuals m^{-3}) or biomass (increase of 0.04 to 0.99 g m^{-3}) concentration. Contrary to predictions, there were no differences between channel treatments for any bulk drift responses following flow reduction.

In the flow increase experiment, total flux increased rapidly by four-fold following the flow manipulation in both channel types (Figure 3.2a and b). Interestingly, the trajectories of the two habitat treatments diverged at night as drift flux continued to increase out of flat channels by an additional 10% relative to daytime, while drift flux from concave channels decreased by ~40% relative to daytime, despite remaining 2-3X higher than controls. In contrast, drift concentration decreased in response to increased flow although drift concentration in flat channels at night remained ~2X greater than control and concave treatment channels (Figure 3.2c and d).

Per Capita Drift Rates

Flow effects on per capita drift varied among the six focal taxa. Following flow reductions, *Baetis* spp. was the only of the six taxa to increase per capita drift rates. Model selection identified flow, time of day, and their interaction as the most important variables to explain *Baetis* spp. drift (Appendix A, Table A2). The top ranked model included a flow x time interaction term, suggesting that per capita drift of *Baetis* spp. increased by 8% (95% CI: 2-13%) when flows were reduced at night (Figure 3.3). In contrast, per capita drift declined for *Zapada* spp. by 1.6% (-3 to -0.3%) and *Corynoneura* spp. by 2.4% (-4 to -0.5%). For *B. retifinis*,

Tanytarsini spp., and *Micrasema* sp., flow reduction had no apparent effects on drift rates. In these cases, flow was not included in the top ranked model and 95% CIs for all terms overlapped zero. In concordance with aggregate flux and concentration results, there was no support for channel architecture effects on per capita drift responses for any taxa.

When flows were increased, per capita drift was consistently elevated and flow was included in the top ranked model for every taxa (Appendix A, Table A2). However, the magnitude of this response varied considerably (Figure 3.4). Per capita drift increased for *Zapada* spp. by 3.5% (1.1 to 5.8%) and *Corynoneura* spp. by 6.4% (1.5 to 11.6%) in flow treatment channels, while most other taxa experienced more substantial flow-induced increases in per capita drift, as high as 30% (11-50%) for *Micrasema* sp. Consistent with predictions, time of day had minimal support for most taxa, providing no evidence for a behavioural lag in drift induction with elevated flows. An exception to this was *B. retifinis*, where a flow x time interaction had substantial support, suggesting per capita drift of *B. retifinis* declined by 14% (-23 to -7%) in flow treatment channels at night, opposite to what would be expected based on behaviourally-induced predator avoidance. Predictions that habitat would mediate drift responses had mixed support. Channel type was not an important predictor for any taxa except *Baetis* spp., where a flow x channel interaction term was included in the top ranked model. Consistent with predictions, *Baetis* spp. drift was elevated 12% (1 to 23%, 95% CIs) in flat channels, which experienced greater increases in velocity.

Trait-Based Analysis of Per Capita Drift Rates

Mobility and drag index both had support to explain variable per capita responses to changing flow among taxa. Mobility appeared to influence whether a given taxa increased drift in response to reduced flow (Figure 3.5 top panel). While per capita drift of all taxa declined by 3.4% on

average with flow reduction, drift increased with higher mobility index values. In addition, diurnal periodicity was also significant under reduced flow, as a flow x time interaction was included in the best approximating model (Appendix A, Table A3), and nocturnal per capita drift rates increased by 4.2% (1.4 to 6.9%) on average following flow reduction.

Under elevated flows, per capita drift increased by 14% on average across all taxa. Consistent with flow reduction, mobility modified responses to flow increase, but the direction of the effect was reversed such that per capita drift rates declined on average for more mobile taxa when flows were increased (Figure 3.5 bottom panel; Appendix A, Table A3). As expected, susceptibility to scour (drag index) emerged as another important trait during flow increases. Taxa with high drag index values experienced higher overall per capita drift rates and responded more strongly on average when flows were elevated as evidenced by a flow x drag index interaction term that was well supported statistically (Appendix A, Table A3).

Potential Impacts of Drift to the Benthos

The potential impacts of flow-induced drift on benthic population size varied among taxa (Figure 3.6). Generally, impacts were strongest where per capita drift changed significantly. Flow reductions resulted in net gains of individuals (emigration < immigration) for three of six taxa (*Zapada* spp. (0.04 ± 0.005 individuals d^{-1}), *Micrasema* sp. (0.08 ± 0.04), and *Corynoneura* spp. (0.05 ± 0.01)). In contrast, flow increases resulted in substantial net losses of individuals for four of six taxa (*Micrasema* sp. (0.31 ± 0.06), *B. retifinis* (0.2 ± 0.03), *Corynoneura* spp. (0.06 ± 0.02) and Tanytarsini spp. (0.07 ± 0.03)). *Baetis* spp., despite increasing per capita drift ~10% following both increased and decreased flow, did not experience changes to its relative rates of immigration and emigration.

Our multivariate analyses indicated that drift community structure diverged from benthic community structure following flow reduction, and converged (became more similar) following flow increases (Table 3.3). During flow reductions, greater proportions of *Baetis* spp. and Simuliidae spp. in the drift in treatment channels relative to control channels and the benthos appeared to drive compositional divergence (Figure 3.7 top panels). In contrast, during flow increases, greater proportions of *Micrasema* sp. and several Chironomid taxa in the drift in treatment channels appeared to drive the compositional convergence with the benthos (Figure 7 bottom row). The PERMANOVA model testing the interaction of flow and sampling interval on drift composition was significant for flow reductions ($F = 2.65$, $P = 0.008$) although the proportion of explained variation was low ($R^2 = 0.03$). The same model was also significant for flow increases ($F = 5.43$, $P = 0.001$, $R^2 = 0.11$); however this difference was likely driven by treatment effects on multivariate dispersion, as drift became more variable in composition when flows were elevated (*betadisper*, $F = 3.55$, $P = 0.02$). Effects of flow manipulations did not extend to the benthos, as composition was not statistically different before to after flow reduction (PERMANOVA, $F = 0.42$, $P = 0.97$) or increase ($F = 0.85$, $P = 0.56$).

3.4 Discussion

Consistent with many of our *a priori* predictions, our results suggest that species traits, and to some extent channel architecture, mediated invertebrate drift responses to flow disturbances. Following flow reductions, drift increased only for the most mobile taxa, with additional evidence that this response was behavioural. First, increased drift occurred primarily at night indicating invertebrates likely waited ~ 12 h from the initial manipulation before responding, although increased night-time drift distances may have played a role (Statzner and Mogel 1985). Second, the divergent community composition between drift and benthos following flow

reduction suggests a smaller component of the benthic assemblage drifted at low flows. The taxa driving this compositional difference, *Baetis* spp. and Simuliidae, are well known to drift behaviourally (Poff et al. 1991, Fonseca and Hart 1996).

Drift responses to increased flow were also in general agreement with predictions as elevated flows increased total drift flux as well as per capita drift rates across all taxa. The rapid response of drift to flow increases, apparent compositional convergence between drift and benthos, and increased dispersion of drift in treatment channels suggests that a larger and more variable component of the benthic assemblage entered the water column through passive drift. This inference is consistent with previous studies that have found drift and benthic composition to converge as flows increased (Imbert and Perry 2000, Gibbins et al. 2007a). The taxa driving convergence in our study, including *Micrasema* sp. and several Chironomid species, are generally more susceptible to scour and are not known to drift behaviourally (Poff et al. 2006).

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

associated with reduced velocity, such as elevated benthic predation risk (Wellnitz 2014) or biofilm depletion (Hintz and Wellnitz 2013), may have played a role but we are unable to distinguish among them.

For the flow increase experiment, there was mixed support for our prediction that flow effects on drift would be amplified in flat channels. *Baetis* spp. experienced a larger increase in per capita drift in flat relative to concave channels as predicted but other supporting evidence was less definitive. For instance, flat versus concave channels displayed contrasting nocturnal responses in total drift flux following flow increases, with reduced night drift in the concave channels. The interpretation of this result is less clear given that the response was not immediate, such that physical dislodgement alone is an insufficient explanation. Possible explanatory mechanisms include active drift associated with larger velocity increases in flat channels and refugia created by expanding habitat area in concave channels, which may have promoted faster recovery from high flows (e.g. Lancaster 2000). Apart from *Baetis* spp., channel architecture was not an important modifier of flow effects on per capita drift rates of any focal taxa, suggesting that velocity increases in concave channels may have been sufficient to induce passive drift for many taxa. However, shear stress values in our concave channels ($\sim 5 \text{ dynes cm}^{-2}$) were below the threshold of passive drift entry (9 dynes cm^{-2}) demonstrated in Gibbins et al. (2007). This may indicate an active drift response to increased flow or from differences (e.g., interstitial refugia, rate of flow increase) between our study and Gibbins *et al.* (2007) such that thresholds of passive drift initiation may not be fully transferable.

Caveats and Implications

While many aspects of our experiment were in the range of natural conditions (e.g. velocity, discharge, benthic densities), substrate and bed topography were considerably simplified to

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

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

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

Our net population impact analysis revealed additional contrasts in the strategies used by invertebrates to cope with flow disturbance. For instance, the magnitude per capita drift rates responded to flow disturbances and the short term impacts to their benthic populations were not necessarily congruent. Specifically, the change in emigration relative to immigration was two-fold higher in *Micrasema* sp. relative to the *B. retifinis* following increased flow, despite similar increases in per capita drift following flow manipulation. We cannot fully resolve the mechanisms responsible for this result but given that Chironomids are known to be rapid

colonizers (Milner 1994) and that *B. retifinis* were more abundant in the drift, we speculate that they mitigated high flow-induced emigration with fast colonization rates. In contrast, *Micrasema* sp. may rely on within-habitat refugium from high flow (Lancaster and Belyea 1997, Lancaster 2000) that was largely absent in our study.

Because we integrated multiple measurements of drift, our results are also useful to examine the interrelationships among drift concentration, flux, and per capita drift rates, and their responses to changing flows. One important implication from our results is that relatively small changes in per capita drift rates from the benthos resulted in disproportionately large changes in drift concentration and flux. For instance, the total flux of *Zapada* spp. increased ~25% when flows were raised, despite an average per capita drift rate increase of only 3% on average. Thus, because benthic standing stock far exceeds drift abundance, even minimal spatiotemporal variation in per capita drift entry rates from the benthos can result in substantial variation in drift concentration or flux.

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

from our study is the need to carefully consider dilution effects when interpreting drift-flow relationships (Hayes et al. 2016; Wooster, Miller and DeBano 2016).

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

3.5 Tables and figures

3.5.1 Tables

Table 3.1 Mean (\pm standard error) benthic densities and trait characteristics of taxa used for trait analysis and per capita analysis (in bold) ranked by % frequency of total drift abundance. Mobility and drag index scores are based off of Rader (1997) and are on a scale from 0 to 9. Note that despite high abundance in drift, we did not include pupal life stages of Chironomids in the per capita analysis due to potentially confounding effects of emergence.

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

Table 3.2 Mean values (\pm standard error in parenthesis) of discharge, velocity and wetted habitat area in each channel type ($n = 12$ each of flow reduction; $n = 6$ each for flow increase) before and after flow manipulations.

Channel Architecture		Discharge (m ³ sec ⁻¹)				Velocity (m sec ⁻¹)				Wetted Area (m ²)			
		Before		After		Before		After		Before		After	
Flow Reduction													
Concave													
	Control	0.32	(0.01)	0.21	(0.01)	0.2	(0.02)	0.13	(0.01)	0.79	(0.02)	0.81	(0.02)
	Reduced	0.35	(0.01)	0.06	(0)	0.22	(0.02)	0.08	(0.01)	0.79	(0.02)	0.58	(0.01)
Flat													
	Control	0.32	(0.02)	0.26	(0.01)	0.17	(0.01)	0.11	(0)	0.76	(0)	0.75	(0)
	Reduced	0.31	(0.02)	0.05	(0)	0.19	(0.01)	0.06	(0.01)	0.76	(0)	0.75	(0)
Flow Increase													
Concave													
	Control	0.21	(0.01)	0.19	(0.01)	0.13	(0.01)	0.13	(0.01)	0.81	(0.02)	0.63	(0.02)
	Increased	0.22	(0.01)	0.78	(0.01)	0.13	(0.01)	0.22	(0.01)	0.8	(0.02)	0.92	(0)
Flat													
	Control	0.26	(0.01)	0.17	(0.01)	0.11	(0)	0.11	(0.01)	0.75	(0)	0.75	(0)
	Increased	0.24	(0.01)	0.79	(0.01)	0.12	(0)	0.28	(0.02)	0.75	(0)	0.75	(0)

Table 3.3 Average pairwise proportional dissimilarities, based on SIMPER analysis, between drift in flow treatment channels compared with benthos and drift from control channels before and after flow manipulations.

	Treatment-Interval	Dissimilarity	
		Benthos	Control
<i>Flow Reduction</i>	Reduced - Before	0.51	0.44
	Reduced - After	0.58	0.52
	Control - Before	0.52	-
	Control - After	0.51	-
<i>Flow Increase</i>	Reduced - Before	0.51	0.43
	Reduced - After	0.33	0.57
	Control - Before	0.49	-
	Control - After	0.58	-

3.5.2 Figures

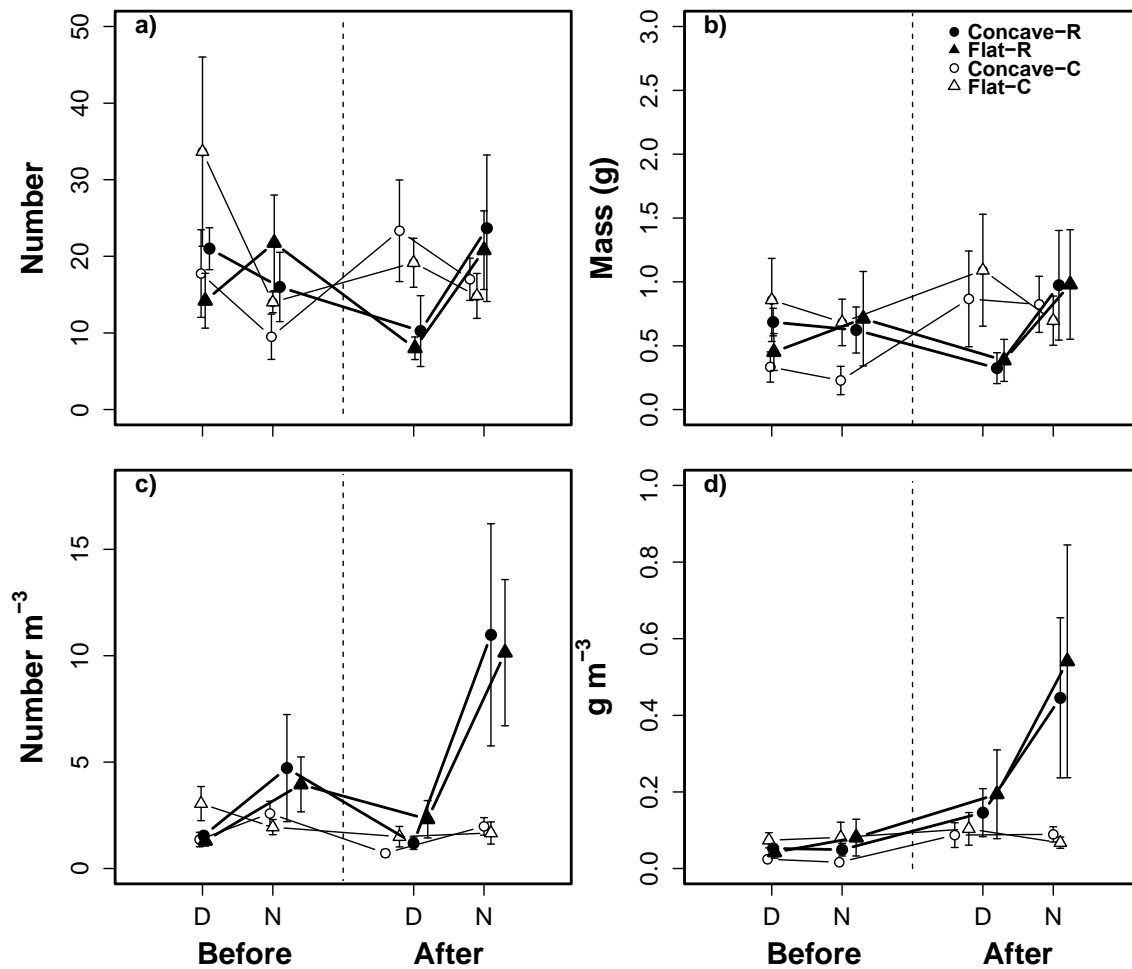


Figure 3.1 Mean (\pm SE) of the total numeric (a) and biomass (b) drift flux, and numeric (c) and biomass (d) drift concentration before and after flow reduction during the day and at night ($n = 6$ per treatment combination). Flow treatment (R) channels have bolded lines relative to controls (C). Points are slightly jittered to ease interpretability.

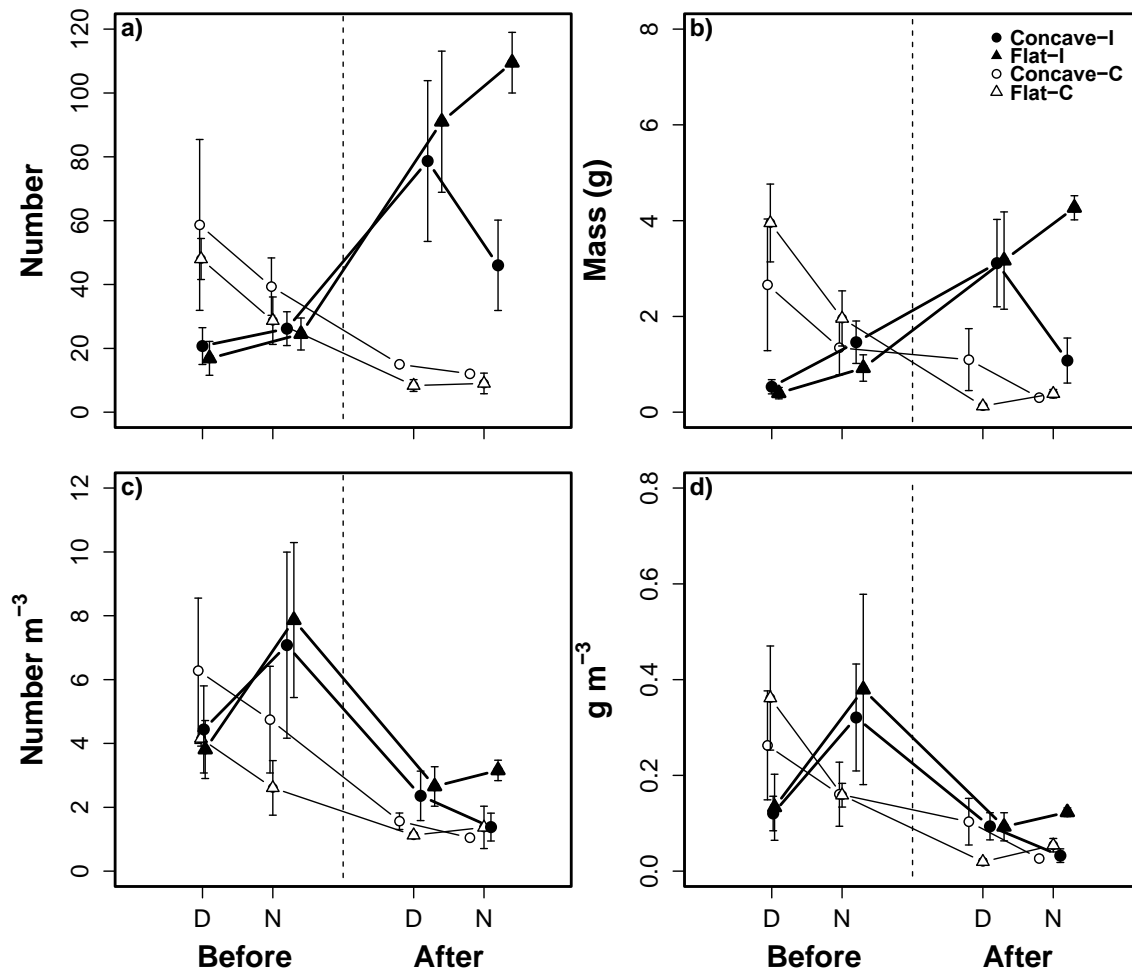


Figure 3.2 Mean (\pm SE) of the total numeric (a) and biomass (b) drift flux, and numeric (c) and biomass (d) drift concentration before and after flow increases during the day and at night ($n = 3$ per treatment combination). Flow treatment channels (I) have bolded lines relative to controls. Symbols are consistent with Figure 3.1.

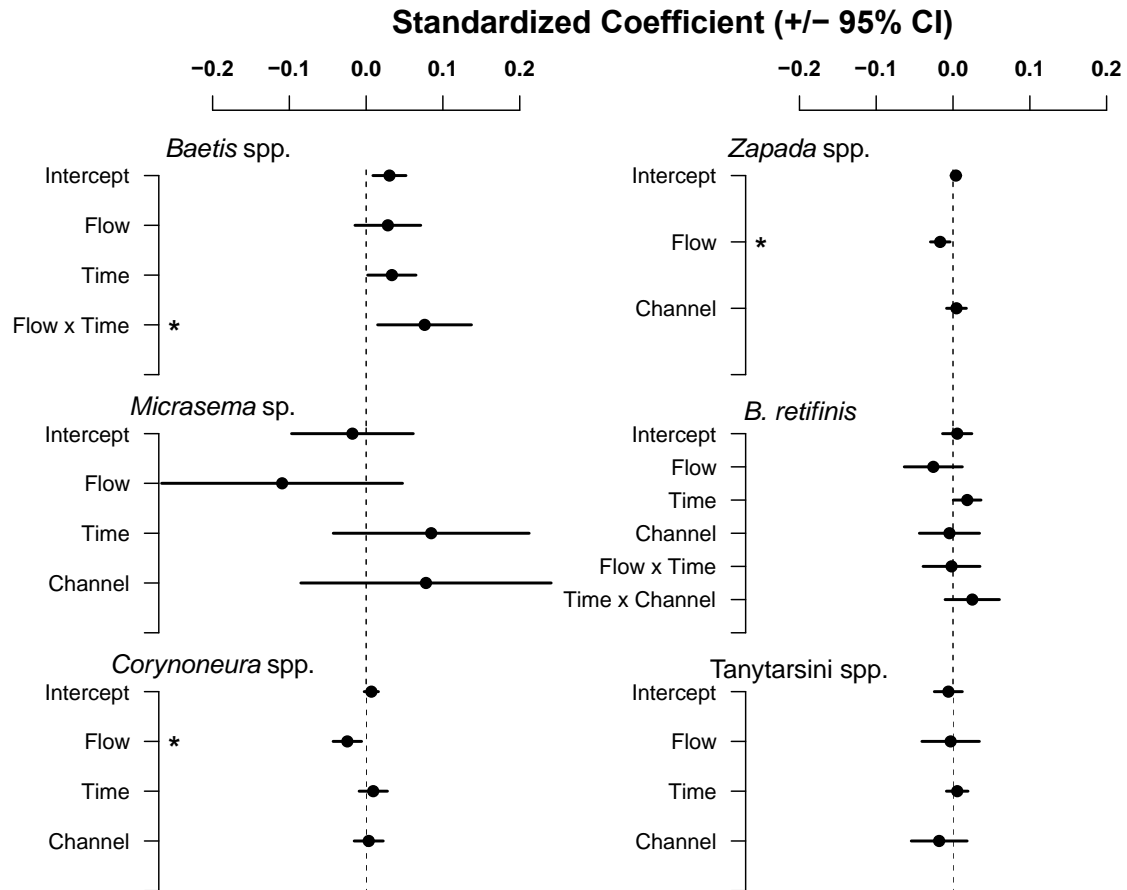


Figure 3.3 Standardized model averaged slope coefficients (\pm 95% CIs) from top ranked models ($\Delta AIC < 4$) explaining the change in per capita drift rates for the six focal taxa from before to after flow reduction. *Flow* represents channels where flow was reduced relative to controls, *Channel* represents flat relative to concave habitat treatments, and *Time* represents night relative to day. Asterisks represent cases where 95% CIs do not overlap zero.

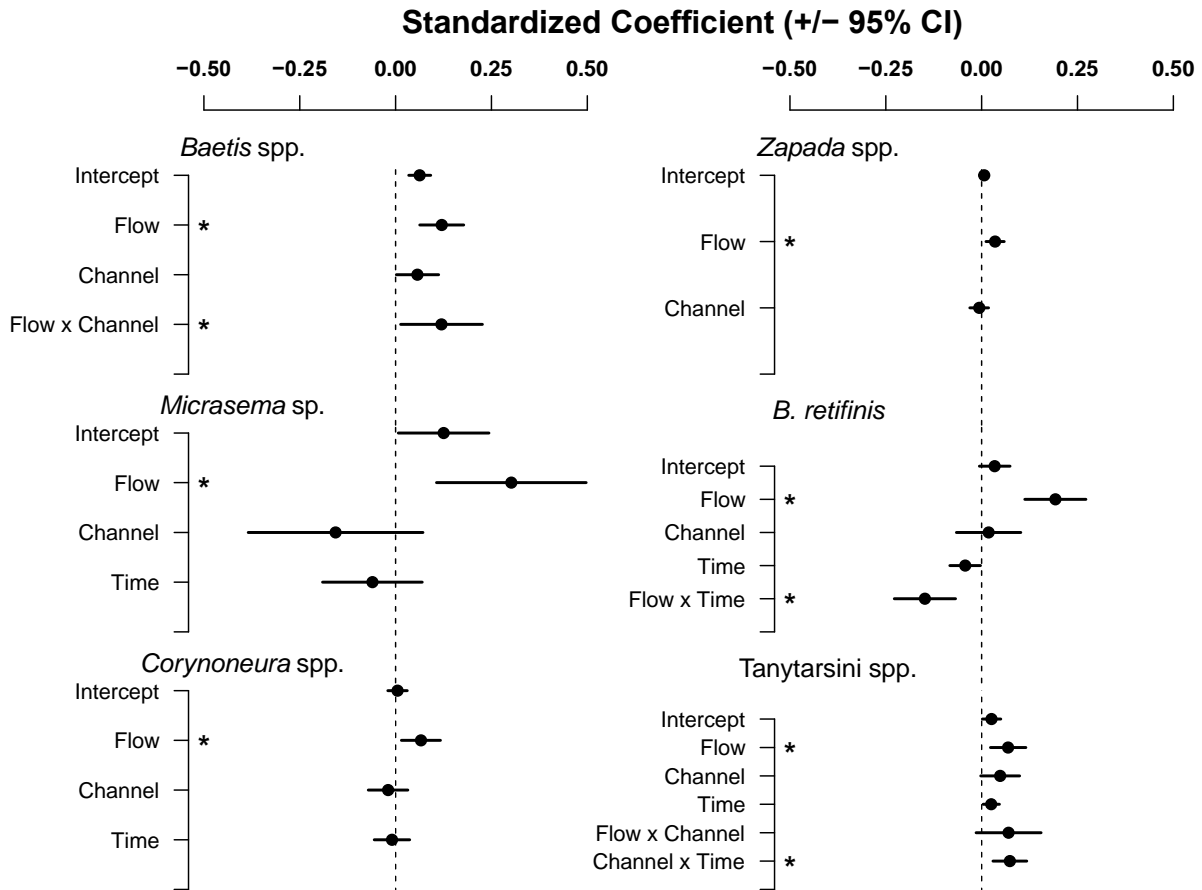


Figure 3.4 Standardized model averaged slope coefficients (\pm 95% CIs) based on models explaining the change in per capita drift rate for the six focal taxa from before to after flow increase. Notation is the same as Figure 3.3

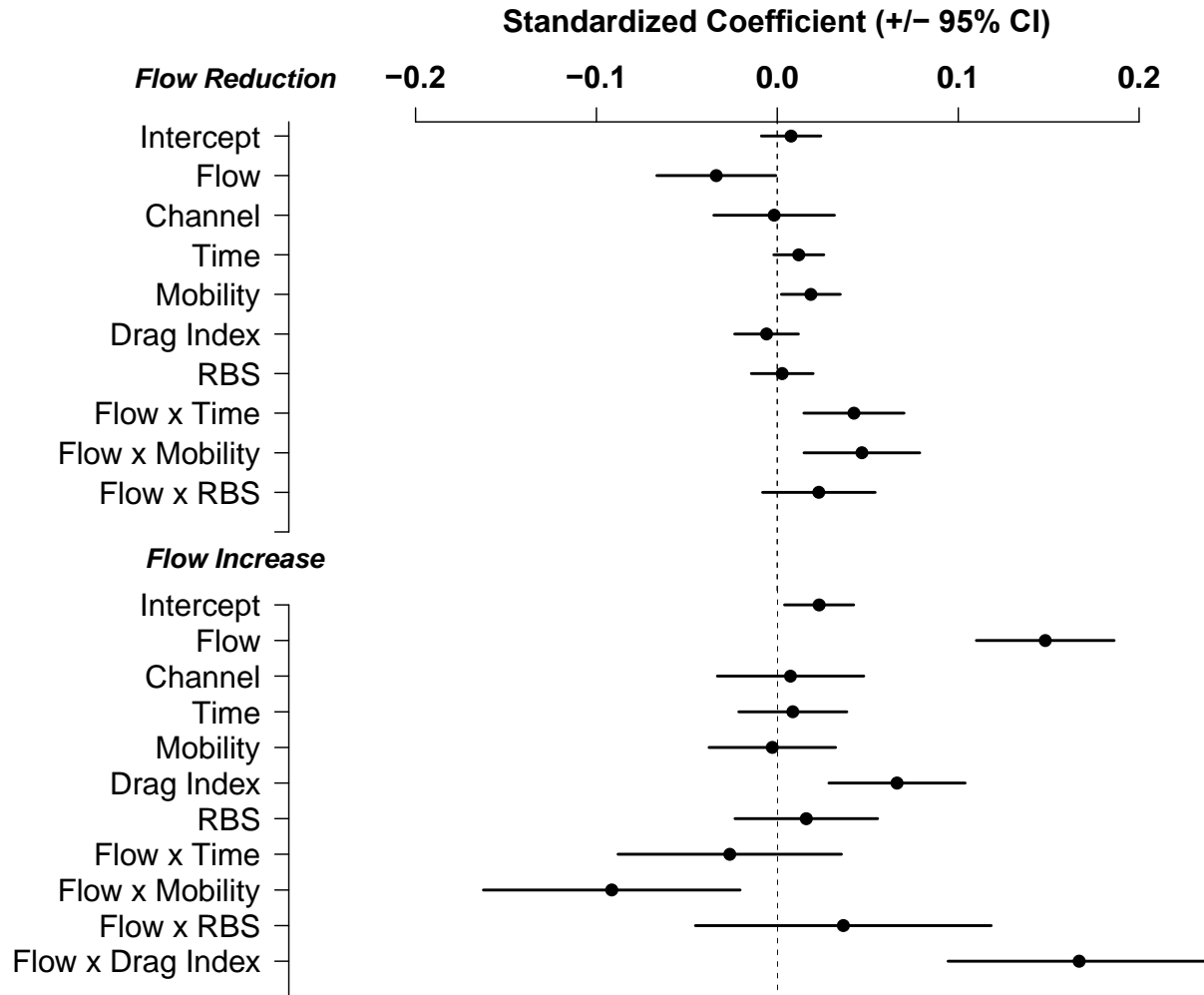


Figure 3.5 Standardized model averaged slope coefficients and 95% confidence intervals for models predicting change in per capita drift across 15 taxa in flow reduction (top panel) and flow increase (bottom panel) experiment. Notation for *Flow*, *Channel* and *Time* are consistent with Figures 3 and 4. *RBS* represents the mean residual body size for drifting taxa relative to their source benthic population.

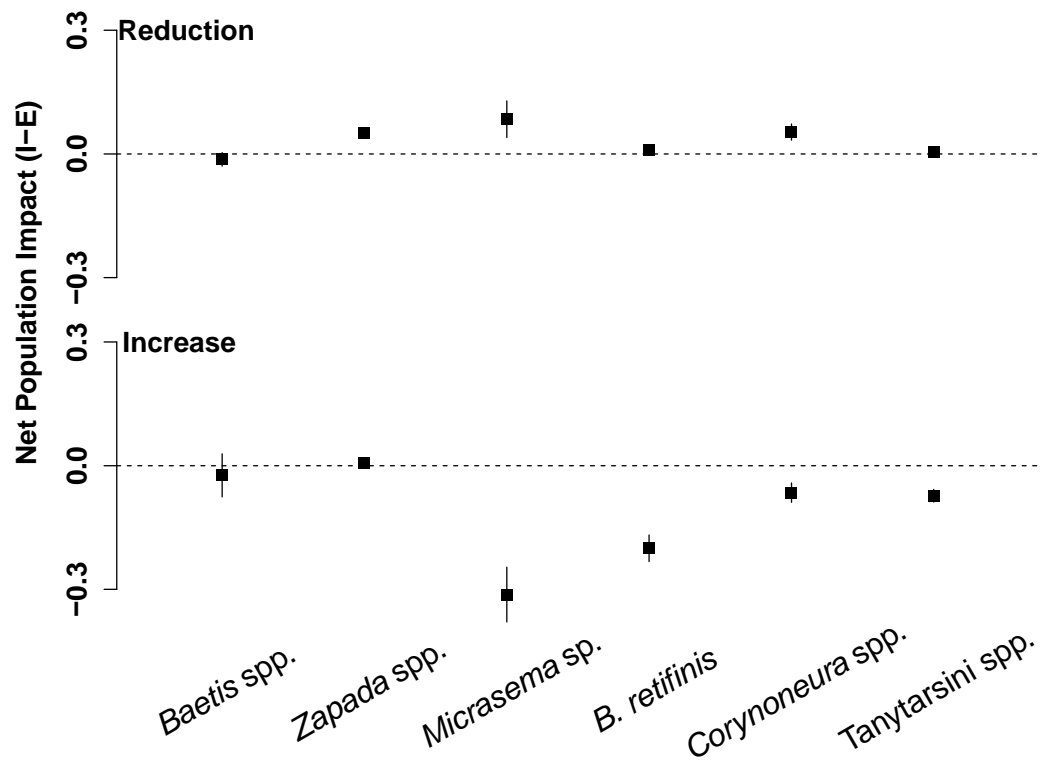


Figure 3.6 Net population impact (\pm SE) of flow reductions (top panel) and increases (bottom panel) on the six focal taxa. Population impact is defined as the difference between per capita emigration rates (number day⁻¹) relative to per capita immigration rates. Negative values indicate net losses of individuals from the benthic population.

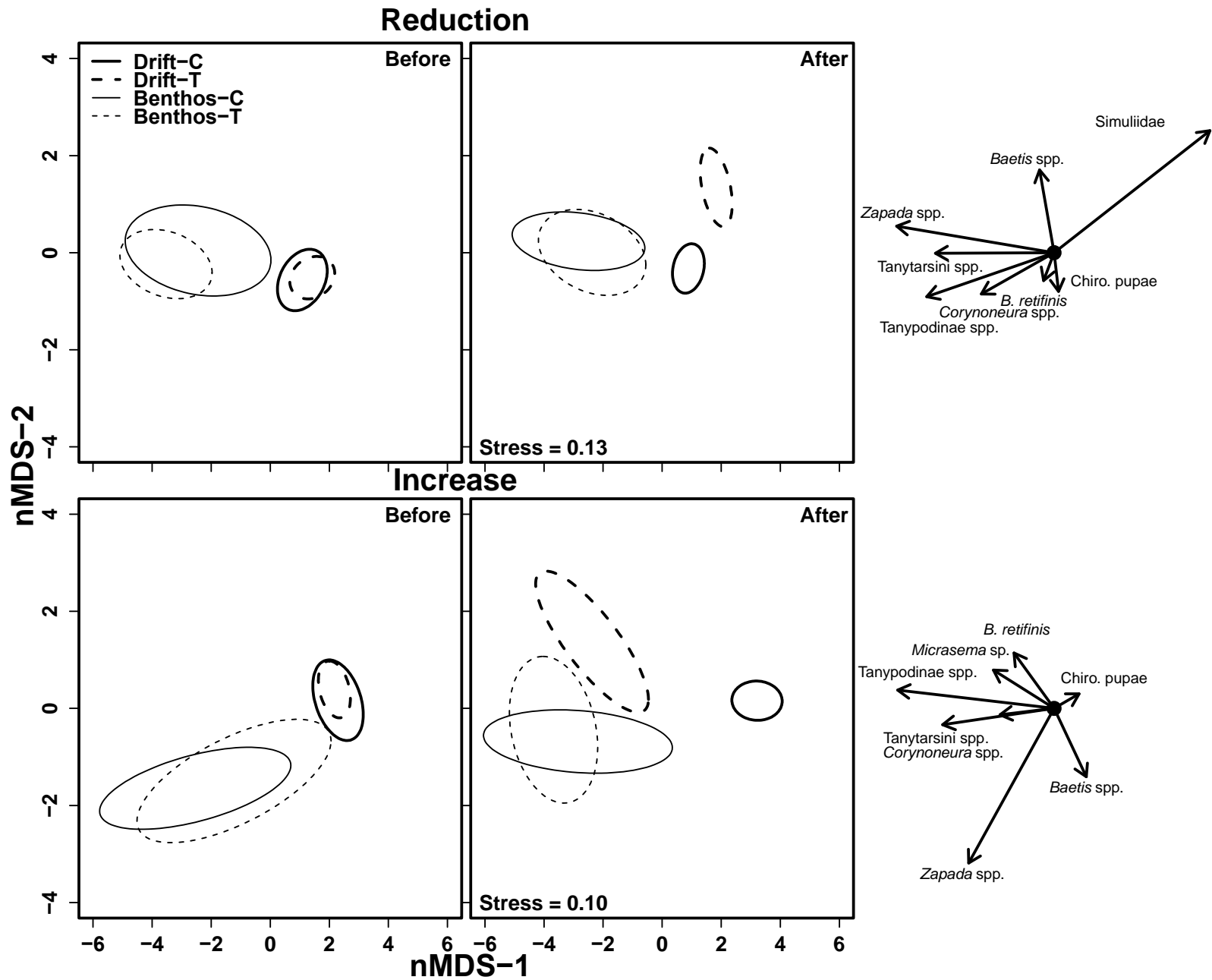


Figure 3.7 Non-metric multidimensional scaling plots showing compositional differences between drift (bolded) and benthos (non-bolded) for flow treatment (T) and controls (C) before and after flow reduction (top panel) and increase (bottom panel). Ellipses represent bivariate 95% confidence regions around the data in multivariate space. Spatial differences in ellipse positions indicate compositional differences among groups. Taxa significantly correlated with the axes are shown for each ordination to the right. Arrows indicate direction of increasing relative abundance.

Chapter 4 Habitat-specific production of aquatic and terrestrial invertebrate drift in small forest streams: implications for drift-feeding fish

4.1 Summary

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

4.2 Introduction

Invertebrate drift, the downstream transport of suspended macroinvertebrates, is a primary source of prey for many stream fishes including salmon and trout (Salmonidae). Together, drift abundance and habitat conditions (e.g., depth, velocity, and temperature) determine the energetic profitability (prey intake) relative to costs (e.g., from swimming) at a given location (Fausch

1984, Hughes and Dill 1990), and ultimately the distribution of usable habitat and potential fish production across a landscape (Chapman 1966, Poff and Huryn 1998, Rosenfeld and Taylor 2009).

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

The abundance of drift, generally measured as a concentration (e.g., number or mass of animals per volume), is determined by the relative rates of invertebrate entrainment into suspension from the benthos (hereafter “drift production”), and exit from suspension through settlement, predation, or emergence (hereafter “depletion”). Because of the well-known influence of hydraulics on both entrainment and settlement, some have posited a source-sink model in which drift abundance (hereafter used synonymously with concentration) increases in riffles and decreases in pools (Poff and Huryn 1998, Rosenfeld and Raeburn 2009). While conceptually intuitive, support for this hypothesis is surprisingly mixed (Naman et al. 2016). One source of ambiguity is that drift production is rarely measured directly; instead, drift concentration is used as a surrogate (e.g., Leung et al. 2009). Thus, it is conceivable that drift

production is spatially homogenous and that it is actually differences in depletion rates that drive spatial variation in abundance (Lancaster et al. 1996, Oldmeadow et al. 2010).

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

Regardless of whether drift production exhibits source-sink or spatially constant patterns, riffles in small streams serve a key function of prey refuge and regeneration because of hydraulically harsh conditions that minimize drift-foraging by fish (Rosenfeld and Boss 2001, Harvey et al. 2006). For a given discharge, the total drift produced and exported from a riffle (hereafter “drift flux”) will influence both the individual growth potential and total capacity of fish occupying suitable habitats downstream (Hayes et al. 2007, Weber et al. 2014). Assuming production and depletion are in equilibrium, drift flux should be a product of the drift production rate and the distance that drift is suspended (Larkin and McKone 1985, Elliott 2002a). This leads to the prediction that drift abundance should increase longitudinally within a riffle and that longer riffles should export more drift on average (Rosenfeld and Raeburn 2009). However, drift distances can be short in small streams (e.g., Elliott 1971) such that riffle length effects on drift flux and concentration may be non-linear, with an asymptote corresponding to the average drift distance. This simple model has some empirical support (Hansen and Closs 2007) but has not been rigorously tested.

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

In addition to total abundance and biomass, the body size distribution of drifting invertebrates is an important determinant of the availability and quality of prey to salmonids (Hayes et al. 2000, Esteban and Marchetti 2004, Dodrill et al. 2016). Larger bodied prey are more easily captured (Wankowski 1981, Bannon and Ringler 1986), provide greater energetic benefits, and influence the distribution of resources among conspecifics (Nielsen 1992). There is some evidence that terrestrial prey are larger than aquatic prey (Nielsen 1992, Li et al. 2016) but there may also be size differences between aquatic invertebrates drifting from pools and riffles due to differences in benthic community structure (Robinson and Minshall 1986), or hydraulic entrainment thresholds (Statzner 1987, Wilzbach et al. 1988) that select for entry of larger bodied individuals into the drift.

To better understand how stream channel structure influences invertebrate drift and prey availability for drift-feeding fish, we used a novel method to estimate production of aquatic and

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

4.3 Methods

Between July 14th and 21st, 2014 we sampled three coastal forest streams in the Sunshine Coast region of southwest British Columbia, Canada, 50 km north of the city of Vancouver, Canada. Streams drained separate catchments composed primarily of second-growth forest dominated by western red cedar *Thuja plicata*, Douglas-fir *Pseudotsuga menziesii*, bigleaf maple *Acer macrophyllum*, and red alder *Alnus rubra*, and had similar physical characteristics including channel gradient, width, and discharge (Table 4.1). In each stream, we selected channel units with the goal of sampling representative pools and a gradient of riffle lengths. To quantify physical habitat characteristics in each channel unit, we measured 3-6 lateral transects of depth and velocity at 20 cm intervals using a Marsh McBirney® flow metre (Hach Company, Loveland, CA), visually estimated substrate composition in each transect, and estimated canopy cover using a densiometer.

Measuring the drift produced in each channel unit necessitated blocking incoming drift from adjacent upstream habitat. To this end, we constructed wide drift nets consisting of 250 µm Nitex mesh attached to wooden rectangular frames that were customized to span the channel width at the upstream and downstream end of each habitat unit. Each frame was designed to fit

into a wooden sill, which we attached to a flat board to function at the upstream and downstream end of each channel unit. Three days prior to drift sampling, we semi-buried the slotted sills in the substrate perpendicular to flow across the upstream and downstream end of each unit, taking care to create minimal disturbance to the benthos (Fig. 4.1a). To ensure that sills were sealed to the benthos, we attached 10 cm strips of pond liner to the wooden sills and buried the liner flush with in the substrate. We avoided structurally complex channel units (e.g., those with wood or undercut banks) because of the difficulty installing block nets with minimal disturbance.

Drift sampling was initiated by carefully sliding the upstream net into the slotted sill from the stream bank (Fig. 4.1b), then repeating this procedure 15 minutes later for the downstream net to allow any disturbance from installing the upper net to subside. Nets remained in place for 2-4 hours between 1100 and 1600 after which we collected the contents of downstream nets. Captured material was stored in 70% ethanol for subsequent identification. To ensure that sampling introduced minimal benthic disturbance, we compared depth and velocity transects (3-6 per habitat) measured 3 days prior to sampling to measurements directly after the downstream nets were removed. We rejected samples where depth or velocity changed more than 10%. While we originally intended to sample 8 pools and 8 riffles in each stream, these screening criteria reduced sample size to 5 riffles in three streams and 3 pools in two streams (Coho Creek and Cook Creek).

Coastal cutthroat trout *Oncorhynchus clarkii clarkii* and coho salmon *O. kisutch* were present in all study streams and could potentially influence results if drift consumption was substantial (e.g., Leung et al. 2009). To minimize this source of bias, we chased fish out of pools from the stream bank using long-handled dip nets prior to installing downstream drift nets, taking care not to disturb the benthos. We then snorkelled through each pool after drift sampling

to account for any remaining fish. Across all pools, only 3 trout (all < 50 mm fork length) were present, suggesting drift predation had minimal influence on our results. To avoid benthic disturbance, we did not attempt to remove fish from riffles, but assume that predation was negligible given shallow depths and high velocities that likely minimized fish foraging.

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

Drift flux was computed as the total number or biomass of drift exported per hour (e.g., Wooster et al. 2016, Naman et al. 2017). To account for size differences among streams, we divided drift flux measurements by the wetted width of each habitat unit to generate a standardized specific flux rate per metre width of channel (number or $\text{mg} \cdot \text{h}^{-1} \cdot \text{m}^{-1}$). Within streams, variation in wetted width was low (i.e., less than 0.3 metres) such that this standardization did not influence relative fluxes among riffles. We also computed drift concentration at the outlet of each riffle as the number or mass of invertebrates per volume of water filtered through each drift net. Drift production was computed as the quotient of drift flux

and the area of habitat over which it was sampled (i.e., drift entry rates $\text{m}^{-2} \cdot \text{h}^{-1}$). Because variation in wetted width among habitats was small relative to variation in length, these estimates also approximated production expressed as drift flux per length of stream channel. Note that our drift production measurements are a net production rate and include both drift entry and resettlement within channel units.

Data Analysis

Drift production in pools and riffles

We used two-way analysis of variance (ANOVA) to test for differences in drift production (number or biomass $\text{m}^{-2} \text{h}^{-1}$) between pools and riffles. Stream was treated as a two-level factor variable (note that pools were only sampled in two of the three study streams). We used Levene's test to validate assumptions of homogenous variances and $\log+1$ transformed any cases that deviated from normality. Because the design was unbalanced ($n = 10$ riffles and 6 pools), we computed F -statistics using Type 3 sum of squares with the *car* package (Fox and Weisberg 2010) in R version 3.2.2 (R Core Team 2013). To quantify uncertainty around drift production estimates for pools and riffles, we computed 95% confidence intervals using a nonparametric bootstrapping procedure ("basic method"; Puth et al., 2015). We did not incorporate the different streams into the bootstrap resampling because we found no differences in drift production between them (see *Results* Table 4.2).

Drift flux and riffle lengths

We used an information theoretic approach with linear mixed effects models to examine how drift flux and concentration varied across a gradient of riffle lengths. Response variables included total drift flux (number or biomass $\text{h}^{-1} \text{m channel width}^{-1}$) and fluxes of aquatic and terrestrial prey categories separately. Because concentration (number and mg m^{-3}) exhibited

responses that were similar to drift flux, we only report results for total concentration to reduce redundancy. For each response we formulated a set of models including riffle length as a fixed effect and stream as a random intercept ($n = 5$ riffles per stream in three streams). We included canopy cover as an additional fixed covariate in models for all responses, and mean velocity (m sec^{-1}) and depth (m) as additional fixed covariates for total and aquatic drift flux. Substrate was similar across all riffles so was not included in the analysis. To address the hypothesis of an asymptotic relationship corresponding to riffle length exceeding average drift distances, some candidate models for each response included $\log(+ 0.5)$ transformed (hereafter “pseudo threshold”) riffle length as a predictor (Franklin et al. 2000). Each candidate set (3-5 models) also included a null model, which included only a random intercept.

We evaluated candidate models using Akaike’s Information Criteria corrected for small sample sizes (AIC_c), with more parsimonious models getting lower AIC_c scores (Burnham and Anderson 2002). We considered a model to have strong support if the deviation of its AIC_c score from that of lowest scoring model in the set (ΔAIC_c) was less than 2 (Burnham and Anderson 2002). We also calculated AIC weights (W_i), which represent the probability a given model is the best fitting model in the candidate model set. For models with strong support, we evaluated fixed effects by examining whether 95% confidence intervals around the slope estimates overlapped zero and overall model fits by computing marginal and conditional R^2 , which represent the variance explained by the fixed and fixed plus random effects, respectively (Nakagawa and Schielzeth 2013). We conducted all analyses in R using the *lme4* (Bates et al. 2015) and *MuMin* packages in R (Bartón 2009).

Many aquatic taxa have behavioural adaptations to shorten or prolong their time in drift (e.g., Elliott, 2002), and variation in drift distances among taxa could obscure community-level

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

Individual body size and community structure

To describe the size structure of drifting invertebrates we compared several attributes of the body mass-frequency distribution between aquatic and terrestrial drift and between aquatic drift in riffles and pools. For mean individual body mass, we first performed two-sample *t*-tests on group means, and then used non-parametric bootstrapping to generate 95% confidence intervals. To examine differences in median body mass, we used a two-way permutation test (10,000 iterations) for group medians following the procedure outlined in Good (2013) and nonparametric bootstrapping to estimate 95% CIs. We were also interested in the skewness of the size distribution, which indicates the degree to which total biomass was driven by large individuals. We used the resampling procedure described above to create distributions based on group means and standard deviations, then used a two-way permutation test to compute exact *P*-values testing differences in skewness between groups. More positive skewness values indicate a more right-tailed distribution (i.e., skewed toward more small invertebrates; Groeneveld and Meedan, 1984).

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

4.4 Results

Across all drift samples, aquatic taxa were four times more abundant than terrestrials. The dominant taxa were larval and adult Chironomidae, Baetidae, Dixidae, and Simuliidae, together comprising over 62% of the total abundance. The three most abundant terrestrial taxa were adult Psocoptera, Collembola, and Araneae, comprising 12% of the total abundance. Despite these large differences in abundance, total biomass was similar between aquatic (total 281 mg dry mass for all samples combined) and terrestrials (261 mg dry mass for all samples). In terms of biomass, the dominant taxa were adult Chironomidae (24%), adult Psocoptera (13%), and Araneae (5%). Larval Baetidae, Simuliidae, and chironomids comprised a combined 11% of total biomass. Contrary to expectations, there was no evidence for distinct drift community structures between pools and riffles (PERMANOVA, $F_{1,14} = 0.83$, $P = 0.62$).

Differences in Drift Production Between Pools and Riffles

Total drift production (biomass and number $\text{m}^{-2} \text{h}^{-1}$) and aquatic drift production (biomass $\text{m}^{-2} \text{h}^{-1}$) were significantly greater in riffles than pools (Table 4.2). Riffles produced 3.5-3.6 times more drift per area of streambed (Fig. 4.2), supporting the source-sink hypothesis. As predicted, terrestrial drift production did not differ significantly between habitat types (Table 4.2).

Although the mean production of terrestrial drift biomass appears larger in riffles (Fig. 4.3), this

was primarily driven by inputs of several anomalously large terrestrial Coleoptera larvae in one riffle in Cook Creek. Interestingly, despite differences in discharge, drift production did not vary significantly among streams (Table 4.2) even when production in riffles were compared separately with Snake Creek included (ANOVA, $F_{2,12} = 1.4$, $P = 0.28$).

Effects of Riffle Length on Drift Flux

As predicted, the total flux of drift out of riffles increased with riffle length (Fig. 4.3). For total numeric flux (number $\text{h}^{-1} \text{m}^{-1}$), the top-ranked model included a linear effect of riffle length ($W_i = 0.54$) and explained 37% of the variation. A non-linear (pseudo-threshold) model also had empirical support ($\Delta\text{AIC} = 0.37$; $W_i = 0.45$), and explained 25% of the variation (Table 4.3). For biomass flux, the top ranked model included a pseudo-threshold term ($W_i = 0.62$), which explained 27% of the variation. For both responses 95% confidence intervals around the slope estimates did not overlap zero (Table 4.3). When we analyzed the aquatic and terrestrial drift separately, there was only weak support for any of the fixed effects (Table 4.3) and top ranked models explained less than 10% of the variation. Canopy cover, mean velocity, and depth had little support to explain drift flux and were not included in plausible models for any responses. Drift concentration was also positively related to riffle length (Fig. 4.4). For numeric concentration, a linear effect of riffle length had the most support ($W_i = 0.67$) and explained 83% of the variation. For biomass concentration, there was support for models including both nonlinear ($W_i = 0.39$) and linear terms ($\Delta\text{AIC} = 1.1$; $W_i = 0.22$) in addition to an intercept only model ($\Delta\text{AIC} = 0.1$; $W_i = 0.38$). 95% confidence intervals did not overlap zero for both numeric and biomass concentration (Table 4.3).

Drift fluxes of individual taxa differed in their response to riffle length. Fluxes of Baetidae and Simuliidae were weakly related to riffle lengths, as the top ranked models explained less than 10% of the variance and confidence intervals around slopes overlapped zero (Table 4.3). In contrast, models including pseudo-threshold terms had the most support explaining longitudinal increases in Chironomidae ($W_i = 0.73$) and Dixidae ($W_i = 0.79$) flux, and 95% CIs around slope estimates did not overlap zero (Table 4.3). Dixidae exhibited the strongest relationship, with riffle length explaining 48% of the variation in drift flux (Fig. 4.5).

Aquatic and Terrestrial Invertebrate Body Size

Individual body mass of aquatic invertebrates drifting from riffles was ~5 times greater on average than those from pools (t -test = 3.15, $df = 493$, $P < 0.01$), and terrestrial body mass was 3.5 times greater on average than aquatic (t -test = 3.44, $df = 185$, $P < 0.01$). Chilopoda, Formicidae, and Hymenoptera were the largest terrestrials, while Gammaridae, Perlidae, and Hydropsychidae were the largest aquatics. Median body mass was also larger for aquatics from riffles relative to pools (Two-way permutation, exact $P = 0.005$), and for terrestrials relative to aquatics (two-way permutation test $P = 0.007$). Body mass-frequency distributions were right tailed for all invertebrates but did not differ between riffles and pools ($P = 0.2$). In contrast, mass-frequency distributions differed between terrestrials and aquatics (Fig. 4.6). Skewness values were ~3 times lower in terrestrials (Table 4.5) indicating that rare, large individuals had a larger influence on overall terrestrial biomass than aquatics.

4.5 Discussion

Our observation of greater drift production in riffles than in pools supports source-sink dynamics and suggests that previously demonstrated differences in drift concentration between habitats (e.g., Leung et al. 2009) may be driven by spatial variation in drift production as well as drift

depletion (i.e. settling or consumption in pools). Given that our study is observational, we cannot confirm the mechanisms that underlie this pattern. One possible explanation is that hydraulic stress and turbulent flows in riffles are more likely to dislodge invertebrates from the benthos as well as make it more difficult for settlement relative to pools, which are more hydraulically benign at low flows (Jowett 1993). In addition, benthic densities and productivity are often greater in riffles (Brown and Brussock 1991; Grubaugh et al. 1997; but see Halwas et al. 2005), which may lead to higher drift (Hammock and Wetzel 2013, Weber et al. 2014).

While pool-riffle differences in drift production could also be influenced by contrasting community structures, e.g., if riffles included more drift prone taxa (Scullion et al. 1982), we were surprised to find similar drift composition between the two channel unit types. Leung et al. (2009) also found similar community structure between drift in pools and riffles, which they attributed to drift being homogenized over short channel units. This is a less plausible explanation for our results given that we blocked drift from adjacent upstream channel units. While differences may have emerged with greater replication, another possibility is that the process of drift essentially selects for a consistent set of taxa from the benthos; for instance, epibenthic taxa prone to dislodgement or behavioural drift entry (Rader 1997). Within this subset of taxa, riffle-pool differences in body size indicate more nuanced effects of habitat type on the physical and behavioural drivers of drift. For example, higher velocities and greater turbulence in riffles may have exceeded entrainment thresholds for larger bodied individuals or reduced their settling rates (Statzner 1987), or larger individuals in pools may have suppressed their tendency to drift as a tactic to reduce predation risk (e.g., Poff et al. 1991, Peckarsky 1996).

Our prediction of greater drift fluxes out of longer riffles was generally supported as the total number and mass of exported drift increased with riffle length. Upstream riffle length was

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

Interestingly, riffle length was a poor predictor of drift flux when categories (aquatic vs. terrestrial) were examined individually. For aquatic-derived drift, the lack of relationship likely results from the integration of multiple taxa with strong differences in ecology, behaviour, and life history. In a similar study in a small New Zealand stream, Hansen and Closs (2007) found that relationships between drift abundance and riffle length were less apparent for Baetid mayflies compared to Trichoptera species, suggesting that behavioural influences on drift distances can obscure longitudinal patterns. Our results support this inference as Baetidae and Simuliidae, which have sophisticated control of resettlement from drift (Otto and Sjostrom 1986, Fingerut et al. 2006), were not influenced by riffle length. In contrast, Dixidae and Chironomidae, which have less control over resettlement (Rader 1997), exhibited positive saturating relationships where drift abundance continued to increase downstream.

For particularly drift-prone taxa like Baetidae, some estimates of drift distances at similar velocities to our study are less than 2 m (Elliott 1971, Townsend and Hildrew 1976), which we

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

Riffle length was a poor predictor of terrestrial drift flux, suggesting that input rates vary strongly over space. In our case, terrestrial drift seemed to vary haphazardly among habitats irrespective of canopy cover. In addition, despite being nearly equal to aquatic drift in terms of total biomass, the contribution of terrestrial invertebrates to drift appeared to be driven by infrequent inputs of large-bodied individuals as evidenced by larger mean and median body sizes, and lower skewness relative to aquatics. While spatial patterns may have emerged with greater replication, other studies have also found substantial variability in terrestrial inputs over relatively small areas (Wipfli 1997, Rosenfeld and Raeburn 2009). Taken together, these results suggest drivers of terrestrial input rates (e.g., invertebrate activity levels, wind and rain; Baxter et al. 2005) are unrelated to pool-riffle channel structure and that this source of prey may not be spatially predictable within stream reaches. However, more work linking input rates to drivers of

riparian arthropod abundance (e.g., vegetation composition, microclimates (Allan et al. 2003, Henshall et al. 2011) could clarify this issue.

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

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

Wallace 1987, Grubaugh et al. 1997). The pool: riffle drift production ratio we observed (~ 3.5 for total drift) is remarkably similar to their estimate suggesting a possible link between benthic and drift production (Waters 1966). However, more data are clearly needed to determine if this result is generalizable.

It is surprising that research into the processes generating spatial heterogeneity in drift is so scarce given that spatial variation in benthic abundance is so well studied (e.g., Downes et al. 1993, Wiens 2002). In principle, spatial variation in drift abundance should occur through changes in the relative rates of production (drift entry) and depletion (Naman et al. 2016). For example, reduced drift abundance in hydraulic dead zones likely results from increased settlement without commensurate increases in production (Bond et al. 2000). In this sense, there may be spatially discrete “patches” of homogeneous drift concentration where production and depletion rates are in relative equilibrium. Our results, along with other work on drift transport (Lancaster et al. 1996, Wilcox et al. 2008) and concentration (Leung et al. 2009), suggests that hydraulic gradients across distinct channel units may contribute to this spatial structure. However, similar to benthic abundance, which differs strongly over microhabitat gradients (Downes et al. 1993, Brooks et al. 2005), rates of drift production and depletion may also vary at small scales *within* channel units; for instance from turbulence (Blanckaert et al. 2013), and lateral settling at channel margins (Ciborowski 1983). In essence, the benthos and drift can be conceptualized as vertically layered patches linked by drift entry and settlement. Whether these patches are spatially congruent is largely an open question and depends on the spatial scale of variation in drift production and depletion and the corresponding extent of homogenous drift patches.

Implications for Drift-Feeding Fish

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

Quantifying source-sink drift patterns may also inform drift-foraging bioenergetics models, an increasingly common strategy to assess habitat capacity for fish (Piccolo et al. 2014, Rosenfeld et al. 2014). Many applications of these models to date make simplifying assumptions that drift concentration is spatially uniform (Stark et al. 2002, Jenkins and Keeley 2010, Urabe et al. 2010). In addition to other factors (e.g., benthic foraging; Harvey and Railsback 2014), assuming spatial uniformity in drift may contribute to deviations between predicted and observed capacity estimates (Wall et al. 2016b). In more complex models that include spatially explicit drift components (Hayes et al. 2007, 2016, Anderson et al. 2013), parameterizing drift entry rates is a crucial source of uncertainty. For small streams, our production estimates could be useful to

validate modelled entry rates if the scale of interest is whole channel units. Alternatively, our predicted drift fluxes at short riffle lengths could provide reasonable estimates of instantaneous drift entry if smaller scales (e.g., foraging territories) are of interest.

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

4.6 Tables and figures

4.6.1 Tables

Table 4.1 Site characteristics of the three sampled streams. Depth and velocity are averaged across each habitat type and stream. Bankfull width and gradient are from Rosenfeld et al.(2000). We did not sample pools in Snake Creek.

Stream	Bankfull width (m)	% Gradient	Q (m ³ sec ⁻¹)	Mean wetted width (m)		Mean velocity (m/s)		Mean depth (cm)	
				Pools	Riffles	Pools	Riffles	Pools	Riffles
Coho	2	1.6	0.05	1.3	1.1	0.12	0.31	14.9	5.1
Cook	2.2	2.5	0.07	0.8	0.96	0.1	0.26	8.6	4.6
Snake	3.5	1.5	0.1	-	1.3	-	0.28	-	6.3

Table 4.2 Results from two-way ANOVAs (type 3 SS) testing the effects of stream and habitat type on various drift production metrics. Significant *P* values (< 0.05) are in bold.

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

Table 4.3 Linear mixed effects models explaining variation in drift flux ranked by AIC_c scores. Abbreviations are as follows: L-L is the log likelihood; ΔAIC_c is the difference between the AIC_c score of a model and the best fitting model in the set; W_i is the probability model i is the best fitting model in the set; R^2_m represents the proportion of variation explained by fixed effects only, and R^2_c represents the amount of variation explained by fixed and random effects. Slopes of fixed effects (β_1) are included when 95% confidence intervals did not overlap zero; β_0 is the fixed intercept. Each model included stream as a random intercept term. The fixed components of the pseudo-threshold models are of the form: $\theta = \beta_0 + \beta_1 \log_e(x_1)$. Only models with ΔAIC_c values less than 2 are shown.

Table 4.3

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

Table 4.4 Estimates of mean and median individual body sizes for drifting invertebrates. Numbers in parentheses are bootstrapped 95% confidence intervals

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

4.6.2 Figures

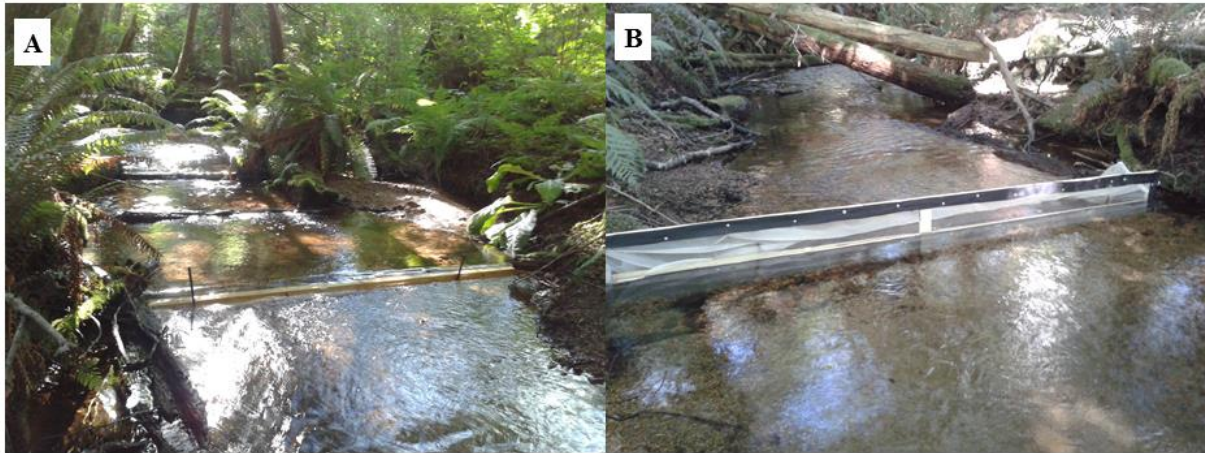


Figure 4.1 Overview of drift sampling protocol. (A) Shows the slotted wooden sill positioned across the top of a riffle. (B) Shows the drift net slid into the slot to intercept drift entering the channel unit. Note that A is looking upstream while B is looking downstream.

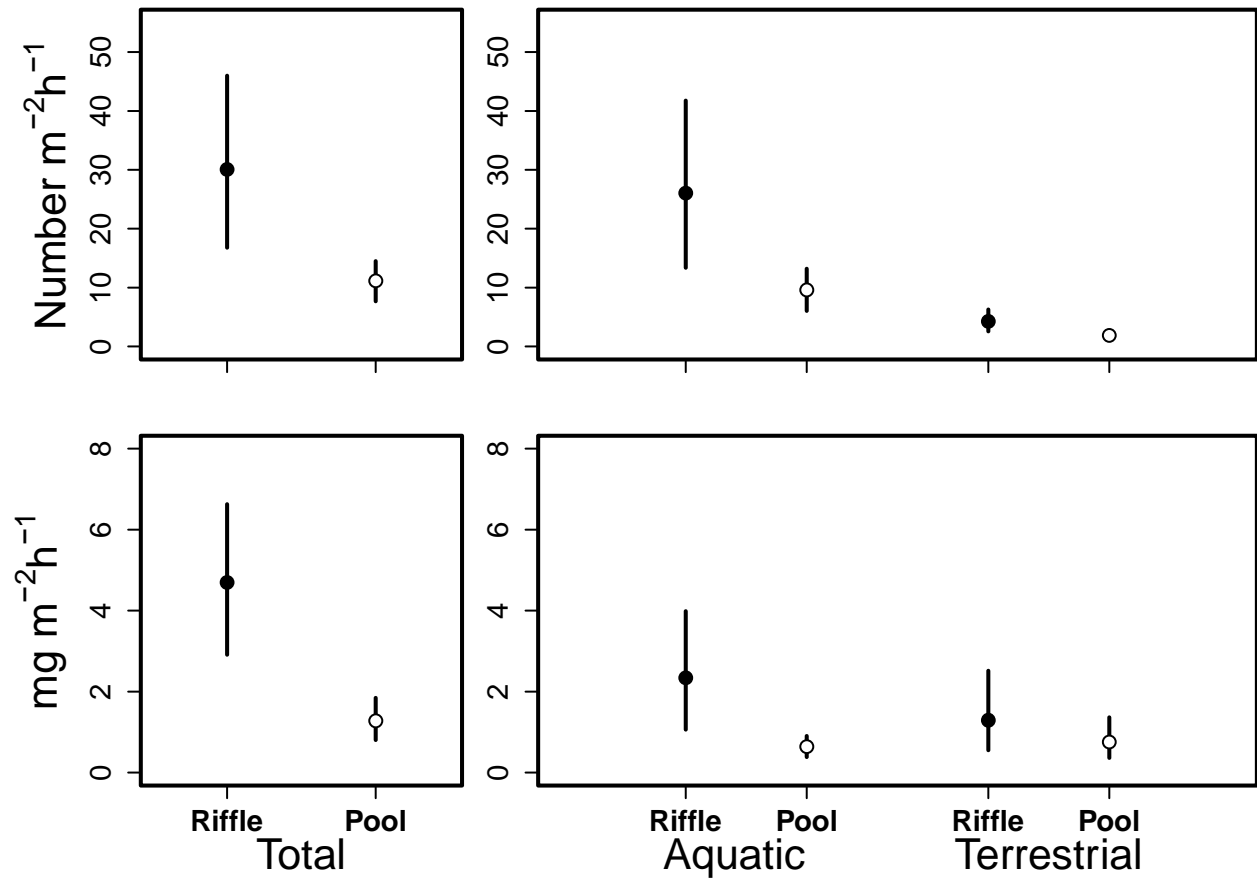


Figure 4.2 Estimates of drift production in riffles (filled circles) and pools (open circles). Left panels are total drift and right panels are separated into aquatic and terrestrial. Error bars represent bootstrapped 95% confidence intervals.

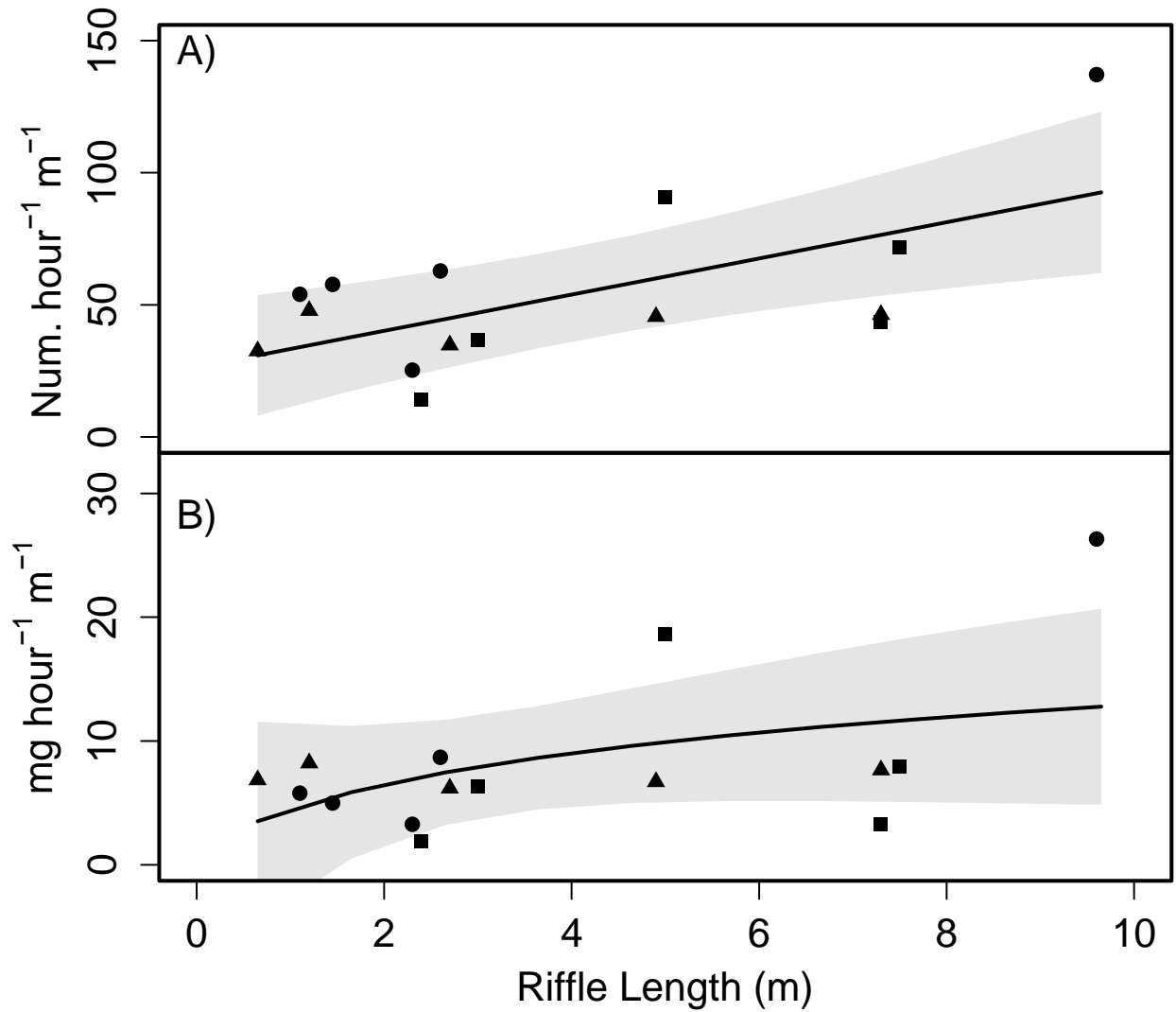


Figure 4.3 Total drift flux in counts (a) and biomass (b) as a function of riffle length. Lines represent the top ranked linear mixed effects model fitted to the entire data set. Shaded areas represent 95% confidence regions. Symbols represent different streams: Coho (triangles), Cook (circles), and Snake (squares).

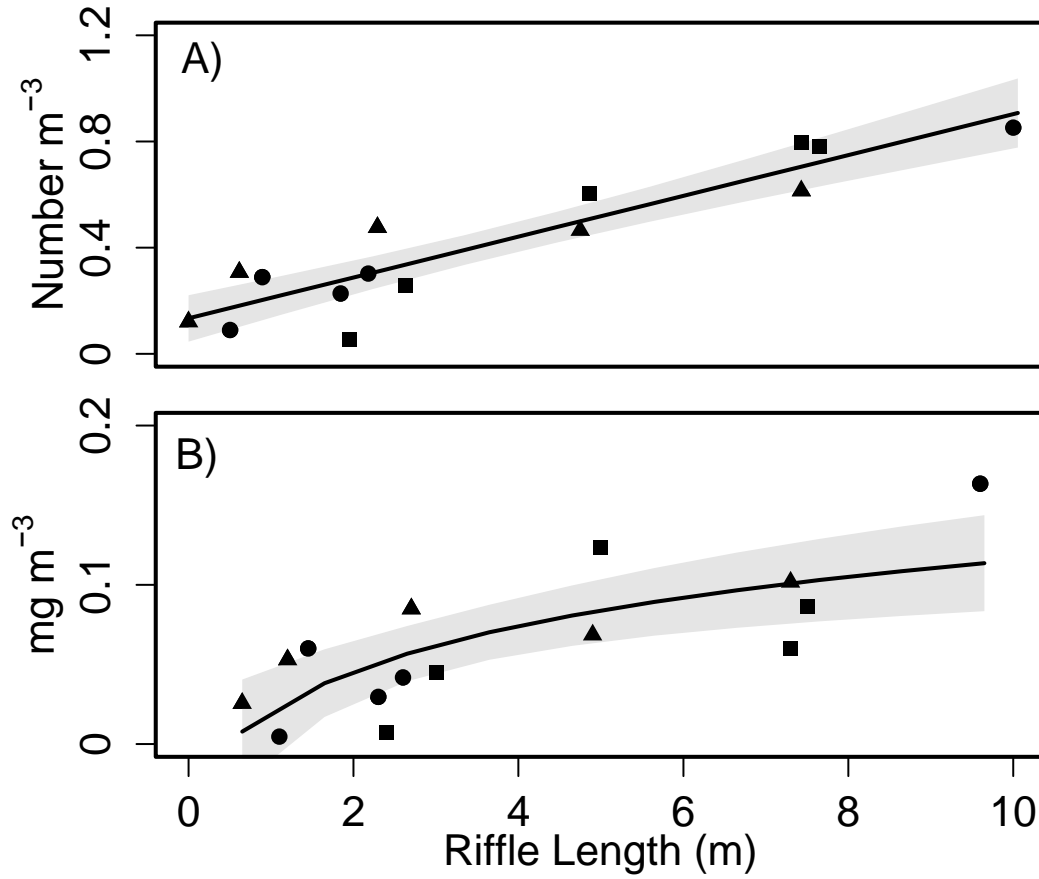


Figure 4.4. Total drift concentration in counts (a) and biomass (b) as a function of riffle length. Lines represent the top ranked linear mixed effects model fitted to the entire data set. Shaded areas represent 95% confidence regions. Symbols are the same as Figure 3.

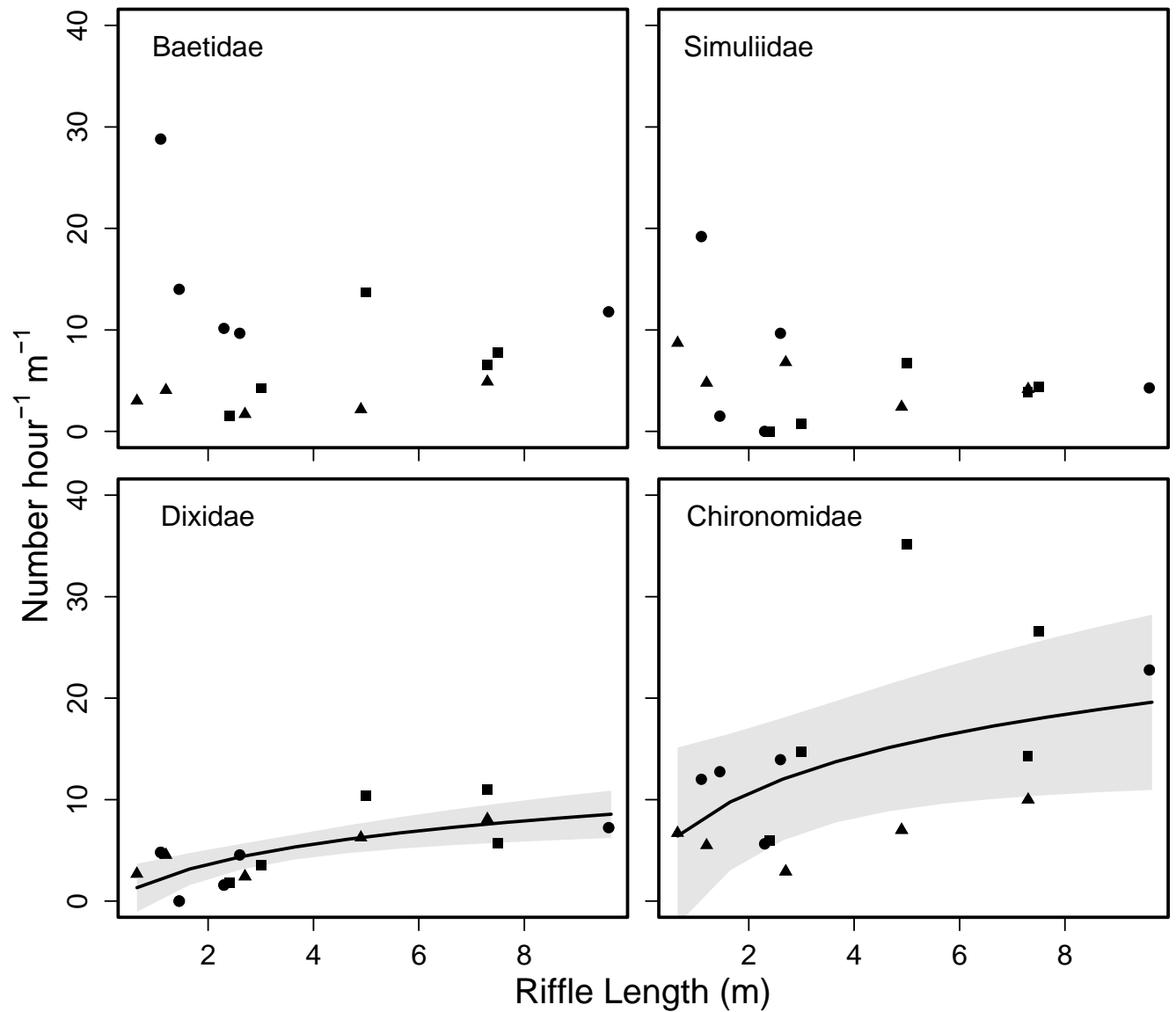


Figure 4.5. Drift flux of Baetidae, Simuliidae, Dixidae, and Chironomidae as a function of riffle length. Lines represent the best fitting mixed effects model fitted to the entire dataset. Shaded area represents the 95% confidence region around the regression line. Regression lines are not shown for Baetidae and Simuliidae because 95% confidence intervals around the slope overlapped zero. Symbols are the same as Figures 3 and 4.

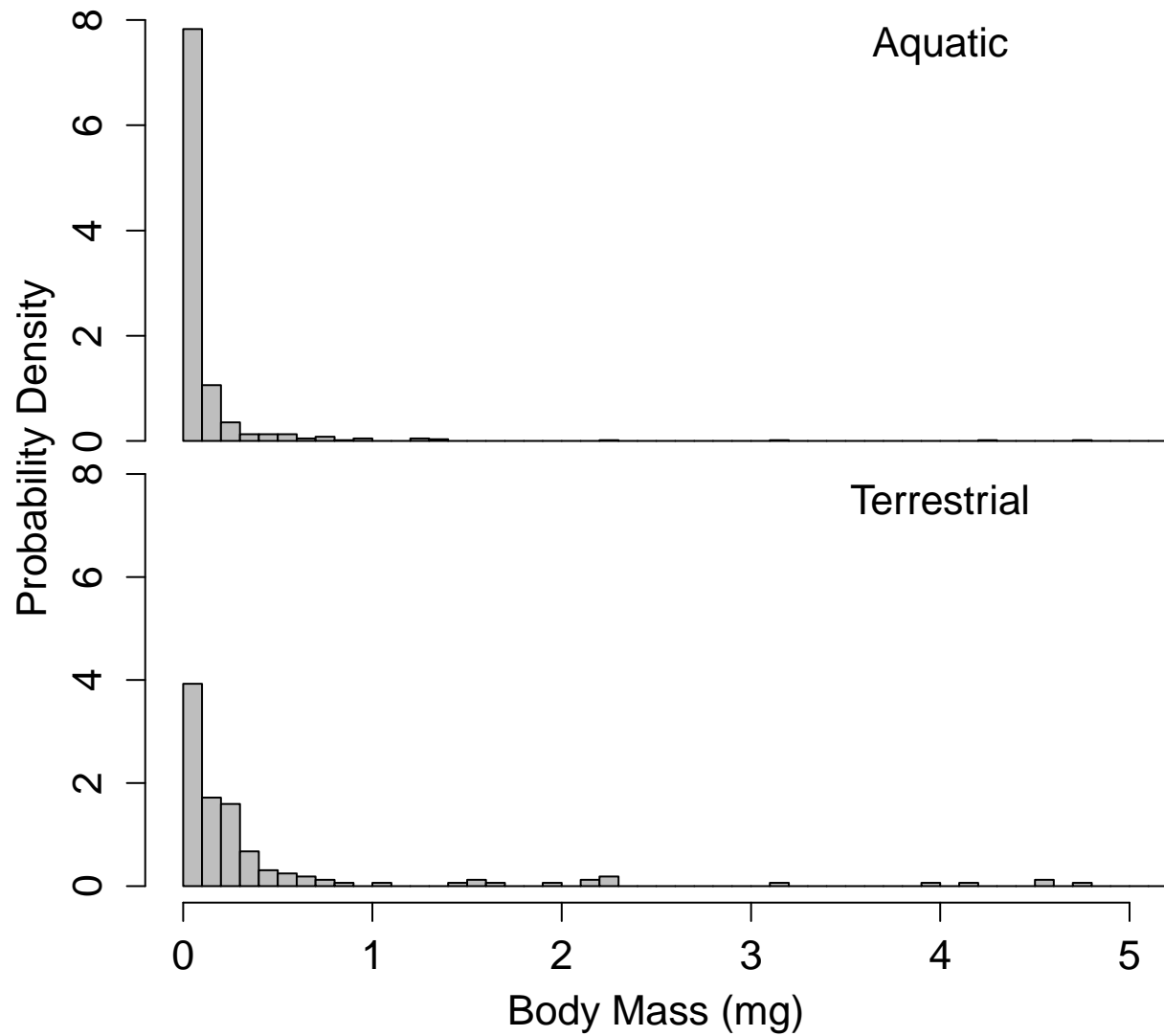


Figure 4.6. Probability density histograms for individual body sizes (mg) of aquatic and terrestrial invertebrates. Body sizes are sorted into 0.1 mg bins. The total area under the bars sums to 1.

Chapter 5 Terrestrial resource subsidies mediate nonlinear effects of habitat heterogeneity on stream-rearing Pacific salmon production

5.1 Summary

Habitat heterogeneity provides refuge from predation, and enhances spatial separation of consumers and their resources. The spatial structure of refuges and foraging habitat patches should therefore mediate energy flow from resources to consumers. However, these effects may diminish if resources are primarily allochthonous and predator consumption is decoupled from local prey production. In small streams, juvenile Pacific salmon (*Oncorhynchus* spp.) typically forage in low velocity pool habitats, which are energetically favourable, while the suspended invertebrates they consume are primarily produced in adjacent high velocity riffles. A trade-off between space (pool habitat) and food limitation (prey production in riffle habitat) therefore predicts a unimodal effect of increasing pool area on juvenile salmonid production. Terrestrial invertebrate inputs can also be an important prey source to stream fish and are unrelated to pool-riffle structure. Consequently, increasing terrestrial prey would predict a linear or saturating effect of pool area on production. To test these contrasting hypotheses and explore the energetic consequences of pool-riffle composition, we enclosed juvenile salmonids across a gradient of relative pool-riffle areas ($n = 13$ enclosures ranging from 14-80 % relative pool area). We then used bioenergetic model simulations to examine the sensitivity of habitat-production relationships to resource delivery mode (aquatic drift vs. terrestrial prey sources). Increasing relative pool area reduced overall prey abundance but increased available habitat, leading to nonlinear positive effects on total fish production and consumption, where increasing pool area

had diminishing returns beyond a threshold of 40-50%. Bioenergetic simulations indicated that increased terrestrial prey inputs linearized the effect of pool area on fish production, while decreased terrestrial inputs resulted in a more 'hump shaped' relationship with a distinct optimum. Our results imply that the composition of distinct habitat patches may have nonlinear effects on consumer productivity due to trade-offs between habitat that generates prey and preferred rearing habitats. However, these relationships were sensitive to cross terrestrial prey inputs, suggesting that habitat configurations that maximize consumer production depend on the mode of resource input.

5.2 Introduction

Habitat heterogeneity -- the diversity, relative abundance, and juxtaposition of structural elements in space -- can strongly influence energy flow and productivity by spatially separating consumers from areas of high resource production (Huffaker 1958, Persson et al. 1996). For instance, if resources primarily originate in refuges that are spatially inaccessible to consumers, e.g., due to harsh abiotic conditions (Menge and Lubchenco 1981, Hixon and Beets 1993), predation may be limited by fluxes of prey from refuges into areas where they are vulnerable (i.e., the foraging arena; Ahrens et al. 2012). In this case, habitat heterogeneity will modulate both resource abundance and the quantity of habitat where consumers can achieve a positive energy balance (Kauffman et al. 2007, Armstrong et al. 2010). If prey flux into vulnerable areas is positively related to the area of prey refuge habitat, a trade-off for consumers may occur whereby increasing the relative area of refuges would elevate food abundance but decrease suitable foraging area (Crowder and Cooper 1982, Heck and Crowder 1991). Consequently, consumer production -- defined as the rate of new tissue accrued across a population -- may peak at an intermediate habitat composition (i.e., the relative areas of distinct habitat patches;

Dunning, Danielson and Pulliam 1992), where energy intake is maximized relative to spatial requirements (e.g., territory size; Grant and Kramer 1990).

The effects of habitat patch composition on consumer production may differ in systems dominated by allochthony, where prey inputs from outside the system of interest subsidize recipient consumers beyond what *in situ* prey could support (Nakano and Murakami 2001, Spiller et al. 2010). These external resource subsidies should be unrelated to recipient habitat structure by definition (Polis et al. 1997, Richardson et al. 2010); consequently, the spatial configuration of prey refuge areas should have less influence on consumer productivity in habitats with high inputs of allochthonous resources.

Mechanistically linking productivity to habitat heterogeneity is a central goal in ecology, with particular relevance to predicting the consequences of habitat alteration on threatened populations (Kovalenko et al. 2011). Indeed, there is a rich literature connecting predation to physical heterogeneity across landscapes (e.g., Irlandi 1994, Hopcraft et al. 2005) or between discrete experimental treatments (e.g., Grabowski 2004; Worischka et al. 2012); however, surprisingly few studies have incorporated gradients of heterogeneity in controlled field experiments. Hence, while nonlinear effects of habitat patch composition on consumer production are evident (e.g., Heck and Crowder 1991, Eklöv and Diehl 1994), the functional form of this relationship is uncertain. In addition, despite a large focus on how allochthonous resources influence recipient food webs (Marczak et al. 2007, Marcarelli et al. 2011), their role in mediating consumer-habitat relationships is less understood.

To address these gaps, we examined the energetic consequences of habitat patch composition and resource delivery mode on juvenile Pacific salmon and trout (Salmonidae) in a temperate forest stream. Stream rearing salmonids are an ideal taxa for testing these ideas given

their performance (e.g., growth) is strongly linked to geomorphic channel structure, which can regulate abundance of both food (prey production) and space (suitable habitat). Salmonids typically forage in dominance hierarchies where they defend fixed central place territories to intercept invertebrate drift, suspended invertebrates in downstream transport (Chapman 1966, Naman et al. 2016). Drift originates primarily in shallow high velocity riffles where epibenthic invertebrates enter drift behaviourally or are dislodged by flow (Leung et al. 2009, Naman et al. 2017b); however, many salmonids preferentially use deeper low velocity pools where higher capture success and reduced swimming costs make drift-foraging more energetically profitable (Fausch 1984, Hill and Grossman 1993). This incongruence leads to the prediction that production of salmonids should peak at intermediate combinations of pool-riffle habitat patches (Poff and Huryn 1998, Rosenfeld and Raeburn 2009).

However, cross-ecosystem inputs of terrestrial invertebrates are also a key property of small streams, often dominating annual energy budgets for salmonids (Kawaguchi and Nakano 2001, Sato et al. 2011). Terrestrial inputs originate from the riparian zone (Wipfli and Baxter 2010, Richardson and Sato 2015) and while they are linked to geomorphology over larger scales (Bellmore and Baxter 2014), they do not vary systematically with pool-riffle channel structure (Gowan and Fausch 2002, Naman et al. 2017b). Consequently, terrestrial inputs could modify the influence of patch configuration on fish production, effectively decoupling the dependence of pool-rearing salmonids from riffle-produced drift.

We conducted a field experiment to test the influence of pool-riffle configuration on consumption, production, and behaviour of two species of drift-feeding Pacific salmon: juvenile coho *Oncorhynchus kisutch* and cutthroat trout *O. clarkii*. We tested two alternative hypotheses of how pool-riffle composition may influence productivity based on contrasting modes of

resource delivery (drift vs. terrestrial drop). We hypothesized that if drift was the primary mode of resource delivery, relative pool-riffle area should impose a food-space trade-off such that (i) usable habitat should increase but energy availability should decline with increasing pool area, and (ii) consumption and production by fish should therefore peak at intermediate pool-riffle combinations. Alternatively, we hypothesized that if terrestrial inputs were the primary mode of resource delivery to fish, pool-riffle composition would limit only the area of suitable habitat, such that increasing pool area would lead to (iii) no changes in energy availability and (iv) a linear or saturating increase in consumption and production (Figure 5.1). Given drift-feeding fish often exhibit plasticity in foraging behaviour (Fausch et al. 1991, Sloat and Reeves 2014), we also made the general prediction that with increasing terrestrial prey, there should be (v) a shift from territorial central place foraging on drift to search foraging on terrestrial prey. We link these hypotheses using bioenergetic model simulations to explore the effects of pool-riffle composition on production across a full gradient of drift vs. terrestrial resource delivery.

5.3 Methods

Study System and Logistics - We conducted our study in Webster Creek, a tributary of the Cedar River, a protected watershed on the west slope of the Cascade Mountains in Washington State, USA (see Kiffney et al. 2009). Webster Creek is a low gradient, pool-riffle gravel-cobble stream draining a conifer dominated second growth catchment, with riparian vegetation typifying similar streams in the region. Bankfull and wetted width at the study site averaged 8 and 2 m, respectively, and summer low flow discharge ranged from 0.01-0.03 m³·s⁻¹. Fish species present in Webster Creek include coho, cutthroat trout, brook lamprey *Lampetra planeri*, and several species of sculpin *Cottus* spp. (P. Kiffney unpublished data). Rainbow trout *O. mykiss* are present lower in the watershed but scarce at the study site.

We selected 13 riffle-pool sequences (*sensu* Frissell *et al.* 1986) as experimental units within a ~2 km reach of stream with the goal of maximizing variation in the relative areas of pools and riffles (14-80% pool area) while minimizing variation in as many other conditions as possible including wood density, canopy cover, pool depth, and riffle velocity (Table 5.1). We installed 2 mm grid wire mesh enclosure fences at the upstream and downstream end of each sequence, which were anchored with rebar stakes and sealed by burying the lower edge 10 cm into the substrate. Fences allowed free passage of drifting invertebrates while preventing movement of fish larger than 20 mm fork length and were cleaned daily during the experiment to prevent clogging.

To quantify differences in hydraulic conditions between riffles and pools, we measured lateral transects of depth and velocity at 20 cm intervals (3-5 per pool or riffle) using a Marsh McBirney flow meter (Hach Company, California). We recorded water temperature continuously with ibutton[®] temperature loggers and measured other physical features including residual pool depth, substrate, wood abundance, and canopy cover according to methods presented in Pess *et al.* (2011) and Kiffney and Roni (2007).

Quantifying Prey Availability - Invertebrate drift was measured three different times during the experiment. Drift sampling involved setting 2-3 nets (306.5 cm² opening) placed across the downstream end of each riffle for 2-4 hours during daylight. We measured terrestrial invertebrate inputs with floating pan traps containing 10 mm of water and soap to reduce surface tension, placed haphazardly within each pool. Pan traps were left for 10-12 h during daylight and were aggregated across three sampling events to calculate a mean value for each pool. Aquatic and terrestrial invertebrates were stored in 75% ethanol and subsequently sorted and identified (typically to family or genus) in the laboratory. We measured the body length of each individual

with a stage micrometer and used allometric equations relating length to mass (Hodar 1996, Benke et al. 1999). Drift and terrestrial inputs were computed as a total energy flux per area of total enclosure ($\text{Joules m}^{-2} \text{ day}^{-1}$), with drift flux calculated as the product of drift concentration and stream discharge. Energy density was used as opposed to biomass as it more explicitly integrates variation in prey quality (Beauchamp 2009). Mass conversion factors from Cummins and Wuycheck (1971) and McCarthy *et al.* (2009) were used to convert biomass to energy density.

Fish Growth, Production, and Habitat use - We collected juvenile coho and cutthroat trout on 22 June 2015 using minnow traps and seine nets. Coho were young of year and ranged from 48-95 mm while cutthroat consisted of young of year and 1-2 year olds and ranged from 50-100 mm. While these species interact and differ slightly in microhabitat use (e.g., Glova 1986) they are treated here as a single drift-foraging assemblage. Fish were held overnight to allow gut clearance, then measured to the nearest mm, weighed to the nearest 0.1 g, and individually marked with elastomer tags (Northwest Marine Technologies, Shaw Island, WA). Equal numbers of coho and cutthroat of a similar size range were stocked at a density of 0.5 fish m^{-2} per area of enclosure (i.e., area of pool and riffle combined). Before stocking, we snorkelled through each enclosure to ensure all salmonids had been removed. We recaptured fish 32 days later on 21 July 2015 and re-measured lengths and weights as described above. We computed instantaneous growth rates ($\% \text{ day}^{-1}$) for individuals as $[\ln(\text{mass final}) - \ln(\text{mass initial})] / \text{duration} \times 100$ and total production as the total mass change of all fish in each enclosure. Because enclosures differed in size, production values were standardized by enclosure area (g m^{-2}). More than 90% of fish were recaptured across all enclosures suggesting terrestrial and avian predation was minimal.

Snorkel surveys were conducted on four occasions to determine pool-riffle habitat preferences and the realized density experienced by individuals. Starting from upstream, we counted all fish through the length of each pool to corroborate the known number of fish stocked into the enclosure. We assumed any unaccounted fish were using riffles, which were too shallow for snorkelling (< 20 cm). Fish densities in pools were then computed as the quotient of the number of fish observed and pool area (number m⁻²).

Behaviour Observations - We conducted observations of territoriality and foraging behaviour on two occasions during the experiment. This involved a snorkelling observer lying motionless at the midsection of each pool for 15 minutes to minimize disturbance artefacts, then recording the number of fish present in the pool and the foraging behaviour of each observed individual. We classified fish as territorial if they maintained consistent foraging positions or non-territorial if they did not hold territories and fed on terrestrial or benthic invertebrates (Nielsen 1992).

Consumption and Exploitation Efficiency - To estimate fish consumption, we used a modified version of a Wisconsin bioenergetics model parameterized for coho salmon (Stewart and Ibarra 1991, Hanson 1997), which we fit to observed growth (Appendix B). There was strong correspondence between fitted and observed growth and production values ($r = 0.98$ for growth, $r = 0.99$ for production, where production is individual growth summed for each pool, Appendix B, Figure B1), suggesting the model approximated true consumption. We report three metrics of consumption in relation to pool-riffle composition. First, we describe bulk energy flow as the *total consumption* of all individuals per area of enclosure (g m⁻²); second, we describe *relative production efficiency* as observed production relative to expected production based on bioenergetics calculations, i.e., the mass produced relative to that expected by the mass

consumed; third, we express *exploitation efficiency* as consumption relative to the energy available from the estimated prey flux. This last ratio was standardized to fall between 0 and 1, where 1 would indicate that 100% of the prey flux was consumed within a pool-riffle sequence. Estimated consumption exceeded prey availability for two of 13 pool-riffle sequences but the estimates were within the range of error for both metrics.

Statistical Analysis – All analyses were conducted in R version 3.3.2 (R Core Development Team). The effect of pool area on total fish production and consumption was determined using ordinary least squares (OLS) regression with three a priori model structures (linear, threshold, and quadratic). To further explore potential unimodal responses to increasing pool area, we also fit a Monod-Haldane function that provides more flexibility in that it allows slopes to differ on the ascending and descending arms of the curve (Bolker 2007). The model was fit with nonlinear least squares (nls) and was constructed as:

$$p(x) = \frac{mx}{a + bx + x^2}$$

where x is relative pool area and m , a , and b are fitted constants. Models were compared with Akaike's Information Criteria corrected for small sample sizes (AIC_c) using the MuMin package (Bartón 2009), which selects the most parsimonious model to explain the data (Burnham and Anderson 2002). For top ranked models (ΔAIC_c within 2 of best model; Burnham and Anderson 2002) we computed 95% confidence intervals around coefficients and evaluated overall fits with R^2 . In the nonlinear case, we evaluated model fits with root mean square error (RSME).

OLS and AIC_c model selection were also used to evaluate the effect of pool area on production efficiency and log transformed energy flux (drift + terrestrial) and fish density in pools. For proportional responses including terrestrial drop proportion, foraging mode, and exploitation efficiency, we used generalized linear models (GLM) with a quasi-binomial

distribution to account for over dispersion. Underlying model assumptions for GLMs were analyzed graphically with diagnostic plots using the R package modEVA (Márcia Barbosa et al. 2013). Each response was compared to a null (intercept only) model with AIC_c (QAIC_c for over-dispersed models) then likelihood confidence intervals were computed around the coefficients and overall fits were evaluated with Pearson r^2 using the *RsqGLM* function in modEVA.

Bioenergetics Model Simulations of Terrestrial Prey Additions - To explore the sensitivity of our results to variable terrestrial subsidies, we used our bioenergetic model to simulate growth at different levels of consumption corresponding to observed terrestrial input rates. Production was computed in each simulation as the sum of growth (mass change) for all individuals in each enclosure. Simulations ranged from no terrestrial inputs (i.e., consumption equivalent to ambient terrestrial drop removed), up to input rates such that all fish were consuming prey at their physiological limit. For each simulation, AIC_c was used as described above to determine the most parsimonious OLS regression model form (linear, threshold, or quadratic) relating relative pool area to production.

Unlike more computationally intensive drift-foraging models, our simulations did not explicitly incorporate constraints on prey capture success, i.e. it assumes all added prey would be captured. This assumption is probably unrealistic given prior empirical work (Piccolo et al. 2008, Neuswanger et al. 2014) and given our exploitation efficiency estimates, which indicated a significant reduction in the proportion of prey flux consumed in smaller pools (see *Results*). To address this issue and explore how prey capture may influence our results, we modelled three potential scenarios: first, where no additional prey capture was allowed in enclosures where less than 95% of the observed prey was consumed; second, where additional prey was allowed to be consumed at the observed efficiency; and third, where all additional prey was consumed.

5.4 Results

Prey Availability – Consistent with our first hypothesis, combined energy flux from drift and terrestrial inputs declined with pool area (Figure 5.2a, OLS, $W_i = 0.99$, $R^2 = 0.60$; full results for all models are in Appendix B, Table B1). This decline was driven by drift, which was the dominant mode of prey delivery (Table 5.1) and declined by an order of magnitude over the gradient of relative pool area (OLS, $W_i = 0.98$, $R^2 = 0.64$). As expected, terrestrial invertebrate inputs were not related to pool-riffle area (OLS, $W_i = 0.99$ for intercept only model); however, the proportion of terrestrial inputs relative to drift increased by ~30% across the gradient of relative pool area (Figure 5.2b, GLM, $W_i = 0.98$, $r^2 = 0.23$). Similar to other studies, drift was composed primarily of larval stages of Ephemeroptera, Diptera, and Trichoptera and terrestrial drop was composed of adult Diptera, Hymenoptera, and Homoptera.

Production, Growth, and Habitat use by Salmonids – Salmonid production (g m^{-2}) exhibited a nonlinear relationship with pool area (Figure 5.3a). A threshold model had the most empirical support ($W_i = 0.38$, $R^2 = 0.71$) but there was also strong support for a quadratic model indicative of a unimodal relationship ($\Delta\text{AIC}_c = 0.24$, $W_i = 0.34$, $R^2 = 0.70$) and some support for a linear model ($\Delta\text{AIC}_c = 0.99$, $W_i = 0.22$, $R^2 = 0.53$). Mean individual growth increased linearly with pool area (Figure 3b; $W_i = 0.55$, $R^2 = 0.75$); however, there was also support for a threshold model suggestive of a saturating relationship ($\Delta\text{AIC}_c = 0.45$, $W_i = 0.44$, $R^2 = 0.72$). Snorkel observations indicated that fish consistently used pools throughout the experiment. Consequently, as the proportion of pool area declined, realized fish density in pools increased by nearly six-fold (Figure 5.3c, GLM, $W_i = 0.99$, $r^2 = 0.98$).

Foraging Behaviour – Fish fed on drift and terrestrial invertebrates during foraging observations with only one benthic foraging attempt observed. The extent fish exhibited territorial central place foraging vs. non-territorial surface foraging was influenced by pool-riffle composition. The proportion of fish holding territories declined by ~60% across the gradient of pool area (Figure 5.3d: GLM $W_i=0.98$, $r^2 = 0.57$), with more fish exhibiting search foraging and occupying areas at the downstream ends of pools.

Consumption and the Efficiency of Exploitation and Production – Total estimated consumption showed a unimodal relationship with pool area, steeply increasing at low pool area then slowly declining after a maximum at intermediate pool area (Figure 5.4a). The Monod-Haldane function had the most support to explain this result (NLS, $W_i = 0.92$, RMSE = 1.96). Relative production efficiency ($\text{g produced} \cdot \text{g consumed}^{-1}$) increased with pool area (Figure 5.4b) indicating that individual fish accrued ~ 0.35 g more biomass per g consumed at the highest relative pool area. Exploitation efficiency also exhibited a strong trend (Figure 5.4c) where less than 10% of available prey was consumed at the lowest pool area, rapidly increasing to consumption of 100% of available prey at intermediate and higher pool areas (GLM $W_i = 0.99$, $r^2 = 0.97$).

Bioenergetic Simulations of Terrestrial Prey Additions – Increasing terrestrial inputs across a gradient of relative pool area generally linearized the relationship with fish production (Figure 5.5); however, the specific shape of the curve, and the input required to change it, differed among prey capture scenarios. In the most restrictive scenario, where no additional prey capture was allowed in enclosures with less than 95% consumption efficiency, it took a 100- fold increase in input rate to alter the curve, and a 1000-fold increase to linearize the relationship (Figure 5.5a). By contrast, in the second scenario where additional prey was consumed at

observed efficiencies, the pool area-production relationship became linear at double the input rate, with subsequent additions increasing the slope (Figure 5.5b). It is important to note that model fits were weaker at 2x and 10x input rates, and that there was also support for threshold models (Appendix B, Table B2), which would have resembled the first scenario. Finally, in the third scenario, where all additional inputs were consumed in all habitats, it required a similar 100-fold increase to linearize the curve; however, the slope of the line gradually diminished and ultimately flattened at the production level expected if all fish were fully satiated, i.e., consuming at their physiological maximum (Figure 5.5c). In all three scenarios, simulating reduced terrestrial inputs caused the relationship to be increasingly unimodal and to decline at the highest relative pool areas.

5.5 Discussion

As predicted, habitat composition (i.e. area of the pool relative to the adjacent upstream riffle) strongly mediated food and space abundance for salmonids. Because fish overwhelmingly preferred pools and were stocked at a constant density over total habitat area (pools and riffle combined), realized fish density strongly declined with increasing relative pool area. However, prey availability correspondingly declined with a decrease in relative riffle area that accompanied increased pool habitat. These opposing responses are consistent with previous work demonstrating strong preference of coho and cutthroat trout for pools (e.g., Lonzarich and Quinn 1995; Roni 2002) and a positive relationship between drift flux and riffle length (Hansen and Closs 2007, Naman et al. 2017b). The resulting trade-off between suitable foraging habitat and resource availability imposed by these contrasting habitat patch types caused a nonlinear response of salmonid consumption and production, whereby increasing pool area had diminishing returns beyond a threshold at an intermediate pool-riffle configuration (~45% pool).

This optimal configuration of habitat types that maximized salmonid production is similar to those observed by Bowlby and Roff (1986) and those predicted by Poff and Huryn (1998) and Rosenfeld (2014).

Our exploitation efficiency estimates corroborate the inference of a trade-off between space (preferred rearing habitat in pools) and food (prey production in riffles); fish experienced a food surplus at reduced pool areas and a food deficit in higher pool areas. In the smallest pools, fish had reduced growth, consumption, and production, yet collectively consumed only ~15% of the total prey flux. This unconsumed surplus was likely due to constraints on prey capture associated with reduced foraging area and higher fish densities. For instance, more individuals may have occupied poorer quality foraging territories at higher realized fish densities (Imre et al. 2004), agonistic interactions may have increased energy expenditures and decreased foraging time (Grant and Kramer 1990, Wood et al. 2012), or a higher proportion of prey may have been able to drift through shorter pools without detection. Increasing pool area appeared to partially relax these constraints as exploitation efficiency reached 100% at an intermediate pool area (45-50% of total area) that corresponded to an asymptote in total fish production.

Beyond an intermediate pool area, fish appeared to become increasingly food limited as the slope of total production diminished. However, despite a clear decline in prey abundance with increasing pool area, it was unclear whether associated fish production also declined or simply levelled off at high pool area. This ambiguity may be associated with increased relative production efficiency in the highest pool areas, where a larger proportion of estimated consumption was converted into biomass. The exact mechanism causing higher efficiency is unclear, but could relate to the reduced territoriality and increased search foraging we observed as pool area increased. Territoriality becomes increasingly costly as prey availability becomes

less predictable (Brown 1969, Grant 1993, Sloat and Reeves 2014); therefore, one interpretation of these results is that fish increased relative production efficiency in larger pools by shifting from defending central place territories to search foraging to exploit the greater proportion of terrestrial drop, which may be less spatially predictable than drift at pool-riffle scales (Nielsen 1992, Gowan and Fausch 2002, Naman et al. 2017b). Since we did not measure the energetic consequences of foraging behaviour on individual fish, this interpretation is speculative and it is possible that other factors such as reduced activity costs could also have increased relative production efficiency at low fish density in larger pools (Li and Brocksen 1977).

Bioenergetic simulations allowed us to explore the sensitivity of habitat composition effects to terrestrial subsidies. Adding subsidies generally linearized the effect of pool area on production as predicted, although the specific form of this effect differed among contrasting capture efficiency scenarios. In any of the three scenarios, however, the absolute magnitude of additional terrestrial inputs required to elicit these effects are well within the range of documented variability across time and space (Wipfli 1997, Nakano and Murakami 2001). By contrast, reducing subsidies accelerated the decline of fish production in high pool area treatments, indicating that large pools may become energetic sinks if terrestrial prey is not available. While our simulation results apply to the range of pool areas measured in the study ($\sim 14\text{-}70\text{ m}^2$), terrestrial inputs may be even more important for sustaining fish production in larger hydraulically benign habitats with low drift fluxes; for instance, pools in large rivers, side-channels, or floodplains (Rosenfeld and Raeburn 2009, Bellmore et al. 2013).

Together, the experiment and simulations suggest a general model for how hydraulic habitat composition and resource delivery shape reach-scale drift-feeding fish production in small streams. When autochthonous invertebrate drift is the primary mode of prey delivery, pool-

riffle composition will govern both suitable habitat area and resource renewal rates, but with increasing allochthonous terrestrial invertebrate inputs, resource availability will become increasingly decoupled from pool-riffle structure. This model is pertinent to defining rearing habitat capacity and quality for salmonids, a continued challenge in both basic and applied contexts (e.g., Rosenfeld 2003; Ayllón et al. 2012). Food and space abundance have long been recognized as key factors regulating stream salmonid populations (Chapman 1966, Keeley 2001, Piccolo et al. 2014) and have been increasingly integrated into assessments of habitat quality (Rosenfeld et al. 2014, McHugh et al. 2017). Our work reinforces the notion that habitat configurations that maximize local salmonid production may involve trade-offs between pools and riffles, which have distinct functional roles (Poff and Huryn 1998, Wipfli and Baxter 2010). Our study also provides new context for the effects of space and food on territorial species like stream salmonids in that optimal habitat configuration is further dependent on the origin and mode of resource delivery (i.e. invertebrate drift vs. terrestrial drop), which is rarely considered in habitat evaluations.

The specific predictions from this model apply to pool-rearing salmonids in small streams. In larger rivers flow patterns may be considerably more complex in vertical and transverse dimensions (Lamouroux et al. 1999); however, the basic trade-off between higher resource fluxes but increased energetic foraging costs in high velocity habitats still apply. Similarly, the shape of non-linear responses to pool-riffle composition may vary with body size or taxon, both of which strongly affect velocity tolerance (Nislow et al. 1999, Rosenfeld and Boss 2001); for instance, we may expect more rapidly decreasing production with pool area for species that also forage at high velocities (e.g., Atlantic salmon). Similarly, predation (Lonzarich and Quinn 1995), temperature (Mejia et al. 2016), discharge (Harvey et al. 2005), and light input

(Kiffney et al. 2004) will further modify the relationship between local productivity and habitat. Therefore, optimal hydraulic configuration that maximizes energy flux relative to spatial requirements may be dynamic and these conditions should be considered in future investigations.

More generally, this study emphasizes the role of habitat patch composition in determining productive capacity for consumers in heterogeneous habitats. In the simplest case, if a single patch type determines useable area for a consumer there should be a simple positive relationship between the area of that habitat type and productivity. In more complex situations, multiple habitat types will determine capacity; for instance in size structured populations where different size or age classes forage in different habitats (Werner and Gilliam 1984, de Roos et al. 2002) or when contrasting patches serve distinct functions (Schindler and Scheuerell 2002, Dolson et al. 2009). In these cases, the relationship between patch composition and productivity is likely nonlinear, with an optimal composition maximizing energy flow to consumers. Better identifying the shape of this relationship is important for understanding how habitat heterogeneity influences trophic dynamics in heterogeneous landscapes (Tunney et al. 2012, Bellmore et al. 2015) and for optimizing the design of restoration projects (e.g. Wall et al. 2016).

Our work also highlights several important yet often underappreciated ways in which resource subsidies interact with habitat heterogeneity. First, while many studies have focused on the direct and indirect effects of subsidies on recipient consumer-resource dynamics and food webs (e.g., Huxel and McCann 1998, Marcarelli et al. 2011), fewer have examined how recipient habitat structure mediates subsidy effects (Orr et al. 2008, Tiegs et al. 2008, Kiffney et al. 2014). Our study indicates that physical habitat heterogeneity may be a key factor modulating subsidy effects on recipient consumers. For instance, terrestrial prey additions may have limited effects in riffle-dominated habitats where foraging efficiency is physically constrained, but strong

effects in pools, which are hydraulically benign yet low in food supply. Second, the sensitivity of optimal habitat composition to simulated prey additions implies that subsidies can decouple not only food web dynamics (Huxel and McCann 1998, Baxter et al. 2005) but also consumer-habitat relationships in recipient ecosystems. This is an intriguing aspect of cross-ecosystem resource subsidies that warrants further study.

5.6 Tables and figures

5.6.1 Tables

Table 5.1 Mean abiotic and biotic and characteristics of enclosures.

Enclosure	Proportion area pool	Total Area (m ²)	Canopy %	Depth (m)		Velocity (m s ⁻¹)		Prey (mg day ⁻¹)	
				Riffle	Pool	Riffle	Pool	Drift	Terrestrial
1	0.66	27.57	70	0.08	0.29	0.31	0.05	315.5	16.1
2	0.22	48.40	60	0.11	0.21	0.30	0.03	763.7	13.5
3	0.51	72.11	55	0.11	0.21	0.36	0.05	559.1	60.4
4	0.82	34.38	65	0.06	0.37	0.24	0.13	141.6	37.2
5	0.20	30.96	80	0.10	0.19	0.24	0.04	1473.9	4.7
6	0.70	18.61	80	0.09	0.26	0.29	0.08	141.0	1.7
7	0.39	19.54	15	0.09	0.22	0.25	0.05	402.7	3.7
8	0.22	41.49	70	0.11	0.22	0.32	0.04	5950.7	32.8
9	0.15	40.25	15	0.11	0.21	0.30	0.05	1167.8	32.5
10	0.48	50.56	5	0.11	0.35	0.35	0.03	498.9	40.5
11	0.27	19.36	60	0.10	0.20	0.35	0.04	775.9	10.9
12	0.45	31.89	30	0.11	0.22	0.24	0.04	833.7	9.7
13	0.27	13.20	70	0.08	0.22	0.37	0.07	552.6	9.5

5.6.2 Figures

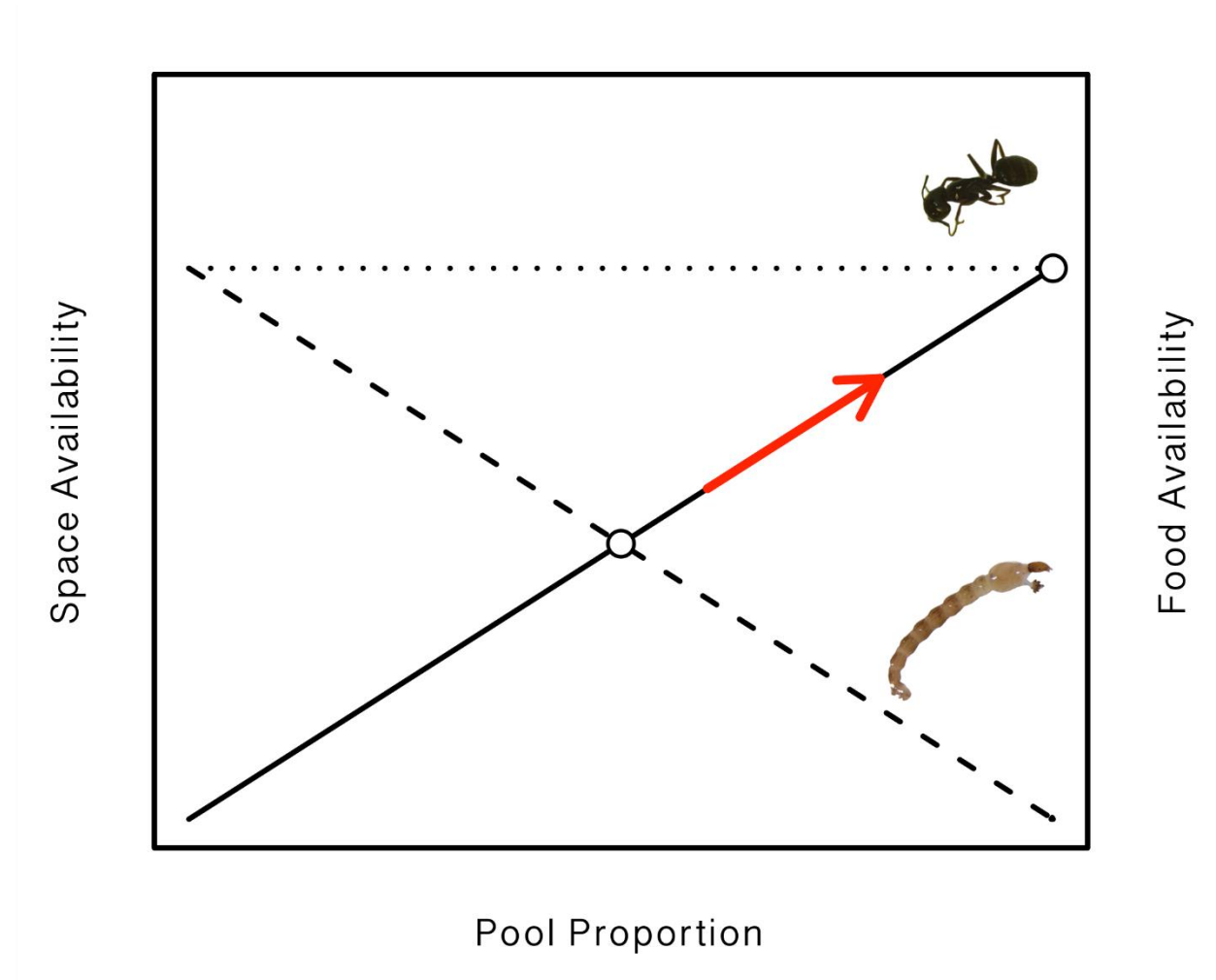


Figure 5.1 Conceptual representation of how pool-riffle configuration may affect salmonid productivity across a gradient of prey delivery mode (drift vs. terrestrial drop). For a given density of fish, as the proportion of pools relative to riffles increases along the x axis, the area of suitable foraging habitat (solid line) increases. When drift is the dominant mode of prey delivery, food availability will decrease as the proportion of pool increases (dashed line). However, if terrestrial subsidies are the primary mode of prey delivery, food availability should be unrelated to pool-riffle configuration (dotted line). Maximum production will occur at the intersection of the two lines (hollow points), where food abundance is optimized relative to habitat availability. This model predicts that adding terrestrial inputs will increase the optimal point to a higher pool area as indicated by the red arrow.

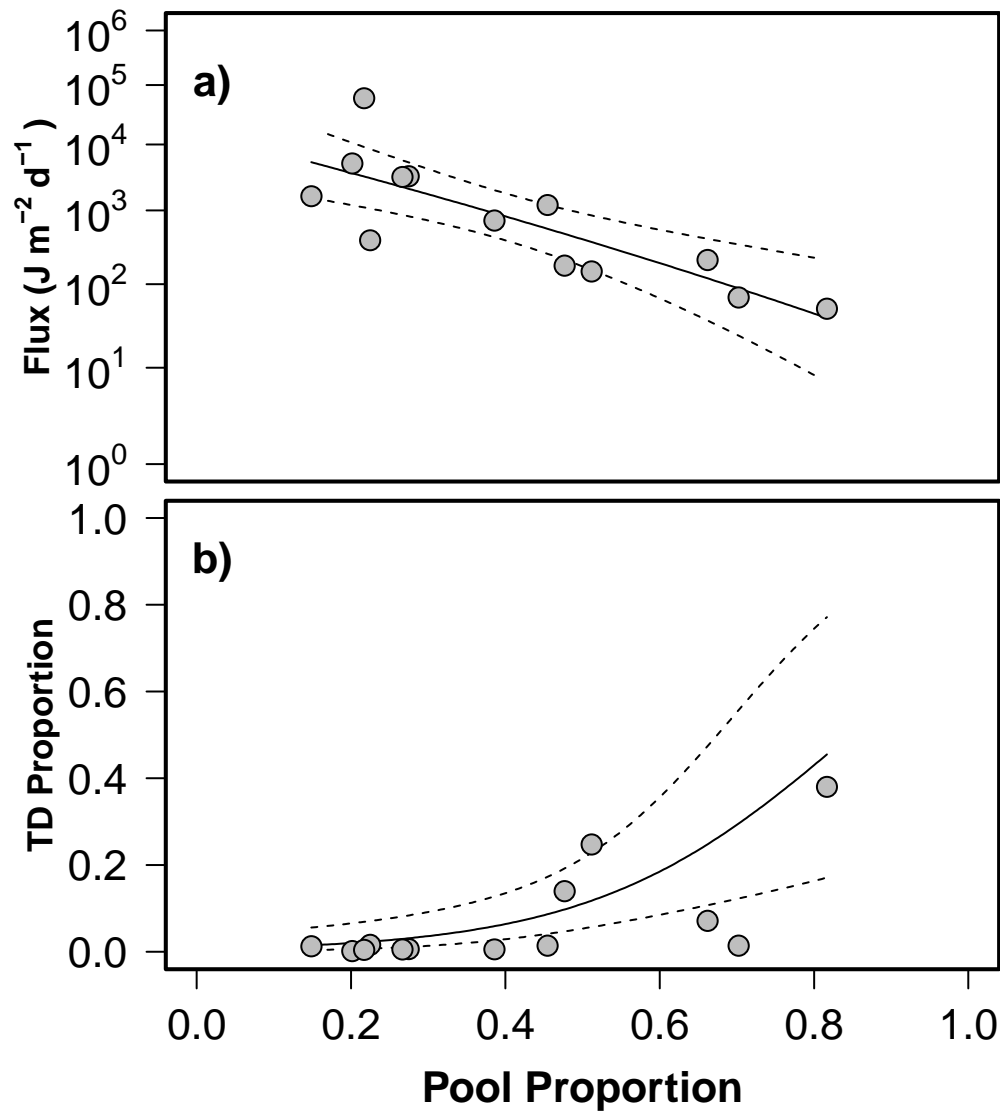


Figure 5.2 (a) Total prey flux (drift and terrestrial combined) in Joules $\text{m}^{-2} \text{day}^{-1}$ and (b) the proportion of total prey from terrestrial drop (TD) across the gradient of relative pool area. Solid lines are based on the top ranked regression models; dashed lines are 95% confidence intervals. Note that panel *a* is on a log scale.

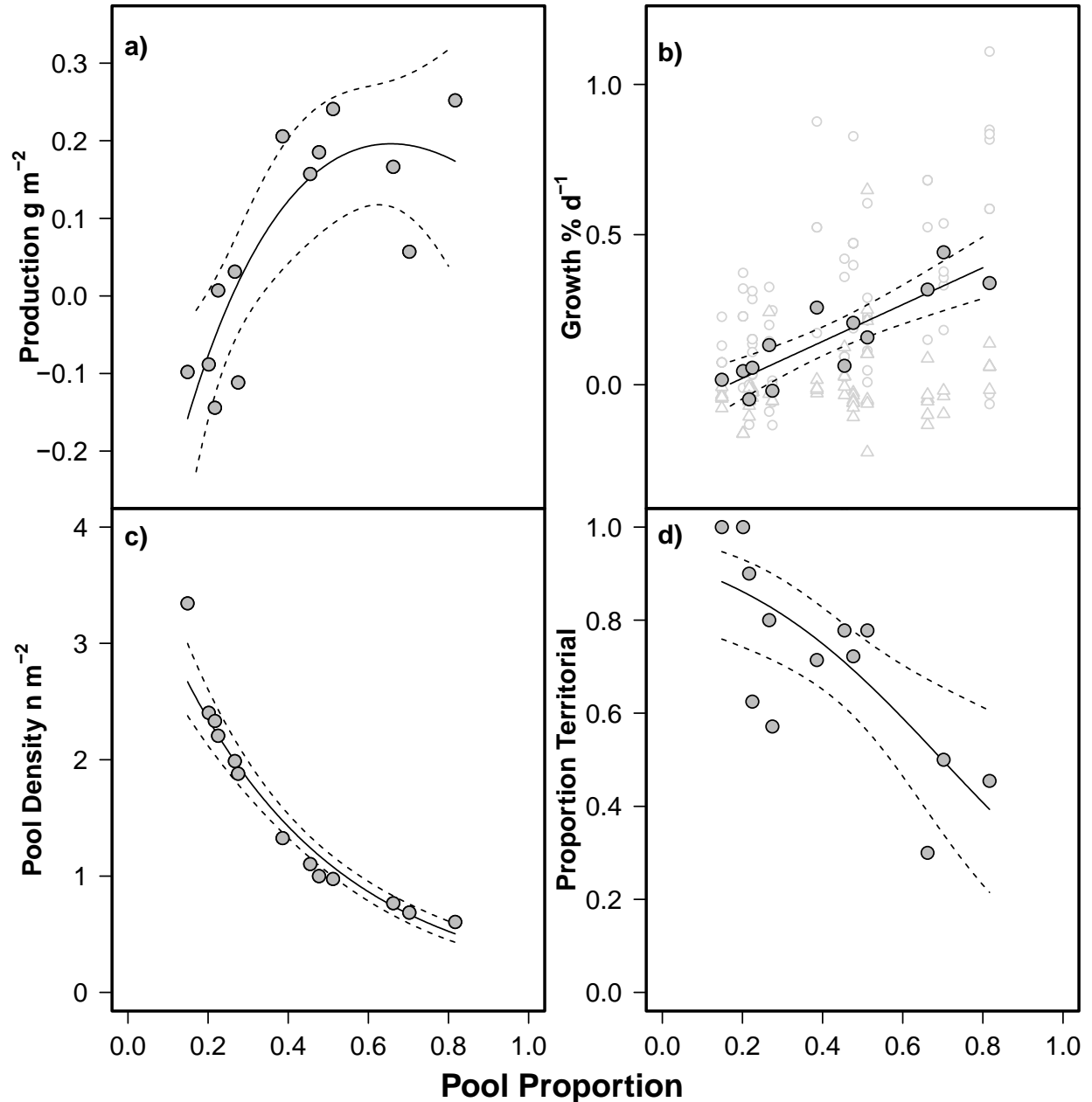


Figure 5.3 The effects of relative pool area on (a) Total fish production (g m^{-2}) of all coho and cutthroat trout in each enclosure; (b) instantaneous growth rates. Bolded points are the mean value across all fish in each enclosure; light points are individual fish (circles for coho; triangles for cutthroat). (c) Density of all fish in pools based on snorkel observations (n m^{-2}) and (d) the proportion of all fish observed in each pool defending territories. In all graphs, solid lines are the top ranked regression models and dashed lines are 95% confidence intervals.

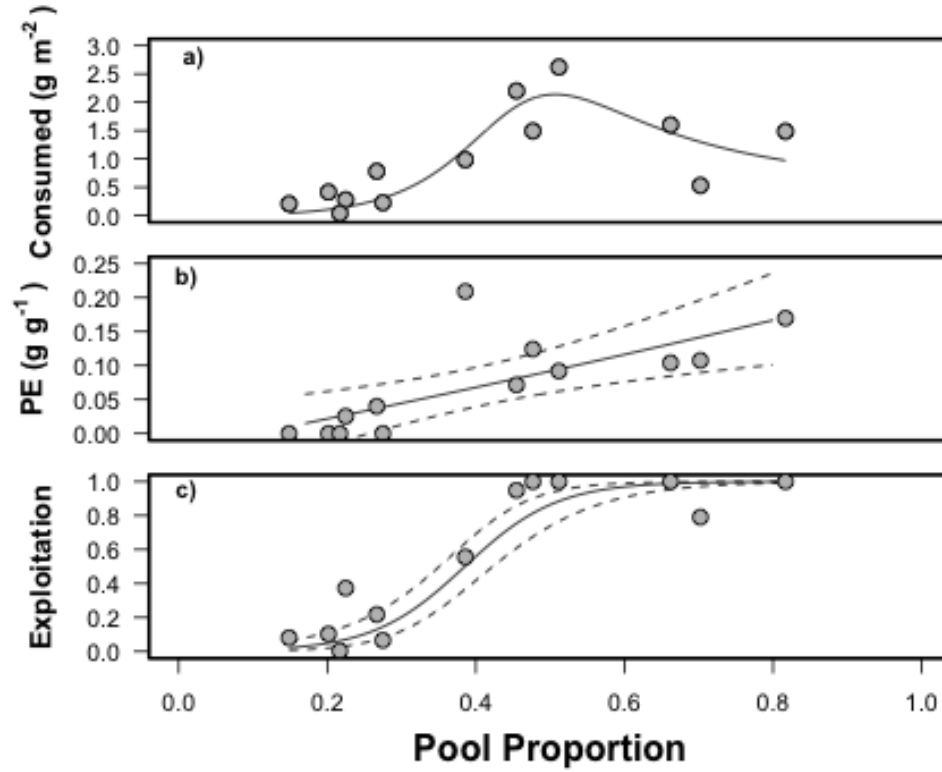


Figure 5.4 The effect of relative pool area on (a) total consumption (g m^{-2}) of all fish in each enclosure throughout the experiment as estimated with the bioenergetics model. Regression line is from the Monod-Haldane function fit by nonlinear least squares; (b) The production efficiency (PE; g produced per g consumed); and (c) The efficiency of prey exploitation expressed as the proportion of total prey flux through each enclosure consumed by fish.

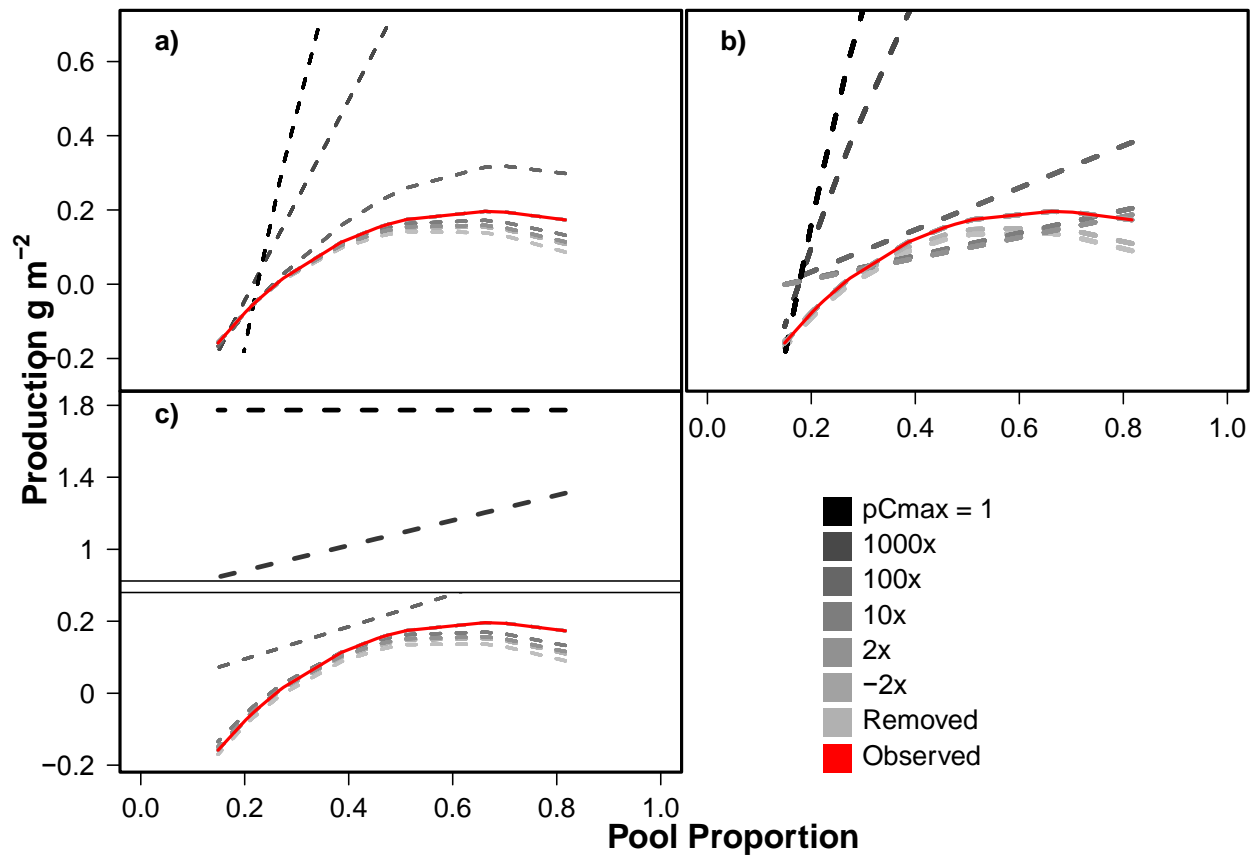


Figure 5.5 Bioenergetic model simulations of production across a gradient of subsidy additions or reductions. The three panels depict three different scenarios of prey capture success: (A) where additional prey are only consumed in enclosures where observed exploitation efficiency was greater than 95%; (B) where additional prey are consumed at the observed exploitation efficiency; and (C) where all additional prey are consumed. Each line represents the most parsimonious (lowest AICc) linear regression model for the relationship between production and relative pool area. pCmax = 1 represents the physiological limit for daily consumption.

Chapter 6 Synthesis and discussion

Habitat science focuses on defining the abiotic requirements of animals, often with specific applications to conservation and management. In lotic ecosystems, this field has largely focused on physical habitat as the key factor limiting focal populations (Roni et al. 2008). However, it has also long been recognized that populations are linked within ecosystems (Lindeman 1942), and that species interactions (e.g., predation, competition), along with abiotic features, strongly determine population performance. Many have called for more explicit consideration of species interactions in management contexts (Palmer et al. 1997, Naiman et al. 2012, Bellmore et al. 2017), yet incorporation of these processes by practitioners has been slow.

In contrast, the field of community ecology is defined by its interest in species interactions and often views population performance in the context of these processes (Werner and Gilliam 1984, Agrawal et al. 2007). The physical environment is well recognized as an important context mediating species interactions and patterns of energy flow through ecosystems (Polis et al. 1997, Holt 2002, Loreau et al. 2003); however, our understanding of the mechanisms behind these linkages is still evolving (Rooney et al. 2008, Kovalenko et al. 2011, McMeans et al. 2016).

The intersection of habitat science and community ecology is an exciting area of research tasked with not only connecting ecological communities to their physical environment but also developing quantitative predictions applicable to conservation and management. This is particularly relevant to lotic ecosystems, which experience significant anthropogenic pressures that often alter their physical character (Poff and Ward 1990, Paul and Meyer 2001). While the effects of habitat structure on stream-rearing Pacific salmon have been well studied in this regard, my dissertation addressed several key gaps in our understanding of the ways that physical

habitat influences invertebrate drift, and in turn salmonid production in forest streams. Here I discuss these advances as well as numerous directions for future studies that could build on my results.

6.1 Re-evaluating invertebrate drift dynamics

One of the primary goals of my thesis was to re-examine the context-dependent processes involved in invertebrate drift. In my Chapter 2 literature review, I particularly highlight the need to better link the physical and behavioural mechanisms underlying drift, primarily from taxon-specific studies, to bulk drift fluxes at scales relevant to drift-feeding fish. Examining my subsequent chapters in this context, several themes emerge. First, incorporating the specific traits influencing both active and passive drift generally improved predictions for individual taxa; however, clear patterns also emerged when taxa were aggregated. For example, the effects of riffle length on the drift of individual taxa in Chapter 4 was contingent on behavioural traits but strong patterns also emerged when taxa were aggregated. This is encouraging with respect to studying drift in an ecosystem context insofar as it suggests that quantitative predictions of bulk drift fluxes may be possible without accounting for the full complexity of taxon-specific drift causation (Weber et al. 2017). Moreover, incorporating species traits and community analysis, as I did in Chapter 3, can be a powerful tool to resolve apparent context dependency in field surveys and experiments.

The second broad message emerging from this work is that inferences with respect to the mechanisms influencing drift are highly dependent on the metric used to compute it. Most notably, in Chapter 3 I demonstrated that drift responses to flow were nearly opposite depending on whether drift was quantified as a concentration (number m^{-3}) or flux (number h^{-1}).

Concentration is often the de facto metric used to quantify drift (Allan and Russek 1985, Weber

et al. 2017) but it is not always the most appropriate. I raised several issues that can confound the relationship between drift concentration and stream habitat features and discharge; these include spatial mismatches between measurement and origin location, confounding drift entry and transport, and reverse dilution effects. Similarly, others have discussed the potential for nonlinear relationships between discharge and numbers of drifting organisms introducing error into concentration estimates (Elliott 2002b, Downes and Lancaster 2010). Therefore, future studies on drift should carefully evaluate the assumptions behind how drift is quantified. Incorporating multiple metrics of drift, as I have done throughout this thesis, may be more informative and help avoid spurious conclusions.

6.2 Channel structure, prey abundance, and drift-feeding fish production

Another one of the main goals of my thesis was to address how physical habitat structure influences prey abundance and production of stream-rearing salmonids. My results from Chapter 4 add to a limited number of studies that suggest invertebrate drift is not spatially uniform (Stark et al. 2002, Leung et al. 2009) and varies systematically with hydraulic channel structure. Specifically, drift production exhibited longitudinal source-sink dynamics across riffles and pools, and drift flux and concentration increased with riffle length. These patterns are intuitive but have rarely been demonstrated empirically (Hansen and Closs 2007). These are an important results in themselves given that drift is considered uniform in most modelling applications (but see Hayes et al. 2007).

It was also especially intriguing that the magnitude of drift production between pools and riffles was strikingly similar to that predicted based on benthic invertebrate production (Grubaugh et al. 1997, Poff and Huryn 1998). If generalizable, this could indicate a novel link between geomorphology and trophic transfer processes in streams. However, this inference is

speculative at this stage as I did not attempt to disentangle the mechanisms generating source-sink drift patterns; for instance, pool-riffle differences in benthic density, species composition, or hydraulic stress. Experiments aimed at teasing apart the individual and interactive influence of these factors would be a logical next step to better understanding underlying processes.

Regardless of the underlying mechanisms, source-sink drift dynamics have important consequences for drift feeding fish. Specifically, in Chapter 5 I suggest that spatial heterogeneity in drift leads to a nonlinear effect of pool-riffle habitat composition on salmonid production. This inference supports the view that drift generated in riffles essentially subsidizes fish in adjacent downstream pools (Cooper et al. 1990, Wipfli and Baxter 2010), leading to pool-riffle structure imposing a reach-scale trade-off between food abundance and usable habitat area (Poff and Huryn 1998, Rosenfeld and Raeburn 2009). The immediate implication of this trade-off is that efforts to increase frequency or area of pool habitat, a common practice in stream restoration (Roni et al. 2008), may have limited success if they come at the expense of prey availability for food-limited fish (Wipfli and Baxter 2010). More generally, by demonstrating a clear link between physical habitat structure, resource abundance, and salmonid production, my work improves our understanding of the physical mechanisms mediating energy flow to top predators in stream ecosystems.

While I focused at the scale of single pool-riffle sequences, mainly for logistical tractability, it would be interesting to explicitly extend my results to larger scales incorporating multiple channel units. For instance, drift produced in non-adjacent upstream habitats may be important to fish if drift distances exceed the length of channel units (Rosenfeld and Raeburn 2009) and if a significant fraction of drift flux through a pool is unconsumed as I demonstrated in Chapter 5. In this context it would be useful to understand how pool-riffle habitat heterogeneity

(e.g., relative areas, adjacency, and interspersions) influences salmonid production across heterogeneous stream networks. For instance, across a 60 m stream reach with equal areas of pool and riffle, how would energy flux and fish production differ if there is one 30 m pool and one 30 m riffle versus three 10 m pools spaced among 10 m riffles? This endeavor would be well suited to a drift foraging model (e.g., Hughes 1998) incorporating the systematic spatial heterogeneity in drift I described. Similarly, it would also be useful to understand how the scale and patch size of source-sink dynamics changes in larger stream and river systems with longer drift distances and a more pronounced lateral and vertical gradients in velocity.

6.2.1 Incorporating terrestrial invertebrates into drift-foraging theory

My work in Chapter 4 and Chapter 5 indicated that terrestrial invertebrate inputs were independent of physical habitat heterogeneity at the scale of individual channel units. These observations are in line with other studies, which have also found seemingly haphazard terrestrial inputs over similar spatial scales (Edwards and Huryn 1995, Gowan and Fausch 2002, Romaniszyn et al. 2007). Gowan and Fausch (2002) suggested that these resources introduce error into predictions of fish habitat use based on net energy intake, concluding that: “*reliable predictions of fish distribution remain elusive, not because we need a better conceptual framework, but because we lack the sampling proficiency of the organisms we hope to understand.*” While I certainly agree that improved sampling techniques are needed, I argue in Chapter 5 that the conceptual framework for predicting drift-foraging fish distribution, growth, and production remains incomplete and should indeed be extended to incorporate the contrasting effects of habitat structure on distinct modes of prey delivery (aquatic drift vs. terrestrial drop).

The conceptual model I present in Chapter 5 builds on previous work on drift-feeding fish (Poff and Huryn 1998) but explicitly incorporates the spatially stochastic nature of terrestrial food resources. Based on both empirical results and bioenergetic simulations, my general

conjecture is that increasing the relative influence of terrestrial resources modifies the relationship between pool-riffle habitat heterogeneity and salmonid production in predictable ways, with the specific form determined by the magnitude of terrestrial inputs and the extent to which they are ingested by fish. In essence, the defining feature of this model is a mismatch in the spatial scale over which these distinct prey sources vary; drift varies across hydraulic gradients imposed by pool-riffle structure (Leung et al. 2009, Chapter 4), while terrestrial inputs vary over larger scales with riparian vegetation and insect activity levels (Allan et al. 2003).

6.3 General relevance beyond streams: habitat constraints on energy flow

Habitat-based constraints on prey accessibility and energy flow are pervasive across many types of ecosystems and provide a broader context to consider my results. Similar to the strong influence of pool-riffle composition on drift-foraging efficiency, there are abundant examples in other systems of physical habitat strongly influencing predation; these include oyster reefs on estuary mudflats constraining the ability of fish and sharks to consume crabs (Grabowski 2004, Byers et al. 2017), forest cover reducing wolf predation on ungulates relative to more open areas (Hebblewhite et al. 2005), and aquatic vegetation in lakes limiting benthic fish predation on macroinvertebrates (Eklöv and Diehl 1994). In addition to supporting these studies, my work in Chapter 5 is relatively unique within this literature insofar as I examined a gradient of habitat composition experimentally, contrasting with most previous experiments with binary designs (e.g., simple vs. complex). One of my most notable results was the nonlinear effect of refuge versus foraging patch area on predator biomass production. In principle, this finding should apply to other systems where spatial mismatches between predator performance and prey abundance occur (Heck and Crowder 1991). However, similar empirical examples of this

phenomena are scarce (but see Crowder and Cooper 1982, Tewfik et al. 2016) and more work is needed to determine the extent to which it applies in other systems.

Another generalizable finding from my work was the complex interaction between habitat structure, prey delivery mode, and consumer production; specifically, that terrestrial subsidies modified consumer-habitat relationships in recipient aquatic ecosystems. Broadening these inferences from Chapters 4 and 5 leads to the more general predictions that: (1) cross ecosystem resource subsidies should differ from autochthonous resources in their relation to habitat structure in recipient systems; (2) consumers in habitats with structural conditions permitting high subsidy retention should benefit disproportionately, and (3) subsidies should modify or decouple the effects of *in situ* habitat structure on consumer production. Prediction 1 is highly intuitive given that the processes influencing production rates of resource subsidies occur outside recipient ecosystems by definition (Marczak et al. 2007, Marcarelli et al. 2011). Similarly, prediction 2 is also well supported in numerous ecosystems (Marczak et al. 2007) including streams (Negishi and Richardson 2003) and beaches (Orr et al. 2008, Barreiro et al. 2011).

By contrast, support for prediction 3 has not been explicitly articulated to my knowledge; however, it should apply in principle whenever subsidy inputs permit recipient consumers to occupy habitats that would otherwise be sub-optimal due to low *in situ* resource abundance or harsh abiotic conditions. For example, beach wrack subsidies (marine macroalgae washing onshore) permit many invertebrates to occupy otherwise inhospitable habitats high in the intertidal by providing food and refuge from desiccation (Bustamante et al. 1995, Spiller et al. 2010). In turn, these subsidies may increase the resource abundance in otherwise unproductive beach habitats for terrestrial consumers (Carlton and Hodder 2003). While the scale and nature

of environmental patchiness affecting recipient consumers is clearly dependent on the ecosystem and specific organisms of interest (Kotliar and Wiens 1990), cross ecosystem subsidies decoupling consumer production from recipient patch structure may be pervasive. Therefore, the sensitivity of consumer-habitat relationships to cross ecosystem subsidies warrants further attention across a variety of ecosystems.

6.4 Potential caveats and limitations

I took a reductionist approach to much of my work; therefore it was necessary to simplify important details of my study system to control for unwanted complexity. Here I consider some of those details. First, throughout much of this thesis, I primarily view habitat as discrete classes (e.g., pools and riffles), which is clearly an oversimplification of reality where habitat conditions vary on a continuous spectrum (Jowett 1993, Inoue and Nunokawa 2002). However, these classes are well established in the scientific literature (Bisson et al. 2006) and are commonplace in assessments of stream habitat conditions (Hawkins et al. 1993); therefore, they provide a tractable and transferable context for results. They also reflect the genuinely patchy nature of stream habitats, where hydraulic forces create greater variation in depth, velocity, and substrate between discrete patches than within them.

Similarly, I did not deal with other important aspects of structural habitat complexity; for instance, wood, submerged vegetation, or substrate size and composition. While these factors are implicitly incorporated insofar as they may covary with or cause habitat heterogeneity in streams (e.g., pool forming wood; Montgomery et al. 1999), I do not consider their more direct influences on either invertebrate drift or fish foraging (Chapter 2, Hafs et al. 2014). I do not suspect any of these factors confounded any of my results given that I attempted to minimize their variation, but they do present important avenues for future research. For instance, as I

discuss in Chapter 2, how large wood abundance affects invertebrate drift is poorly understood but may be crucial to predicting the effects of wood additions as a restoration measure (e.g., Roni et al. 2015).

6.4.1 Considering processes at multiple spatial and temporal scales

I primarily addressed my study questions at scales relevant to interactions among individual organisms (e.g., a riffle-pool sequence) over relatively short time periods. However, watersheds are intrinsically hierarchical in space and time and ecological processes are often determined by factors acting across scales (Fausch et al. 2002, Thorp et al. 2006). Viewing my results in this light, several notable caveats become apparent. First, the spatial habitat heterogeneity in which much of my work is premised can be strongly influenced by seasonal changes in hydrology. For instance, at high flows, hydraulic differences between pools and riffles often become homogenized or even reversed beyond a threshold discharge (Keller 1971). Consequently, my work is mainly applicable to low flow conditions, when abiotic differences among stream habitats are most pronounced.

Second, the abundance of invertebrates available in drift as fish food ultimately depends on their source populations in the benthos. Hence, the local physical features (e.g., pool-riffle composition) where I focused my work may only be proximate drivers of drift supply. The abiotic and biotic processes determining the local abundance and production of benthic invertebrates operate across multiple spatial and temporal scales (Benke et al. 1984, Malmqvist 2002, Benke and Huryn 2010). The premise that these scales generally match pool-riffle morphology is well supported (Huryn and Wallace 1987, Brown and Brussock 1991, Grossman 2014), but this may not always be the case. For instance, within-reach heterogeneity in canopy cover, groundwater exchange, or detrital inputs can strongly influence primary production and benthic invertebrate abundance (Hawkins et al. 1982, Kiffney et al. 2004, Kaylor and Warren

2017), which could potentially degrade predictions of drift fluxes based on channel hydraulics alone.

Finally, both resident and anadromous stream salmonids have incredibly complex life cycles that can integrate many habitats over large landscapes (Quinn 2011). Consequently, a wide array of processes at different scales can influence their individual- and population-level performance (Fausch et al. 2002). My work focused on a narrow range of processes at local scales over short timeframes; as such, making assumptions about larger scale processes was necessary. Most notably, my conceptual model described in Chapter 5 assumes that stream habitats are saturated and that food and space are the primary factors limiting salmonid biomass production. While this appears to be a common scenario (e.g., Grant and Kramer 1990), exceptions may also occur; for instance, due to recruitment limitation by environmental factors (e.g., ocean conditions or high stream flows; Beamish et al. 1997, Lobón-Cerviá and Rincón 2004), lack of suitable spawning habitat (Geist and Dauble 1998), or predation (Milner et al. 2003). In these cases, low densities should allow a greater proportion of individuals to access profitable foraging areas, resulting in less influence on reach-scale production of food and space limitation imposed by pool-riffle structure.

These scaling considerations place limits on the inferences that can be directly drawn from my work; however, they also open the door to future research opportunities. In particular, my work is relevant to drift foraging models applied over larger scales (Wall et al. 2016b, McHugh et al. 2017), that currently do not include local heterogeneity in prey abundance. In addition, my work may be complementary to more holistic food web approaches that describe how distinct trophic pathways supporting salmon production vary across space and time through whole watersheds (Wipfli and Baxter 2010, Cross et al. 2011). These efforts are more spatially

and temporally extensive but do not explicitly incorporate the role of finer scale channel hydraulics at the scales I consider (Bellmore et al. 2013). Linking my work to these approaches could help explain the mechanisms generating variation in biomass production of drift-feeding salmonids, and ultimately, patterns of food web structure across riverine landscapes.

6.4.2 Behavioural plasticity and movements of drift-feeding fish in relation to spatial heterogeneity

While not a central aim of my thesis, the behaviour of drift-feeding fish strongly interacts with habitat structure and food supply, with significant consequence for energy flow and production (White et al. 2014). Consequently, several attributes of fish behaviour deserve attention. First, territorial animals like stream salmonids often include subsets of individuals with non-territorial foraging tactics (Grant 1997). These alternative strategies arise if the energetic benefit of defending foraging territories drops below a threshold value, which is often a consequence of less predictable resources that are more difficult to defend (Brown 1969, Grant 1993), or intense competition for high-quality drift-feeding stations. In natural populations of stream salmonids, search foraging is often observed, where fish do not defend territories and opportunistically feed on terrestrial invertebrate drop or benthic invertebrates (Puckett and Dill 1985, Fausch et al. 1991, Nielsen 1992). The proportion of individuals adopting these strategies is clearly linked to the extent that resources are spatially predictable (Sloat and Reeves 2014); therefore in Chapter 5, I contend that a reduction in drift (a predictable resource) relative to terrestrial drop, (an unpredictable resource) resulted in reduced territoriality in larger pools.

Contrasting foraging strategies within populations of stream salmonids can potentially mediate the effects of physical habitat on production. Non-territorial individuals often have slower growth rates relative to territorial conspecifics (Nielsen 1992, Nakano 1995, Rosenfeld and Raeburn 2009); however, they may grow more efficiently given reduced activity costs

(Puckett and Dill 1985). In Chapter 5, I speculated that the increased proportion of non-territorial fish in the largest pools grew more efficiently, and in turn, caused total fish production in these habitats to be greater than predicted relative to bioenergetic estimates for drift-foragers with potentially higher activity costs. This suggests that in addition to relaxing upper limits of salmonid density set by minimum territory sizes (Grant and Kramer 1990), flexible foraging tactics can relax the limits of biomass production set by the higher activity costs associated with drift feeding. Or more simply put, reduced territoriality in larger pools may permit higher biomass production than would otherwise be expected. Unfortunately, logistical constraints during the experiment prevented me from fully confirming this mechanism; thus, it remains an intriguing loose end to address in the future.

In addition to shifts in foraging mode within pools, drift-feeding fish are also known to move across larger scales to exploit foraging opportunities (e.g., Gowan and Fausch 2002, Armstrong et al. 2013). How fish accomplish this is a multidimensional problem that would also be interesting to address in the context of my assertion that invertebrate food resources vary in their predictability within stream networks. It is particularly intriguing to consider how resource delivery mode and predictability influence the specific cues or strategies that fish use to evaluate habitat. For instance, fish might evaluate foraging profitability based on average drift supply rates (Hansen and Closs 2009) or abiotic conditions (Brewitt et al. 2017); alternatively, they may bet hedge to exploit more stochastic, but higher quality, terrestrial inputs. Progress on this front would be very relevant for better understanding the influence of behaviour on habitat-production relationships and the potential limitations of habitat selection models based on net energy intake (Railsback and Harvey 2011).

6.4.3 Drift-foraging and consumer-resource dynamics

Throughout this thesis, I view fish-invertebrate interactions as instantaneous energy flows as opposed to dynamic consumer-resource coupling. This implicitly treats drift-foraging dynamics as donor controlled, where drift is essentially an infinitely renewable resource lacking fully coupled dynamics (Strong 1992, Abrams and Walters 1996). While this assumption is intuitive based on the premise that the majority of benthic stream invertebrates are inaccessible to fish, and that structural prey refuges cause donor controlled consumer-resource dynamics (Persson et al. 1996), the extent to which this assumption is empirically justified is an open question. The literature I reviewed on this subject in Chapter 2 was wildly inconsistent, with some studies finding that drift foraging was indeed donor controlled while others finding strong evidence for strong top down effects of fish predation (see section 2.5).

Aside from differences in methodology, design, and interpretation of experiments (discussed in Cooper et al. 1990, Englund and Cooper 2003, Englund 2005), the ecological factors responsible for discrepancies in the strength of fish-invertebrate interactions among studies are not well resolved. Similarly, it is unclear how different forms of consumer-resource dynamics might alter current drift-foraging predictions. In the context of my results, for example, how would the effects of pool-riffle composition on fish production change if consumer-resource dynamics were tightly coupled over longer time scales? Addressing these types of questions empirically is fraught with logistical challenges but a simulation approach combining consumer-resource models with established empirical drift relationships could be a good starting place (Anderson et al. 2006a, 2013). For instance, simulating consumer-resource dynamics across gradients of predation pressure, drift components (i.e., entry and settlement rates), and habitat structure could add definition to the parameter space in which drift-foraging may or may not impact benthic populations, and ultimately feedback to drift supply.

It is also important to place drift-foraging consumer-resource dynamics in the context of specific invertebrate taxa and their unique sets of ecological traits. As I demonstrated in Chapter 3, the impact of drift predation on benthic populations will surely vary along axes of individual and population-level traits, such as mobility, dislodgement susceptibility, or colonization rates (Rader 1997, Elliott 2003). Consequently, incorporating these traits into future drift-foraging predation studies should be highly informative. A particularly exciting opportunity on this front may be to combine drift foraging with response length theory (Anderson et al. 2005, Diehl et al. 2008), which integrates individual and population-level traits to characterize the spatial scale over which population demographics or consumer-resource dynamics respond to environmental perturbations (Anderson et al. 2006a).

6.5 Concluding thoughts

My dissertation addressed several fundamental gaps in our understanding of invertebrate drift and drift-foraging dynamics in small streams. Generally my data support the premise that hydraulic heterogeneity imposed by physical channel structure not only influences fish directly but is also a strong determinant of their prey availability. To increase the predictive power of habitat selection models and ultimately the effectiveness of stream habitat conservation and restoration, we need to consider the individual and population level mechanisms linking habitat to drift-feeding fish and their invertebrate prey.

References

- Abrams, P. A., and C. J. Walters. 1996. Invulnerable Prey and the Paradox of Enrichment. *Ecology* 77:1125–1133.
- Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, S. John, D. A. Soluk, J. F. Addicott, J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological Neighborhoods : Scaling Environmental Patterns. *Oikos* 49:340–346.
- Agrawal, A. A., D. D. Ackerly, F. Adler, E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. a. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5:145–152.
- Ahrens, R. N. M., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. *Fish and Fisheries* 13:41–59.
- Allan, D., and E. Russek. 1985. The quantification of stream drift. *Canadian Journal of Fisheries and Aquatic Sciences* 42:210–215.
- Allan, J. D. 1978. Trout predation and the size composition of stream drift. *Limnology and Oceanography* 23:1231–1237.
- Allan, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology* 63:1444–1455.
- Allan, J. D., and M. M. Castillo. 2007. *Stream Ecology: The Structure and Function of Running Waters*. 2nd edition. Springer, Dordrecht, The Netherlands.
- Allan, J. D., and B. P. Feifarek. 1989. Distances travelled by drifting mayfly nymphs: factors influencing return to the substrate. *Journal of the North American Benthological Society* 8:322–330.
- Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 60:309–320.
- Anderson, K. E., L. R. Harrison, R. M. Nisbet, and A. Kolpas. 2013. Modeling the influence of flow on invertebrate drift across spatial scales using a 2D hydraulic model and a 1D population model. *Ecological Modelling* 265:207–220.
- Anderson, K. E., R. M. Nisbet, and S. Diehl. 2006a. Spatial scaling of consumer-resource interactions in advection-dominated systems. *The American naturalist* 168:358–72.
- Anderson, K. E., R. M. Nisbet, S. Diehl, and S. D. Cooper. 2005. Scaling population responses to spatial environmental variability in advection-dominated systems. *Ecology Letters* 8:933–943.
- Anderson, K. E., A. J. Paul, E. Mccauley, L. J. Jackson, R. M. Nisbet, and J. R. Post. 2006b. Instream flow needs in streams and rivers: the importance of understanding ecological dynamics. *Frontiers in Ecology and the Environment* 4:309–318.
- Anderson, M. J. 2001a. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.

- Anderson, M. J. 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626–639.
- Anderson, N. H., and D. M. Lemkuhl. 1968. Catastrophic drift of insects in a woodland stream. *Ecology* 49:198–206.
- Anholt, B. R. 1995. Density dependence resolves the stream drift paradox. *Ecology* 76:2235–2239.
- Armstrong, J. B., and M. H. Bond. 2013. Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. *Journal of Animal Ecology* 82:966–975.
- Armstrong, J. B., and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. *Nature* 476:84–87.
- Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91:1445–1454.
- Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. E. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94:2066–2075.
- Ayllón, D., A. Almodóvar, G. G. Nicola, I. Parra, and B. Elvira. 2012. Modelling carrying capacity dynamics for the conservation and management of territorial salmonids. *Fisheries Research* 134–136:95–103.
- Bannon, E., and N. H. Ringler. 1986. Optimal prey size for stream resident brown trout (*Salmo trutta*): tests of predictive models. *Canadian Journal of Zoology* 64:704–713.
- Barbero, M., A. M. Oberto, and M. C. Gualdoni. 2013. Spatial and temporal patterns of macroinvertebrates in drift and on substrate of a mountain stream (Cordoba, Central Argentina). *Acta Limnologica Brasiliensia*, 25:375–386.
- Barreiro, F., M. Gomez, M. Lastra, J. Lopez, and R. De La Huz. 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. *Marine Ecology Progress Series* 433:65–74.
- Bartón, K. 2009. MuMIn: Multi-model inference in R.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67.
- Baxter, C. V, K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Baxter, C. V, T. A. Kennedy, S. W. Miller, J. D. Muehlbauer, and L. A. Smock. 2017. Macroinvertebrate drift, adult insect emergence and oviposition. Pages 435–456 in G. A. Lamberti and F. R. Hauer, editors. *Methods in Stream Ecology*, Volume 1. Third edition. Academic Press.
- Beale, C. M. 2007. The behavioral ecology of disturbance responses. *International Journal of Comparative Psychology* 20:111–120.
- Beamish, R. J., C. E. M. Neville, and a J. Cass. 1997. Production of Fraser River sockeye

- salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 54:543–554.
- Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium* 70:1–19.
- Beechie, T. J., G. R. Pess, M. M. Pollock, M. H. Ruckelshaus, and P. Roni. 2009. Restoring Rivers in the Twenty-First Century : Science Challenges in a Management Context. Pages 697–717 *in* R. J. Beamish and B. J. Rothschild, editors. *The Future of Fisheries Science in North America*. Springer Science and Business Media.
- Beisel, J., P. Usseglio-polatera, S. Thomas, and J. Moreteau. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 389:73–88.
- Bellmore, J. R., and C. V. Baxter. 2014. Effects of geomorphic process domains on river ecosystems: A comparison of floodplain and confined valley segments. *River Research and Applications* 30:617–630.
- Bellmore, J. R., C. V. Baxter, and P. J. Connolly. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology* 96:274–283.
- Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. *Ecological applications* 23:189–207.
- Bellmore, J. R., J. R. Benjamin, M. Newsom, J. A. Bountry, and D. Dombroski. 2017. Incorporating food web dynamics into ecological restoration : a modeling approach for river ecosystems. *Ecological Applications* 27:814–832.
- Benke, A. C., T. C. Van Arsell Jr., D. M. Gillepsie, and F. K. Parrish. 1984. Invertebrate productivity in a subtropical Blackwater River: the importance of habitat and life history. *Ecological Monographs* 54:25–63.
- Benke, A. C., and A. D. Huryn. 2010. Benthic invertebrate production — facilitating answers to ecological riddles in freshwater ecosystems. *Journal of the North American Benthological Society* 29:264–285.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308–343.
- Benke, A. C., and B. Wallace. 2003. Influence of wood on invertebrate communities in streams and rivers. Pages 149–177 *in* S. V. Gregory and A. M. Gurnell, editors. *The Ecology and Management of Wood in World Rivers*. American Fisheries Society, Bethesda, Maryland.
- Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* 62:1234–1243.
- Bilton, D. T., J. R. Freeland, B. Okamura, and R. Freeland. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32:159–181.
- Bishop, J. E. 1969. Light control of aquatic insect activity and drift. *Ecology* 50:371–380.

- Bisson, P. A. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society* 117:262–273.
- Bisson, P. A., D. R. Montgomery, and J. M. Buffington. 2006. Valley Segments, Stream Reaches, and Channel Units. Pages 23–50 in R. F. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*. 2nd edition. Elsevier.
- Blanckaert, K., X.-F. Garcia, A.-M. Ricardo, Q. Chen, and M. T. Pusch. 2013. The role of turbulence in the hydraulic environment of benthic invertebrates. *Ecohydrology* 6:700–712.
- Bohonak, A. J., and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6:783–796.
- Bolker, B. M. 2007. *Ecological Models and Data in R*. Princeton University Press.
- Bond, N. R., G. L. W. Perry, and B. J. Downes. 2000. Dispersal of organisms in a patchy stream environment under different settlement scenarios. *Journal of Animal Ecology* 69:608–619.
- Boss, S. M., and J. S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1044–1053.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology* 48:1173–1185.
- Boulton, A. J., S. Findlay, P. Marmonier, E. H. Stanley, A. J. Boulton, S. Findlay, P. Marmonier, E. H. Stanley, and H. M. Valett. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* 29:59–81.
- Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society* 115:503–514.
- Brewitt, K. S., E. M. Danner, and J. W. Moore. 2017. Hot eats and cool creeks: juvenile Pacific salmonids use mainstem prey while in thermal refuges. *Canadian Journal of Fisheries and Aquatic Sciences* 15:1–15.
- Brittain, J. E., and T. J. Eikeland. 1988. Invertebrate drift - a review. *Hydrobiologia* 166:77–93.
- Brooks, A. J., T. Haeusler, I. Reinfelds, and S. Williams. 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology* 50:331–344.
- Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220:99–108.
- Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. *The Wilson Bulletin* 81:293–329.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information theoretic approach*. Springer Science and Business Media.
- Bustamante, R. H., G. M. Branch, and E. S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76:2314–2329.
- Byers, J. E., Z. C. Holmes, and J. C. Malek. 2017. Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. *Oecologia*.

- Cardinale, B. J., K. Nelson, and M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* 91:175–183.
- Cardinale, B. J., M. a Palmer, C. M. Swan, S. Brooks, and L. Poff. 2010. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *America* 83:412–422.
- Carlton, J. T., and J. Hodder. 2003. Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256:271–286.
- Chang, W. Y. B., and D. W. Sell. 1984. Determining the density dependence of immigration and emigration of benthic stream invertebrates: theoretical considerations. *Hydrobiologia* 108:49–55.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist* 100:345–357.
- Ciborowski, J. J. H. 1983. Downstream and lateral transport of nymphs of two mayfly species (Ephemeroptera). *Canadian Journal of Fisheries and Aquatic Sciences* 40:2025–2029.
- Ciborowski, J. J. H. 1987. Dynamics of drift and microdistribution of two mayfly populations: a predictive model. *Canadian Journal of Fisheries and Aquatic Sciences* 44:832–845.
- Ciborowski, J. J. H., P. J. Pointing, and L. D. Corkum. 1977. The effect of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* (Mcdunnough). *Freshwater Biology* 7:567–572.
- Clarke, K. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian journal of ecology* 18:117–143.
- Closs, G. P. 1994. Feeding of galaxias olidus (Gunther) (pisces: Galaxiidae) in an intermittent australian stream. *Marine and Freshwater Research* 45:227–232.
- Cooper, S. D., S. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. *Ecology* 71:1503–1514.
- Corkum, L. D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. *Canadian Journal of Zoology* 56:1201–1206.
- Corrarino, C. A., and M. A. Brusven. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. *Freshwater Invertebrate Biology* 2:88–98.
- Crespo, J. G. 2011. A review of chemosensation and related behavior in aquatic insects. *Journal of insect science* 11:1–39.
- Cross, W. F., C. V Baxter, K. C. Donner, E. J. Rosi-Marshall, T. a Kennedy, R. O. Hall, H. a W. Kelly, and R. S. Rogers. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological applications* 21:2016–33.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.
- Culp, J. M., N. E. Glozier, and G. J. Scrimgeour. 1991. Reduction of predation risk under the cover of darkness: avoidance responses of mayfly larvae to a benthic fish. *Oecologia* 86:163–169.

- Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10:147–72.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *International Association of Theoretical and Applied Limnology* 18:1–158.
- Dahl, J., and L. Greenberg. 1996. Impact on stream benthic prey by benthic vs drift feeding predators: a meta-analysis. *Oikos* 77:177–181.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology* 21:271–282.
- Demes, K. W., J. N. Pruitt, C. D. G. Harley, and E. Carrington. 2013. Survival of the weakest: increased frond mechanical strength in a wave-swept kelp inhibits self-pruning and increases whole-plant mortality. *Functional Ecology* 27:439–445.
- Dewson, Z. S., A. B. W. James, and R. G. Death. 2007a. Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology* 52:357–369.
- Dewson, Z. S., A. B. W. James, R. G. Death, and S. Dewson. 2007b. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the American Water Resources Association* 26:401–415.
- Diehl, S., K. E. Anderson, and R. M. Nisbet. 2008. Population responses of drifting stream invertebrates to spatial and environmental variability: an emerging conceptual framework. Pages 158–183 *in* J. Lancaster and R. . Briers, editors. *Aquatic Insects: Challenges to Populations*. Wallingford.
- Diehl, S., S. D. Cooper, K. W. Kratz, R. M. Nisbet, S. K. Roll, S. W. Wiseman, and T. M. Jenkins, Jr. 2000. Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *The American Naturalist* 156:293–313.
- Dimand, J. B. 1967. Evidence that drift of stream benthos is density related. *Ecology* 48:855–857.
- Dodrill, M. J., C. B. Yackulic, T. A. Kennedy, and J. W. Hayes. 2016. Prey size and availability limits maximum size of rainbow trout in a large tailwater: insights from a drift-foraging bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 73:759–772.
- Dolson, R., K. McCann, N. Rooney, and M. Ridgway. 2009. Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos* 118:1230–1238.
- Douglas, P. L., G. E. Forrester, and S. D. Cooper. 1994. Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia* 98:48–56.
- Downes, B. J. 1990. Patch dynamics and mobility of fauna in streams. *Oikos* 59:411–413.
- Downes, B. J., P. S. Lake, and E. S. Schreiber. 1993. Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshwater Biology* 30:119–132.
- Downes, B. J., and J. Lancaster. 2010. Does dispersal control population densities in advection-dominated systems? A fresh look at critical assumptions and a direct test. *Journal of Animal Ecology* 79:235–48.
- Dudgeon, D. 1990. Seasonal dynamics of invertebrate drift in a Hong Kong stream. *Journal of*

- the Zoological Society of London 222:187–196.
- Dunbrack, R. L., and L. M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. *Environmental Biology of Fishes* 8:203–216.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Edwards, E. D., and A. D. Huryn. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *New Zealand Journal of Marine and Freshwater Research* 29:467–477.
- Eklöv, P., and S. Diehl. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98:344–353.
- Elliott, J. M. 1967a. Invertebrate drift in a Dartmoor stream. *Archiv für Hydrobiologie* 63:202–237.
- Elliott, J. M. 1967b. The life histories of drifting Plecoptera and Ephemeroptera in a Dartmoor Stream. *Journal of Animal Ecology* 36:343–362.
- Elliott, J. M. 1970. Methods of Sampling Invertebrate Drift. *Annales de Limnologie*:133–159.
- Elliott, J. M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. *Oecologia* 6:350–379.
- Elliott, J. M. 2002a. Time spent in the drift by downstream-dispersing invertebrates in a Lake District stream. *Freshwater Biology* 47:97–106.
- Elliott, J. M. 2002b. A continuous study of the total drift of freshwater shrimps, *Gammarus pulex*, in a small stony stream in the English Lake District:75–86.
- Elliott, J. M. 2002c. The drift distances and time spent in the drift by freshwater shrimps, *Gammarus pulex*, in a small stony stream, and their implications for the interpretation of downstream dispersal. *Freshwater Biology* 47:1403–1417.
- Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology* 48:1652–1668.
- Elliott, J. M. 2011. A comparative study of the relationship between light intensity and feeding ability in brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology* 56:1962–1972.
- Englund, G. 2005. Scale dependent effects of predatory fish on stream benthos. *Oikos* 111:19–30.
- Englund, G., and S. D. Cooper. 2003. Scale effects and extrapolation in ecological experiments. *Advances in Ecological Research* 33:161–213.
- Esteban, E. M., and M. P. Marchetti. 2004. What's on the menu? Evaluating a food availability model with young-of-the-year Chinook salmon in the Feather River, California. *Transactions of the American Fisheries Society* 133:777–788.
- Fausch, K. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441–451.
- Fausch, K. D. 2013. A historical perspective on drift foraging models for stream salmonids.

Environmental Biology of Fishes.

- Fausch, K. D., S. Nakano, and S. Khano. 1991. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. *Behavioral Ecology* 8:414–420.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–498.
- Fenoglio, S., F. Boano, T. Bo, R. Revelli, and L. Ridolfi. 2013. The impacts of increasing current velocity on the drift of *Simulium monticola* (Diptera: Simuliidae): a laboratory approach. *Italian Journal of Zoology* 80:443–448.
- Ferguson, R. I. 2003. The missing dimension: effects of lateral variation on 1-D calculations of fluvial bedload transport. *Geomorphology* 56:1–14.
- Fingerut, J. T., D. D. Hart, and J. N. McNair. 2006. Silk filaments enhance the settlement of stream insect larvae. *Oecologia* 150:202–12.
- Flecker, A. S. 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology* 73:438–448.
- Fonseca, D. M. 1999. Fluid mediated dispersal in streams: models of settlement from the drift. *Oecologia* 121:212–223.
- Fonseca, D. M., and D. D. Hart. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* 75:49–58.
- Fonseca, D. M., and D. D. Hart. 2001. Colonization history masks habitat preferences in local distributions of stream insects. *Ecology* 82:2897–2910.
- Forrester, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. *Ecology* 75:1208–1218.
- Fox, J., and S. Weisberg. 2010. *An R companion to applied regression*. Sage, Thousand Oaks, CA.
- Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- Fraser, F., and A. Huntingford. 1986. Feeding and avoiding predation hazard: the behavioral response of the prey. *Ethology* 8:56–68.
- Fraser, N. H. C., and N. B. Metcalfe. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. *Functional Ecology* 11:385–391.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10:199–214.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *Research techniques in animal ecology: controversies and consequences*. Columbia University Press.
- Gause, G. F. 1934. *The struggle for existence*. The Williams and Wilkins Company, Baltimore.

- Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall chinook salmon: The importance of geomorphic features in large rivers. *Environmental Management* 22:655–669.
- Gelman, A., S. Yu-Sung, Y. Masanao, J. Hill, M. Pittau, J. Kerman, T. Zheng, and V. Dorie. 2009. arm: data analysis using regression and multi-level/heirarchical models. R package version 1.15.1.
- Gibbins, C. N., and R. J. Batalla. 2010. Invertebrate drift and benthic exhaustion during disturbance: response of mayflies (Ephemeroptera) to increasing shear stress and river-bed instability. *River Research and Applications* 511:499–511.
- Gibbins, C. N., D. Vericat, and R. J. Batalla. 2007a. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology* 52:2369–2384.
- Gibbins, C. N., D. Vericat, and R. J. Batalla. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. *Journal of the North American Benthological Society* 29:945–958.
- Gibbins, C. N., D. Vericat, R. J. Batalla, and C. Gomez. 2007b. Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1–5.
- Gilliam, J., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68:1856–1862.
- Gippel, C. J., and M. J. Stewardson. 1998. Use of wetted perimeter in defining minimum environmental flows. *Regulated Rivers: Research & Management* 67:53–67.
- Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*) in a laboratory stream. *Hydrobiologia* 131:155–168.
- Good, P. 2013. Permutation tests: a practical guide to resampling methods for testing hypotheses. Second. Springer Science and Buisness Media.
- Gowan, C., and K. D. Fausch. 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes* 64:139–153.
- Grabowski, J. H. G. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.
- Grant, J. W. A. 1993. Whether or not to defend? The influence of resource distribution. *Marine Behaviour and Physiology* 23:137–153.
- Grant, J. W. A. 1997. Territoriality. Pages 81–103 in J.-G. Godin, editor. *Behavioural ecology of teleost fishes*. Oxford University Press, Oxford.
- Grant, J. W. A., and D. L. Kramer. 1990. Density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1724–1737.
- Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem: Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. *Fisheries* 25:15–21.

- Groeneveld, R. A., and G. Meedan. 1984. Measuring skewness and kurtosis. *Journal of the Royal Statistical Society* 33:391–399.
- Grossman, G. D. 2014. Not all drift feeders are trout: a short review of fitness-based habitat selection models for fishes. *Environmental Biology of Fishes* 97:465–473.
- Grubaugh, J. W., B. J. Wallace, and E. S. Houston. 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. *Freshwater Biology* 37:581–596.
- Gunderson, L. H. 2000. Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics* 31:425–439.
- Gustafsson, P., L. A. Greenberg, and E. Bergman. 2014. Woody debris and terrestrial invertebrates – effects on prey resources for brown trout (*Salmo trutta*) in a boreal stream. *Environmental Biology of Fishes* 97:529–542.
- Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. a. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* 11:348–356.
- Hafs, A. W., L. R. Harrison, R. M. Utz, and T. Dunne. 2014. Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. *Ecological Modelling* 285:30–38.
- Halwas, K. L., M. Church, and J. S. Richardson. 2005. Benthic assemblage variation among channel units in high-gradient streams on Vancouver Island, British Columbia. *Journal of the North American Benthological Society* 24:478–494.
- Hammock, B. G., N. Y. Krigbaum, and M. L. Johnson. 2012. Incorporating invertebrate predators into theory regarding the timing of invertebrate drift. *Aquatic Ecology* 46:153–163.
- Hammock, B. G., and W. C. Wetzel. 2013. The relative importance of drift causes for stream insect herbivores across a canopy gradient. *Oikos* 122:1586–1593.
- Hansen, E. A., and G. P. Closs. 2007. Temporal consistency in the long-term spatial distribution of macroinvertebrate drift along a stream reach. *Hydrobiologia* 575:361–371.
- Hansen, E. A., and G. P. Closs. 2009. Long-term growth and movement in relation to food supply and social status in a stream fish. *Behavioral Ecology* 20:616–623.
- Hanson, P. C. 1997. *Fish Bioenergetics 3.0 for Windows*.
- Hart, D. D., and C. M. Finelli. 1999. Physiobiological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* 30:363–395.
- Harvey, B. C., R. J. Nakamoto, and J. L. White. 2006. Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. *Transactions of the American Fisheries Society* 135:998–1005.
- Harvey, B. C., and S. F. Railsback. 2014. Feeding modes in stream salmonid population models: is drift feeding the whole story? *Environmental Biology of Fishes* 97:615–625.
- Harvey, B. C., J. L. White, and R. J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream.

- Canadian Journal of Fisheries and Aquatic Sciences 62:650–658.
- Harvey, B. C., J. L. White, and R. J. Nakamoto. 2009. The effect of deposited fine sediment on summer survival and growth of rainbow trout in riffles of a small stream. *North American Journal of Fisheries Management* 29:434–440.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press.
- Hawkins, C., J. Kershener, P. Bisson, M. D. Bryant, L. Decker, S. Gregory, D. McCullough, C. K. Overton, G. Reeves, R. Steedman, and M. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18:3–12.
- Hawkins, C., M. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840–1856.
- Hayes, J. W., E. Goodwin, J. Hay, K. A. Shearer, and L. H. Kelly. 2012. Minimum flow requirements of trout in the Mataura river: comparison of traditional habitat and net rate of energy intake modelling. Prepared for Environment Southland. Cawthron Report No. 1957.
- Hayes, J. W., E. Goodwin, K. A. Shearer, J. Hay, and L. Kelly. 2016. Can weighted useable area predict flow requirements of drift-feeding salmonids? Comparison with a net rate of energy intake model incorporating drift–flow processes. *Transactions of the American Fisheries Society* 145:589–609.
- Hayes, J. W., N. F. Hughes, and L. H. Kelly. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecological Modelling* 207:171–188.
- Hayes, J. W., J. D. Stark, and K. A. Shearer. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society* 129:315–332.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* 111:101–111.
- Heck, K. L., and J. L. B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Pages 281–299 in S. S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. *Habitat structure: the physical arrangement of objects in space*. Springer Science and Buisiness Media.
- Henshall, S. E., J. P. Sadler, D. M. Hannah, and A. J. Bates. 2011. The role of microhabitat and food availability in determining riparian invertebrate distributions on gravel bars: a habitat manipulation experiment. *Ecohydrology* 4:512–519.
- Herder, F., and J. Freyhof. 2006. Resource partitioning in a tropical stream fish assemblage. *Journal of Fish Biology* 69:571–589.
- Hieber, M., C. T. Robinson, and U. Uehlinger. 2003. Seasonal and diel patterns of invertebrate drift in different alpine stream types. *Freshwater Biology* 48:1078–1092.
- Hildebrand, S. G. 1974. The relation of drift to benthos density and food level in an artificial

- stream. *Limnology and Oceanography* 19:951–957.
- Hildrew, A. G., and C. R. Townsend. 1980. Aggregation, interference and foraging by the larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodinae). *Animal Behaviour* 28:553–560.
- Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74:685–698.
- Hillebrand, H. 2005. Light regime and consumer control of autotrophic biomass. *Journal of Ecology* 93:758–769.
- Hintz, W. D., and T. Wellnitz. 2013. Current velocity influences the facilitation and removal of algae by stream grazers. *Aquatic Ecology*.
- Hixon, M. A., and J. B. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hodar, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologia* 17:421–433.
- Holomuzki, J. R., and A. S. Van Loan. 2002. Effects of structural habitat on drift distance and benthic settlement of the caddisfly, *Ceratopsyche sparna*. *Hydrobiologia* 477:139–147.
- Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecology* 17:261–273.
- Hoover, T. M., and J. S. Richardson. 2009. Does water velocity influence optimal escape behaviors in stream insects? *Behavioral Ecology* 21:242–249.
- Hopcraft, J. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* 74:559–566.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predatory-prey oscillations. *Hilgardia* 27:343–383.
- Hughes, N. F. 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1999–2008.
- Hughes, N. F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology* 79:281–294.
- Hughes, N. F., and L. M. Dill. 1990. Position choice by drift feeding salmonids: a model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2039–2048.
- Huhta, A., T. Muotka, and P. Tikkanen. 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biology* 45:33–42.
- Humphries, S. 2002. Dispersal in drift-prone macroinvertebrates: a case for density-independence. *Freshwater Biology* 47:921–929.
- Humphries, S., and G. D. Ruxton. 2002. Is there really a drift paradox? *Journal of Animal Ecology* 71:151–154.
- Humphries, S., and G. D. Ruxton. 2003. Drift distances and mortality risk for of

- intergenerational estimation dispersal aquatic macroinvertebrates. *Limnology and Oceanography* 48:2117–2124.
- Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography* 41:243–252.
- Huryn, A. D., and B. J. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68:1932–1942.
- Hutchinson, G. E. 1958. Concluding remarks. *Quant. Biol* 22:415–427.
- Huxel, G. R., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. *The American naturalist* 152:460–9.
- Imbert, J., and J. Perry. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* 436:191–208.
- Imre, I., J. W. A. Grant, and E. R. Keeley. 2004. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). *Oecologia* 138:371–378.
- Inoue, M., and M. Nunokawa. 2002. Effects of longitudinal variations in stream habitat structure on fish abundance: an analysis based on subunit-scale habitat classification. *Freshwater Biology* 47:1594–1607.
- Irlandi, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98:176–183.
- Jackson, J. K., E. P. McElravy, and V. H. Resh. 1999. Long-term movements of self-marked caddisfly larvae (Trichoptera: Sericostomatidae) in a California coastal mountain stream. *Freshwater Biology* 42:525–536.
- James, A. B. W., Z. S. Dewson, and R. G. Death. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications* 35:22–35.
- James, A. B. W., Z. S. Dewson, and R. G. Death. 2009. The influence of flow reduction on macroinvertebrate drift density and distance in three New Zealand streams. *Journal of the North American Benthological Society* 28:220–232.
- Jenkins, A. R., and E. R. Keeley. 2010. Bioenergetic assessment of habitat quality for stream-dwelling cutthroat trout (*Oncorhynchus clarkii bouvieri*) with implications for climate change and nutrient supplementation. *Canadian Journal of Fisheries and Aquatic Sciences* 67:371–385.
- Jowett, I. G. 1993. A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research* 27:241–248.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* 10:690–700.
- Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual

- resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology* 46:303–316.
- Kaylor, M. J., and D. R. Warren. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. *Ecosphere* 8:e01845.
- Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* 82:1247–1259.
- Keeley, E. R., and J. W. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:1894–1902.
- Keller, E. A. 1971. Areal sorting of bed-load material: the hypothesis of velocity reversal. *Bulletin of the Geological Society of America* 82:753–756.
- Kennedy, B. P., K. H. Nislow, and C. L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. *Ecology* 89:2529–41.
- Kennedy, T. A., C. B. Yackulic, W. F. Cross, P. E. Grams, M. D. Yard, and A. J. Copp. 2014. The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. *Freshwater Biology* 59:557–572.
- Kerans, B. L., P. L. Chesson, and R. A. Stein. 2000. Assessing density-dependent establishment and dispersal: an example using caddisfly larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1190–1199.
- Keupp, L. E. 1988. Invertebrate fish food resources of lotic environments. Susitna-Watana Hydroelectric Project: River Productivity Study:42.
- Kiffney, P. M., E. R. Buhle, S. M. Naman, G. R. Pess, and R. S. Klett. 2014. Linking resource availability and habitat structure to stream organisms: an experimental and observational assessment. *Ecosphere* 5:39. <http://dx.doi.org/10.1890/ES13-00269.1>.
- Kiffney, P. M., G. R. Pess, J. H. Anderson, and P. Faulds. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. *River Research and Applications* 452:438–452.
- Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. *Journal of the North American Benthological Society* 23:542–555.
- Kiffney, P. M., and P. Roni. 2007. Relationships between Productivity, Physical Habitat, and Aquatic Invertebrate and Vertebrate Populations of Forest Streams: An Information-Theoretic Approach. *Transactions of the American Fisheries Society* 136:1088–1103.
- Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* 66:1749–1761.
- Kohler, S. L. 1992. Competition and the structure of a benthic stream community. *Ecological Monographs* 62:165–188.
- Kohler, S. L., and M. Mcpeek. 1989. Predation risk and the foraging behavior of competing stream insects. *Ecology* 70:1811–1825.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260.

- Kovalak, W. P. 1978. Effects of a pool on stream invertebrate drift. *American Midland Naturalist* 99:119–127.
- Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2011. Habitat complexity: approaches and future directions. *Hydrobiologia* 685:1–17.
- Kratz, K. 1996. Effects of stoneflies on local prey populations: mechanisms of impact across prey density. *Ecology* 77:1573–1585.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573–592.
- Lamouroux, N., J. Olivier, H. Persat, M. Pouilly, Y. Souchon, and B. Statzner. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biology* 42:275–299.
- Lancaster, J. 2000. Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. *Journal of Animal Ecology* 69:442–457.
- Lancaster, J., and L. R. Belyea. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society* 16:221–238.
- Lancaster, J., B. J. Downes, and A. Arnold. 2011. Lasting effects of maternal behaviour on the distribution of a dispersive stream insect. *The Journal of animal ecology* 80:1061–9.
- Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* 12:385–393.
- Lancaster, J., A. G. Hildrew, and C. Gjerlov. 1996. Invertebrate drift and longitudinal transport processes in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 53:572–582.
- Larkin, P. A., and D. W. McKone. 1985. An evaluation by field experiments of the McLay model of stream drift. *Canadian Journal of Fisheries and Aquatic Sciences* 42:909–918.
- Larsen, S., and S. J. Ormerod. 2010. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology* 55:476–486.
- Lauridsen, R. B., and N. Friberg. 2005. Stream macroinvertebrate drift response to pulsed exposure of the synthetic pyrethroid lambda-cyhalothrin. *Environmental toxicology* 20:513–21.
- Leeseberg, C. A., and E. R. Keeley. 2014. Prey size, prey abundance, and temperature as correlates of growth in stream populations of cutthroat trout. *Environmental Biology of Fishes* 97:599–614.
- Leung, E. S., J. S. Rosenfeld, and J. R. Bernhardt. 2009. Habitat effects on invertebrate drift in a small trout stream: implications for prey availability to drift-feeding fish. *Hydrobiologia* 623:113–125.
- Li, H. W., and R. W. Brocksen. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *Journal of Fish Biology* 11:329–341.
- Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed forest watershed. *Canadian Journal of Fisheries and Aquatic Sciences*.

- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lindeman, R. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–417.
- Lobón-Cerviá, J., and P. A. Rincón. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos* 105:641–646.
- Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Canadian Journal of Zoology* 73:2223–2230.
- Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6:673–679.
- Lutscher, F., R. M. Nisbet, and E. Pachepsky. 2010. Population persistence in the face of advection. *Theoretical Ecology* 3:271–284.
- Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617–628.
- Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology* 47:679–694.
- Malmqvist, B., and P. Sjöström. 1987. Stream drift as a consequence of disturbance by invertebrate predators. *Oecologia* 74:396–403.
- Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92:1215–1225.
- Márcia Barbosa, A., R. Real, A. R. Muñoz, and J. A. Brown. 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions* 19:1333–1338.
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web Effects of resource subsidies. *Ecology* 88:140–148.
- Martin, J. C., and A. W. Knight. 1989. The effect of long pools on the drift of macro-invertebrates in a mountain stream. *Hydrobiologia* 185:63–70.
- McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the south fork Trinity River watershed, California. *Transactions of the American Fisheries Society* 138:506–521.
- McCoy, E. D., and S. S. Bell. 1991. Habitat structure: the evolution and development of a complex topic. Pages 1–27 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky, editors. *Habitat structure: the physical arrangement of objects in space*. Springer Science and Business Media.
- McHugh, P. A., W. C. Saunders, N. Bouwes, C. E. Wall, S. Bangen, J. M. Wheaton, M. Nahorniak, J. R. Ruzyski, I. A. Tattam, and C. E. Jordan. 2017. Linking models across

- scales to assess the viability and restoration potential of a threatened population of steelhead (*Oncorhynchus mykiss*) in the Middle Fork John Day River, Oregon, USA. *Ecological Modelling* 355:24–38.
- McIntosh, A., and B. Peckarsky. 1996. Differential behavioural responses of mayflies from streams with and without fish to trout odour. *Freshwater Biology* 35:141–148.
- McIntosh, A. R., and B. L. Peckarsky. 2004. Are mayfly anti-predator responses to fish odour proportional to risk? *Archiv für Hydrobiologie* 160:145–151.
- McLaughlin, R. L., J. W. Grant, and D. L. Noakes. 2000. Living with failure: the prey capture success of young brook charr in streams. *Ecology of Freshwater Fish* 9:81–89.
- McLay, C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *J. Fish. Res. Bd. Canada* 27:359–370.
- McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. P. Lester, B. J. Shuter, and N. Rooney. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. *Ecological Monographs* 95:833–844.
- McNair, J. N., and J. D. Newbold. 2001. Turbulent transport of suspended particles and dispersing benthic organisms: the hitting-distance problem for the local exchange model. *Journal of theoretical biology* 209:351–69.
- McNair, J. N., and J. D. Newbold. 2012. Turbulent particle transport in streams: can exponential settling be reconciled with fluid mechanics? *Journal of Theoretical Biology* 300:62–80.
- Meissner, K., and T. Muotka. 2006. The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology* 75:421–33.
- Mejia, F. H., C. V. Baxter, E. K. Berntsen, and A. K. Fremier. 2016. Linking groundwater-surface water exchange to food production and salmonid growth. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1650–1660.
- Melbourne, B. A., and P. Chesson. 2005. Scaling up population dynamics: integrating theory and data. *Oecologia* 145:179–87.
- Melbourne, B. A., and P. Chesson. 2006. The scale transition: scaling up population dynamics with field data. *Ecology* 87:1478–1488.
- Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* 51:429–450.
- Merritt, R., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall Hunt.
- Miller, S. W., and S. Judson. 2014. Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking. *Canadian Journal of Fisheries and Aquatic Sciences* 71:675–687.
- Milne, J. A. 1982. Bed-material size and the riffle-pool sequence. *Sedimentology* 29:267–278.
- Milner, A. M. 1994. Colonization and succession of invertebrate communities in a new stream in Glacier Bay National Park, Alaska. *Freshwater Biology* 32:387–400.

- Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton, and M. Ladle. 2003. The natural control of salmon and trout populations in streams. *Fisheries Research* 62:111–125.
- Minshall, W. G., and P. V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49:580–582.
- Montgomery, D. R., and J. Buffington. 1997. Channel-reach morphology in mountain drainage basins. *GSA Bulletin* 109:596–611.
- Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. R. Pess. 1995. Pool spacing in forest channels. *Water Resources Research* 31:1097–1105.
- Moore, R. D., P. Sutherland, T. Gomi, and A. Dhakal. 2005. Thermal regime of a headwater stream within a clear-cut, coastal British Columbia, Canada. *Hydrological Processes* 19:2591–2608.
- Müller, K. 1954. Investigations on the organic drift in North Swedish streams. Rep. Inst. Freshwat. Res. Drottningholm 35:133–148.
- Müller, K. 1982. The colonization cycle of freshwater insects. *Oecologia* 52:202–207.
- Naiman, R. J., J. R. Alldredge, D. a Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggione, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the United States of America* 109:21201–7.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Nakano, S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology* 64:75–84.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98:166–170.
- Naman, S. M., J. S. Rosenfeld, and J. S. Richardson. 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1292–1305.
- Naman, S. M., J. S. Rosenfeld, J. S. Richardson, and J. L. Way. 2017a. Species traits and channel architecture mediate flow disturbance impacts on invertebrate drift. *Freshwater Biology* 62:340–355.
- Naman, S. M., J. S. Rosenfeld, L. C. Third, and J. S. Richardson. 2017b. Habitat-specific production of aquatic and terrestrial invertebrate drift in small forest streams: implications for drift-feeding fish. *Canadian Journal of Fisheries and Aquatic Sciences* 74:1208–1217.
- Negishi, J. N., and J. S. Richardson. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 258:247–258.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads:

- stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4–21.
- Neuswanger, J., M. S. Wipfli, A. E. Rosenberger, and N. F. Hughes. 2014. Mechanisms of drift-feeding behavior in juvenile Chinook salmon and the role of inedible debris in a clear-water Alaskan stream. *Environmental Biology of Fishes* 97:489–503.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* 121:617–634.
- Nikora, V., K. Koll, I. McEwan, S. McLean, and A. Dittrich. 2004. Velocity distribution in the roughness layer of rough-bed flows. *Journal of Hydraulic Engineering* 130:1036–1042.
- Nislow, K. H., C. L. Folt, and D. L. Parrish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecological Applications* 9:1085–1099.
- Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 127:116–127.
- O' Hop, J., and J. B. Wallace. 1983. Invertebrate drift, discharge and sediment relations in a southern Appalachian headwater stream. *Hydrobiologia* 98:71–84.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. Simpson, P. Solymos, H. Stevens, and H. Wagner. 2013. Vegan community ecology package. R package version 2.0–9,.
- Oldmeadow, D. F., J. Lancaster, and S. P. Rice. 2010. Drift and settlement of stream insects in a complex hydraulic environment. *Freshwater Biology* 55:1020–1035.
- Orr, M., M. Zimmer, D. E. Jelinski, and M. Mews. 2008. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. *Ecology* 86:1496–1507.
- Otto, C., and P. Sjostrom. 1986. Behaviour of drifting insect larvae. *Hydrobiologia* 86:77–86.
- Pachepsky, E., F. Lutscher, R. M. Nisbet, and M. A. Lewis. 2005. Persistence, spread and the drift paradox. *Theoretical population biology* 67:61–73.
- Palmer, M. A., J. D. Allan, and C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in ecology & evolution* 11:322–326.
- Palmer, M. A., R. F. Ambrose, and N. L. R. Poff. 1997. Ecological theory and community restoration ecology. *Restoration ecology* 5:291–300.
- Patterson, R. J., and K. E. Smokorowski. 2011. Assessing the benefits of flow constraints on the invertebrate drifting community of a regulated river. *River Research and Applications* 112:99–112.
- Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333–365.
- Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61:932–943.
- Peckarsky, B. L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecological Monographs* 77:1888–1905.

- Perkin, E. K., F. Hölker, K. Tockner, and J. S. Richardson. 2014. Artificial light as a disturbance to light-naïve streams. *Freshwater Biology* 59:2235–2244.
- Perry, S. A., and W. B. Perry. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the. *Hydrobiologia* 134:171–182.
- Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation- concepts, patterns, and mechanisms. Pages 396–434 in G. A. Polis and K. . Winemiller, editors. *Food Webs*. Springer.
- Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The influences of body Size, habitat quality, and competition on the movement and survival of juvenile coho Salmon during the early stages of stream recolonization. *Transactions of the American Fisheries Society* 140:883–897.
- Peterson, J. T., and C. F. Rabeni. 2001. Evaluating the physical characteristics of channel units in an Ozark stream. *Transactions of the American Fisheries Society* 130:37–41.
- Piccolo, J. J., B. M. Frank, and J. W. Hayes. 2014. Food and space revisited: the role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. *Environmental Biology of Fishes* 97:475–488.
- Piccolo, J. J., N. F. Hughes, and M. D. Bryant. 2008. Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). *Canadian Journal of Fisheries and Aquatic Sciences* 65:266–275.
- Pickett, S. ., and P. A. White. 1985. The ecology of natural disturbance and patch dynamics. Page (S. T. . Pickett and P. A. White, Eds.). Elsevier.
- Ploskey, G. R., and A. V Brown. 1980. Downstream drift of the mayfly *Baetis flavistriga* as a passive phenomenon. *American Midland Naturalist* 104:405–409.
- Poff, N. L., R. D. Decino, J. V Ward, S. Url, and N. Leroy. 1991. Size-dependent drift responses of mayflies to experimental hydrologic variation: active predator avoidance or passive hydrodynamic displacement? *Oecologia* 88:577–586.
- Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:201–217.
- Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, P. Mark, and B. C. Kondratieff. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society* 25:730–755.
- Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629–645.
- Poff, N. L., and V. Ward. 1989. Implications of streamflow variability and predidability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 1:1805–1818.

- Poff, N. L., and V. Ward. 1991. Drift responses of benthic invertebrates to experimental streamflow reduction in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1926–1936.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. Richard, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. W. De Badgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456–459.
- Pringle, C. M., and A. Ramirez. 2001. Spatial and temporal patterns of invertebrate drift in streams draining a Neotropical landscape. *Freshwater Biology* 46:47–62.
- Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho Salmon (*Oncorhynchus kisutch*). *Behaviour* 92:97–111.
- Pulliam, H. R. 1988. sources, sinks, and population regulation. *The American Naturalist* 132:652–661.
- Puth, M. T., M. Neuhauser, and G. D. Ruxton. 2015. On the variety of methods for calculating confidence intervals by bootstrapping. *Journal of Animal Ecology* 84:892–897.
- Quinn, T. P. 2011. The behavior and ecology of Pacific salmon and trout. UBC Press, Vancouver, BC.
- R Core Team. 2013. R: a language for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1211–1234.
- Railsback, S. F., M. Gard, B. C. Harvey, J. L. White, and J. K. H. Zimmerman. 2013. Contrast of Degraded and Restored Stream Habitat Using an Individual-Based Salmon Model. *North American Journal of Fisheries Management* 33:384–399.
- Railsback, S. F., and B. C. Harvey. 2011. Importance of fish behaviour in modelling conservation problems: Food limitation as an example. *Journal of Fish Biology* 79:1648–1662.
- Railsback, S., H. Stauffer, and B. Harvey. 2003. What can habitat preference models tell us? Tests using a virtual trout population. *Ecological Applications* 13:1580–1594.
- Reisen, W. K., and R. Prins. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County. *Ecology* 53:876–884.
- Resh, V. H., A. V Brown, A. P. Covich, M. E. Gurtz, W. Hiram, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, C. Robert, M. E. Gurtz, H. W. Li, and G. W. Minshall. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72:873–887.

- Richardson, J. S., and T. Sato. 2015. Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology* 8:406–415.
- Richardson, J. S., Y. Zhang, and L. B. Marczak. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications* 66:55–66.
- Rincón, P. A., and J. Lobon-Cervia. 1997. Temporal patterns in macroinvertebrate drift in a northern Spanish stream. *Marine and Freshwater Research* 48:455–464.
- Robinson, C. T., and W. G. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society* 5:237–248.
- Robson, B. J. 1996. Small spate disturbance and the complexity of habitat architecture in Mountain River, Tasmania. *Marine and Freshwater Research* 47:851–855.
- Romaniszyn, E. D., J. J. Hutchens, and B. J. Wallace. 2007. Aquatic and terrestrial invertebrate drift in southern Appalachian Mountain streams: implications for trout food resources. *Freshwater Biology* 52:1–11.
- Roni, P. 2002. Habitat use by fishes and Pacific giant salamanders in small Western Oregon and Washington streams. *Transactions of the American Fisheries Society* 131:37–41.
- Roni, P., T. Beechie, G. Pess, and K. Hanson. 2015. Wood placement in river restoration : fact , fiction , and future direction. *Canadian Journal of Fisheries and Aquatic Sciences* 478:466–478.
- Roni, P., K. Hanson, and T. Beechie. 2008. Global Review of the Physical and Biological Effectiveness of Stream Habitat Rehabilitation Techniques. *North American Journal of Fisheries Management* 28:856–890.
- Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:282–292.
- Rooney, N., K. S. McCann, and J. C. Moore. 2008. A landscape theory for food web architecture. *Ecology Letters* 11:867–881.
- de Roos, A., K. Leonardsson, L. Persson, and G. G. Mittelbach. 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Ecological Monographs* 4:189–217.
- Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. *Transactions of the American Fisheries Society* 132:37–41.
- Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:766–774.
- Rosenfeld, J. S. 2014. Modelling the effects of habitat on self-thinning, energy equivalence, and optimal habitat structure for juvenile trout. *Canadian Journal of Fisheries and Aquatic*

Sciences 71:1395–1406.

- Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic Sciences* 58:585–593.
- Rosenfeld, J. S., N. Bouwes, C. E. Wall, and S. M. Naman. 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. *Environmental Biology of Fishes* 97:551–574.
- Rosenfeld, J. S., T. Leiter, G. Lindner, and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:1691–1701.
- Rosenfeld, J. S., J. Post, G. Robins, and T. Hatfield. 2007. Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 64:755–767.
- Rosenfeld, J. S., and R. Ptolemy. 2012. Modelling available habitat versus available energy flux: do PHABSIM applications that neglect prey abundance underestimate optimal flows for juvenile salmonids? *Canadian Journal of Fisheries and Aquatic Sciences* 1934:1920–1934.
- Rosenfeld, J. S., and E. Raeburn. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. *Ecology of Freshwater Fish* 18:572–584.
- Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. *Fisheries Management and Ecology* 16:202–218.
- Rowe, L., and J. S. Richardson. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. *Oecologia* 129:473–480.
- Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665–706.
- Ruetz, C. R., and D. W. Stephens. 2003. Site selection under differential predation risks by drifting prey in streams. *Oikos* 102:85–94.
- Rundio, D. E., and S. T. Lindley. 2008. Seasonal patterns of terrestrial and aquatic prey abundance and use by *Oncorhynchus mykiss* in a California coastal basin with a Mediterranean climate. *Transactions of the American Fisheries Society* 137:467–480.
- Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-Mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society* 21:336.
- Sagar, P. M., and G. J. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 33:643–653.
- Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. *Ecology* 92:201–

- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. *Oikos* 98:177–189.
- Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1:31–37.
- Scrimgeour, G. J., and J. M. Culp. 1994a. Foraging and evading predators: the effect of predator foraging species on a behavioural trade-off by a lotic mayfly. *Oikos* 69:71–79.
- Scrimgeour, G. J., and J. M. Culp. 1994b. Feeding while evading predators by a lotic mayfly : linking short-term foraging behaviours to long-term fitness consequences. *Oecologia* 100:128–134.
- Scullion, J., C. A. Parish, N. Morgan, and R. W. Edwards. 1982. Comparison of benthic macroinvertebrate fauna and substratum composition in riffles and pools in the impounded River Elan and the unregulated River Wye, mid-Wales. *Freshwater Biology* 12:579–595.
- Sharma, R., and R. Hilborn. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1453–1463.
- Shearer, K. A., J. D. Stark, J. W. Hayes, and R. G. Young. 2003. Relationships between drifting and benthic invertebrates in three New Zealand rivers: implications for drift-feeding fish. *New Zealand Journal of Marine and Freshwater Research* 37:809–820.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043.
- Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour* 63:437–443.
- Siler, E. R., J. B. Wallace, and S. L. Eggert. 2001. Long-term effects of resource limitation on stream invertebrate drift. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1624–1637.
- Sloat, M. R., and G. Reeves. 2014. Demographic and phenotypic responses of juvenile steelhead trout to spatial predictability of food resources. *Ecology* 95:2423–2433.
- Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173–180 in D. Noakes, D. Lindquist, D. Helfman, and J. Ward, editors. *Predators and prey in fishes*. Dr. W Junk Publishers, The Hague.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- Speirs, D. C., and W. S. C. Gurney. 2001. Population persistence in rivers and estuaries. *Ecology* 82:1219–1237.

- Spiller, D. A., J. Piovato-scott, A. N. Wright, L. H. Yang, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology* 91:1424–1434.
- Stark, J. D., K. A. Shearer, and J. W. Hayes. 2002. Are aquatic invertebrate drift densities uniform? Implications for salmonid foraging models. *Verh. Internat. Verein. Limnol.*:988–991.
- Statzner, B. 1987. Growth and Reynolds number of lotic macroinvertebrates: a problem for adaptation of shape to drag. *Oikos* 51:84–87.
- Statzner, B., C. Dejoux, and J. Elouard. 1984. Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast) I. Introduction: review of drift literature, methods and experimental conditions. *Reviews of Tropical Hydrobiology* 17:319–334.
- Statzner, B., J. Elouard, and C. Dejoux. 1987. Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). III. Trichoptera. *Freshwater Biology* 17:391–404.
- Statzner, B., and R. Mogel. 1985. An example showing that drift net catches of stream mayflies (*Baetis* spp., Ephemeroptera, Insecta) do not increase during periods of higher substrate surface densities of the larvae. *Verhandlungen der Internationalen Vereinigung für Theoretische Angewandte Zoologie* 22:3238–3243.
- Steingrimsson, S. O., and J. W. a. Grant. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *Journal of Animal Ecology* 68:17–26.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. *Canadian Journal of Fisheries and Aquatic Sciences* 48:909–922.
- Stoneburner, D. L., and L. A. Smock. 1979. Seasonal fluctuations of macroinvertebrate drift in a South Carolina Piedmont stream. *Hydrobiologia* 63:49–56.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754.
- Stubbington, R. 2012. The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research* 63:293–311.
- Sweka, J. A., and K. J. Hartman. 2008. Contribution of terrestrial invertebrates to yearly brook trout prey consumption and growth. *Transactions of the American Fisheries Society* 137:224–235.
- Syms, C., and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral- reef fish community. *Ecology* 81:2714–2729.
- Syrjanen, J., K. Korsu, P. Louhi, R. Paavola, and T. Muotka. 2011. Stream salmonids as opportunistic foragers: the importance of terrestrial invertebrates along a stream-size gradient. *Canadian Journal of Fisheries and Aquatic Sciences* 68:2146–2156.
- Tewfik, A., S. S. Bell, K. S. McCann, and K. Morrow. 2016. Predator diet and trophic position modified with altered habitat morphology. *PLoS ONE* 11:1–22.
- Thorp, J. H., M. C. Thoms, and M. D. DeLong. 2006. The riverine ecosystem synthesis:

- biocomplexity in river networks across space and time. *River Research and Applications* 22:123–147.
- Tiegs, S. D., D. T. Chaloner, P. Levi, R. Janine, J. L. Tank, and G. A. Lamberti. 2008. Timber harvest transforms ecological roles of salmon in Southeast Alaska rain forest streams. *Ecological Applications* 18:4–11.
- Tonkin, J. D., and R. G. Death. 2013. Macroinvertebrate drift-benthos trends in a regulated river. *Fundamental and Applied Limnology* 182:231–245.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36–50.
- Townsend, C. R., and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* 45:759–772.
- Townsend, C. R., and A. G. Hildrew. 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biology* 31:265–275.
- Trinci, G., G. L. Harvey, A. J. Henshaw, W. Bertoldi, and F. Hölker. 2017. Life in turbulent flows: interactions between hydrodynamics and aquatic organisms in rivers. *Wiley Interdisciplinary Reviews: Water* 4:e1213.
- Tunney, T. D., K. S. McCann, N. P. Lester, and B. J. Shuter. 2012. Food web expansion and contraction in response to changing environmental conditions. *Nature communications* 3:1105.
- Turner, D., and D. Williams. 2000. Invertebrate movements within a small stream: density dependence or compensating for drift? *Internat. Rev. Hydrobiol.* 85:141–156.
- Urabe, H., M. Nakajima, M. Torao, and T. Aoyama. 2010. Evaluation of habitat quality for stream salmonids based on a bioenergetics model. *Transactions of the American Fisheries Society* 139:1665–1676.
- Verberk, W. C. E. P., H. Sijpeel, and H. Esselink. 2008. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* 53:1722–1738.
- Vinson, M. R. 2001. Long term dynamics of an invertebrate assemblage downstream of a large dam. *Ecological Applications* 11:711–730.
- Vogel, S. 1994. *Life in moving fluids: the physical biology of flow*. Princeton University Press.
- Wall, C. E., N. Bouwes, J. M. Wheaton, S. N. Bennett, W. C. Saunders, P. A. McHugh, and C. E. Jordan. 2016a. Design and monitoring of woody structures and their benefits to juvenile steelhead trout (*Oncorhynchus mykiss*) using a net rate of energy intake model. *Canadian Journal of Fisheries and Aquatic Sciences* 12:1–12.
- Wall, C. E., N. Bouwes, J. M. Wheaton, W. C. Saunders, and S. N. Bennett. 2016b. Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1081–1091.
- Walters, D. M., D. S. Leigh, M. C. Freeman, B. J. Freeman, and C. M. Pringle. 2003. Geomorphology and fish assemblages in a Piedmont river basin, USA. *Freshwater Biology* 48:1950–1970.

- Wankowski, J. 1981. Behavioral aspects of predation by juvenile Atlantic salmon (*Salmo salar*) on particulate drifting prey. *Animal Behaviour*:557–571.
- Waters, T. F. 1965. Interpretation of invertebrate drift in streams. *Ecology* 46:327–334.
- Waters, T. F. 1966. Production rate, population density, and drift of a stream invertebrate. *Ecology* 47:595–604.
- Waters, T. F. 1969. Invertebrate drift ecology and significance to stream fishes. Page in T. G. Northcote, editor. *Symposium on Salmon and Trout in Streams*.
- Weber, N., N. Bouwes, and C. Jordan. 2017. Accounting for spatial and temporal variation in macroinvertebrate community abundances when measuring the food supply of stream salmonids. *Freshwater Science* 36:364–376.
- Weber, N., N. Bouwes, and C. E. Jordan. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1158–1170.
- Wellnitz, T. 2014. Can current velocity mediate trophic cascades in a mountain stream? *Freshwater Biology* 59:2245–2255.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche shift and species interactions in size structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- White, S. M., G. Giannico, and H. Li. 2014. A “behaviorscape” perspective on stream fish ecology and conservation: linking fish behavior to riverscapes. *Wiley Interdisciplinary Reviews: Water* 1:385–400.
- Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47:501–515.
- Wilcox, A. C., B. L. Peckarsky, B. W. Taylor, and A. C. Encalada. 2008. Hydraulic and geomorphic effects on mayfly drift in high-gradient streams at moderate discharges. *Ecohydrology* 186:176–186.
- Williams, D. D., and G. P. Levens. 1988. Evidence that hunger and limb loss can contribute to stream invertebrate drift. *Journal of the North American Benthological Society* 7:180–187.
- Wilzbach, M. 1990. Nonconcordance of drift and benthic activity in *Baetis*. *Limnology and Oceanography* 35:945–952.
- Wilzbach, M. A., K. W. Cummins, and R. A. Knapp. 1988. Toward a functional classification of stream invertebrate drift. *Verh. Internat. Verein. Limnol.* 23:1244–1254.
- Wilzbach, M., K. Cummins, and J. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology* 67:898–911.
- Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29:84–99.
- Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*:1259–1269.

- Wipfli, M. S., and C. V Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* 35:373–387.
- Wood, J. L., J. W. Grant, and M. H. Belanger. 2012. Population density and territory size in juvenile rainbow trout, *Oncorhynchus mykiss*: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1121–1128.
- Wooster, D., S. W. Miller, and S. J. DeBano. 2016. Impact of season-long water abstraction on invertebrate drift composition and concentration. *Hydrobiologia* 772:15–30.
- Worischka, S., C. Koebsch, C. Hellmann, and C. Winkelmann. 2012. Habitat overlap between predatory benthic fish and their invertebrate prey in streams: the relative influence of spatial and temporal factors on predation risk. *Freshwater Biology* 57:2247–2261.

Appendices

Appendix A Supporting information for Chapter 3

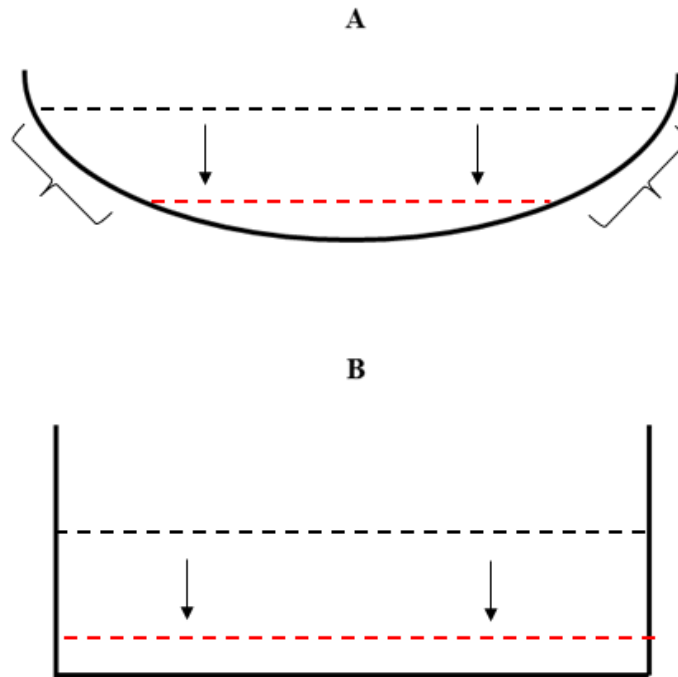


Figure A1: Conceptual representation of the rationale behind the habitat treatments used in the experiments. Dashed lines in represent the water level under stable (black lines) and reduced (red lines) flows. When flows decline, concave channels (A) with gently sloping banks will lose more wetted streambed area (highlighted in brackets) than channels with vertically sloping banks and flat bottoms (B). Similarly, when flows increase, wetted streambed area will increase in concave channels more than flat channels. The converse is true with velocity; when flows decline, velocity will decrease more in flat channels than concave channels, and conversely velocity will increase more in flat relative to concave channels when flows are elevated.

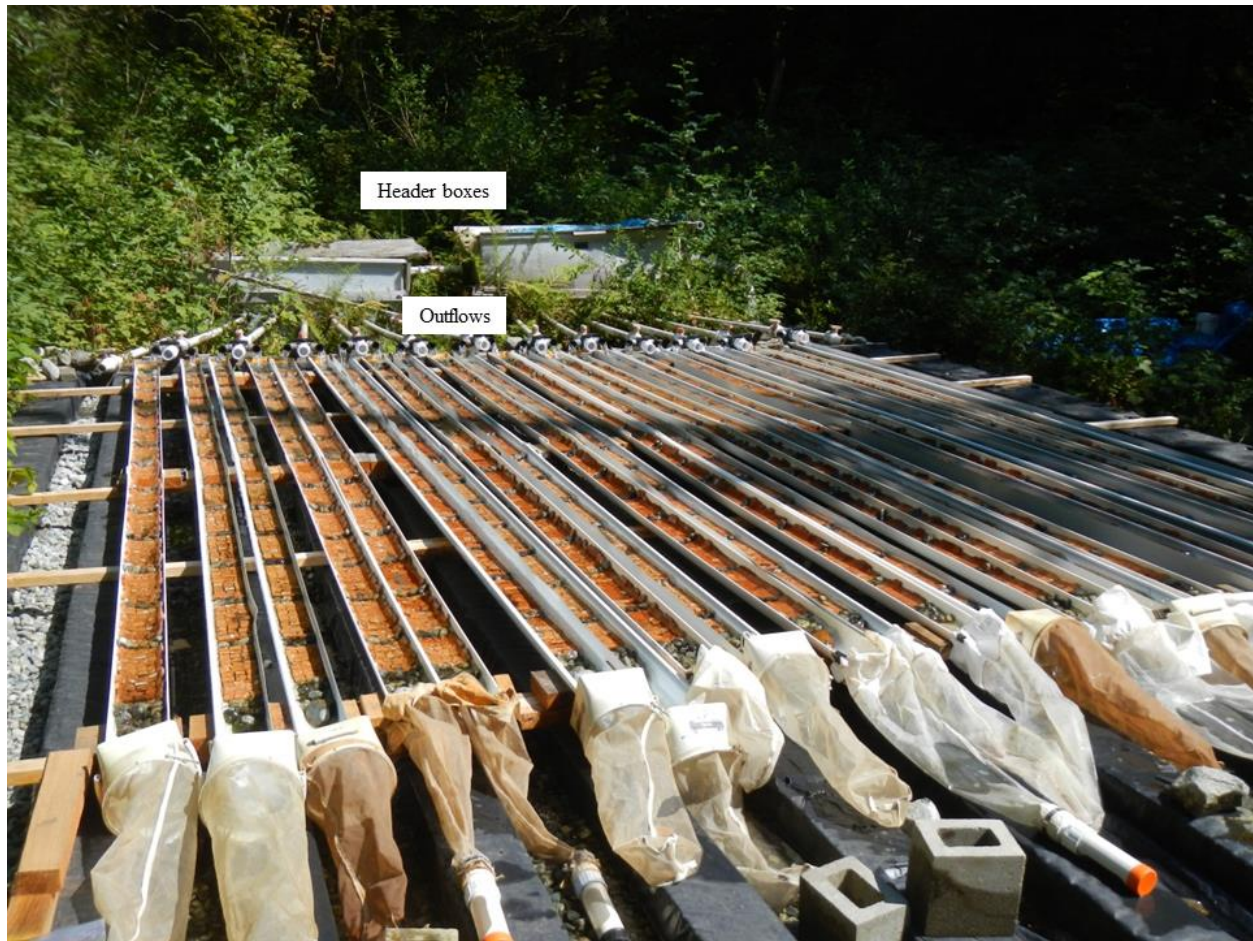


Figure A2: Photograph of drift sampling of all 24 stream mesocosms. Water from Mayfly Creek was piped into the two header boxes, which then distributed flow into twelve outflow spigots that fed one concave and one flat channel.



Figure A3: Photograph of outflow spigots feeding a concave and flat channel before (top) and after (bottom) flow reduction. We reduced flows by opening the middle valve of the three-way splitter, which released flow in between the channels and lowered discharge $\sim 75\%$.



Figure A4: Photographs showing fine inorganic and organic matter on substrate before and after (from left to right) flow increases in flat (top row) and concave (bottom row) channels.

Table A1: AIC_c scores for models explaining variation in the change in aggregate drift measures from before to after flow manipulations. Models are ranked by AIC_c and are listed from most plausible to least plausible based on ΔAIC_c values. AIC_c weights (W_i) represent a probability of model i being the best fitting model within each candidate set. Each model included a random intercept term grouped by channel. Marginal (R^2_m) and conditional (R^2_c) R^2 values represent the proportion of variance explained by the fixed and fixed plus random model components respectively. Other abbreviations are as follows: $L-L$ is the log likelihood; and k is the number of parameters.

Model	k	L-L	AIC _c	ΔAIC_c	W_i	R^2_m	R^2_c
Flow Reduction							
<i>Flux (n 12 h⁻¹)</i>							
Channel + Time	5	-159.98	345.86	0.00	0.41	0.21	0.52
Channel	4	-164.11	346.62	0.76	0.28	0.16	0.35
Flow + Channel + Time	6	-157.10	348.37	2.51	0.12	0.21	0.55
Channel + Time + Channel x Time	6	-156.80	348.50	2.64	0.11	0.21	0.47
Channel + Flow	5	-161.25	348.99	3.13	0.09	0.17	0.39
<i>Flux (g 12 h⁻¹)</i>							
Intercept	3	-69.40	144.24	0.00	0.36	0.00	0.00
Time	4	-68.61	145.22	0.98	0.22	0.04	0.04
Flow	4	-68.89	145.83	1.59	0.16	0.02	0.02
Channel	4	-69.25	146.58	2.34	0.11	0.00	0.00
Flow + Time	5	-68.15	147.04	2.80	0.09	0.05	0.06
Channel + Time	5	-68.40	147.60	3.36	0.07	0.04	0.05
<i>Concentration (n m⁻³)</i>							
Flow + Time + Flow x Time	6	-102.97	228.78	0.00	0.99	0.52	0.85
<i>Concentration (g m⁻³)</i>							
Flow + Time + Flow x Time	6	-23.67	52.73	0.00	0.59	0.32	0.48
Flow + Time	5	-25.31	54.55	1.82	0.24	0.04	0.04
Flow	4	-25.74	55.10	2.38	0.18	0.02	0.02
Flow Increase							
<i>Flux (n 12 h⁻¹)</i>							
Flow	4	-86.23	196.73	0.00	0.64	0.58	0.87
Flow + Channel	5	-82.14	199.65	2.92	0.15	0.58	0.87
Flow + Time	5	-83.20	200.25	3.53	0.11	0.58	0.86
Flow x Time	6	-77.87	200.43	3.70	0.10	0.57	0.91
<i>Flux (g 12 h⁻¹)</i>							
Flow	4	-103.35	229.72	0.00	0.65	0.65	0.87
Flow + Channel	5	-99.29	231.92	2.21	0.22	0.65	0.87
Flow + Time	5	-100.48	232.87	3.15	0.13	0.64	0.86
<i>Concentration (n m⁻³)</i>							
Intercept	3	-34.07	75.39	0.00	0.35	0.00	0.35
Time	4	-32.62	75.91	0.52	0.27	0.08	0.51
Flow	4	-33.14	77.81	2.42	0.11	0.05	0.38
Channel	4	-33.34	78.30	2.91	0.08	0.02	0.38
Flow + Time + Flow x Time	6	-29.06	78.49	3.10	0.07	0.18	0.73
Flow + Time	5	-31.70	78.85	3.46	0.06	0.11	0.53
Channel + Time	5	-31.88	79.29	3.89	0.05	0.09	0.54

Model	k	L-L	AIC _c	ΔAIC _c	W _i	R ² _m	R ² _c
<i>Concentration</i> (g m ⁻³)							
Flow	4	1.97	-0.92	0.00	0.58	0.30	0.30
Channel + Flow	5	0.65	2.27	3.20	0.12	0.31	0.31
Flow + Time	5	0.57	2.40	3.33	0.11	0.30	0.30
Flow + Channel + Flow x Channel	6	1.45	2.51	3.43	0.11	0.41	0.41
Intercept	3	0.28	2.98	3.90	0.08	0.00	0.26

Table A2: Top ranked candidate models explaining variation in per capita drift rates for the six focal taxa. Format and abbreviations are the same as Table A1.

Model	k	L-L	AIC _c	ΔAIC _c	W _i	R ² _m	R ² _c
Flow Reduction							
<i>Baetis</i> spp.							
Flow + Time + Flow x Time	6	52.63	-116.08	0	0.71	0.18	0.46
Time	4	54.33	-113.25	2.83	0.17	0.06	0.31
Flow + Time	5	52.28	-112.57	3.51	0.12	0.11	0.33
<i>Zapada</i> spp.							
Flow	4	80.09	-168.88	0	0.75	0.18	0.18
Flow + Channel	5	76.19	-166.67	2.22	0.25	0.19	0.19
<i>Micrasema</i> sp.							
Intercept	3	7.25	-11.64	0	0.35	0	0.44
Flow	4	6.55	-10.52	1.12	0.2	0.12	0.49
Time	4	6.22	-10.22	1.42	0.17	0.06	0.53
Channel	4	6.08	-9.42	2.22	0.11	0.06	0.48
Flow + Time	5	5.81	-9.38	2.26	0.11	0.19	0.57
Channel + Time	5	5.18	-7.9	3.74	0.05	0.12	0.56
<i>B. retifinis</i>							
Time	4	73.32	-152.81	0	0.29	0.03	0.65
Flow + Time	5	71.2	-152.28	0.53	0.22	0.09	0.66
Intercept	3	75.11	-151.14	1.67	0.13	0	0.59
Flow	4	72.96	-150.65	2.16	0.1	0.06	0.61
Channel + Time	5	70.33	-150.35	2.45	0.08	0.03	0.66
Channel + Time + Channel x Time	6	68.21	-149.86	2.94	0.07	0.05	0.68
Flow + Time + Flow x Time	6	68.12	-149.67	3.14	0.06	0.09	0.64
Channel + Flow + Time	6	68.17	-149.64	3.17	0.06	0.09	0.67
<i>Corynoneura</i> spp.							
Flow	4	82.79	-173.09	0	0.56	0.15	0.15
Flow + Time	5	79.52	-171.6	1.49	0.27	0.16	0.16
Flow + Channel	5	79.09	-170.65	2.44	0.17	0.15	0.15

Model	k	L-L	AIC _c	ΔAIC _c	W _i	R ² _m	R ² _c
Tanytarsini spp.							
Intercept	3	62.2	-125.19	0	0.44	0	0.84
Channel	4	59.6	-123.65	1.53	0.2	0.04	0.85
Time	4	58.43	-123.26	1.92	0.17	0	0.82
Flow	4	59.12	-122.58	2.6	0.12	0	0.85
Channel + Time	5	55.84	-121.64	3.55	0.07	0.05	0.83
Flow Increase							
<i>Baetis</i> spp.							
Flow + Channel + Flow x Channel	6	22.88	-50.99	0	0.69	0.59	0.59
Flow + Channel	5	22.38	-48.51	2.48	0.2	0.5	0.54
Flow	4	23.15	-47.39	3.61	0.11	0.42	0.57
<i>Zapada</i> spp.							
Flow	4	43.45	-92.18	0	0.83	0.39	0.6
Flow + Channel	5	40.05	-89.01	3.17	0.17	0.38	0.6
<i>Micrasema</i> sp.							
Flow	4	3.86	-3.46	0	0.59	0.39	0.84
Flow + Channel	5	3.61	-1.89	1.58	0.27	0.49	0.85
Flow + Time	5	2.47	-0.57	2.9	0.14	0.43	0.83
<i>B. retifinis</i>							
Flow + Time + Flow x Time	6	21.6	-47.96	0	0.77	0.69	0.88
Flow	4	21.54	-44.29	3.67	0.12	0.64	0.66
Flow + Channel + Time + Flow x Time	7	19.39	-44	3.96	0.11	0.68	0.89
<i>Corynoneura</i> spp.							
Flow	4	30.02	-62.62	0	0.6	0.27	0.36
Flow + Channel	5	27.55	-60.06	2.56	0.17	0.28	0.39
Flow + Time	5	27.2	-59.67	2.96	0.14	0.27	0.34
Intercept	3	29.79	-58.93	3.69	0.09	0	0.35
Tanytarsini spp.							
Flow + Channel + Time + Channel x Time	7	23.73	-55.65	0	0.66	0.66	0.89
Flow + Channel + Time + Channel x Time + Flow x Channel	8	22.84	-53.14	2.51	0.19	0.75	0.89
Channel + Time + Channel x Time	6	23.25	-52.61	3.04	0.15	0.36	0.9

Table A3: Top ranked candidate models explaining variation in mean per capita drift rates across 15 taxa. Formatting and abbreviations are the same as Tables 3 and 4. *RBS* is the mean residual body size of a given taxa in the drift relative to the benthos. Each model includes a random intercept grouped by taxa nested within a random intercept grouped by stream.

Model	k	L-L	AIC _c	ΔAIC _c	W _i	R ² _m	R ² _c
Flow Reduction							
Flow + Time + Mobility + Flow x Time + Flow x Mobility	9	343.8	-712.08	0	0.34	0.11	0.45
Flow + Time + Mobility + Drag + Flow x Time + Flow x Mobility	10	340.19	-710.47	1.61	0.15	0.11	0.45
Flow + Time + Mobility + RBS + Flow x Time + Flow x Mobility	10	340.02	-710.2	1.88	0.13	0.11	0.45
Flow + Time + Mobility + RBS + Flow x Time + Flow x Mobility + Flow x RBS	11	337.76	-709.97	2.11	0.12	0.12	0.45
Channel + Flow + Time + RBS + Flow x Time + Flow x Mobility	10	340.63	-709.84	2.23	0.11	0.11	0.46
Flow + Time + Mobility + Drag + RBS + Flow x Time + Flow x Mobility	11	336.48	-708.31	3.77	0.05	0.11	0.45
Flow + Time + Mobility + Drag + RBS + Flow x Time + Flow x Mobility + Flow x RBS	12	334.29	-708.23	3.85	0.05	0.12	0.45
Channel + Flow + Time + Drag + RBS + Flow x Time + Flow x Mobility	11	337.02	-708.22	3.86	0.05	0.11	0.46
Flow Increase							
Flow + Drag + Mobility + Flow x Drag + Flow x Mobility	9	117.19	-251.01	0	0.31	0.46	0.57
Flow + Drag + Mobility + RBS + Flow x Drag + Flow x Mobility	10	114.46	-249.2	1.81	0.12	0.46	0.57
Flow + Time + Drag + Mobility + Flow x Drag + Flow x Mobility	10	114.06	-249.01	2	0.11	0.46	0.57
Flow + Drag + Flow x Drag	7	119.56	-248.91	2.1	0.11	0.43	0.58
Flow + Channel + Drag + Mobility + Flow x Drag + Flow x Mobility	10	114.27	-248.7	2.31	0.1	0.45	0.57
Flow + Drag + Mobility + RBS + Flow x Drag + Flow x Mobility + Flow + RBS	11	112.58	-247.64	3.37	0.06	0.46	0.57
Flow + Drag + RBS + Flow x Drag	8	116.98	-247.43	3.58	0.05	0.43	0.58
Flow + Time + Drag + Mobility + Flow x Time + Flow x Drag + Flow x Mobility	11	111.87	-247.37	3.64	0.05	0.46	0.57
Flow + Time + Drag + Mobility + RBS + Flow x Drag + Flow x Mobility	11	111.4	-247.29	3.72	0.05	0.46	0.57
Flow + Time + Drag + Flow x Drag	8	116.46	-247.05	3.96	0.04	0.43	0.58

Appendix B Supporting information for Chapter 5

Additional description of bioenergetic model

We used a modified version of the Wisconsin bioenergetics model (Stewart and Ibarra 1991, Hanson 1997) to estimate consumption from observed growth. The Wisconsin model is an energetics budget model that assumes that the sole energy source for an animal is from its food and that all energy consumed must be used for basic metabolic processes (metabolism and specific dynamic action), lost through excretion or egestion, or accumulated as somatic growth. These components form the basic energy balance equation:

$$C = R + SDA + F + E + G$$

C is consumption, R is metabolism through respiration, SDA is specific dynamic action, F is egestion, E is excretion, and G is growth. Within the bioenergetics framework, each of these processes is modelled as a function of body size and temperature with specific equations and parameters developed for various species and environmental conditions based on physiology studies in controlled laboratory conditions (described in Hanson 1997).

In our case, since growth rates were measured empirically in the experiment, we estimated specific daily consumption C ($\text{g g}^{-1} \text{ day}^{-1}$) as:

$$C = C_{max} \cdot p \cdot f(T)_c$$

where C_{max} is the maximum daily consumption, an allometric function of fish size and temperature (Table A1, equation 2), p is the proportion of C_{max} actually realized, and $f(T)_c$ is a temperature dependence function for consumption (Table A1, equation 3). We fit the model by iteratively adjusting p such that predicted growth matched observed growth. The model was built with custom functions written in R (version 3.2.3) and ran at daily time steps over the experimental period using mean daily temperature and fish mass (g) as inputs. There was

generally strong correspondence between predicted and observed final mass for each individual fish (Figure B1); however, the model underestimated the magnitude of mass loss for some cutthroat trout ($n = 5$). These individuals were removed for subsequent simulations.

To simulate the influence of altered prey inputs on fish production, we re-arranged the model to predict growth when consumption varied. Here, growth is defined as a function of consumption less the costs of basic metabolism and energy lost to waste.

$$G = C - R + SDA + F + E$$

We used the mean observed terrestrial input rate of $0.005 \text{ g m}^{-2} \text{ day}^{-1}$ as a baseline value, then examined the sensitivity of growth to prey alterations by adding or subtracting multiples of this baseline to consumption. We bounded simulations by restricting p to a maximum of 1; in other words, fish were not allowed to consume more than their maximum daily ration. This may be conservative given the considerable plasticity in digestive capacity observed for salmonids (e.g., Armstrong and Schindler 2011, Armstrong and Bond 2013); however, given the short time frame of our experiment and simulations, we assumed constraining consumption to C_{\max} would give a reasonable approximation. Furthermore, it is likely that physical constraints on prey capture success in flowing water (e.g., Piccolo et al. 2008), which we did not account for in the model, would limit prey intake at augmentation levels near or below the physiological maximum.

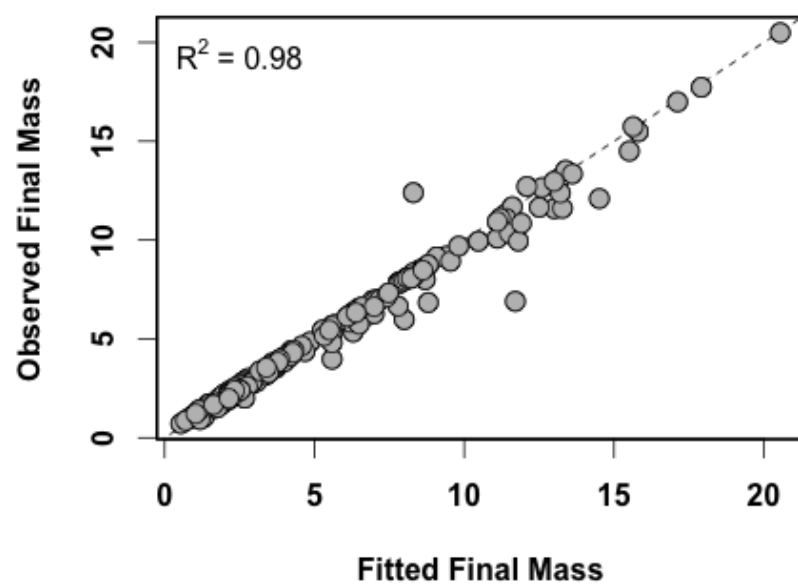


Figure B1 Final mass (g) of each individual fish predicted by the bioenergetic model plotted against the final mass of each fish observed at the end of the experiment. The dotted line represents a 1:1 relationship.

Table B1. Output from model selection for main experimental responses. Abbreviations are as follows: LL is the log likelihood; OLS is ordinary least squares; NLS is nonlinear least squares; GLM is generalized linear model; ΔAICc is the difference between a given model and the top ranked model in each candidate model set; W_i (0-1) is the probability a given model is the most parsimonious model in a candidate model set; RSME is the root mean square error, which was used to evaluate the fit of nonlinear models. All responses for GLM models are on a logit scale. ** We did not attempt to estimate parameters from the M-H model due to parameter autocorrelation.

Response	Parameters	Form	Fit	LL	ΔAICc	W_i	R^2	r^2	RSME	β (\pm 95% CI)	β_0
Total production (g m⁻²)		Gaussian									
	log(Pool area + 0.5)		OLS	15.42	0	0.38	0.71			2.55 (0.02-5.08)	1.27
	Pool area ²		OLS	15.31	0.22	0.34	0.7			-1.39 (-2.77--0.003)	-0.38
	Pool area		OLS	12.77	0.98	0.22	0.53			0.51 (0.22-0.79)	-0.14
	M-H		NLS	12.93	4.98	0.03					
	Intercept only		OLS	7.27	8.5	0.001					
Total consumption (g m⁻²)		Gaussian									
	M-H		NLS	-6.61	0	0.93			1.96	**	**
	Pool area ²		OLS	-9.41	6.5	0.04					
	log(Pool area + 0.5)		OLS	-12.15	7.6	0.02					
	Pool area		OLS	-12.78	8.7	0.01					
	Intercept only		OLS	-15.44	10.7	0					
Total prey flux (J m⁻² day⁻¹)		Gaussian - log transformed									
	(Pool area)		OLS	-9.53	0	0.99	0.6			-0.32 (-4.82--1.59)	10.19
	Intercept only		OLS	-16.05	11.03	0.01					
Terrestrial proportion		Quasibinomial									
	Pool area		GLM	-90549	0	0.98		0.2		6.0 (2.68 - 9.67)	-5.08
	Intercept only		GLM	-207764	8.53	0.02					

Response	Parameters	Form	Fit	LL	ΔAIC_c	W_i	R^2	r^2	RSME	β (\pm 95% CI)	β_0
Pool density (fish m ⁻²)		Gaussian - log transformed									
	Pool area		OLS	10.47	0	0.99	0.95			-2.49 (-2.84 - 2.14)	3.87
	Intercept only		OLS	-10.1	37.68	0.01					
Prey exploitation (consumption g prey ⁻¹)		Quasibinomial									
	Pool area		GLM	-64.54	0	1				0.99 (0.98 - 1.00)	0.002
	Intercept only		GLM	-511.71	105.12	0					
Efficiency (g produced g consumed ⁻¹)		Gaussian									
	Pool area		OLS	23.1	0	0.97	0.52			0.45 (0.40 - 0.52)	-0.02
	Intercept only		OLS	17.8	7.09	0.02					
Proportion holding territories		Quasibinomial									
	Pool area		GLM	-20.42	0	0.98		0.6		0.02 (0.002-0.18)	0.93
	Intercept only			-27.1	8.19	0.02					

Table B2 The form and R^2 of the most plausible regression model (ranked by AIC_c) relating simulated fish production to pool area for each level of subsidy addition or reduction. In scenario 1, no effects of subsidy additions were allowed in enclosures where consumption efficiency was less than 95%; in scenario 2, additional subsidies were assumed to be consumed at observed efficiency; and in scenario 3, all additional subsidies were allowed to be consumed in all enclosures.

Subsidy Level	Form	R²
<i>Scenario 1</i>		
Increased 2x	Threshold	0.59
Increased 10x	Threshold	0.62
Increased100x	Linear	0.78
Increased 1000x	Linear	0.82
Max consumption	Linear	0.86
Reduced 2x	Threshold	0.58
No subsidy	Quadratic	0.55
<i>Scenario 2</i>		
Increased 2x	Linear **	0.44
Increased 10x	Linear **	0.48
Increased100x	Linear	0.71
Increased 1000x	Quadratic	0.86
Max consumption	Quadratic	0.86
Reduced 2x	Threshold	0.63
No subsidy	Quadratic	0.63
<i>Scenario 3</i>		
Increased 2x	Threshold	0.63
Increased 10x	Threshold	0.63
Increased100x	Linear	0.52
Increased 1000x	Linear	0.46
Max consumption	No relationship	0
Reduced 2x	Threshold	0.63
No subsidy	Quadratic	0.63