Evaluating barriers to dispersal: weirs and tributaries in the montane rivers of the Australian Alps

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Abstract

Dispersal involves the movement of individuals between established populations or colonisation of uninhabited areas and is a key organising process underpinning patterns in populations and communities. Dispersal is a fundamental component of metapopulation and metacommunity theory, central to explaining the underlying the patterns of abundance and distribution of species, both spatially and temporally. Furthermore, dispersal is a main determinant of community assembly, governing how communities are constructed and maintained through immigration.

Barriers that limit or prevent species from dispersing to a location can have a major influence on population dynamics and how communities assemble. In a restoration context, this can result in delayed or poor restoration outcomes due to a lack of dispersing colonists preventing colonisation. In freshwater environments, one key hypothesis describing how dams and weirs affect rivers is that they disrupt longitudinal connectivity, fragmenting river ecosystems, potentially limiting dispersal of biota along rivers. In this thesis, I asked three main questions: 1) Are there natural barriers to dispersal in advective systems? 2) Do artificial barriers hinder dispersal more than natural barriers? 3) Do artificial barriers constrain dispersal in ways that affect population and communities, especially community assembly?

The study focused on rivers located mostly within Kosciuszko National Park, in the Snowy Mountains region of south-east Australia. Many rivers in this area are affected by the Snowy Mountains Hydro-electric Scheme and associated culverts, weirs and dams, which capture and divert numerous alpine and montane streams, severing flow connections between much of the Snowy River catchment and its headwaters.

First, I tested how species dispersal between suitable habitats was influenced by the characteristics of the intervening matrix of unsuitable habitat. Specifically, I examined whether stream insect drift was constrained by natural river features, potentially limiting connectivity within rivers. I found that natural, slow moving pools may limit the connectivity of benthic invertebrate populations in rivers by reducing drift rates between riffle habitats. Furthermore, I determined that the hydraulic conditions within a pool limit drift dispersal and total distance between riffle habitat patches was not an important factor in limiting dispersal via drift.

Secondly, I tested whether species dispersal was constrained by a human-made barrier, potentially limiting connectivity between populations more than natural landscape structures. In a natural river system, I studied whether a weir and associated pool reduced the drift rates of insects to a greater degree than natural pools. This component addressed a major knowledge gap about the effect of weir structures on downstream dispersal of stream biota. The weir consistently reduced numbers of drifting insects for 3 of 4 study taxa, exceeding the reduction of drifters in natural pools. The morphology of the weir pool was substantially deeper and wider and slower than the majority of studied natural pools. The combined effects of much lower average water velocity, multiple large low velocity areas within the weir pool and the weir wall were likely to be central causes of the reduction stream insect drift through the weir.

Lastly, in a multi-year study, I tested whether and how the removal of dispersal constraints affected community assembly in new habitats and whether changed dispersal can alter existing communities. In this study, I investigated the patterns and mechanisms of freshwater invertebrate community assembly after the reintroduction of water to 2 streams downstream of weirs that were previously dry for over 50 years. Colonisation of the newly formed habitat in the tributaries downstream of the weirs was rapid and strongly influenced by dispersal via drift from upstream. Even with some dispersal constraint via reduced drift rates, the new communities rapidly resembled unimpacted communities that were the source of colonists. In the regulated rivers, a reduction in environmental constraints had a much greater influence on the trophic structure of established communities than increased dispersal from the newly formed community in the tributaries.

Collectively, this research has overturned important, pre-existing assumptions about dispersal in advective systems by identifying and quantifying the influence of different types of barriers on movement and the effect of altered dispersal rates on community

assembly. This information can inform the development of river restoration strategies in rivers affected by weirs and dams and elucidate how and why restoration measures may have been unsuccessful in the past.

Declaration

This is to certify that:

1. The thesis comprises only my original work towards the PhD except where indicated.
2. Due acknowledgement has been made in the text to all other material used.
3. The thesis is fewer than 100 000 words in length, exclusive of tables, maps, bibliographies and appendices.

Signed ___________________

Andrew John Brooks

Preface

i) Contributions of all persons involved in any multi-authored publications or articles in preparation included in the thesis

Andrew John Brooks designed the research, conducted the field work, carried out the analysis of data and was the primary author of the papers.

Benjamin Wolfenden assisted in the design of the study, conducted the field work and contributed to manuscript revisions.

Barbara Downes assisted in the design of the study and contributed to manuscript revisions.

Jill Lancaster assisted in the design of the study and contributed to manuscript revisions.

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Chapter 1. Introduction, barriers to dispersal, research aims and summary

1.1. The role of dispersal in population and community ecology

The aim of ecology is to understand the processes underlying the patterns of abundance and distribution of species, both spatially and temporally. A central question ecology seeks to answer is how and why species occur in certain locations and not others. Despite the numerous mechanisms thought to underpin patterns in populations and communities, dispersal is a key organising process (Vellend, 2010). Dispersal can be defined as the movement of individuals between established populations or colonisation of uninhabited areas (immigration and emigration) (Bohonak & Jenkins, 2003). However, dispersal information is limited for many species. Specifically, we require greater knowledge of the innate dispersal abilities of species, species dispersal rates between habitats and the effect of the intervening habitat matrix, the barriers that may impede dispersal (both natural and human-made), and whether dispersal to a location is actually successful (i.e. movement results in colonisation) (Logue *et al.*, 2011; Driscoll *et al.*, 2014; Caplat *et al.*, 2016; Urban *et al.*, 2016). This information is fundamental to increasing our understanding of population and community dynamics, and vital to addressing the challenges of addressing human impacts on ecosystems.

In this chapter, I first summarise how and why dispersal is a fundamental component of population and community ecology. In particular, I focus on the integration of the role of dispersal between local populations and communities into metapopulation and metacommunity theory. Second, I discuss how the lack of knowledge of dispersal rates and the factors that impede dispersal are major challenges to unravelling the relative influence of dispersal on population and community dynamics. Third, I introduce my chosen study systems – rivers – and then discuss how dispersal may be impeded in river systems fragmented by weir and dam structures. I focus on how weir and dam structures may disrupt connectivity between stream insect populations by obstructing downstream movement of larvae via drift, impacting communities and inhibiting the success of river restoration activities. I then outline the major aims and research questions of the thesis and the individual studies I have undertaken to address them. Finally, I summarise the main findings of my studies and how they collectively answer key gaps in our understanding of dispersal and connectivity.

1.1.1. Dispersal and population ecology

The rates of four fundamental processes – births, deaths, emigration and immigration – are principal drivers of populations. Ecological theory historically viewed that population dynamics were primarily governed by species niches, competition and predation in small, ecologically homogenous areas (Ricklefs, 1987). Species niches and competition and predation largely influence birth and death rates, and so the effect of immigration and emigration (i.e. dispersal) was considered minimal. Therefore, most of the ecological research focused on the relative importance of biotic and abiotic processes at local scales affecting birth and death rates. However, the perspective that local populations frequently become extinct and are recolonised by dispersal from other populations had been advocated for decades (Andrewartha & Birch, 1954). The importance of such regional factors gained greater recognition with the development of island biogeography theory (MacArthur & Wilson, 1967), where dispersal (immigration and emigration) was crucial in explaining species diversity patterns.

From the 1970s onwards, the role of dispersal between locations was a significant topic of study for different species and ecosystems. This significantly advanced population ecology through its emphasis on the role of immigration in population dynamics (Ricklefs, 2008). Studies in marine systems showed that although local processes could have substantial effects on the structure rocky intertidal communities, at many locations the supply of larvae was limiting, and regional processes (e.g. such as wind-driven upwelling of offshore waters), explain the composition of local communities (Connell, 1985; Roughgarden, Gaines & Possingham, 1988). Seed dispersal is also one of the key processes determining the spatial structure of plant populations (Eriksson & Ehrlén, 1992). In mangrove species, the dispersal of propagules combined with tidal patterns influenced the establishment of seedlings (Sousa *et al.*, 2007) and the regional species pool and dispersal was strongly related to local species richness of plants in California (Harrison *et al.*, 2006). These studies demonstrated that in some situations the supply of new individuals arriving and recruiting to a location influences populations more strongly than post-recruitment processes, such as mortality resulting from predation, competition or by abiotic conditions causing physical stress.

The mounting empirical evidence of the importance of regional dispersal showed that the view of populations governed almost exclusively by local processes was inadequate to explain population abundance and distribution. Mismatches between species distributions and habitat suitability also further emphasise the deficiency of concentrating predominantly on local factors. For instance, a savanna violet species was often absent from locations with suitable habitat (i.e. favourable environmental conditions) and its distribution was therefore only weakly matched with habitat, reflecting exclusion due to dispersal limitations rather than environmental constraints (Pinto & MacDougall, 2010). Similarly, there was a mismatch between suitable habitat and the distribution of a North American orchid, a result consistent with dispersal limitation (Diez *et al.*, 2014).

Metapopulations

Overcoming the shortfalls of the historical focus on local factors, metapopulation theory highlighted the significance of dispersal as a component of population dynamics. In metapopulation theory, a local population of a species is embedded within a larger group of populations, which are distributed across the landscape in suitable habitat patches, surrounded by a matrix of sub-optimal habitat and are linked by dispersal (Levins, 1969). Metapopulations are thus defined as a set of populations of a single species that are connected by dispersal (Hanski, 1998). In metapopulations, local extinctions following natural and anthropogenic disturbances can be offset by dispersal and recolonisation from other populations.

There are a number of categories that have been used to describe metapopulation dynamics (Harrison, 1991). In classic metapopulations (Levins, 1969), all local populations are similar in size and equally prone to local extinction and the metapopulation persists through continuous recolonisation amongst patches. In contrast, mainland-island metapopulations describe a population spatial structure where a large, permanently occupied habitat patch is surrounded by smaller patches of similar habitat quality with temporary populations. These smaller habitat patches can be recolonised by the larger habitat patch which provides a source of colonists. The mainland-island concept incorporates source-sink dynamics, whereby individuals may occur in "sink" habitats (i.e. “islands”), where local reproduction is too low to balance local mortality, possibly due to unsuitable habitat or small population size, but populations may persist, being locally maintained by continued dispersal and recolonisation from "source" populations (i.e. “mainland”) (Pulliam, 1988; Eriksson, 1996). In the patchy population concept, local populations are so strongly connected by dispersal that local extinctions rarely occur due to frequent colonists, and they are effectively a single population. Non-equilibrium metapopulations consist of local populations with more frequent extinctions than recolonisations and consequently the species is declining regionally (Harrison, 1991). Finally, local populations may be isolated and individuals rarely disperse amongst them. In this situation, local populations are sustained by recruitment from local dispersers rather than other populations and are called “closed” or “isolated” (e.g. marine fishes; Swearer *et al.*, 1999).

Empirical evidence for classic metapopulations (*sensu* Levins, 1969) is scarce and suggests that they are rare in nature, however dispersal is generally found to influence population dynamics to some degree (Baguette, 2004; Fronhofer et al., 2012). For example, a study of 44 beetle species found almost no evidence of classic or source-sink metapopulation structure in a large, naturally fragment landscape, and that local habitat conditions (e.g. vegetation type) commonly influenced populations (Driscoll et al., 2010). Dispersal between patches was an important factor for 30% of beetle species, suggesting that dispersal limitation influenced community development, but classic or source-sink metapopulations were not common. This example and others (see Baguette, 2004; Fronhofer *et al.*, 2012) indicate that only a small proportion of populations may fit neatly into a classic metapopulation model. However, the main metapopulation categories are not mutually exclusive and represent a continuum of processes, with many populations intermediate between categories or exhibiting characteristics of several population processes. Where the spatial structure of a population fits on the continuum will depend on the amount of dispersal between populations and the susceptibility of local populations to extinction (Thomas & Kunin, 1999).

In summary, metapopulation theory emphasises the role of dispersal, which can affect population dynamics as much as local processes (e.g. competition and predation, abiotic conditions) influence average birth and death rates (Hanski, 1998). Given that dispersal rates are one of the main factors influencing the spatial structure of populations (Ovaskainen & Saastamoinen, 2018), knowledge of species dispersal rates are critical to fully understanding population dynamics.

The metapopulation concept focuses on single species and their persistence in spatially distinct habitats linked by dispersal. However, this view ignores the possibility that species may affect each other’s birth and death rates and may be a significant source of variation affecting community composition (Wilson, 1992). I now consider how species interactions and dispersal processes are integrated into community ecology.

1.1.2. Dispersal and community ecology

Communities comprise groups of populations of different species occupying the same geographical area. The importance of regional factors (i.e. dispersal) in governing the structure and dynamics of ecological communities has also developed in tandem with metapopulation theory over recent decades, leading to the concept of a “metacommunity” (Leibold *et al.*, 2004). A metacommunity is defined as a network of local communities that are linked by dispersal of multiple species, and is comparable to a metapopulation, expanded from single to multiple species. Metacommunity theory provides a framework to explain the linkage between local processes (intra- and inter-specific interactions, abiotic conditions) and regional processes (e.g. dispersal) (Logue *et al.*, 2011). Therefore, the central premise of metacommunity theory is that the composition and dynamics of communities cannot be understood by focusing solely on local-scale processes, and that regional processes must be equally considered.

Community assembly and priority effects

The metacommunity concept emphasises the need to examine multiple, spatially distinct communities and how they are linked by dispersal. The metacommunity approach builds upon community assembly concepts by recognising that dispersal to and from a local community may vary (i.e. sources or sinks for dispersers), and dispersal may play a dissimilar role in community dynamics in different habitat patches. Community assembly, which predated the metacommunity approach, seeks to explain variations in local community composition relative to the influence of local and regional processes, bridging the gap between large and small spatial scales. Community assembly is defined as the process by which local communities are constructed and maintained through immigration from the regional species pool in combination with extinctions (Patrick & Swan, 2011; Fukami, 2015). The regional species pool is the set of species from within the metacommunity that could potentially colonise and establish at a local site (Cornell & Lawton, 1992; Lessard *et al.*, 2012). There are substantial empirical studies supporting the concept that the dispersal from the regional species pool strongly influences local biodiversity (see Cottenie, 2005). For example, Myers and Harms (2011) found seed dispersal increased species richness in plant communities. In zooplankton communities, an experimental study showed that even under similar environmental conditions, very different communities developed as a result of variation in species dispersal (Chase, 2007).

There are three principal determinants of community assembly: dispersal constraints, environmental constraints (abiotic conditions) and biotic constraints, although the term ‘filters’ is often used (Belyea & Lancaster, 1999). The first two factors are external to the community while biotic constraints refer to the internal dynamics of a community (interactions among species), all of which sort and narrow the pool of potentially establishing species. Dispersal constraints determine which species from the pool of potential colonists can disperse to a location. Once a species arrives, it must possess the appropriate traits to establish and survive the environmental conditions present at that site (environmental constraints) (Poff, 1997; Lake, Bond &

Reich, 2007). Subsequently, competition and predation can interact to determine species composition and abundance within a local community (Chesson & Kuang, 2008).

The order and timing of arrival of species is directly influenced by dispersal constraints and is an important element of community assembly. Known as priority effects, these effects can lead to local communities diverging in composition in locations with similar environmental conditions and which share the same species pool (Chase, 2003; Fukami, Mordecai & Ostling, 2016). Priority effects can occur when the species that first colonise a location obtain an advantage over subsequent competitors by monopolising space or resources (De Meester *et al.*, 2016). In these situations, the establishment, growth, or reproduction of the species arriving later is affected by high densities of the first colonisers, altering community assembly (Waters, Fraser & Hewitt, 2013). In addition to influencing the structure of communities, community assembly history can also alter ecosystem functions. For example, altering immigration patterns of wood-decaying fungi resulted in large differences in the rate of decomposition and carbon released from wood (Fukami *et al.*, 2010). In plants, above-ground plant biomass was higher when legumes were sown prior to other functional groups (Weidlich *et al.*, 2017). Consequently, in addition to understanding the intrinsic abilities of species to move between habitats (i.e. dispersal rates), the factors that influence the order and timing of species immigration (e.g. barriers) are an equally important area of research in community ecology. However, the use of empirically derived knowledge about dispersal is often lacking, and this means population and community models often make untenable assumptions.

1.1.3. Challenges to integrating dispersal into population and community ecology

Dispersal is clearly a fundamental component of population and community ecology, underpinning metapopulation and metacommunity theory. However, there are four major aspects of dispersal research that have serious deficiencies, and addressing these knowledge gaps are necessary to progress our understanding of dispersal.

First, a major challenge to unravelling population and community processes is that for many species, knowledge of dispersal is either not available or is of poor quality, particularly for organisms other than birds and mammals (see review: Driscoll et al., 2014). This comprehensive review of 655 dispersal research papers found only 14 % of studies used direct measurements of dispersal. Similarly, a review of empirical studies of metacommunities also found few direct measures of dispersal, where only 5 of 74 studies measured dispersal rates (Logue *et al.*, 2011). As a consequence, population and community models often lack information on rates of dispersal for most species of interest and often incorporate oversimplified measures of dispersal, such as assuming that all organisms disperse similarly across any landscape. For instance, in a recent study of 32 species of birds endemic to mangroves, due to a lack of species specific information on dispersal rates, the same average dispersal distance (317 m) was used for each bird species to derive a dispersal function for use in a metapopulation model (e.g. Huang, Pimm & Giri, 2020). However, a review examining dispersal variation within and between species, found models using species-specific dispersal produced more accurate predictions of range shifts due to climate change than models applying unrealistic measures of dispersal (Urban, Zarnetske & Skelly, 2013).

Furthermore, the use of proxies has been advocated in the absence of direct measures of dispersal. Spatial metrics using the distance between habitat patches are used as a surrogate for connectivity between populations and communities. These types of proxies do not incorporate any species specific dispersal data and assume that smaller distances equate with greater dispersal. Moreover, mathematical approaches used to estimate dispersal distances do not take into account variations in organism or vector behaviours (e.g. Humphries & Ruxton, 2003; Hawkes, 2009). However, species behaviours may drastically alter dispersal distances and the location of colonisation (e.g. Zimmer, Fingerut & Zimmer, 2009; Oldmeadow, Lancaster & Rice, 2010). Dispersal proxies such as body-size and dispersal trait groups (e.g. dispersal *mode* or dispersal *ability*) are also commonly used in metacommunity studies, often in combination with spatial metrics (Jacobson & Peres-Neto, 2010; Urban *et al.*, 2016). However, larger body size may reflect increased dispersal distances for mammals (Sutherland *et al.*, 2000), but may not be a suitable proxy for smaller organisms where larger body size may actually constrain dispersal distances (e.g. bark-living oribatid mites; Bailey *et al.*, 2018). Dispersal traits, such as dispersal *mode* (e.g. swimming, flying, walking), may not relate to actual dispersal rates or distances (Heino *et al.*, 2017). Dispersal *ability* traits are often assigned to species or groups of organisms in the absence of detailed dispersal information (Jacobson & Peres-Neto, 2010) and may similarly fail to accurately estimate dispersal rates between locations. Despite the widespread use of dispersal proxies in population and community studies (see Heino *et al.*, 2017) and call for caution in their use (e.g. Sekar, 2012), there is a risk they are viewed as acceptable descriptors of dispersal and not as interim measures. As such, the use of dispersal traits without supporting empirical evidence could lead to distorted conclusions about dispersal patterns and connectivity between communities.

The second major deficiency in dispersal knowledge is an accurate understanding of which elements of the landscape moderate the movement of individuals. Importantly, a species dispersal ability is not a constant trait, and will vary considerably depending on landscape structure and any alterations to the landscape (Fahrig, 2007). Dispersal constraints or limitations will determine the frequency of dispersal of individuals between populations, affecting the connectivity within metapopulations and metacommunities (Harrison & Hastings, 1996). Consequently, dispersal constraints will influence both the ability of populations to persist through time and the processes that drive community patterns. Landscape features that limit or block an organism from moving are defined as dispersal barriers (Caplat *et al.*, 2016). Barriers can completely block dispersal or may be partial, whereby dispersal rates are lower than would occur in the absence of the barrier, and may be human-made or natural. Large natural features, such as the Amazon River, have been found to limit the dispersal of passerine birds based on distributional range maps(Hayes & Sewlal, 2004) and mountain barriers and dry forest habitat have limited gene flow between populations three congeneric frog species (Crawford, Bermingham & Carolina, 2007). Human made barriers can also limit movement. Dissimilarities in species composition on different sides of a large road indicate that these structures may act as barriers on the movement of bees and wasps (Andersson *et al.*, 2017). In freshwater systems, dams have fragmented rivers, isolating char fish populations and leading to their decline (Morita & Yamamoto, 2002).

However, direct measures of the effect of barriers on dispersal are rare, except for some larger organisms (e.g. turtles, Shepard *et al.*, 2008; fish, Junge *et al.*, 2014). In general, dispersal is assumed to be limited or blocked by a barrier when a species is absent from an area (or in reduced in density) compared to locations with similar suitable habitat. Similarly, dispersal barriers can be inferred by identifying differences in genetic structure between populations (Baguette *et al.*, 2013). Whilst both types of indirect measures are commonly used, only direct measures of the effect of barriers on species dispersal rates will provide actual information of the demographic consequences (i.e. immigration) and thus on population dynamics and community assembly.

The third area that poses a major challenge to evaluating the role of dispersal is distinguishing between successful dispersal and failed dispersal. Although an individual may disperse to a location with suitable habitat, it may fail to reproduce or alternatively, not find a suitable habitat to colonise and thus fail to establish (Bonte *et al.*, 2012; Lancaster & Downes, 2017). The use of dispersal proxies only consider the movement phase of dispersal, and cannot differentiate between the possible mechanisms of failed dispersal. This is an important, but rarely considered, distinction and is a key information gap, requiring not only the study of the movement of individuals, but also of subsequent recruitment.

Lastly, the current information about the influence of dispersal on community assembly processes has significant limitations because of the nature of the studies from which data are gathered. Many of these types of studies are carried out in unnatural environments and by artificially manipulating dispersal. For example, a microcosm study of the effects of species arrival history on the structure and function wood-decomposing fungi was restricted to 10 of 96 naturally occurring species, conducted on small wood disks within a laboratory, and dispersal was manipulated via inoculation (Leopold *et al.*, 2017). The use of mesocosms in community assembly research also illustrates the artificial nature of these types of studies. Louette & De Meester (2007), in their investigation of priority effects, predation and community assembly, used plastic barrels in an outdoor setting, limited the study to three laboratory reared zooplankton species and artificially manipulated dispersal by using different inoculation sequences. In both these examples, dispersal events were completely unnatural and new dispersers arrived to a simplified community and the extension of the results of these types of experiments into the natural world is questionable. Importantly, studies have shown that the strength of species interactions can be dependent on the type of study (i.e. laboratory, mesocosm, field manipulation), with mesocosm studies greatly overestimating the effects of species interactions (Skelly & Kiesecker, 2001; Skelly, 2002). This raises questions about the relevance of conclusions from laboratory and mesocosm studies to community assembly processes occurring in natural environments. Field based studies which include both natural local and landscape process are likely to offer the greatest insight into the role of dispersal in population and community processes. However, this type of investigation is rare because dispersal of multiple species can seldom be manipulated at the landscape scale with any level of replication and over appropriate temporal and spatial scales. The information gained by studies of this nature, although infrequent and difficult, will be invaluable and will address significant gaps in dispersal knowledge.

1.2. River systems and aquatic insect dispersal

Riverine systems have a unique spatial structure that is characterised by a hierarchical branching geometry, described as dendritic ecological networks (Peterson *et al.*, 2013). These systems possess characteristics that make dispersal and connectivity patterns differ from other landscape types, such as patch-like systems common in terrestrial and marine environments. In particular, the dendritic spatial structure and strong unidirectional water flow is thought to impose constraints on the connectivity and dispersal of biota within rivers (Grant, Lowe & Fagan, 2007). In dendritic river systems, the movement of biota is primarily restricted to the river network (Rodriguez-Iturbe *et al.*, 2009). However, overland dispersal between river corridors is possible for some organisms, such as aquatic insects with flying adult life stages (Hughes *et al.*, 2003). Therefore, the connectivity within and between rivers varies depending on the dispersal abilities of an organism at different life stages, the position of populations within the stream network and the extent of stream a species occupies (Hughes, Schmidt & Finn, 2009; Brown & Swan, 2010). Consequently, rivers provide a unique system with which to undertake tests of hypotheses about dispersal.

Freshwater insects are suitable model organisms to evaluate questions about dispersal between populations and the effect of dispersal barriers. They comprise a major component of freshwater biodiversity and have a significant role in a number of different riverine processes as primary consumers, detritivores and predators, influencing nutrient and carbon cycling, primary productivity and decomposition of organic material (Wallace & Webster, 1996; Malmqvist, 2002; Dijkstra, Monaghan & Pauls, 2014). These organisms have complex lifecycles and with varying modes of dispersal. Many stream insects have a relatively long aquatic juvenile stage (either larva or nymph) with a shorter flying adult period (e.g. mayflies). However, the lifecycle of other insects is entirely aquatic (e.g. elmid beetles). For insect species or life stages that are exclusively aquatic, dispersal will be restricted within the river channel, but for species with an adult flying stage, there is the possibility of dispersal between river systems. These differences in life history strategies will determine a species major dispersal mechanisms and its capability to disperse between populations and colonise habitats (Hughes *et al.*, 2008).

1.2.1. Mechanisms of aquatic insect dispersal

There are a number of reasons why stream insects may disperse, such as avoiding inbreeding, locating a new site with fewer resource competitors, and potentially escaping from predators and limited resources (Bilton, Freeland & Okamura, 2001).. Dispersal of aquatic insects can occur through a number of mechanisms: drift, swimming, crawling, and adult flight (Mackay, 1992). In general, crawling and swimming are thought to be small-scale movements of less than a few metres (Freilich, 1991; Mackay, 1992), associated with food resources and foraging behaviour (Kohler, 1984). Therefore, I discuss the two dispersal mechanisms most likely to result in long distance movement, drift and adult flight.

Drift

Drift of stream insects is probably one of the most ubiquitous forms of downstream dispersal and has been frequently reviewed, focusing on the mechanisms that potentially cause drift (see Waters, 1972; Brittain & Eikeland, 1988). Drift is common both in juvenile stages as larvae or nymphs (e.g. baetid mayflies: Wilcox *et al.*, 2008) and also in adults that are fully aquatic (e.g. elmids: Elliott, 2008). There are many complex biotic and abiotic factors that can initiate drift such as discharge (O'Hop & Wallace, 1983; Gibbins, Vericat & Batalla, 2007), resource limitation (Kohler, 1985; Siler, Wallace & Eggert, 2001), predation (Peckarsky, 1980; McIntosh & Townsend, 1998) and competition (Fonseca & Hart, 1996). Drift is also predominately diurnal, with maximum numbers of drifters occurring after sunset, and thought to occur to avoid predation by visual predators like fish (Lancaster, 1992; Schreiber, 1995).

Whilst the causes of entering the drift have been well studied, the role that drift plays in the dispersal of stream insects and metapopulation and community assembly processes, recolonisation and river restoration is not well understood. A key piece of information is the distances insects disperse via drift. Total lifetime drift distances are the sum of numerous small drift movements, and it is unlikely that invertebrates drift for long distances in a single movement (Englund & Hambäck, 2004). Stream insects also possess behavioural ability to exit the drift, and so can control to some extent their drift distance in an individual drift event (Allan & Feifarek, 1989; Oldmeadow *et al.*, 2010). The drift distances of most stages of insects is relatively short, ranging from a few centimetres to several metres (Brittain & Eikeland, 1988; Elliott, 2003). However, despite small individual movements, the combined drift distance during a life-time may be in the range of kilometres (Hershey *et al.*, 1993). However, there is a paucity of knowledge about how barriers, natural and human-made, may reduce drift rates. There is some evidence natural features, such as pools, reduce numbers of larvae of a baetid species drifting between consecutive riffles (Lancaster, Downes & Arnold, 2011). However, this information is restricted to a single species. There are also no current data on the effect of dams or weirs on drift rates, and therefore little understanding of how these structures limit connectivity between populations and communities (see Section 1.1.3).

Adult flight

Insects flying during adult life stages are also important in the dispersal of stream insects. Adult aerial dispersal can occur among riffles within a stream and also among streams (Heino & Peckarsky, 2014). For aquatic insects with aerial adult stages, flying appears to be the main method of dispersal over moderate distances up to 5km. A study of adult caddisflies and mayflies found average inland dispersal distances of between 0.6-1.8km (Kovats, Ciborowski & Corkum, 1996) and strong patterns of genetic differentiation in a predatory caddisfly were detected in streams separated at distances of >3.5km (Addison *et al.*, 2015). For stoneflies, maximum adult dispersal distances of 0.7-1.1km were estimated by stable isotope (^{15}N) enrichment (Briers *et al.*, 2004; MacNeale, Peckarsky & Likens, 2005). However, the majority of stonefly and caddisfly adults (90%) seem to only travel distances of less than 50m (Petersen *et al.*, 1999; Briers, Cariss & Gee, 2002).

In contrast to the estimates of small aerial adult dispersal distances, analyses of multiple studies of genetic variation in a number of stream insects have shown that adults disperse over large distances amongst streams and possibly even catchments (Hughes, Huey & Schmidt, 2013). Surprisingly, genetic differentiation of insect populations between sites within a stream are often greater than differentiation between streams and catchments (Bunn & Hughes, 1997; Hughes *et al.*, 2011). This has been attributed to local populations being the offspring of relatively few females dispersing from other locations within the same stream. A study of the patterns of oviposition and emergence further supports this hypothesis, showing recruitment of baetid mayfly eggs was likely to be a function of the regional supply of dispersing adults rather than from the local supply of adults (Peckarsky, Taylor & Caudill, 2000).

These findings suggest that insect populations are connected primarily by flying adults. Adult insect flight for some species can be mostly restricted to stream corridors (Petersen *et al.*, 2004), and if dams and weirs restrict this mechanism of dispersal along river channels, there could be profound consequences on population and community processes. However, as with drifting insects, there is no information about how dispersal rates may be affected by these structures. Culverts can impede the movement of flying insect adults, possibly due to predation from spiders (Blakely *et al.*, 2006), indicating that in-stream structures have the potential to block dispersal, but we lack detailed information on whether dams and weirs also affect the dispersal of flying insects.

Despite the research on the different modes of dispersal of aquatic insects, it is still unclear at what spatial scale insect populations are connected in freshwater systems (see Downes & Reich, 2008). The lack of dispersal information about aquatic insects and how natural and human-made features limit or constrain successful dispersal are critical issues for understanding connectivity patterns within rivers and fundamental to managing freshwater ecosystems, but remain largely unanswered.

1.2.2. Human impacts on river systems

Freshwater ecosystems are some of the most altered ecosystems worldwide and are experiencing significant declines in biodiversity (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010). Three major factors have been attributed to causing biodiversity declines: catchment alteration, introductions of non-native species and excessive water use by humans (Light & Moyle, 2015). One of the main stressors on river systems caused by human water use is the construction of dams and other instream structures. More than half the world’s large rivers are regulated by dams (Nilsson *et al.*, 2005; Grill *et al.*, 2019) and there are estimated to be over 800,000 weirs and low head dams existing worldwide (Rosenberg, McCully & Pringle, 2000).

Barriers to dispersal – dams and weirs

Dams and weirs regulate river flows, modifying the natural flow regime, reducing species diversity and altering community composition in river ecosystems (Poff *et al.*, 1997; Magilligan & Nislow, 2005). A literature review of ecological responses caused by dams and weirs found 92% of papers reported decreased values of these ecological metrics (Poff & Zimmerman, 2010), and there are multiple hypotheses to explain how species diversity is reduced (Bunn & Arthington, 2002). Dams and weirs are thought to damage aquatic ecosystems by modifying local environmental conditions through excessive sedimentation (Baker *et al.*, 2011) and can reduce geomorphic and hydraulic habitat complexity (Graf, 2006). In addition, the release of water from dams can alter the thermal characteristics of a river by releasing cold or warm water from thermally stratified reservoirs (Olden & Naiman, 2010). One major hypothesis how dams and weirs damage rivers is that they disrupt longitudinal connectivity, fragmenting river ecosystems (Ward & Stanford, 1995), potentially limiting dispersal of aquatic biota along rivers (Ward & Stanford, 1995; Lake *et al.*, 2007) and affecting metapopulation and metacommunity processes (With & King, 1999).

Flow restoration below dams aims to mimic some elements of the pre-regulation flow regime, resulting in changes to the ecosystem so that it resembles a more natural state (Poff *et al.*, 1997; Arthington *et al.*, 2006). Environmental flows generally focus on restoring in-stream physical habitat (i.e. environmental constraints) with little thought given to dispersal constraints, and assumes that species will return and ecological processes will re-establish (Parkyn & Smith, 2011). However, focusing solely on improving local environmental conditions while ignoring larger scale dispersal processes, assumes that dispersal is frequent between populations and unimpeded by barriers. Nonetheless, much of stream restoration is built on the assumption that improvement of local habitat will lead to recovery (e.g. increased biodiversity). Metapopulation and community assembly theory would suggest that rehabilitating local environmental conditions alone may not be sufficient to produce a successful outcome, and that addressing dispersal constraints may be equally critical. Indeed, a review of 78 river habitat restoration projects found almost all but 2 failed to increase biodiversity (Palmer, Menninger & Bernhardt, 2010). There is also limited evidence of the success of environmental flows in restoring rivers and achieving their ecological goals (Souchon *et al.*, 2008). This suggests that dispersal limitation is likely to be an important factor constraining ecological responses to improvements in local environmental conditions (Bond & Lake, 2003; Brederveld *et al.*, 2011; Gray & Arnott, 2011; Brown *et al.*, 2011). In regulated rivers, if dam and weir structures impede dispersal of larvae and adults from upstream source populations, there will be few dispersers to recolonise degraded river sections and restoration may be constrained by a lack of dispersing colonists (Öster *et al.*, 2009). Disentangling the different mechanisms of how dispersal is affected by dams and weirs is critical to understanding how rivers are impacted by regulation and how river restoration techniques are implemented.

Dams can limit the downstream dispersal of aquatic organisms such as plants (e.g. Jansson, Nilsson & Renöfält, 2000) and fish (e.g. Liermann *et al.*, 2012). However, dispersal is rarely directly measured and the barrier effect of dams is inferred from the presence or absence of species, differences in community composition or models which include oversimplified estimates of dispersal (see Section 1.1.1 above).This is a major handicap both to understanding how ecosystems are impacted and determining appropriate river restoration methods. Knowledge of the effect of dispersal constraints on species movement can also inform why a restoration strategy was successful or not (Hulvey & Aigner, 2014), and so I now consider how dams specifically affect dispersal by aquatic insects.

Barriers to aquatic insect dispersal

Despite being a pivotal component of river ecosystems, there are no studies which empirically test whether and how stream insect movement is impeded by dams and weirs, and thus the effect of obstructed dispersal on downstream ecosystem processes (Web of Science search: [dispersal and {weir* or dam*} and barrier* and {river* or freshwater* or stream*}, and {insect* or invertebrate*}]). Seven papers were returned by this search and only one directly measured dispersal. In this study, mass swarmings of an adult mayfly species was observed using cameras, and the authors found that a large bridge functions as an optical barrier for female mayflies during their upstream flight (Málnás *et al.*, 2011). Of the remaining studies, indirect methods were used to determine the influence of barriers on dispersal distances and site occupancy (two used genetic methods, three used modelling approaches and one used differences in community composition) (Monaghan *et al.*, 2001; Dedecker *et al.*, 2007; Brooks *et al.*, 2011; Keller, Strien & Holderegger, 2012; Tonkin *et al.*, 2014; Sondermann *et al.*, 2015). None of these studies provide estimates of rates of dispersal and do not provide useful information about how a barrier may influence population dynamics. Without realistic data on the effect of barriers on dispersal rates, models are unlikely to provide accurate estimates of the impacts of barriers. Therefore, how dams and weirs affect the major pathways and mechanisms of stream insect dispersal and influence downstream population and community processes remains a major knowledge gap.

Connectivity with the regional species pool is a critical requirement for population persistence from disturbances, both natural and anthropogenic, by providing a source of colonists to re-establish after a disturbance (Sedell *et al.*, 1990). Therefore, successful river restoration is reliant on the dispersal of biota from extant populations elsewhere in the river system (Bond & Lake, 2003). If dams and weirs impede the downstream dispersal of aquatic insects then there will be few dispersers to recolonise degraded river sections from upstream even with the provision of environmental flows. Consequently, tributaries are the only likely source of potential aquatic insect colonists, while also providing energy resources, sediment and augmenting flows (Kiffney *et al.*, 2006; Rice, Ferguson & Hoey, 2006; Wilson & McTammany, 2014). Thus, aquatic insect communities in rivers impacted by dams are thought to recover downstream of unregulated tributaries due to dispersal and recolonisation (Storey, Edward & Gazey, 1991; Stanford & Ward, 2001; Katano *et al.*, 2009). However, for tributaries to successfully provide colonists to the main-stem river, their connectivity must remain intact (Stanford *et al.*, 1996).

It is unknown whether and how dams or weirs block or impede dispersing aquatic insect species. Dams can potentially impede the drift of aquatic insects, but could also be barriers to adult insect flight (e.g. Blakely *et al.* 2006). We also know little about how tributaries contribute insect colonists to main-stem rivers. These uncertainties raise questions about the ability of stream insects to disperse long distances and restore regulated rivers. If environmental flows cannot address dispersal constraints or barriers to dispersal, then degraded stream sections will remain disconnected from insect populations required for recolonisation, and biological recovery will not occur regardless of any improvement to the local habitat.

1.3. Research aims and thesis structure

The central question of this thesis is how do natural and human-made features within the landscape influence the dispersal of organisms, and are community assembly processes affected by these alterations to dispersal?

This research is comprised of three components, each of which test key hypotheses about factors that may constrain dispersal and limit colonisation and collectively fill major knowledge gaps regarding the role of dispersal in population and community ecology (outlined in Section 1.1.3):

> **Question 1.** Are there natural barriers to dispersal in advective systems?
>
> **Question 2.** Do artificial barriers hinder dispersal more than natural barriers?
>
> **Question 3.** Do artificial barriers constrain dispersal in ways that affect population and communities, especially community assembly?

Question 1 – Are there natural barriers to dispersal in advective systems? First, I tested whether there are barriers to dispersal caused by natural components of the landscape (Chapter 2 – Paper 1). In terrestrial environments, natural features are known to be barriers to movement. For instance, dry forest habitat can limit the dispersal of wet-forest frog species (Crawford *et al.*, 2007) and large rivers can be a barrier to the dispersal of forest birds (Hayes & Sewlal, 2004). For species that use advection (e.g. by wind or water) to disperse, the effects of the landscape on advective currents and dispersal can be also important. For example, ocean currents can be barriers to the dispersal of planktonic larvae and affect their geographical distribution (Gaylord & Gaines, 2000; Wares, Gaines & Cunningham, 2001). In natural rivers, the flow of water is assumed to transport larval organisms downstream as long as water remains flowing and populations and communities remain connected by this process. Models of connectivity in rivers and streams often make this assumption (e.g. stream hierarchy model; Hughes *et al.*, 2009), and lack consideration of instream barriers to dispersal. However, water currents can be influenced by river morphology, such as deep pools, and it is unknown how these habitat patches impede downstream movement of larvae. In this investigation, I directly measured dispersal between multiple habitat patches and determined how a natural landscape feature modifies dispersal, providing new empirically derived information on whether natural pools reduce the rates of downstream movement via drift of stream insects.

Question 2. Do artificial barriers hinder dispersal more than natural barriers? The understanding of natural dispersal constraints gained in Chapter 2 allowed me to test whether species dispersal was constrained by a human-made barrier to a greater degree than natural landscape structures, again possibly limiting connectivity between populations (Chapter 3 – Paper 2). In terrestrial environments, non-natural structures have been shown to limit the movement of animals, potentially fragmenting populations (e.g. roads, urbanisation, deforestation; Caplat *et al.*, 2016). In advective systems, human-made structures may alter currents in ways that are not found in natural settings, creating greater impediments to dispersal than would be found in unaltered ecosystems. These structures could create environmental conditions that are barriers to an organism's movement either because of behavioural avoidance or mortality when attempting to disperse across the modified environment, but these effects have rarely been studied. This study quantified the effect of a non-natural barrier on the dispersal rates of multiple species in a freshwater system, providing directly measured data about how artificial barriers may affect demographic processes compared to natural barriers.

Question 3. The third component of the thesis tested whether and how the removal of dispersal constraints caused by artificial structures affected community assembly in new habitats and whether changed dispersal can alter existing communities (Chapter 4 – Paper 3). The newly assembled communities may diverge in structure from the source of colonists because the artificial barrier varies the order, frequency and identity of species arrival and monopolisation by early colonists (Chase, 2003; Schröder, Persson & Roos, 2005). The composition of existing communities may change in response to increased numbers and diversity of dispersers or could be resistant to colonisation because the new dispersers arrive in an already colonised, densely occupied habitat and fail to become established (Waters *et al.*, 2013). These are major hypotheses that are rarely tested in natural systems at landscape scales.

Dispersal is a three-stage process beginning with the initial departure or emigration stage, the movement or transport stage and finally, the settlement stage at a new location (i.e. immigration) (Ronce, 2007). Chapters 2 and 3 answered questions about whether and how natural and human-made barriers impede organisms during the movement phase of dispersal, but do not provide a complete picture of the consequences of these potential dispersal impediments. In Chapter 4 (Paper 3), I quantified the how changes to dispersal affected the final stage of dispersal – settlement. By measuring both dispersal rates during movement and colonisation in newly formed habitats and compositional changes in existing communities, this study also determined whether priority effects are influential or not in natural systems that are re-assembling.

1.4. Study area

The study focused on rivers located mostly within Kosciuszko National Park, in the Snowy Mountains region of south-east Australia (Figure 1). In this area, the Snowy Mountains Hydro-electric Scheme captures and diverts the headwaters of numerous alpine and montane streams (12 rivers and 71 creeks). The Scheme includes 16 dams, 18 aqueducts, 19 trans-mountain tunnels, 7 power stations and 2 pumping stations. In addition to generating electricity, the Scheme is used to regulate the supply of water for irrigation in the Murrumbidgee and Murray valleys in conjunction with downstream irrigation dams. Impoundments and diversions throughout the Snowy River catchment have severed flow connections between much of the Snowy River catchment and its headwaters. Ninety-nine percent of mean annual flows from the upper catchment are diverted to the Murrumbidgee and Murray Rivers through a series of weirs and impoundments, disrupting the natural flow regime to downstream reaches and impacting on aquatic communities. Mowamba River is the first major tributary of the Snowy River downstream of Jindabyne Dam and the only potential snowmelt tributary within 180km of the dam. Mowamba River weir diverts all flows up to $5.7m^3s^{-1}$ from the river to Jindabyne Dam via an aqueduct (Figure 1).

Similarly, the weirs on Middle Creek and Diggers Creek (tributaries of the Geehi River and Snowy River below Island Bend Dam respectively) were used to divert almost all stream flows into nearby dams for hydropower generation and diversion to different catchments for irrigation (Figure 1). Thus, the stream sections downstream of these weirs have previously been dry for > 50 years and contributed no flow to the downstream regulated rivers except during floods. The regulated river sections also received no flow from the upstream dams except for small volumes from seepage.

Collectively, these rivers and human-made barriers provided a rare opportunity to conduct a unique set of hypothesis tests in ways that have never been undertaken before.

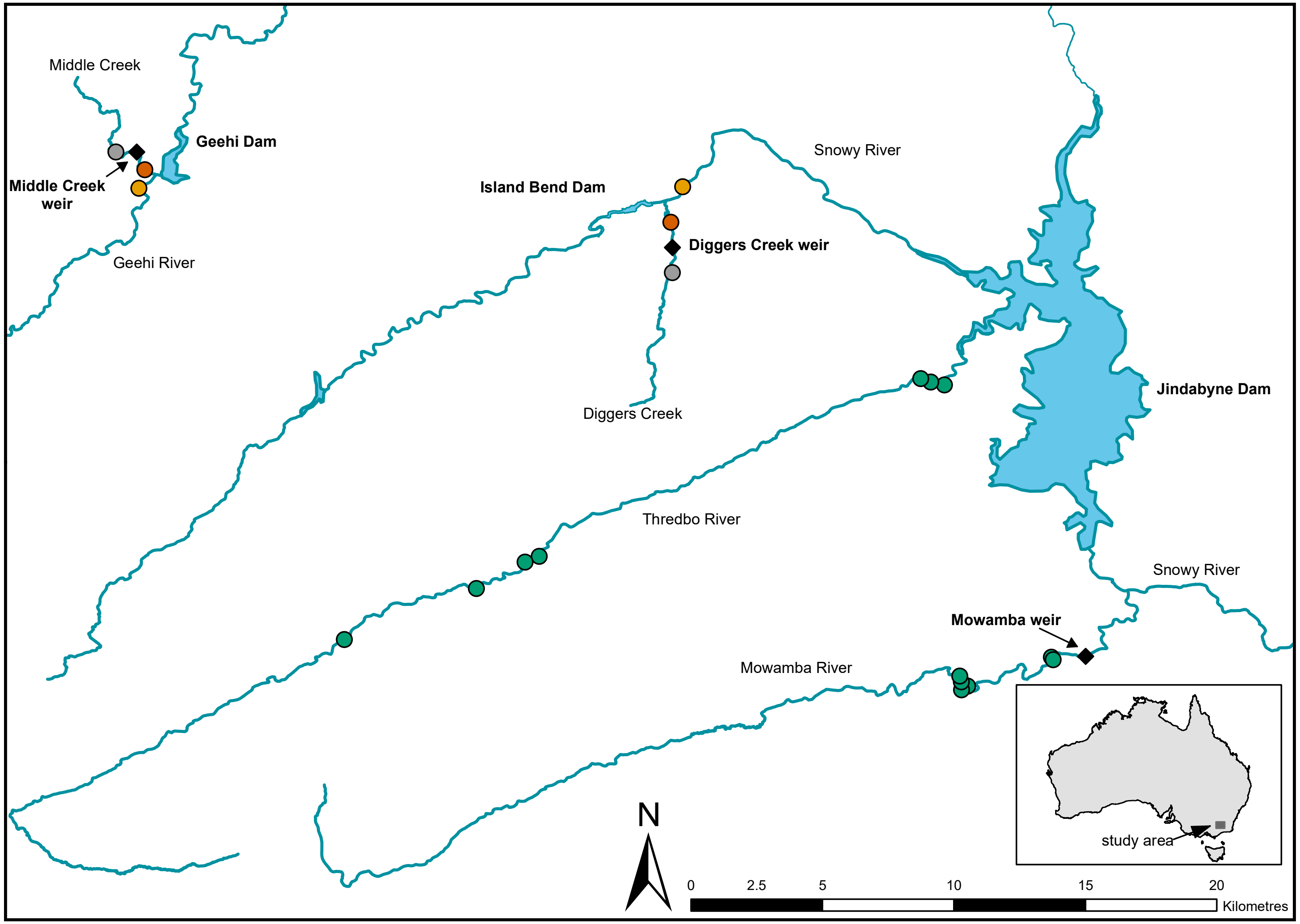

Figure 1 Location of sampling sites within Kosciuszko National Park in the Snowy Mountains region of NSW, Australia. Location of natural pool sampling sites on the Thredbo and Mowamba rivers (green circles) and the Mowamba River weir (black diamond) used in Chapters 2 and 3. Location of sampling sites on Diggers Creek and Geehi River, Middle Creek and Snowy River (orange, vermillion and grey circles) and the Diggers Creek and Middle Creek weirs (black diamonds) used in Chapter 4.

1.5. Summary of findings

1.5.1. Dispersal constraints caused by natural pools

In Chapter 2 (Paper 1), I tested the hypothesis that dispersal between suitable habitats is constrained by natural features, potentially limiting connectivity between populations. Specifically, I determined whether multiple species of riffle dwelling insects drifting between riffle habitats (i.e. patches of suitable habitat) were impeded by natural pools with slow-flowing water (i.e. unsuitable habitat) that limited or prevented dispersal between riffle habitats. This study was undertaken in 13 sites within two unregulated tributaries (Thredbo River, Mowamba River) of the Snowy River on 2 occasions (Figure 1). Whether or not pools impeded drift dispersal was expected to be related to the hydraulic conditions experienced by the organism while attempting to traverse the pool and the distance between riffle habitat patches.

I concluded that stream insect drift between riffle habitats was constrained by the intervening pool habitats between these habitat patches. I found that deep, slow moving pools can substantially limit drift rates and connectivity between riffles. Importantly, I showed that the hydraulic conditions within a pool limit drift dispersal and total distance between riffle habitat patches was not important factor in limiting dispersal via drift.

Quantifying how pools, a natural river feature, constrain stream insect dispersal has provided new empirically derived information on how pools are semi-permeable barriers, changing our perception rivers as simple, connected advective systems. This study avoided the pitfalls of mathematical approaches using distances between habitat patches to estimate dispersal by directly quantifying dispersal rates amongst patches (e.g. Altermatt, Seymour & Martinez, 2013). These results indicated that drift may have a limited role in defining the large-scale population structure of stream insects. Many models of community connectivity in rivers assume distance between locations are a surrogate for connectivity and that drift is unimpeded (e.g. Sarremejane *et al.*, 2017). My research has showed a landscape feature (i.e. pools), is one mechanism that could limit connectivity within river systems, and that distance alone may not reflect dispersal limitations. This finding, while restricted to rivers with distinct pool-riffle sequences, can be generalised because this study was undertaken in multiple different pools within two rivers over two occasions. My findings also support studies which have found genetic differentiation of juvenile insect populations between sites within a stream is often greater than between streams and catchments (Hughes *et al.*, 2011). There should be little genetic difference at this scale if drift was frequent and common over large distances, and my research indicated limited dispersal by drift of aquatic insects within a stream caused by pools could contribute to these genetic patterns.

1.5.2. Dispersal constraints caused by weirs

Despite hypotheses about the effects of human-made structures acting as a barrier to movement, there are few empirical studies of their significance on dispersal. To address this knowledge gap, I specifically tested whether a weir (on the Mowamba River; Figure 1) and associated pool reduced the drift rates of insects to a greater degree than natural pools in Chapter 3 (Paper 2).

The weir consistently reduced the numbers of drifting insects for 3 of 4 study taxa to a greater degree than natural pools. The pool morphology of the weir pool was substantially deeper and wider and slower than the majority of studied natural pools. The combined effects of much lower average water velocity, multiple large low velocity areas within the weir pool and the weir wall were likely to be central causes of the reduction stream insect drift through the weir.

In Paper 3, I also assessed whether invertebrates drift rates were affected by weir pools. In two weirs on different rivers (Middle Creek, Diggers Creek; Figure 1), I found altered drift community composition and reduced drift rates of 5 of 8 study taxa. Although pool morphology was not directly measured in Paper 3, the main mechanism of drift reduction in Paper 2 – the areas of low velocity in the weir pools – were likely to be responsible for reduced drift rates in these weir pools.

The results of Paper 2 and Paper 3 indicate that weirs can be a significant barrier to drift of some stream insects under moderate flow conditions, and may disrupt downstream movement to a greater degree than natural river features that create slow moving water (i.e. pools). My research is the first to provide a direct measure of the effect of multiple weirs on dispersal rates of freshwater invertebrates. This information is important, because dispersal limitation caused by weirs may result in delayed or poor restoration outcomes due to a reduction of dispersing colonists (Hulvey & Aigner, 2014), and flying adults will become the primary source of colonists to restored stream sections. The focus of much of stream restoration is on rehabilitating in-stream physical habitat or providing a more natural flow regime to hydrologically altered rivers (i.e. environmental contraints; Palmer, Hondula & Koch, 2014). My research has shown that dispersal limitations caused by weirs and similar structures will need to be considered, in addition to environmental constraints, in any river restoration program. This is particularly important in river systems where there are weirs on tributaries of main-stem rivers with large dams. In these situations, the tributary is expected to provide a source of colonists to the regulated river, aiding in downstream recovery, but the presence of weirs may interfere with this process.

1.5.3. Effect of dispersal constraints caused by weirs on downstream community assembly after flow restoration

Chapter 4 (Paper 3) tested two general hypotheses in community assembly: (i) whether removal of dispersal constraints affected community assembly in new habitats and (ii) whether changed dispersal can alter existing communities. In both hypotheses, priority effects may play a role in community assembly

Firstly, this study tested whether changes to dispersal rates and the species dispersing to a location are influential in communities that are re-assembling in newly formed habitat. I specifically investigated the patterns and mechanisms of freshwater invertebrate community assembly after the reintroduction of water to 2 streams downstream of weirs that were previously dry for over 50 years (Figure 1). The community in the new habitat may be influenced the order, frequency and identity of species arrival, with early-arriving species gaining precedence to resources and becoming dominant in the community and excluding later arriving species. Secondly, I explored whether the obstruction to downstream dispersal by weirs had consequences for recolonisation from upstream sources into established communities. An increase in numbers and diversity of dispersers to an existing community may change their composition. However, many of the new arriving species will be confronted by an existing community with many species monopolising similar niches, potentially limiting the establishment of the new species dispersing from the tributaries.

This study was carried out over 2 years post-flows, and so encompassed sufficient time for different colonisation mechanisms to occur: dispersal by drift and recruitment from flying adults dispersing and laying eggs. Thus, the major shortcomings of many dispersal studies (see Section 1.1.3) were overcome by (i) directly measuring species dispersal rates of (ii) two different life stages in (iii) natural systems at appropriate spatial (i.e. landscape) and temporal scales.

I found successful colonisation of benthic communities in the tributary stream sections below the weirs after the release of water, and the communities became similar to upstream sites after 2 years. Colonisation of the newly formed habitat in the tributaries downstream of the weirs was rapid and strongly influenced by dispersal via drift from upstream. Therefore, even with some dispersal constraints via reduced drift rates, the new communities rapidly resembled unimpacted upstream communities that were the source of colonists.

Thus, the findings of Paper 3 regarding colonisation in the tributary downstream of weirs were in contrast to the conclusions I made in both Paper 1 and 2, where I hypothesised that the reduction in invertebrate drift caused by natural river features (i.e. pools) and weirs may have persistent effects on downstream colonisation patterns. My research indicates that in newly created stream habitat, there were no long lasting effects of reduced dispersal or order of species arrival on freshwater invertebrate community assembly (i.e. priority effects). This finding is contrary to many studies of priority effects conducted in artificial ecosystems such as mesocosms or microcosms, where variations in dispersal history were found to cause divergence in community composition (e.g. Chase, 2007; Fukami *et al.*, 2010). These conflicting results may be attributable to laboratory and mesocosm studies of species interactions yielding unrealistic responses (Skelly & Kiesecker, 2001; Skelly, 2002). Additionally, some studies had artificial dispersal that does not reflect natural variation and most studies are carried out small spatial scales relative to those over which populations extend. Thus, the outcomes of mesocosm and microcosm experiments may not be an accurate guide to the effect of dispersal history on community assembly occurring in natural environments.

The presence of unaltered upstream communities providing a pool of colonists was critical to successful tributary community assembly in the tributary. The continuous dispersal from upstream of the weir, despite reductions in drift rates, was sufficiently high that early colonising species did not have time to dominate and preclude colonisation by subsequently arriving species. An alternative explanation is that invertebrates drifted through the weir irregularly (e.g. during high flows) and colonised the tributary during times that we did not sample drift from the weir. Research quantifying drift rates during high flow events and subsequent colonisation would help unravel the potentially different contributions of continuous daily invertebrate drift and episodic drift events.

Additionally, I argued that based on the results of Paper 1 and 2 and recent literature (see Lancaster, Downes & Arnold, 2010; Encalada & Peckarsky, 2012; Macqueen & Downes, 2015), adults would play a significant role in the recolonisation of restored river sections. After 2 years of recolonisation in the tributary, the results of Paper 3 indicate that drift may be the primary mechanism for the recovery of benthic invertebrates in areas where new habitat is created, and flying adults have little role in initial colonisation success. Further exploration of the role of flying adults in colonisation of new habitats relative to drift from upstream sources, would provide valuable information for understanding the population dynamics of freshwater invertebrates and potential constraints on successful river restoration.

Paper 3 also tested the hypothesis that increased flows and dispersal from the tributaries would alter existing downstream regulated river communities. Overall, there was a 28 to 56-fold increase in discharge in the regulated rivers, resulting in gradual changes (i.e. assembly) to the existing communities, increasing community similarity to upstream sites to approximately 65% similar after 22 months.

For regulated rivers, a reduction in environmental constraints had a much greater influence on the trophic structure of established communities than increased dispersal from the newly formed community in the tributaries. In particular, some trophic groups (gatherers and scrapers) did not respond to increased dispersal from the tributary into the regulated location (i.e. a reduction in dispersal constraints). This finding indicates that environmental or biotic constraints may have prevented the new dispersers from the tributaries from establishing in the regulated locations.

A notable change in the existing benthic community was an increase in densities of filter feeders, despite no increase in dispersal of this group from the tributaries. One possible explanation is that increased flows reduced environmental constraints by increasing the area of fast-flowing habitat in what was previously a predominantly lentic environment, resulting in more space for filter feeders (Brooks & Haeusler, 2016; Wallace & Merritt, 1980).

This study suggests that small tributary sourced flows were successful in alleviating environmental constraints for some taxa (i.e. filter feeders), but were not sufficient to create an adequate disturbance in extremely hydrologically altered rivers to create additional habitat to benefit other invertebrate groups (i.e. gatherers and scrapers). Recovery of regulated rivers downstream of unregulated tributaries is a fundamental component of the Serial Discontinuity Concept (Ward & Stanford, 1983) and associated theories such as the Link Discontinuity Concept (Rice, Greenwood & Joyce, 2001). However, successful restoration may require large releases of water from dam structures to create a disturbance in regulated systems and initiate a new round of community assembly, provided there is an adequate source of colonists (i.e. from tributaries).

1.5.4. Summary

Collectively, this research has overturned important, pre-existing assumptions about dispersal in advective systems by identifying and quantifying the influence of different types of barriers on movement and the effect of altered dispersal rates on community assembly. Field research to date has often used unsuitable or untested dispersal metrics or dispersal traits, while laboratory research frequently used simplified communities with few species where dispersal is carried out by researchers and is hence completely artificial. Some valuable and interesting work has been accomplished using field mesocosms, but the small spatial scales and manipulated dispersal may not reflect natural dispersal mechanisms and thus community assembly processes. In contrast, my studies were carried out at landscape scales using direct measures of dispersal and so provide realistic estimates of dispersal rates and direct evidence of the effects of barriers on dispersal and colonisation patterns. This understanding of how barriers impede the movement phase of dispersal provides vital information with which to improve models of population and community connectivity in river systems. Current models of connectivity in rivers and streams often assume that downstream advective dispersal is relatively uninterrupted by physical features, but my research has shown that barriers are key factors limiting movement amongst populations and communities. Moreover, my research has revealed that certain types of geomorphic channel units can act as barriers, not just physical structures such as human-made walls. This study has also provided new information on dispersal constraints and community assembly, data that is critical to improving methods of river restoration. I found that communities can quickly recover when natural channels that have been dry for decades are re-wetted (i.e. restored), but this outcome was reliant on flows that deliver dispersers from upstream, unimpacted communities. In contrast, boosting dispersal did not greatly alter the composition of existing communities in highly modified river systems. Therefore, increases in discharge and dispersal produced different outcomes in new versus established communities. This research has shown that, providing there is a source of drifters, successful restoration may require large releases of water from dam structures to provide diverse microhabitats and initiate a new round of community assembly. This novel finding will aid the development of restoration strategies in rivers affected by weirs and dams and will help elucidate how and why restoration measures may have been unsuccessful in the past.

Chapter 2. Paper 1 – Do pools impede drift dispersal by stream insects?

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Summary

1. Drift of stream insects is one of the most ubiquitous forms of downstream dispersal and thought to be a key factor influencing the persistence of local populations. Identifying the factors that limit drift dispersal between habitat patches is needed to understand the connectivity of insect populations along river channels.

2. We determined whether insects drifting between riffle habitats (i.e. patches of suitable habitat) were impeded by natural, slow-moving pools (i.e. unsuitable habitat), limiting dispersal to the next downstream riffle, by estimating drift rates entering and exiting pools. We also investigated whether the frequency of drift dispersal between riffle habitats decreased with increasing pool size (length, width, depth), resulting from increasing areas of low or zero current velocity and/or distance between habitat patches. We then used this information to estimate drift distances of each taxon by modelling the distances downstream that a proportion of individuals arising from a source riffle will remain in the drift.

3. We found that for the majority of study taxa (7 of 8 taxa), drift dispersal between riffles was significantly hindered by the intervening pool habitat, supporting our prediction that natural, large slow-moving pools impede the number of invertebrates drifting between riffle habitats. There were three taxa whose drift rates were significantly reduced by increasing pool depth or width – *Offadens hickmani*, *Austrophlebioides* spp. and *Austrosimulium* spp., and weak relationships ($P<0.10$) were also found for *Coloburiscoides munionga* and *Asmicridea edwardsii*. Drift was not associated with pool length for any species, suggesting that hydraulic conditions within a pool limit drift dispersal and not the total distance between riffle habitat patches.

4. Overall, our results suggest drift dispersal seems unlikely to be a major mechanism of long distance dispersal, for at least some common insects. These findings indicate that drift may play a more limited role in stream insect dispersal than is commonly considered and that flying adults may therefore have much greater influence on connectivity amongst populations.

Introduction

Dispersal of biota is one of the key factors influencing the spatial structure and persistence of local populations. This is because local extinctions following natural and anthropogenic disturbances can be overcome by recolonisation from other populations that are linked by dispersal (Hanski, 1998; Leibold *et al.*, 2004). Within riverine systems, dendritic network structure and strong unidirectional water flow can restrict dispersal, particularly for organisms with life stages that are strictly aquatic (Grant, Lowe & Fagan, 2007; Heino *et al.*, 2015).

The drift of stream insects, downstream movement while entrained in stream currents, is common in many lotic species (Waters, 1972; Brittain & Eikeland, 1988). Drift is thought to be initiated by interacting biotic and abiotic factors including discharge and its associated hydraulic forces (e.g. O'Hop & Wallace, 1983; Gibbins, Vericat & Batalla, 2007), resource limitation (e.g. Kohler, 1985; Siler, Wallace & Eggert, 2001), predation (e.g. Peckarsky, 1980; McIntosh & Townsend, 1998) and competition (e.g. Fonseca & Hart, 1996). Drift occurs both in juvenile stages as larvae or nymphs (e.g. baetid mayflies: Wilcox *et al.*, 2008) and also in adults that are predominately aquatic (e.g. elmids: Elliott, 2008b). Consequently, drift is thought to be one of the main dispersal mechanisms for the redistribution of some stream insects (Mackay, 1992).

While drift has the potential to exert an overarching unidirectional control on population connectivity, recent evidence suggests dispersal by drift of aquatic insects within a stream may be minimal. For example, genetic differentiation of juvenile insect populations between sites within a stream is often greater than between streams and catchments, but if drift was widespread, there should be little genetic difference at this scale (Bunn & Hughes, 1997; Hughes, Huey & Schmidt, 2013). Studies of baetid larvae have also found dispersal distances can be shorter than routinely assumed (Lancaster, Downes & Arnold, 2011). For stream insects, it is unclear at what spatial scale populations are connected within river networks. To help resolve these uncertainties, measuring the rates of movement of stream insects between patches of suitable habitat is necessary (Downes & Reich, 2008). Therefore, identifying the factors that limit drift dispersal between habitat patches is critical for greater understanding of the connectivity of insect populations at broader spatial scales.

Natural river features can influence drift dispersal, potentially limiting connectivity within rivers (Alp *et al.*, 2012). In particular, the spatial configuration of low and zero flow areas throughout a stream channel will have a strong influence on drift dispersal distances (Lancaster, Hildrew & Gjerlov, 1996; Bond, Perry & Downes, 2000). Pools are regions of deeper, slower moving water and have been suggested as areas of drift deposition (Martin & Knight, 1989). The patterns of low velocity areas throughout a pool will be determined by the morphology of the pool, in particular its depth and width (Emery *et al.*, 2003; Gordon, McMahon & Finlayson, 2004). Pool length could also affect drift dispersal rates because successful movement between habitats is expected to reduce as the costs of movement (e.g. exposure to predation, energy expenditure) increase (Bowler & Benton, 2005). The degree to which pool morphology affects drift dispersal will be dependent on species behaviours such as altering body posture and swimming ability, and decisions about whether to continue or exit the drift (Allan & Feifarek, 1989; Oldmeadow, Lancaster & Rice, 2010).

The aim of this study was to determine whether stream insect drift is constrained by natural river features, potentially limiting connectivity within rivers. Specifically, we determined whether lotic insects drifting between riffle habitats (i.e. patches of suitable habitat) were impeded by natural, slow-moving pools (i.e. unsuitable habitat) that limited or prevented dispersal between riffle habitats. Whether or not pools impede drift dispersal is expected to be related to the hydraulic conditions experienced by the organism while attempting to traverse the pool and the distance between riffle habitat patches

We investigated the drift dispersal of stream insects between riffle habitat patches by testing two *a priori* predictions. (i) If natural, large slow-moving pools impede the number of drifters, there will be greater numbers of drifting insects entering a pool from an upstream riffle (immigrants) than leaving the same pool (emigrants). This would indicate that drift dispersal between riffle habitat patches is limited. Alternatively, if pools do not impede drift then dispersal and emigration will equal or sometimes exceed immigration. To further explore the mechanisms that may influence the drift dispersal between riffles, we predicted, (ii) the frequency of drift dispersal between riffle habitats will decrease with increasing pool size (length, mean width, mean depth). This would result from the increasing areas of slow- or non-flowing water and increasing distance between habitat patches limiting drift dispersal distances (Lancaster *et al.*, 1996; Bond *et al.*, 2000).

Methods

Study area and sites

In order to test our predictions, drift entering and exiting thirteen natural pools were sampled in the Mowamba (6 pools) and Thredbo (7 pools) rivers. These rivers are located mostly within Kosciuszko National Park, in the Snowy Mountains region of south-east Australia (Fig. 1) and are snowmelt driven systems with highest discharge during spring (September-November). The catchment area of Mowamba River is 222 km^2 and Thredbo River is 243 km^2. The study pools in both rivers ranged in length from 36 m to 352 m, mean depth ranged from 0.5 m to 1.79 m and mean width ranged from 7.3 m to 33.4 m.

Field sampling

Sites were sampled on two occasions: early autumn (April) and early summer (December) of 2011. Discharge in Mowamba River sites ranged from 0.97 m^3s^{-1} – 1.23 m^3s^{-1} during autumn sampling and 0.85 m^3s^{-1} – 1.01 m^3s^{-1} during summer sampling. In the Thredbo River sites, discharge ranged 3.61 m^3s^{-1} – 6.75 m^3s^{-1} during autumn and 2.28 m^3s^{-1} – 4.27 m^3s^{-1} during summer. These flows equated to the 50-60th percentile in both rivers (see Fig. S1 in Supporting Information). Invertebrate drift was sampled using drift nets (25 x 25 cm opening) fitted with 1.5 m long nets with 250 µm mesh. Drifting invertebrates were sampled entering and exiting each pool using six nets located along a transect above the upstream margin of each pool and immediately below the upstream riffle (immigration) and six nets at the downstream end of each pool and above the next downstream riffle (emigration). We expected there may be differences in the composition and density of drifting insects throughout the water column (see Fenoglio *et al.*, 2004). To ensure we collected a representative sample of drift, drift nets were stratified with three completely submerged at approximately 0.6 of maximum depth and at least 3 cm from the bottom, and three sampling the top 10-15 cm of the water column. For each pool, drift was collected on a single night over three hours starting fifteen minutes prior to sunset. Sunset was defined as the instant the upper edge of the sun's disk was coincident with the horizon. This time period was chosen because the majority of invertebrate drift occurs just after dusk (Brittain & Eikeland, 1988). All samples were preserved in 70% ethanol for laboratory sorting and identification.

Stream discharge was calculated at each sampling transect (entering and exiting each pool) on the day of sampling using standard river gauging methods (Gordon *et al.*, 2004). The bathymetry of each pool was measured using a Lowrance Elite-5 HDI chartplotter fitted to a kayak. Between 700 and 2000 measures of depth and position were taken in each pool by multiple longitudinal and diagonal passes of the pool. Mean depth and mean width were calculated and FRAGSTATS v4 was used to calculate length of pool between riffle habitat patches (McGarigal, Cushman & Ene, 2012). These three pool morphological measures were not significantly correlated (Pearson correlation, $P > 0.05$).

Laboratory procedures

In this study design, individual pools are replicates, not individual drift nets, and the *Statistical analysis* section will explain this in greater detail. Therefore for each transect, the contents of the 6 individual nets were composited. Each composited sample was 30% subsampled using the methods and equipment described by Marchant (1989) and identified to species level where possible and enumerated.

Study species

We limited our analysis to 8 taxa from the families Baetidae, Coloburiscidae, Elmidae, Gripopterygidae, Hydropsychidae, Leptophlebiidae and Simuliidae (Table 1) that were commonly found across all sites and on the majority of sample occasions. These taxa are more prevalent in riffle habitats than pools in the study rivers (Brooks *et al.*, 2011), and more generally the focal genera are found in fast-flowing, well oxygenated waters such as riffles (CSIRO Division of Entomology, 1991), indicating riffles are a more suitable habitat than pools for these organisms. Some of the study taxa comprised multiple species, but we expected support for our hypotheses if drift behaviours were consistent within such taxonomic groups. Alternatively, non-support of hypotheses (i.e. no effect of pools on drift) implies either that species drift consistently through pools or that species respond in various ways, producing an average response that does not support our hypotheses.

Statistical analysis

For drift, the proportion of the cross-sectional area of the water column that was sampled by drift nets was calculated, and total drift numbers of each taxa were multiplied by its inverse to estimate total numbers drifting past each sampling location. Thus, drift rates were the total number of insects drifting past the total cross-sectional area of the river per three hours. We did not use volume of water passing through the nets in our calculations for two reasons. First, our hypotheses require us to estimate the numbers of insects drifting into or out of pools per unit time; the volume of water in which they travel is not directly relevant to our hypotheses. Secondly, while it is commonly assumed that it is necessary to correct drift numbers because of the different volumes of water that pass through nets, in actuality this correction requires there to be a tight and largely linear relation between drift numbers and volumes (Downes, 2010). Such relations may be poor given that drift nets have to be placed in flows sufficient for them to function i.e. drift nets cannot sample drifters in slow flows. If there is no relation between drift numbers and volume (e.g. as shown in Downes, 2010), then dividing the former by the latter adds a lot of noise that can blur any underlying patterns. We deemed it simpler to work with drift rates.

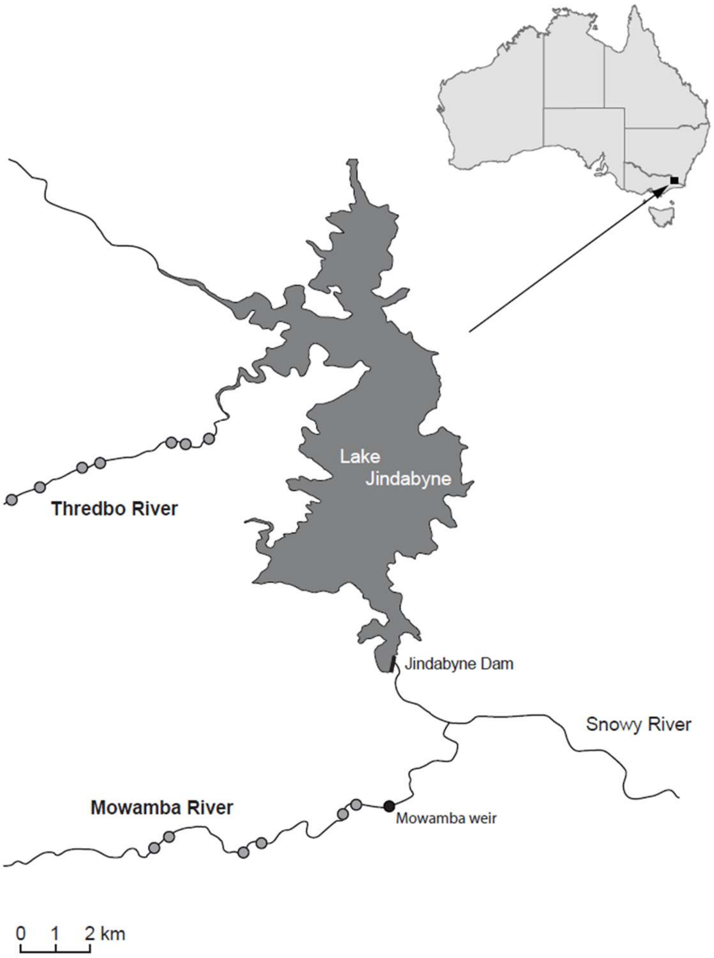

Figure 1. Location of the 13 sampling sites within the Mowamba and Thredbo Rivers.

For each study species, drift rates from a riffle into a pool (immigration, N_I) and drift rates exiting the same pool to the next downstream riffle (emigration, N_E) were calculated. Using these estimates we calculated a source/sink index (SS) for each pool after Lancaster *et al.* (2011):

$$SS = (N_E - N_I) / N_E \text{ if } N_I < N_E \text{, and } SS = (N_E - N_I) / N_I \text{ if } N_I > N_E$$

This index ranges between -1 and 1. Pools are sinks if SS < 1 (immigration > emigration) and SS represents the proportion of immigrating insects that did not drift through the pool. In contrast, pools are a source of drifting insects if SS > 0 (i.e. emigration > immigration) and SS reflects the proportion of emigrants that originated in the pool. Values of SS = 0 indicate comparable immigration and emigration rates.

Therefore, if pools impede drift dispersal between riffles for a particular species, then SS averaged over all pools will be < 0. Alternatively, drift dispersal between riffle patches is not impeded by pools when the average SS > 0.

To test prediction (i), *t*-tests were used to determine whether the mean SS for each study species was significantly less than 0, and thus whether large natural pools impeded drift dispersal between riffle habitats. One-tailed tests ($P < 0.05$) were used because we were only interested in determining if SS was less than 0 to test this hypothesis.

To determine whether increasing pool size affected dispersal between riffles (prediction (ii)), we tested for associations between SS values for each species and each of the pool morphological measures. Associations between SS values and mean depth and mean width were tested using least squares linear regression. Associations between pool length and SS were tested as a non-linear relationship using a negative exponential function. This form was chosen because exponential models of drift – distance relationships have been supported empirically (see McLay, 1970).

Results

There were no significant differences between SS and time of sampling or between rivers for all taxa except for *Coloburiscoides munionga*, which had a significantly lower SS in March (mean SS = -0.62) compared to December (mean SS = -0.07). We found that a significant proportion of drifters for 7 of the 8 focal taxa failed to disperse from the upstream riffle through the pools to the next riffle (*t*-tests: mean SS values < 0, $P < 0.05$; Table 1; Fig. 2). These results indicate that on average, there was between 29% and 60% fewer drifters exiting a pool than entering a pool. The exception was *Austrophlebioides* spp. where the number of drifters entering a pool equalled the number exiting (mean SS = -0.13). *Offadens hickmani* had the lowest mean SS (SS = -0.6; Fig. 2, Table 1) and significantly lower than *Austrophlebioides* spp. (Tukey HSD test, P < 0.05). For neither of these taxa, however, was SS significantly different from any other species (Fig. 2).

Table 1. Summary of drift dispersal results for the 8 study stream insects. *t*-tests comparing the mean source/sink index (SS) for each invertebrate taxa to zero. *P* values are significant at 0.05 (1-tailed test). Least squares regression relationships between SS and pool morphology are also summarised. Mean depth and mean width were tested as linear responses and length as a negative exponential response. Relationships 0.05 < *P* < 0.10 are shown in italics and relationships P<0.05 are indicated in bold.

Taxon	*t*-tests				Regression analysis									
					length				mean depth			mean width		
	Mean SS	df	t-value	*P*	df	F	*P*	R^2	F	*P*	R^2	F	*P*	R^2
Ephemeroptera														
Offadens hickmani (Baetidae)	**-0.60**	22	-10.1	**<0.01**	21	1.9	0.22	0.07	**8.1**	**<0.01**	**0.28**	1.6	0.22	0.07
Coloburiscoides munionga (Coloburiscidae)	**-0.30**	20	-2.2	**0.04**	19	2.6	0.12	0.12	*4.2*	*0.05*	*0.18*	0.1	0.80	0.01
Austrophlebioides spp. (Leptophlebiidae)	-0.13	23	-1.1	0.27	22	0.8	0.37	0.04	**11.0**	**<0.01**	**0.33**	0.7	0.41	0.03
Plecoptera														
Dinotoperla spp. (Gripopterygidae)	**-0.43**	24	-4.0	**<0.01**	23	0.4	0.51	0.02	1.8	0.20	0.07	0.2	0.66	0.01
Trichoptera														
Asmicridea edwardsii (Hydropsychidae)	**-0.38**	24	-3.3	**<0.01**	23	1.9	0.18	0.07	*3.1*	*0.09*	*0.12*	<0.1	0.86	0.00

Taxon	*t*-tests				Regression analysis									
					length				mean depth			mean width		
	Mean SS	df	t-value	*P*	df	F	*P*	R^2	F	*P*	R^2	F	*P*	R^2
Cheumatopsyche sp. AV4 (Hydropsychidae)	**-0.38**	19	-2.6	**0.02**	18	0.3	0.57	0.02	0.2	0.67	0.01	<0.1	0.99	0.00
Coleoptera														
Simsonia spp. (adult) (Elmidae)	**-0.41**	24	-3.8	**<0.01**	23	0.7	0.42		<0.1	0.95	0.00	1.8	0.20	0.07
Diptera														
Austrosimulium spp. (Simuliidae)	**-0.29**	24	-3.6	**<0.01**	23	0.1	0.83		**5.1**	**0.03**	**0.18**	**8.7**	**<0.01**	**0.27**

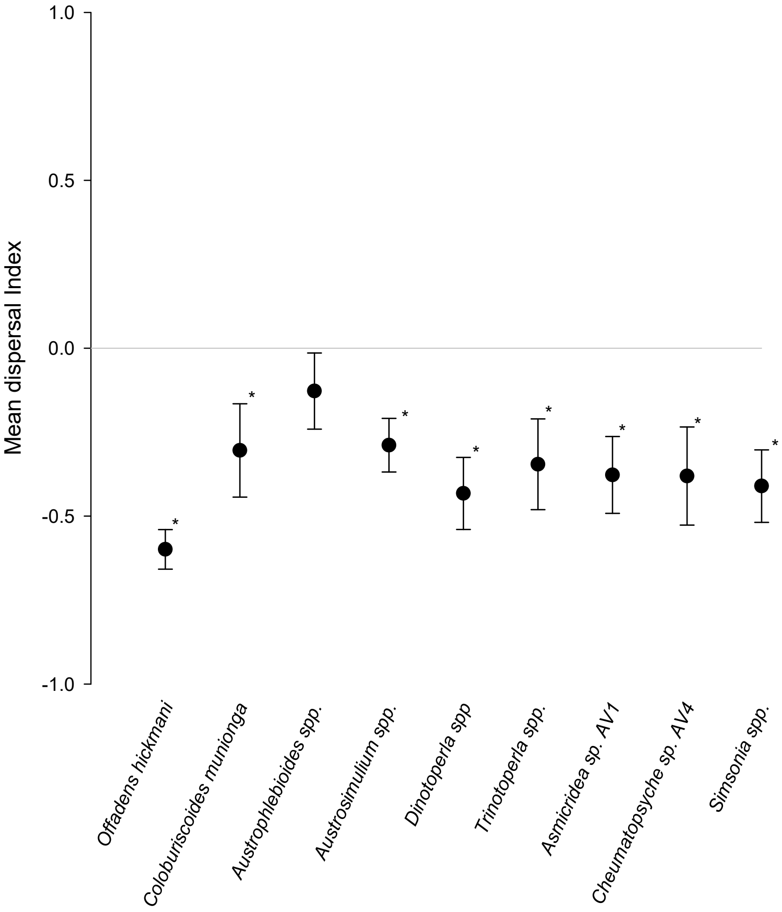

Figure 2. Mean source/sink index (SS) for study taxa. Error bars are standard errors. * indicates mean SS is significantly < 0 (*t*- tests). Grey line shows SS=0.

There were three taxa that had significant relationships between SS and mean depth – *Offadens hickmani*, *Austrophlebioides* spp. and *Austrosimulium* spp (Table 1). Additionally, mean depth was associated with *Coloburiscoides munionga* and *Asmicridea edwardsii*, but more weakly (*P* < 0.10: Table 1). The direction of all relationships (with slopes significantly less than zero) indicated the proportion of individuals drifting between riffles was reduced as pool depth increased. *Austrophlebioides* spp. had the strongest relationship (β = -0.83) with mean depth (Table 1, Fig. 3). Even though SS for *Austrophlebioides* spp. was approximately zero when averaged across all pools (Table 1), deeper pools strongly reduced the proportion of individuals drifting between riffles (Fig. 3). The simulids, *Austrosimulium* spp., was the only species to be significantly related to mean width (Fig. 3, Table 1). Length was not significantly related to the drift dispersal of any study species (e.g. Fig. 3e).

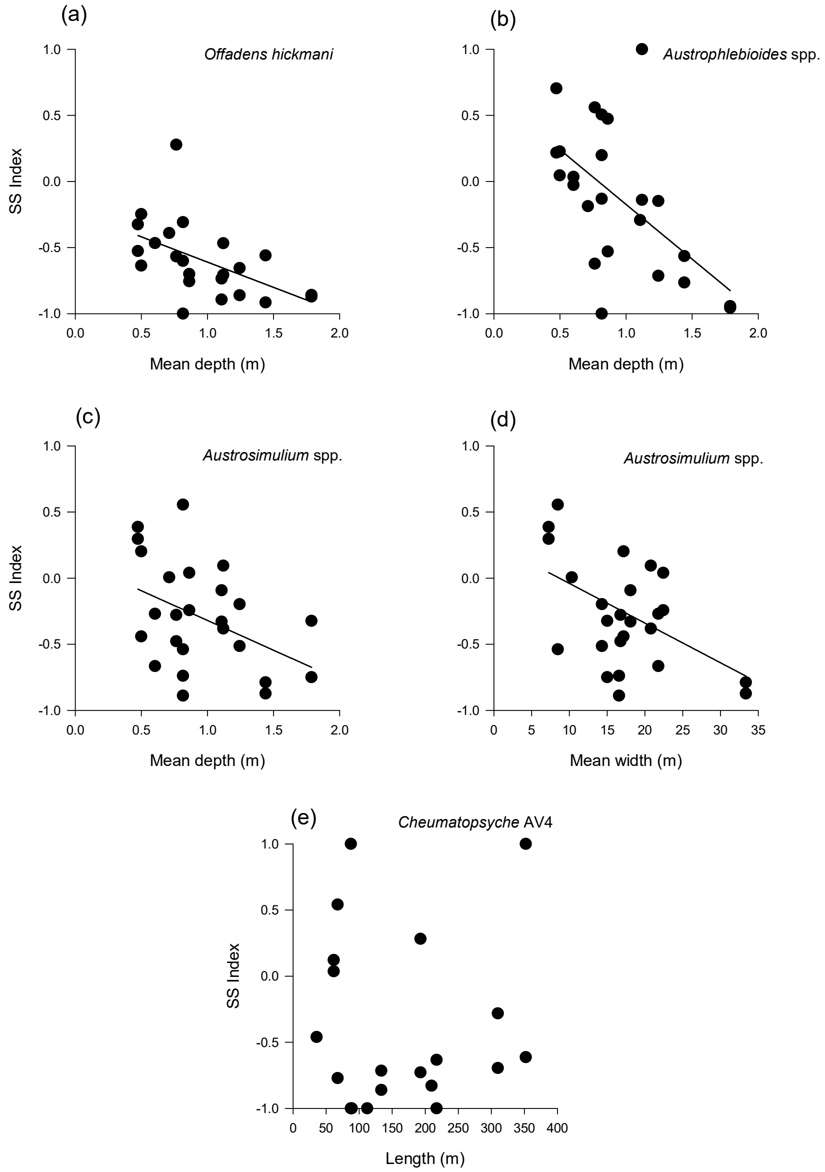

Figure 3. Regression relationships between source/sink index (SS) and measures of pool morphology. Significant relationships between SS and mean pool depth (a – c) and mean pool width (d). Example of non-significant relationship between SS and pool length for

Cheumatopsyche AV4 (e). Note that SS – length relationships were tested as negative exponential functions.

Discussion

Identifying the limits or constraints to successful dispersal remains a critical issue for the understanding of connectivity patterns across landscapes (Vasudev *et al.*, 2015). In freshwater systems, understanding the degree of connectivity between populations is fundamental to population ecology (Fagan & Lutscher, 2006; Hughes, Schmidt & Finn, 2009). A key piece of information is the distances insects disperse via drift, which is dependent on the dispersal capabilities of an insect, the frequency of dispersal and barriers to dispersal. We asked a number of questions that investigated stream insect drift between riffle habitats and the possible mechanisms by which intervening pool habitats could constrain dispersal between these habitat patches.

Are stream insects drifting between riffle habitats impeded by pools?

We found that for the majority of study taxa, drift dispersal between riffles (i.e. patches of suitable habitat) was hindered by the intervening pool habitat. These findings supported our first prediction that natural, large slow-moving pools impede the number of invertebrates drifting between riffle habitats.

The baetid, *Offadens hickmani*, showed the greatest reduction in drift (60% reduction). Lancaster *et al.* (2011) studied drift rates of the baetid, *Baetis rhodani,* through seven pools and found similar declines in drift numbers, suggesting that pools were sinks for this species. In general, for our study taxa, there are few published studies of drift of stream insects between riffles separated by pools, and therefore limited results with which to compare our findings. The few relevant studies rarely sampled more than one or two pools and the results were often contradictory. For example, Kovalak (1978) found that a pool was a source of a number of rheophilic invertebrates (*Baetis*, *Simulium*, *Hydropsyche*). Similarly, Campbell (1985) concluded that drift of *Baetis* through a pool was not reduced. However, their study pools were relatively short (<17 m) compared to our study where the pool lengths were >35 m and mean depths >0.5 m. In contrast, Martin & Knight (1989) showed two long pools (45 m and 90 m) were barriers to drift for *Simulium* and *Baetis* and it was hypothesised that low water velocities through the pools limited drift distances of insects.

Is drift affected by pool morphology?

Drift dispersal between riffle habitats for many of the study species (5 of 8 taxa) were associated with one aspect of pool morphology - mean depth. For each of these species, the direction of the relationship indicated that drift was reduced with deeper pools. *Austrosimulium* spp. drift was also significantly reduced with increasing mean width. Pool cross-sectional area increases with increasing depth, and therefore pool velocity also declines with increasing depth in accordance with the continuity equation (discharge = velocity*area; see Gordon et al., 2004). Therefore, our findings were consistent with the prediction that dispersal was increasingly impeded by declining velocity associated with increasing pool depth (prediction (ii)). Interestingly, there were few significant relationships between drift and pool length. The lack of associations was because velocity at any location within a pool is a function of discharge, width and depth (i.e. discharge / cross sectional area), and length will have minimal influence on velocity through a pool. This further supports our hypothesis that the area and arrangement of low and zero flow zones within a pool limit drift dispersal between riffles, and not the total distance between riffle habitat patches. The lack of any length-SS relationships also suggests that these species ability to drift through pools independently of velocity patterns within pools is limited and drift distances are highly dependent on water current.

Variations in SS - pool morphology relationships between the study insects may be attributed to differences in a species' body morphology, drift behaviours and swimming abilities (Lancaster & Downes, 2013). For baetid mayflies, a combination of swimming and body posturing is used to manage drift time and distances (Oldmeadow *et al.*, 2010). These behaviours can both prolong drift and also allow exit the drift (Allan & Feifarek, 1989). The baetid, *Offadens hickmani*, is likely to use similar mechanisms when drifting. *O. hickmani* may have actively chosen to exit the drift when initially exposed to slow or zero velocity areas by swimming to the substrate (Otto & Sjöström, 1986), possibly to avoid the risk of settlement in slow flow habitats where the risk of predation can be greater (Wellnitz, 2014). Actively settling from the drift may well have increased when encountering progressively slower flows in deeper pools. *Austrosimulium* spp., a simulid, increase their chances of transiting pools using silk threads, which diminish their fall velocities, making them more likely to drift through a pool before being deposited (Fingerut *et al.*, 2009). This may explain why proportionally more *Austrosimulium* spp. (SS = -0.29) drifted through pools compared to any other study species, but the effectiveness of silk threads helping larvae moving between riffles was reduced in deeper, slower flowing pools. Drift of *Austrophlebioides* spp. was not significantly reduced by pools on average, but was greatly reduced by the deeper pools and associated low and zero flow areas. Leptophlebiids use dorso-ventral undulations to swim in low velocity areas (Otto & Sjöström, 1986; Barmuta, Mckenny & Swain, 2001), and presumably swimming was used to disperse across the shallower pools, but was less effective when drifting into the deepest pools in our study.

We found the ability of hydropsychids (*Asmicridea* AV1, *Cheumatopsyche* AV4), mayfly (*Coloburiscoides munionga*), stonefly (*Dinotoperla* spp.) and adult elmid (*Simsonia* spp.) to drift through pools was limited, but the degree of impediment did not increase with increasing pool size (Table 1). Hydropsychidae larvae are inefficient swimmers (e.g. *Hydropsyche* sp.; Otto & Sjöström, 1986) and avoid areas of slow flow and move to areas of faster flow by walking (e.g. *Asmicridea* AV1; Sharpe & Downes, 2006). Elmid adults also predominantly disperse by walking rather than drifting (Elliott, 2008a). The capacity to walk from pool habitats after settlement to seek faster flowing riffle areas may explain why there was no association between pool size and drift for these species. Stonefly nymphs have the capability to swim in still water using lateral undulations (Otto & Sjöström, 1986). Similarly, Coloburiscidae mayfly nymphs have some capacity to swim, albeit poorly (Phillips, 1931). Despite the potential for both these taxa to swim, drift was reduced by pool habitats, and shallower pools did not increase their likelihood of drifting to the next downstream riffle.

Our results also highlight questions about the fate of the individuals that unsuccessfully drifted from a source riffle to the next downstream riffle. There are a number of potential explanations for the loss of drifters. An unlikely reason for the reductions is fish predation during drift. In our study rivers, the major fish predators were heavily stocked non-native rainbow and brown trout (NSW Department of Primary Industries - Fisheries, 2014) with few native fish. However, trout feeding generally does not occur after twilight (Angradi & Griffith, 1990) when drift numbers are at their highest, and overall losses of invertebrates are likely to be only a negligible fraction of the drift (Naman, Rosenfeld & Richardson, 2016). A more likely explanation is that an individual will settle from the drift in the lateral margins of the river (Ciborowski, 1983) and crawl or swim upstream, returning to the upstream riffle, as small-scale upstream movements of benthic invertebrates are reasonably common (Elliott, 2003). Alternatively the adverse environmental conditions and/or increased predation may result in many of these individuals dying before moving out of pools (Wellnitz, 2014).

Most measurements of drift distances of stream insects have been experimental studies in depths <0.5m (e.g. McLay, 1970; Elliott, 1971; Larkin & McKone, 1985), with settlement estimates subsequently used to model drift distances (e.g. Anderson et al., 2013). Our study has shown that deep, slow moving pools can substantially limit drift dispersal distances. Therefore, accurate models of drift dispersal need to incorporate the influence of pools, otherwise drift distances may be substantially overestimated.

Gathering information about dispersal rates between habitat patches, and distinguishing the major mechanisms that insects use to disperse between them, is key to predicting and understanding population dynamics (Downes & Reich, 2008; Hughes *et al.*, 2008). We found drift dispersal seems unlikely to be a major mechanism of long distance dispersal, with a significant proportion of drifters failing to disperse between riffles separated by a deep pool. Our findings support recent observations that dispersal of freshwater insects is not as wide-spread as was assumed, and that drift may have a limited role in defining the large-scale population structure of stream insects (Bohonak & Jenkins, 2003; Downes & Lancaster, 2010; Lancaster *et al.*, 2011; Naman *et al.*, 2016). This is consistent with mounting evidence that the larval distribution patterns within rivers may be more influenced by adult behaviours (successful mating and oviposition of adult females) than drift (Encalada & Peckarsky, 2012; Lancaster & Downes, 2014). As a consequence, connectivity amongst populations over large spatial scales is most probably determined by movements of flying adults (Hughes *et al.*, 2013). However, for insects with adult stages that are fully aquatic or poor fliers, the spatial extent of their population may be even more limited. We acknowledge that our results and conclusions are limited to stream systems with well-defined pool-riffle sequences. Drift patterns may vary strongly between rivers with different geomorphological characteristics and is an area that is in need of further research.

Detailed knowledge of the primary mechanisms of stream insect dispersal is also vital to understand how populations may be restored following anthropogenic disturbances (Palmer, Ambrose & Poff, 1997; Parkyn & Smith, 2011). Dams and weirs can fragment populations and alter the ability of animals to move through river networks (Dudgeon *et al.*, 2006; Lake, Bond & Reich, 2007; Erős & Campbell Grant, 2015). If stream insect dispersal between habitat patches is impeded by natural river features such as pools, then weir pools and dam lakes may obstruct drift dispersal to an even greater extent, and any attempts at downstream river restoration may become predominantly reliant on dispersal of flying adults from populations elsewhere within the river system. Therefore, a key area of is research understanding how these structures affect the major pathways and mechanisms of successful stream insect dispersal (both aquatic and terrestrial), and will be critical to successful river restoration.

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Supplementary information

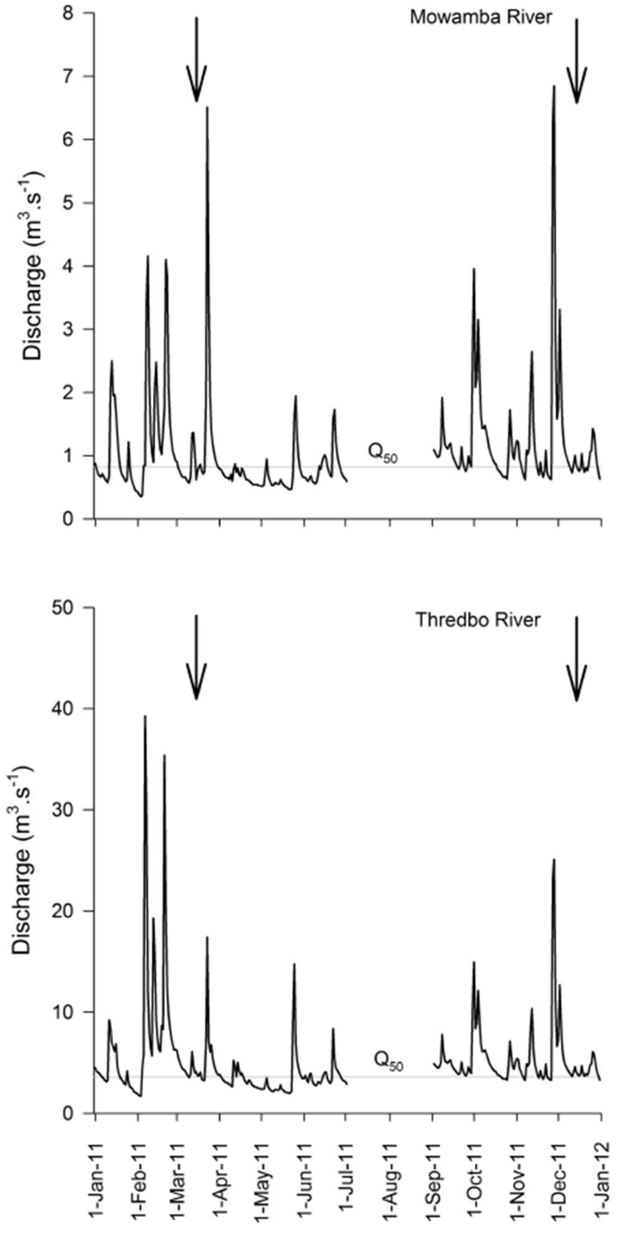

Figure S1. Mean daily discharge in the Thredbo River (gauge no. 222451) and Mowamba River (gauge no. 222546) for the period of this study. Flow data was missing for the period between July and September. The horizontal grey line indicates the Q_{50} (median) discharge. Arrows indicate sampling occasions.

Chapter 3. Paper 2 – Barriers to dispersal: the effect of a weir on stream insect drift

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Abstract

Dams and weirs degrade river ecosystems, reducing diversity and altering the assemblage composition of aquatic biota. These structures may damage rivers by disrupting longitudinal connectivity, fragmenting rivers and isolating populations. We tested whether a weir could impede the downstream dispersal of stream insects by comparing drift rates through natural pools and through a weir pool. For 3 of 4 of our study taxa (*Offadens* spp., *Austrosimulium* spp. and *Simsonia* spp.), we found the numbers of drifters were consistently reduced by the weir across multiple occasions (reduction ranging from 68% - 98%) to a higher degree than natural pools (reduction ranging from 24% - 41%). Drift of *Cheumatopsyche* spp. through the weir was greatly reduced in December (-95%) compared to natural pools, but the weir had little effect during April (-9%). There were size related patterns in drift through the weir pool for some taxa. In the weir pool, emigrating individuals of *Austrosimulium* spp. were significantly smaller than immigrating individuals, which was not observed in natural pools. In contrast, significant reductions of *Cheumatopsyche* spp. drifters through the weir only occurred when individuals were small (December). Within the weir pool, the combined effects of lower average water velocity, multiple large low velocity areas and the weir wall were likely to be the cause of the reduction in stream insect drift through the weir. The impediment of drift of some taxa by weirs may affect dispersal and colonisation processes. This obstruction of downstream movement could undermine the outcomes of river restoration projects.

Introduction

Dams and weirs degrade river ecosystems, reducing diversity and altering the assemblage composition of aquatic biota (Poff & Zimmerman, 2010). There are multiple hypotheses to explain how dams and weirs reduce species diversity such as altering the flow regime (Magilligan & Nislow, 2005), reducing downstream habitat complexity (Graf, 2006), increasing sedimentation (Baker, Bledsoe, Albano, & Poff, 2011), and also modifying the thermal regime (Olden & Naiman, 2010). One major hypothesis how dams and weirs damage rivers is that they disrupt longitudinal connectivity, fragmenting river ecosystems and isolating populations of aquatic biota (Ward & Stanford, 1995), potentially limiting dispersal of biota along rivers (Lake, Bond, & Reich, 2007). If the movement of individuals and genes among resource patches is impeded, the extent, viability, and ultimately persistence of populations could be greatly affected (Erős & Campbell Grant, 2015; Fagan, 2002).

Drifting downstream while entrained in stream currents is frequent among some lotic species and is one mechanism for the redistribution of stream insects (Brittain & Eikeland, 1988; Waters, 1972). These organisms also disperse by swimming, crawling, and adult flight (Bilton, Freeland, & Okamura, 2001). The role of flying adults in insect dispersal is clearly important for some species (Hughes, Schmidt, & Finn, 2009), but despite the capacity to fly as adults, dispersal can be much more limited for other species (Wilcock, Bruford, Nichols, & Hildrew, 2007), and drift may have a significant influence on population connectivity.

Within rivers, pools are regions of deeper, slower moving water and are areas of drift deposition, reducing downstream movement and potentially limiting connectivity within rivers (Brooks, Wolfenden, Downes, & Lancaster, 2017; Martin & Knight, 1989). Weirs create unnaturally wide and deep pools, resulting in patterns of low velocity areas throughout the weir pool that may be substantially different to natural pools. The spatial configuration of low and zero flow areas throughout a stream channel have a strong influence on drift dispersal distances (Bond, Perry, & Downes, 2000; Lancaster, Hildrew, & Gjerlov, 1996), and weir pools may affect drift to a greater degree than natural pools.

Dams have been reported to limit the downstream dispersal of aquatic organisms such as plants (e.g. Jansson, Nilsson, & Renöfält, 2000), fish (e.g. Liermann, Nilsson, Robertson, & Ng, 2012) and aquatic insects (e.g. Sondermann, Gies, Hering, Schröder, & Feld, 2015), but dispersal is rarely directly measured. There are no studies which empirically test whether and how stream insect drift is impeded by dams and weirs, and thus the effect of obstructed dispersal on downstream ecosystem processes (Web of Science search: *(drift AND (weir* OR dam*) AND barrier* AND (river* OR freshwater* or stream*) AND (insect* OR invertebrate*))*). Therefore, how weirs affect the major pathways and mechanisms of stream insect dispersal, such as drift, remains a major knowledge gap.

Therefore, the aim of this study was to test whether a weir and its associated pool impedes drift of stream insects. We predicted that (i) drift would be impeded by the large slow-moving weir pool. Weirs create unnaturally wide and deep pools, and therefore, we predicted the weir pool and associated areas of slow moving water would limit drift dispersal to a greater extent than natural pools (Prediction (ii)). The degree to which the weir pool and natural pools affects drift will depend on pool characteristics and species' behaviours and swimming ability (Oldmeadow, Lancaster, & Rice, 2010). In addition, the body size of an insect may influence the distance an individual can drift (Allan & Feifarek, 1989; Campbell, 1985). Smaller individuals may be able to drift for longer (and further) due to their lower mass and reduced ability to exit the drift through swimming or body posturing (Malmqvist & Sjöström, 1987). Therefore, we predicted that (iii), smaller individuals would drift out of a pool compared to those entering, and that drifters exiting the weir pool would be smaller than individuals drifting out of natural pools because of the weir pool’s greater size.

Methods

Study area and sites

We sampled drifting stream insects entering and exiting the pool of a weir on the Mowamba River, a tributary of the regulated Snowy River. The weir has a spillway 50.2 m wide and the weir wall is 2.7 m high. In addition, we used data collected from a previously published study which sampled drifting stream insects entering and exiting thirteen natural pools in the Mowamba (6 pools upstream of the weir) and Thredbo (7 pools) rivers (Brooks et al., 2017). The catchment area of Mowamba River is 222 km^2 and Thredbo River is 243 km^2, and sites were located between elevations of 980 m to 1300 m, mostly within Kosciuszko National Park in south-east Australia.

Field sampling

Sites were sampled twice: autumn (April) and early summer (December) of 2011 with discharge ranging between the 50-60th percentile in both rivers. Mowamba weir diverts all stream flow (up to 5.7 m^{3}s^{-1}) through an aqueduct into a nearby dam. The aqueduct was closed and the weir was overtopped for 1 month prior to sampling and then returned to its original operation. Therefore, a longer term study of downstream colonisation was not possible. Drifting invertebrates were sampled entering and exiting natural pools using six drift nets (25 x 25 cm opening, 250 µm mesh) along a transect across the upper end of a pool and six drift nets along a transect at the lower end of a pool. For natural pools, drift was collected on a single night over three hours starting fifteen minutes prior to sunset. This was carried out in both April and December. More detail of the methods for drift sampling in natural pools are described in Brooks et al. (2017). Weir pool drift was sampled on three nights over a period of seven days within both April and December, coinciding with sampling of natural pools. The weir was sampled over three nights to calculate an accurate estimate of drift rates through the weir and samples were pooled for analysis (see below *Laboratory Procedures*). Drift entering the weir pool was sampled using the same methods as the natural pools described above. For drift exiting the weir, metal frames were used to position drift nets perpendicular to the flow overtopping the weir wall. Six to ten nets were placed in random positions beneath the flow of water falling from the weir. All samples were preserved in 70% ethanol for sorting and identification in the laboratory.

The bathymetry of the weir pool and each natural pool was measured using a Lowrance Elite-5 HDI chartplotter fitted to a kayak. Between 700 and 2000 measures of depth and position were taken in each pool by multiple longitudinal and diagonal passes of the pool. From this data, we calculated surface area, mean and maximum width, median depth, 25th % depth, 75th % depth and length of each pool. In addition, the distance to deepest and widest sections of each pool, measured from the upstream limit of the pool, were also calculated.

Laboratory procedures

The contents of the 6-10 individual nets from the three nights were composited, 30% subsampled using the methods described by Marchant (1989), identified to genus level and enumerated. Size measurements of individuals were performed using a Leica M165C Dissecting Stereomicroscope. All animals were measured from the top of the head capsule to the tip of the abdomen.

Study species

We limited our analysis to *Offadens* spp. (Baetidae), *Simsonia* spp. (adult Elmidae), *Cheumatopsyche* spp. (Hydropsychidae) and *Austrosimulium* spp. (Simuliidae) (Table 2). These taxa were commonly found drifting into the weir pool and across the majority of natural pool sites and sampling occasions. They are more prevalent in fast-flowing riffle habitats than pools in the study rivers (Brooks, Russell, Bevitt, & Dasey, 2011), indicating pools are likely to be unsuitable habitat for these taxa.

Statistical analysis

Using the pool morphological measures, principal components analysis (PCA) using a correlation matrix was then undertaken to investigate differences in morphology between the weir pool and natural pools. The mean cross sectional water velocity was calculated for each natural pool and the weir pool for the night of sampling in both April and December.

For drift, the proportion of the cross-sectional area of the water column that was sampled by drift nets was calculated, and total drift numbers of each taxon were multiplied by its inverse to estimate total numbers drifting through each transect. Thus, drift rates were the total number of insects drifting past the total cross-sectional area of the river per three hours (Brooks et al., 2017; Downes, 2010).

For each study genus, drift rates from a riffle into a pool (immigration, N_I) and drift rates exiting the same pool to the next downstream riffle (emigration, N_E) were calculated. Using these estimates we calculated a source/sink index (SS) for each pool and the weir pool after Lancaster *et al.* (2011):

$$SS = (N_E - N_I) / N_E \text{ if } N_I < N_E, \text{ and } SS = (N_E - N_I) / N_I \text{ if } N_I > N_E$$

This index ranges between -1 and 1. Pools are sinks if SS < 0 (immigration > emigration) and SS represents the proportion of immigrating insects that did not drift through the pool. In contrast, pools are a source of drifting insects if SS > 0 (i.e. emigration > immigration) and SS reflects the proportion of emigrants that originated in the pool. Values of SS = 0 indicate comparable immigration and emigration rates. Therefore, if natural pools impede drift between riffles for a particular genus, then SS averaged over all pools will be < 0. Alternatively, drift between riffle patches is not impeded by pools when the average SS > 0. Similarly, if the average SS for the weir pool < 0, the drift has been impeded.

An SS value was calculated for the weir for each sampling occasion (April & December). The SS value for each occasion was the mean of the three weir SS values collected on each occasion. We determined on each occasion if the values of the mean SS for each study genus were consistently lower than 0 (prediction (i)) , and tested if the SS for the weir pool was less than mean SS for natural pools using *t*-tests (prediction (ii)).

We also tested whether body size influenced the ability of a stream insect to drift through natural pools and the weir pool (prediction (iii)). We compared the size frequency distribution of insects entering and exiting pools using the two-sample Kolmogorov-Smirnov test (KS test; bootstrapping n=5000). This is a non-parametric procedure that tests for differences between two distributions and is sensitive to differences in location, dispersion and skewness (Sokal & Rohlf, 1995). The test statistic, D_n, is the maximum absolute difference between the two cumulative distributions, and can be considered a measure of effect size (ranging between 0-1). Both the significance value and the D_n value were evaluated to aid in the interpretation of the results. The KS test was performed separately on natural pools and the weir pool. The size frequency analysis was not conducted on the adult elmid *Simsonia* spp. because adults do not vary much in body size. Therefore, there was little expectation that differences in body size between immigrating and emigrating drifters could be detected.

Results

Pool morphology of natural pools and the weir pool

The Mowamba weir pool was 420 m long, mean depth was 1.5 m, mean width was 33.2 m, and surface area was 22092 m^2, and exceeded the depth, width, length and surface area measures of the majority of natural pools (Table 1, Figure 1). Twenty-five percent of depth measurements in the weir pool were greater than 2 m (25th % depth), almost twice as deep as the 25th % depth of natural pools. The distances to the widest and deepest sections in the weir pool were 302 m and 359 m respectively, and were substantially greater than natural pools both in absolute distances and as a proportion of the total length of the pool.

The principal components analysis showed that pool morphology differed considerably between the weir pool and the natural pools (Figure 2). The first principal component (PC1) explained 68% of the variation in pool morphological measures and the second principal component (PC2) explained just 16% of variation. The weir pool was predominately separated from natural pools along PC1, which was negatively associated with all variables, indicating weir pool was wider, deeper and larger than the range of natural pools sampled in the study.

Table 1. Pool bathymetry and flow in natural pools and Mowamba weir pool. Averages and ranges were calculated for each morphological measure for natural pools.

Pool morphology	natural pools (range)	Mowamba weir pool
mean depth (m)	0.9 (0.5 - 1.8)	1.5
maximum depth (m)	3.1 (0.7 - 5.5)	4.1
median depth (m)	0.8 (0.4 - 1.2)	1.5
25th percentile depth	1.1 (0.6 – 2.5)	2.0
75th percentile depth	0.5 (0.4 – 0.8)	1.0
mean width (m)	17.1 (7.3 – 33.4)	33.2
maximum width (m)	25.5 (20.2 - 30.7)	89.3
length (m)	156.9 (35.8 - 352.3)	419.8
downstream distance to widest point in pool (m)	58.0 (26.2 – 118.0)	302.0
downstream distance to deepest point in pool (m)	63.5 (26.2 – 149.7)	358.7
mean velocity (ms^{-1})	0.2 (0.15 - 0.25)	0.015 (0.014 – 0.017)

The mean flow velocity of the weir pool was significantly lower than the velocity of natural pools on both occasions (*t* tests: $p < .05$; Table 1), resulting from the differences in the pool bathymetry (Table 1, Figures 1 & 2).

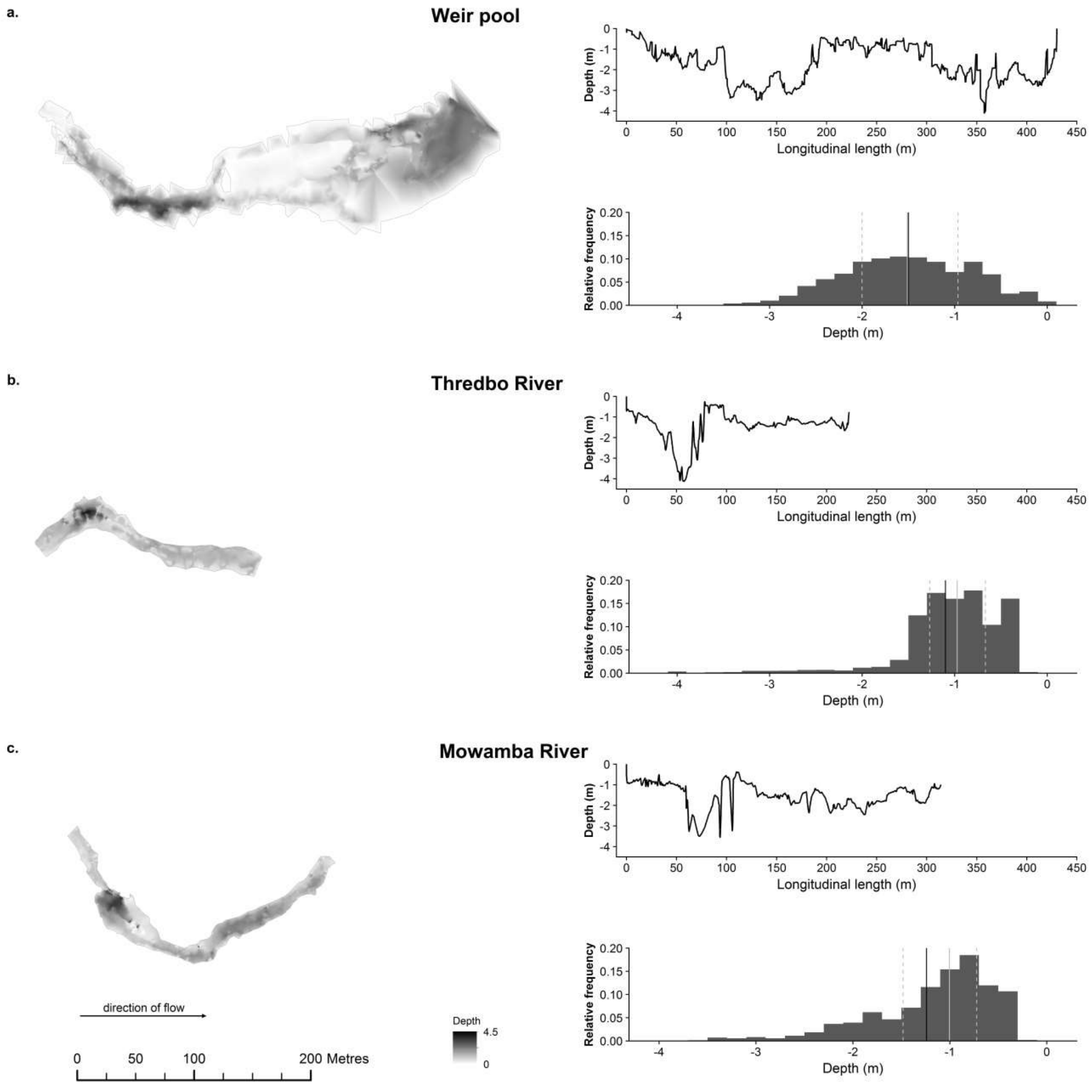

Figure 1. Pool bathymetry and depth frequency distributions of the Mowamba weir (a) and examples of natural pools within the Thredbo (b) and Mowamba (c) rivers. Black line (histograms) = mean, grey line = median and grey dotted lines = 25th percentile and 75th percentile.

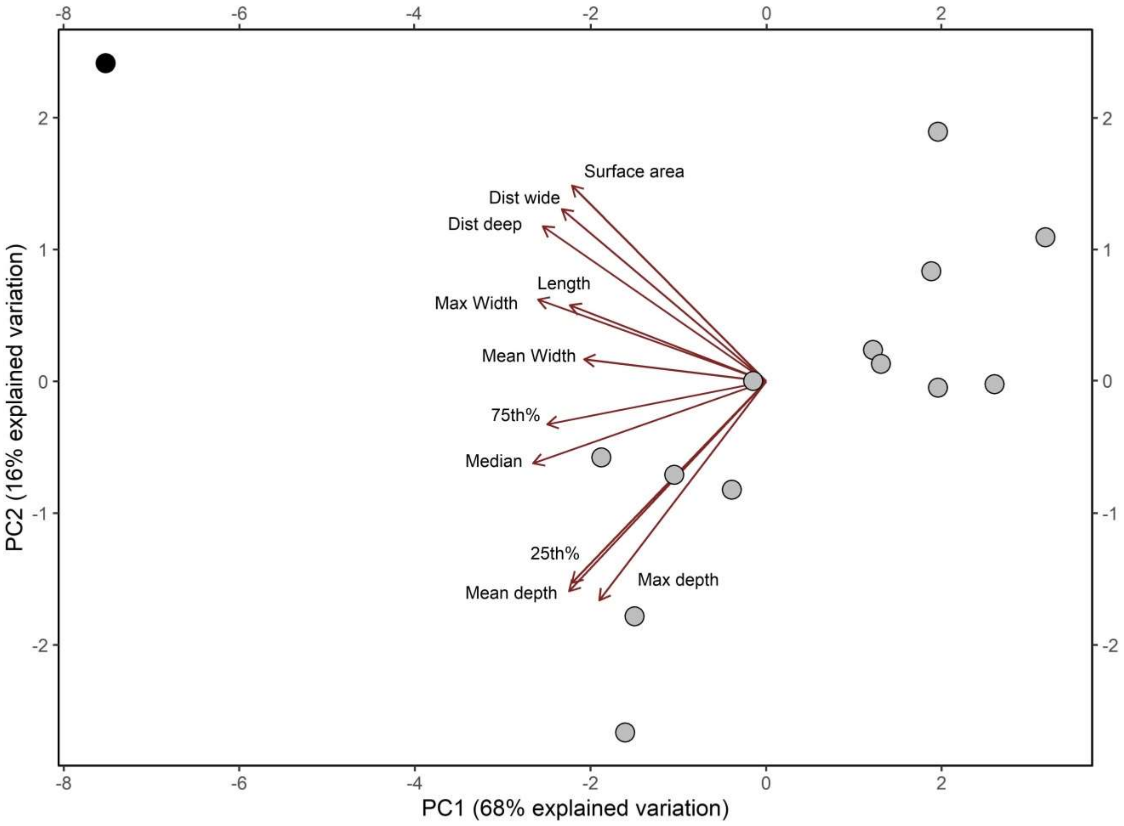

Figure 2. Principal components analysis (PCA) of pool morphological measures. Grey circles = natural pools, black circle = weir pool. Arrows are vectors of loadings of individual pool morphological measures.

The effect of natural pool and the weir pool on the numbers of drifting stream insects

Offadens spp. was the most numerous invertebrate drifting into and out of both natural pools and the weir pool and *Simsonia* spp. (adult) was the least numerous (Table 2). The standard deviation of the mean was high for all taxa, indicating substantial variation between pools and sampling times.

Table 2. Mean number of drifters per 3 hours (standard deviation) of the four focal stream insect genera drifting into and out of natural pools and a weir pool.

	natural pools		weir pool	
	In	Out	In	Out
Ephemeroptera				
Offadens spp. (Baetidae)	8,742.0 (11,840.1)	4,930.5 (4,479.5)	5,580.7 (4,972.1)	875.1 (1,167.2)
Trichoptera				
Cheumatopsyche spp. (Hydropsychidae)	2,601.3 (4,233.9)	1,572.9 (2,806.4)	1,549.2 (783.1)	470.6 (511.7)
Coleoptera				
Simsonia spp. (adult) (Elmidae)	1,455.7 (1,412.4)	872.9 (895.6)	1,711.8 (864.7)	457.2 (212.6)
Diptera				
Austrosimulium spp. (Simuliidae)	3,375.5 (4,331.9)	2,296.9 (3,025.6)	1,525.5 (1,278.6)	89.0 (73.8)

As reported in Brooks et al. (2017), a significant proportion of drifters of all four focal taxa failed to disperse from the upstream riffle through natural pools to the next riffle (see Brooks et al., 2017 for results of *t* - tests; Table 3, Figure 3), but the weir pool presented an even greater barrier. On average, the numbers of drifters emigrating from a natural pool were between 24% and 41% less than immigrating into a pool.

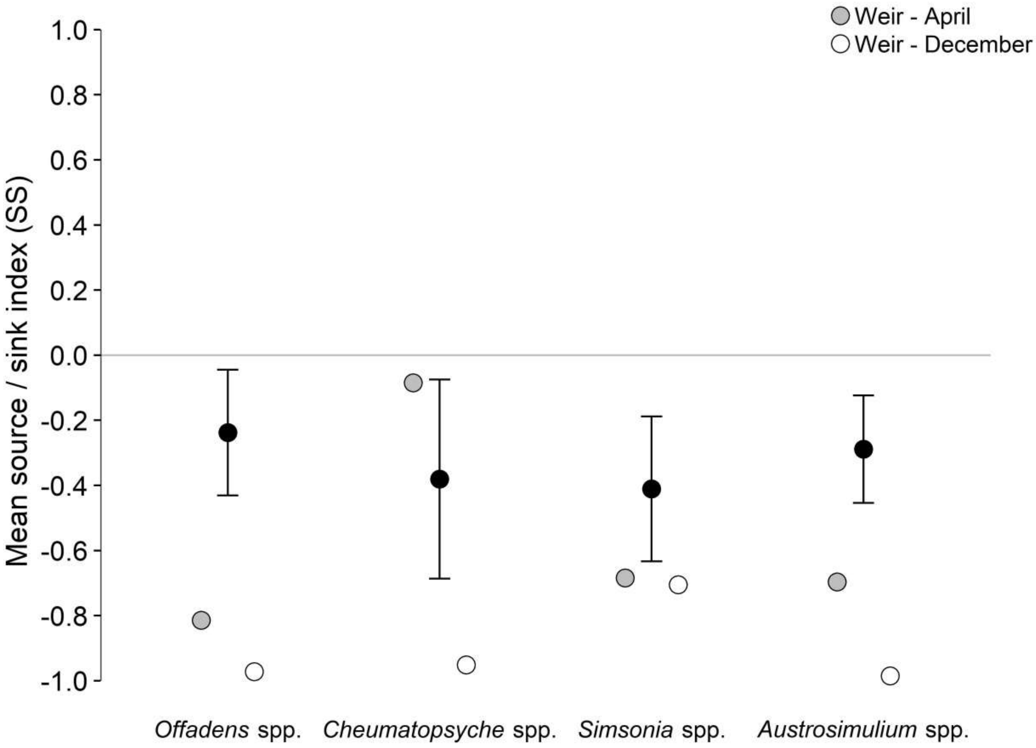

Figure 3. Mean source/sink index for drifting study taxa in natural pools and Mowamba weir. Natural pools are solid black circles and error bars are 95% confidence intervals (Brooks et al., 2017). Mowamba weir SS values are in grey circles (December) and open circles (April). Grey line shows SS = 0.

A large percentage of drifters of all study stream insects failed to disperse through the Mowamba weir pool (all SS values < 0; Figure 3, Table 3). There was between 68% and 98% fewer drifters of *Offadens* spp., *Austrosimulium* spp. and *Simsonia* spp. exiting the weir pool than entering on both sampling occasions, and was significantly greater than drift reductions in natural pools (Table 3). *Cheumatopsyche* spp. drift through the weir pool was reduced by 95% in December, significantly lower than drift in natural pools, but only 9% in April (non-significantly different to natural pools; Figure 3, Table 3).

Table 3. Summary of drift dispersal of the four focal stream insect genera. SS values for natural pools were reported in Brooks et al. (2017). *t* – tests comparing the mean source/sink index (SS) for each taxon in natural pools with the Mowamba weir pool. *p* values are significant at .05 and indicated in bold.

		mean source / sink index (SS)		*t*-tests		
Taxon		weir pool	natural pools	*df*	*t* value	*p*
Offadens spp. (Baetidae)	April	-0.81	-0.24	23	6.16	**< 0.01**
	December	-0.97		23	7.84	**< 0.01**
Cheumatopsyche spp. (Hydropsychidae)	April	-0.09	-0.38	19	-1.99	0.97
	December	-0.95		19	3.90	**< 0.01**
Simsonia spp. (adult) (Elmidae)	April	-0.68	-0.41	24	2.50	**< 0.01**
	December	-0.70		24	2.68	**< 0.01**
Austrosimulium spp. (Simuliidae)	April	-0.70	-0.29	24	5.14	**< 0.01**
	December	-0.98		24	8.64	**< 0.01**

The effect of stream insect body size on drift through natural pools and the weir pool

Natural pools

Within natural pools, the difference in the size distributions between drifters entering and exiting natural pools was significantly different for each genus (KS test; Table 4, Figures 4 & 5). However, the D_n test statistic indicated these differences were very small (natural pool D_n between 0.08 – 0.12). The statistical significance of tests in the natural pools, despite the small differences in insect sizes, was probably because of the high statistical power due to the large numbers of individuals collected in the study.

Weir pool

Table 4. Differences in body size between immigrating and emigrating drifters in natural pools and the Mowamba weir pool. Kolmogorov-Smirnoff test comparing the body size frequency distribution of immigrating and emigrating drifters. *p* values are significant at .05 and indicated in bold. *Simsonia* spp. was not assessed as adult elmids do not vary sufficiently in size to warrant analysis.

			Kolmogorov-Smirnoff test	
Taxon			D_n statistic	Bootstrap *p*
Ephemeroptera				
Offadens spp. (Baetidae)	natural pools		0.12	**< 0.01**
	weir pool		0.08	> 0.05
Trichoptera				
Cheumatopsyche spp. (Hydropsychidae)	natural pools		0.08	**0.02**
	weir pool	April	0.15	0.24
		Dec	0.11	0.60
Diptera				
Austrosimulium spp. (Simuliidae)	natural pools		0.11	**< 0.01**
	weir pool		0.35	**< 0.01**

Austrosimulium spp. drifters exiting the weir pool were significantly smaller (≈20% smaller) than those entering, with no individuals drifting through the weir exceeding 4 mm in length (KS test, Table 4, Figure 4). In contrast, larvae greater than 4 mm were frequently observed drifting into and out of natural pools. The D_n statistic was almost three times as large as the values for natural pools, indicating this result reflects a large reduction in the size of emigrating drifters. The sizes of *Offadens* spp. individuals entering and exiting the weir pool were not significantly different.

The sizes of *Cheumatopsyche* spp. individuals drifting through the weir were compared separately for April and December. This was done because differences in total drift numbers through the weir (SS values) between the two sampling times were detected, and analysing size frequency separately for each time may help explain the contrasting patterns in drift rates. There were no significant size differences of *Cheumatopsyche* spp. entering and exiting the weir pool in both April and December (Table 4, Figure 5). However, *Cheumatopsyche* spp. was considerably smaller in December (≈40% smaller).

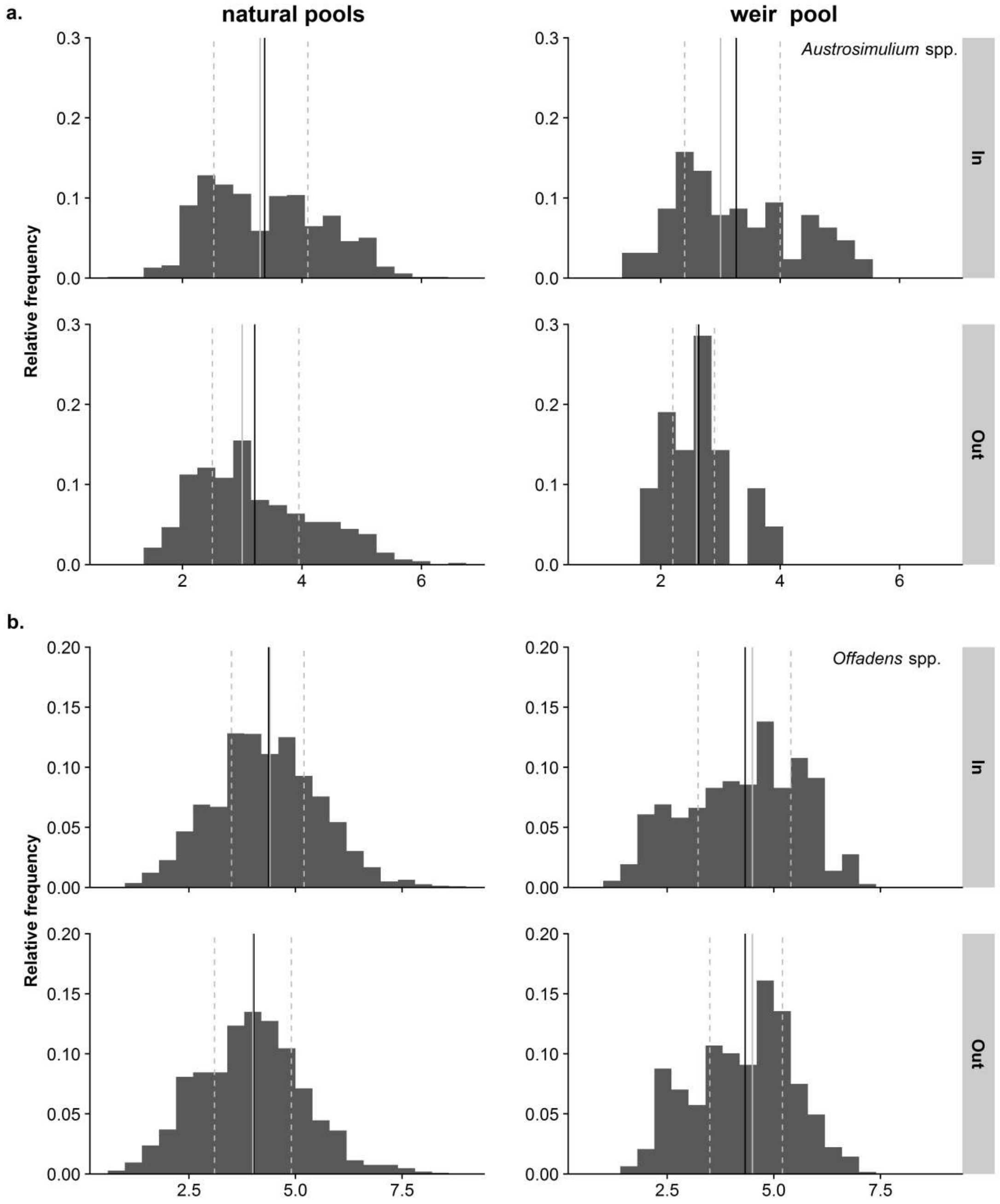

Figure 4. Size frequency distributions of drifting stream insects immigrating and emigrating from natural pools and Mowamba weir. a) *Austrosimulium* spp. b) *Offadens* spp. Black line = mean, grey line = median and grey dotted lines = 25th% and 75th%.

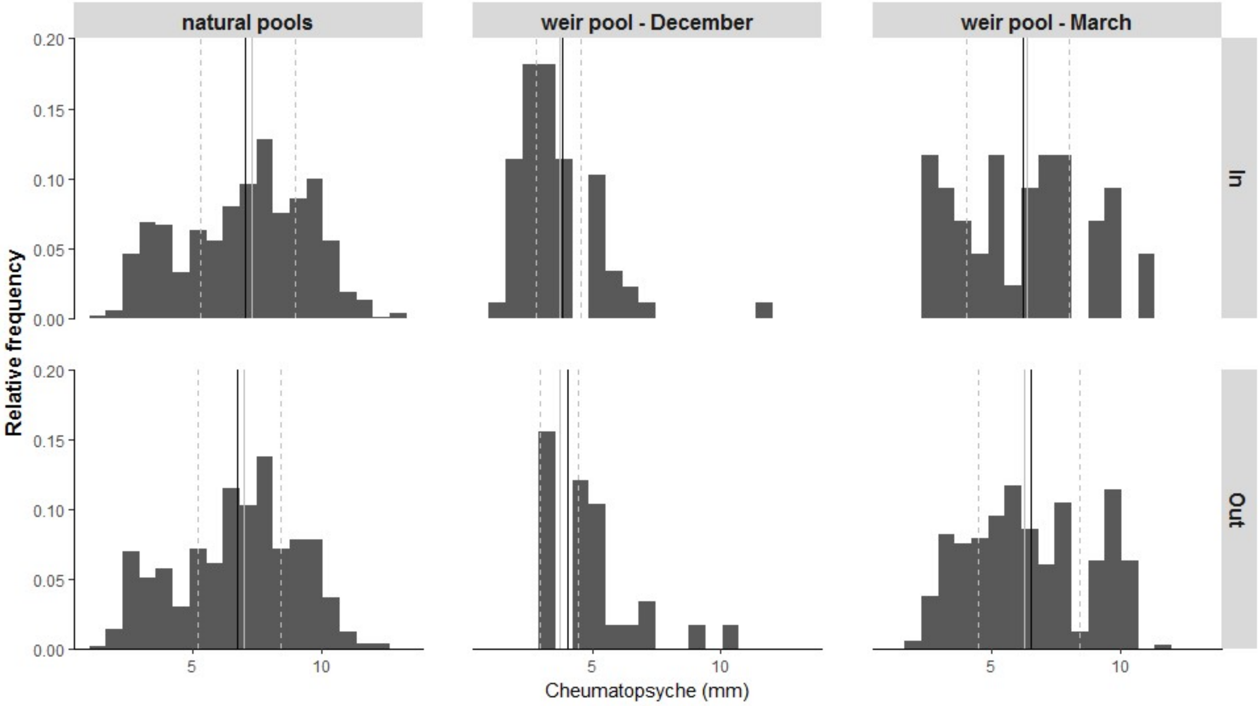

Figure 5. Size frequency distribution of drifting *Cheumatopsyche* spp. immigrating and emigrating from natural pools and Mowamba weir in April and December. Black line = mean, grey line = median and grey dotted lines = 25th percentile and 75th percentile.

Discussion

There are more than 800,000 weirs and low head dams estimated to exist across the globe (Rosenberg, McCully, & Pringle, 2000). Despite hypotheses about the barrier effect of these structures, there are few empirical studies of their significance on downstream dispersal. We addressed the possible impacts of weirs on dispersal stream insects by directly testing whether a weir and its associated pool impeded the drift of stream insects.

For 3 of 4 of our study taxa (*Offadens* spp., *Austrosimulium* spp. and *Simsonia* spp.), the numbers of drifting insects were consistently reduced by the weir, supporting prediction (i). This decline in drift numbers exceeded the reduction within natural pools (prediction (ii) supported). These results indicate that the weir is a significant barrier to drift under moderate flow conditions in autumn and early summer, and may disrupt downstream movement to a greater degree than other natural river features that create similar slow moving water (i.e. pools). It is possible that drift during high flows may overcome the effects of the weir. However, drift densities peak and decline quickly after the onset of high flows and increased shear stress (Gibbins, Batalla, & Vericat, 2010; Imbert & Perry, 2000), and may not provide substantial numbers of colonists to downstream sections of rivers. Furthermore, other studies have shown drift rates of hydropsychids were lower at higher discharges than base flows, possibly due to behaviours such as moving into the substratum to avoid increased shear stresses (Downes & Lancaster, 2010).

Dispersal distances are influenced by the spatial configuration of low water velocity areas as much as the overall proportion of low velocity within a stream reach (Bond et al., 2000; Lancaster et al., 1996). Mowamba weir pool was substantially deeper and wider and slower than the majority of sampled natural pools. The weir pool had two areas where flows would be very slow - a deep region towards the start of the weir pool and another deep and wide area at the most downstream end adjacent to the weir wall. In this second downstream area, the weir wall at the end of the pool created an abrupt depth change from approximately 3 m to 0 m over less than a metre. In the natural pools, generally there was only a single deep and wide region and the downstream end of the pool became gradually shallower before the next riffle. Furthermore, the length of the deep, wide areas in natural pools was much shorter than the weir pool. Therefore, the combined effects of much lower average water velocity, multiple large low velocity areas within the weir pool and the weir wall are likely to be central causes of the reduction in drift through the weir.

For baetid mayflies, a combination of swimming using dorso-ventral undulations and body posturing is used to manage drift time and distance (Campbell, 1985; Oldmeadow et al., 2010; Otto & Sjöström, 1986). These behaviours can both prolong drift and allow exit from the drift (Allan & Feifarek, 1989). Baetid species of the genus *Offadens* are likely to use similar mechanisms when drifting and may have actively chosen to exit the drift when exposed to slow or zero velocity areas by swimming to the substrate. Actively seeking the substrate is possibly to avoid settling in slow flow habitats where resource quality is low or difficult to acquire, and may have become more pronounced in the weir pool, where there were higher number and greater proportion of slow water zones. The size of *Offadens* spp. individuals did not influence their ability to drift through the low water velocity areas. This result is contrary to findings for another species of baetid, *Baetis rhodani*, where smaller larvae drift from riffles into slower flowing areas, remaining there to grow, and later drifting into riffles as large larvae (Lancaster et al., 2011). It is possible that the slow, deep pools in our study did not provide the same between-riffle habitat for small larvae to develop, resulting in no size differences between immigrating and emigrating larvae.

Austrosimulium spp. (Simuliidae) increase their chances of transiting pools using silk threads, which diminish their fall velocities, making them more likely to drift through a pool before being deposited (Fingerut, Schamel, Faugno, Mestrinaro, & Habdas, 2009). This mechanism appeared to provide some success in transiting natural pools (SS = -0.29), but most likely the efficacy was reduced in the weir pool by the much deeper, slower flowing water. The number of *Austrosimulium* spp. drifters was reduced in the weir pool, but the few emigrating drifters were significantly smaller than immigrating individuals. The difference in drift distances due to the presence of silk varies greatly with larval size, with smaller larvae having decreased fall velocities and increased drift distances compared with larger larvae (Fingerut et al., 2009). Therefore, silk threads may provide an important mechanism for smaller larvae to successfully drift through the slow flowing areas of weir pools.

Drift numbers of *Simsonia* spp. were significantly reduced by both weir pools and natural pools, but the weir reduced drifters to a greater extent. Elmid adults predominantly disperse by walking rather than drifting (Elliott, 2008) and have the capacity to walk from pool habitats after settlement to seek faster flowing riffle areas. The reduced drift through the weir pool may have been due to the unusual morphology of the downstream end of the weir pool. In this part of the weir pool, the abrupt change in depth at the weir wall and deep wide cross-section may have limited the ability of the elmid to walk downstream and re-enter the drift and disperse downstream.

We found the effect of the weir pool on *Cheumatopsyche* spp. drifters was inconsistent and possibly related to the size of individuals. Drift of *Cheumatopsyche* spp. through the weir was greatly reduced in December (-95%) but reduced by very little during April (-9%). In contrast, drift of this genus through natural pools did not differ between sampling times. There was little difference in daily flow between the two sampling events (December = 0.85 m^3s^{-1}, April = 0.72 m^3s^{-1}), and flow could not explain the temporal inconsistencies in drift rates through the weir pool. There were no differences in the size of *Cheumatopsyche* spp. larvae entering and exiting the weir pool on either sampling occasion. However, larvae in December were significantly smaller than April. December corresponded to a significant reduction in drift numbers through the weir pool, while in April individuals were much larger when there was little effect of the weir pool on drift. In contrast, similar differences in larval size between April and December did not appear to have any differential effect on drift through natural pools. This suggests the weir pool impedes the drift of smaller individuals to a much greater degree than large larvae, and that natural pools do not have a size related effect on drift. This finding is contrary to our prediction that smaller individuals would drift further and be more likely to drift through the weir pool.

This unexpected observation suggests that the larger larvae possess abilities to drift through the weir pool that small larvae do not. Filter-feeding Hydropsychidae larvae are inefficient swimmers (Otto & Sjöström, 1986) and avoid areas of slow flow and move to areas of faster flow by walking (Sharpe & Downes, 2006). Hydropsychids, while possessing little directional swimming ability, have some behavioural control of drift time such as curling into a ball, which increases settlement from the drift, or stretching out their body to prolong drift time (Oldmeadow, 2005). It is possible that smaller larvae actively exit the drift as soon as they drift into slow flow areas and walk upstream (Elliott, 2003), preventing settlement in pools where filter feeding is difficult. Also, smaller larvae may have more difficulty moving through slowly flowing water than larger larvae, because smaller organisms experience water as more viscous (Kutash & Craig, 1998). In addition, larger larvae have greater energy stores, and thus may have greater capacity to move through the weir pool through a combination of drifting, walking and swimming, and then re-enter the drift, passing over the weir wall.

The weir pool reduced the numbers of drifting invertebrates of three focal genera (*Offadens* spp., *Austrosimulium* spp., adult *Simsonia* spp.) from three different orders (Ephemeroptera, Diptera, Coleoptera), despite their diverse methods of drift and downstream movements. This suggests that there are multiple mechanisms by which the weir pool impedes drift. Reductions in numbers of drifting *Offadens* spp. and *Austrosimulium* spp. have previously been found to be related to increases in pool depth and width (Brooks et al., 2017), indicating that their contrasting drifting methods are equally diminished by slow moving water. The greater areas and multiple zones of zero and low flow areas in the weir pool appear to have exacerbated this effect, particularly on larger *Austrosimulium* spp. In contrast, declines in the number of drifting *Simsonia* spp. and *Cheumatopsyche* spp. through natural pools are unrelated to pool depth and width (Brooks et al., 2017). Therefore, the higher drift reductions through the weir pool cannot be explained by the slower flow in the weir, but possibly caused by the weir wall at the downstream end of the weir pool blocking downstream movement by walking and drifting. The most surprising result was that the weir pool impeded the drift of small *Cheumatopsyche* spp., suggesting the drift behaviours of larger individuals could overcome both the slow flowing pool and the weir wall.

The outcome of weirs reducing drift dispersal on downstream population dynamics and recovery following disturbances remains unexplored. Dispersal limitation is likely to be an important impediment to recovery for freshwater insects in rivers fragmented by weirs and dams (Brederveld, Jähnig, Lorenz, Brunzel, & Soons, 2011), but empirical studies remain scant. Therefore, a deeper understanding of how weirs and dams affect downstream colonisation and recruitment processes (both aquatic and aerial) will be critical to successful river restoration.

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Chapter 4. Paper 3 – Just add water: Rapid assembly of new communities in previously dry riverbeds, and limited long-distance effects on existing communities.

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Key words: community assembly, colonisation, dispersal, freshwater invertebrates, barriers

Abstract

Barriers preventing species from dispersing to a location can have a major influence on how communities assemble, resulting in delayed or poor restoration outcomes due to a lack of dispersing colonists. One key hypothesis describing how dams and weirs affect rivers is that they disrupt longitudinal connectivity, limiting dispersal of biota along rivers. Decommissioning aqueducts on two weirs, each within a tributary of different regulated rivers, delivered flow to previously dry riverbeds and additional flows to the main-stem regulated rivers further downstream. This provided an opportunity to test how removal of dispersal constraints affected community assembly in new habitats and whether changed dispersal can alter existing communities. The results were very similar for the two systems. Even with dispersal constraint via reduced drift rates, the new communities in the newly formed habitat in tributaries rapidly resembled upstream unimpacted communities that were the source of colonists. For established communities (regulated rivers), increased flow from the tributary changed the trophic structure of communities. In particular, densities of filter feeders increased due to increased areas of fast-flowing habitat (a change in environmental constraints) rather than higher dispersal rates. Our study illustrates that communities can quickly re-assemble when natural channels that have been dry for decades are re-wetted by flows that deliver dispersers from intact locations upstream. Boosting dispersal had no strong effects on existing communities. Instead, increased discharges effected a reduction in environmental constraints, which altered trophic structure. Thus, increases in discharge and dispersal produced different outcomes in new versus established communities.

Introduction

Community assembly theory describes the processes by which local communities are constructed and maintained through sequential and repeated immigration from the regional species pool (Patrick and Swan 2011; Fukami 2015). Community assembly is governed by three main determinants: dispersal constraints, environmental constraints and biotic constraints (interactions among species), although the term ‘filters’ is often used, all of which sort and narrow the pool of species that might establish (Belyea and Lancaster 1999; Chase 2003). Dispersal constraints will limit the frequency and timing of individuals dispersing into a location from the pool of potential colonists (Harrison and Hastings 1996). Once a species arrives, it must possess the appropriate traits to establish and survive the abiotic environmental conditions present at that site (environmental constraints) (Poff 1997; Lake et al. 2007). Biotic interactions such as predation and competition among species for limiting resources can also affect the assembly of a community (Chase et al. 2009; Myers and Harms 2009). Dispersal constraints determine the order and identity of species arrival to a location and in combination with biotic interactions, may result in priority effects (Belyea and Lancaster 1999). Priority effects often occur when high densities of initial colonisers at a site can affect the establishment, growth, or reproduction of the species that arrive later, influencing further community assembly (Waters et al. 2013). Priority effects can lead to communities diverging in composition in locations with similar environmental conditions and which share the same species pool (Chase 2003; Fukami et al. 2016). Understanding how these different constraints affect community assembly in natural and human – altered environments is central to advancing community ecology.

Barriers that limit or prevent species from dispersing to a location can have a major influence on how communities assemble. In a restoration context, this can result in delayed or poor restoration outcomes due to a lack of dispersing colonists or priority effects preventing colonisation (Funk et al. 2008; Öster et al. 2009; Hulvey and Aigner 2014). In freshwater environments, one key hypothesis describing how dams and weirs affect rivers is that they disrupt longitudinal connectivity, fragmenting river ecosystems, potentially limiting dispersal of biota along rivers (Ward and Stanford 1995; Lake et al. 2007). In effect, dams and weirs – beyond their effects on discharge and hydraulic habitat – may influence community assembly by limiting dispersal and the arrival of species to sites. Therefore, rivers and their associated in-stream barriers provide an ideal system to test questions of community assembly and dispersal limitation. Here, we undertook a study that aimed to determine (a) the patterns of assembly of a community in new habitat, (b) whether barriers to dispersal affected community assembly within the new habitat and (c) whether dispersal from the newly formed community can successfully colonise and alter existing communities in nearby established habitats.

This study focusses on two upland streams within a national park, each with a diversion weir and associated aqueduct that had previously removed all water from downstream sections for over 50 years (Fig. 1). In each case, the stream affected by the weir was the first major tributary downstream of a large dam. The river sections below the dams also received no water, however, in these areas there was a small amount of flowing water from groundwater inputs, and benthic invertebrate communities were present. A decision to decommission the aqueducts on the weirs provided flow over the top of the weirs and to the previously dry riverbeds of the tributaries and additional flows to the main-stem regulated rivers further downstream (Fig. 1). This provided a unique opportunity to study the patterns and mechanisms of community assembly of freshwater invertebrates in new and existing habitats within two river systems unaffected by human influences, except flow regulation and diversion by dams and weirs.

Overall, after the commencement of flows over the weir, we expected that the weirs would limit the downstream dispersal of invertebrates by reducing drift rates (see Brooks et al. 2018). Therefore, we anticipated that dispersal constraints would play a dominant role in the assembly of benthic communities in the tributary, potentially leading to communities dissimilar to reference locations. In the regulated sites, we expected increased dispersal from the new tributary communities would alter the established communities, but changes would depend on the patterns of colonisation in the tributary. Thus, the effect of adverse abiotic environmental conditions (environmental constraint) and competition and predation (biotic constraints) on community assembly, although possible, were likely to be less influential than dispersal constraints. First, we examined patterns of community structure in the tributaries and in the regulated locations after flows commenced. We also assessed changes in the trophic structure of benthic communities by examining densities of different functional feeding groups (predators, scrapers, gatherers, filter feeders) in the tributary and regulated locations over time. Some taxa may drift to a location but fail to establish, and functional feeding groups may provide insight into what factors limit colonisation. For example, greater flow may increase the availability and supply of food and flowing water habitat, creating more favourable environmental conditions for colonisation of filter feeders and herbivores (Robson and Matthews 2004; Kiffney et al. 2006; Wilson and McTammany 2014). Also, predator colonisation may be delayed until prey populations have established in new habitats (Malmqvist et al. 1991). Second, we tested for dispersal constraints. If drifting invertebrates were impeded by water over-topping the weirs, we expected composition of the drift assemblage over the weirs to be altered compared to assemblages upstream, and drift rates of some taxa to be reduced. Additionally, if drift was impeded by the weirs or dispersal from the tributary into regulated rivers was limited, drift composition at tributary and regulated locations would be dissimilar to upstream locations. Winged adults play an important role in recolonisation of rivers via oviposition (Bogan and Boersma 2012), and are a potential source of colonists if they are present at downstream locations after flows increased. If dispersal of winged adults was limited in this system, then we expected adults would be present at upstream but not downstream locations.

Materials and methods

Study area and sampling design

This study was centred upon two cobble-bed creeks, Middle Creek and Diggers Creek, which are tributaries of the regulated Geehi River (regulated by Geehi Dam) and Snowy

River (regulated by Island Bend Dam), respectively and situated in different catchments approximately 16 km apart (Fig.1, Table 1). These structures form part of the Snowy Mountains Hydro-electric Scheme, which was built between 1949 to 1974, collecting and storing water from the headwaters of the Snowy River and diverting it through tunnels and power stations to the Murrumbidgee and Murray River valleys in the west (NSW Office of Water 2010). The scheme comprises 16 dams, 18 aqueducts, 19 trans-mountain tunnels, 7 power stations and 2 pumping stations.

Diversion of water was stopped on 1 May 2012 (Middle Creek weir) and 1 May 2013 (Diggers Creek weir), allowing all flows to overtop the weirs, providing flows to the previously dry tributary stream sections and also the regulated river downstream of the tributary. Flows increased 28 – 56 fold in the regulated river sections, equating to 5 – 10 % of natural flows (Table 1).

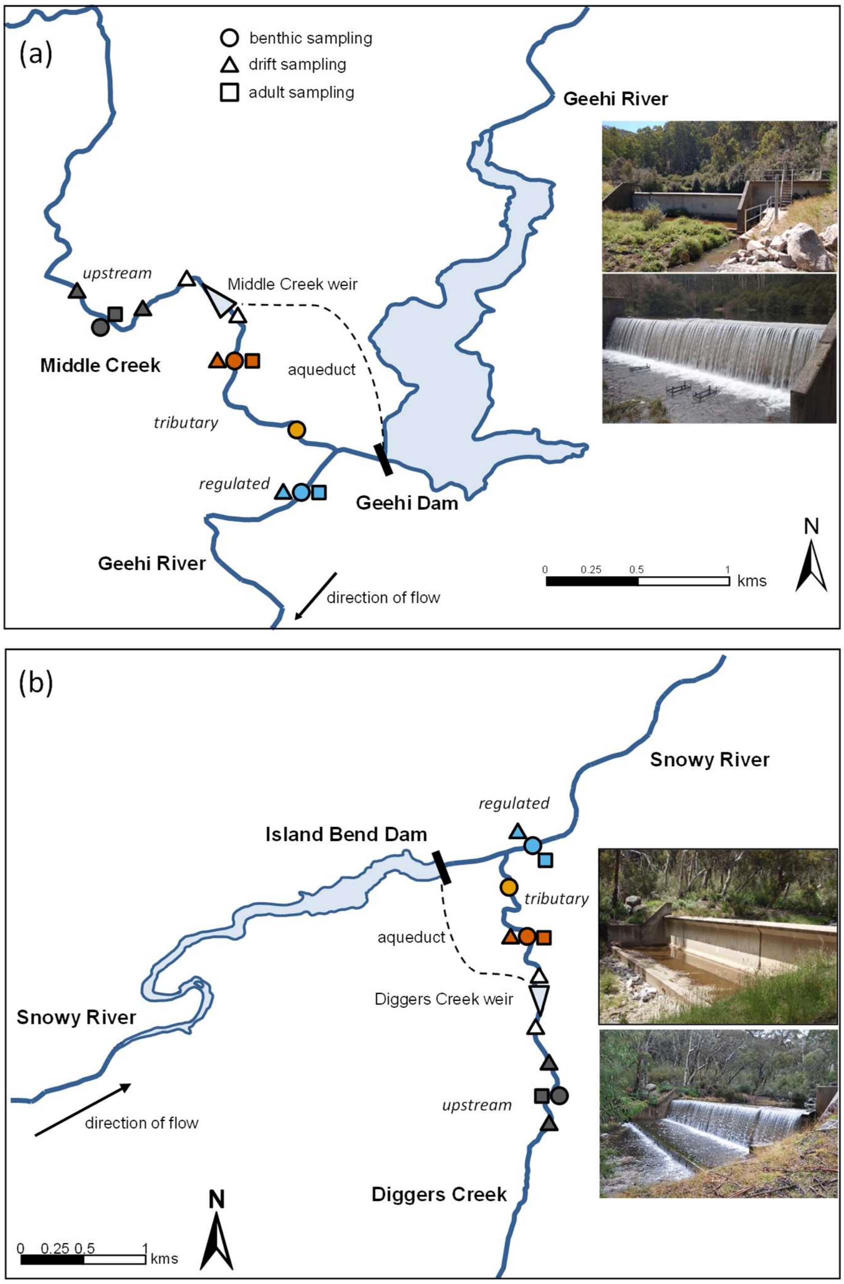

Figure 1. Map of sampling sites on (a) Middle Creek and Geehi River, and (b) Diggers Creek and Snowy River. Circles = benthic sampling sites, triangles = drift sampling sites and squares = flying adult sampling sites. Photographs show each weir pre- and post-decommissioning of the aqueducts.

The weirs on both rivers were approximately 1 km upstream from the confluence with the regulated rivers. The Middle Creek-Geehi River confluence was 60 m downstream of Geehi Dam and the Diggers Creek-Snowy River confluence was 400 m downstream of Island Bend Dam. The study rivers are located entirely within montane woodland zone of the Kosciuszko National Park in the Snowy Mountains region of south-east Australia (Doherty et al. 2015), and consequently are unaffected by any other human impacts. Rivers are snowmelt driven systems with highest discharge during spring (September – November). The water temperature ranged from 4 °C to 17.4 °C over the duration of the study.

Table 1. Flow in tributary and regulated locations after water released from weirs, and size of weir and dam structures. Post-release flows are mean daily flows calculated over the two years of study (Source: SnowyHydro Ltd).

	mean flow (m^3/s)		weir or dam dimensions (m)	
Location	pre-release	post-release	length	height
tributary				
Middle Creek	0	0.55	12	2.8
Diggers Creek	0	0.27	18	3
regulated				
Geehi River	0.01	0.56	265	91
Snowy River	0.01	0.28	146	49

Sample sites (elevation 1100 m – 1250 m) were grouped into upstream (i.e. reference), tributary and regulated locations with a different number of sites in each location for each method of sampling (Fig. 1). Benthic samples were collected upstream of the weirs (100 – 250 m upstream) and two sites in the tributaries below the weirs (Fig. 1). The upper-tributary sites were situated 100 m downstream of the weirs and lower-tributary sites within 50 m of the confluence with the regulated rivers (Fig. 1). Regulated sites were 130 – 150 m downstream of the tributary confluence (Fig. 1). Drift samples were collected at two sites upstream of the weir separated by 100 m. These samples were situated where the uppermost benthic samples were taken. Drift samples were also collected at the upper-tributary site and the regulated sites corresponding to the location of benthic samples. In addition, drift was sampled immediately upstream of the weir pools and also exiting the weir pools (see *Drift sampling* for details). No benthic or drift samples could be taken in the regulated river upstream of the tributary confluence because there was no flowing water in this area. Flying adults of aquatic insects were sampled at the upstream, upper-tributary and regulated sites matching the location of the benthic samples.

Benthic samples were taken twice in the upstream and regulated locations in both rivers prior to the decommissioning of the aqueducts. Samples were collected 41 and 3 days prior to decommissioning in Middle Creek / Geehi River, and 141 and 26 days prior to decommissioning in Diggers Creek / Snowy River. Drift samples were taken prior to flows only in Diggers Creek/Snowy river upstream and regulated locations. Benthic and drift samples were collected from all locations on 6 occasions after flows from the weir began (approximately 1, 7, 11, 16, 20, 22 months post-release).

Benthic invertebrate sampling

On each sampling occasion at each site, we collected 6 benthic invertebrate samples from 6 random points within a 20 m length of river. Each sample was collected over 1 minute using a suction sampler (area sampled 0.07 m^2, 250 µm mesh) (Brooks, 1994) and preserved in 70% ethanol. In this study design, individual sites are replicates, not individual samples. Therefore, the 6 samples were composited to provide a single estimate of densities per site (no./0.42 m^2). Each composited sample was subsampled (20% – 50%) following the methods of Marchant (1989), invertebrates were identified to genus and enumerated, except for Chironomidae, which were identified to sub-family. Invertebrates were assigned to one of four functional feeding groups (predators, filter feeders, gatherers and scrapers) based on Chessman (1986), Gooderham and Tsyrlin (2002), and Phillips and Smith (2018).

Drift sampling

Invertebrate drift was sampled using drift nets (25 x 25 cm opening) fitted with 1.5 m long nets with 250 µm mesh. At each site, three nets were located along a transect perpendicular to the flow of water. Nets were completely submerged at approximately 0.6 of maximum depth and at least 3 cm above the stream bed. Drift was collected on two nights over 3 hr starting 15 min prior to sunset. This time period was chosen because the majority of invertebrate drift occurs just after dusk (Brittain and Eikeland 1988). Sample methods for drift exiting the weirs were slightly different, with metal frames used to orient drift nets perpendicular to the flow overtopping the weir wall. Six nets were placed in random positions beneath the flow of water falling from the weir. All samples were preserved in 70% ethanol and samples collected at a site (3 or 6 nets and 2 nights) were composited, subsampled, identified and enumerated in the laboratory using the protocols as for benthic samples. Chironomidae were not identified in drift samples due to resource constraints.

To estimate drift rates, we calculated the proportion of the cross-sectional area of the water column sampled by drift nets, and used this to estimate the total number of individuals of each taxon drifting at each sampling location (Downes 2010). Thus, drift rates were the total number of insects drifting past the total cross-sectional area of the river per 3 hr.

Adult sampling

We sampled flying invertebrate adults using light traps (8 W, 12 V ultraviolet fluorescent tube) placed above a white bucket with an ethanol wick dispenser, which released ethanol fumes into the bucket and killed trapped insects. A single light trap was placed overnight at each site, and each site was sampled on 2 nights. Samples were preserved in 70 % ethanol and composited over the 2 nights and identified to genus level.

Statistical analysis

First, statistical tests were undertaken on benthic community composition and structure to determine the pattern of community assembly in the tributary and community change in the regulated locations after flows increased. Tests were also conducted on densities of functional feeding groups to further examine community assembly patterns and the possible influence of environmental or biotic constraints on communities. Second, to determine if there were constraints to dispersal, the effect of the weir on drift rates was analysed. The presence or absence of flying adults was also examined as a potential dispersal constraint.

Prior to each statistical analysis, we determined if the relationship between the response variables and predictors at each location were consistent between the two study rivers (i.e. whether the two rivers responded differently). Analysis of covariance (ANCOVA) was used to test for a significant River x Time interaction for each location for the analysis outlined in *Patterns of community assembly* and *Assembly of trophic structure* sections below. ANCOVA was used to test for River x Location interactions when examining the impact of the weir on drifting invertebrates (*Evidence of dispersal constraints* section). Where interaction terms were not significant, data from both rivers were pooled and analysed. Where interaction terms were significant, each river was analysed separately.

Patterns of community assembly in tributary and regulated locations following increased flows

We determined whether benthic invertebrate community composition in tributary and regulated sites became more similar to upstream (reference) communities after water began to flow over the weirs. In all statistical analyses, the upstream sites were reference locations, representing a natural community. First, non-metric multidimensional scaling ordination (NMDS, Clarke 1993) was used to visualise overall macroinvertebrate community patterns in each location and river after flows increased. Ordinations were carried out separately for each location and river combination.

Second, community similarity between pairs of samples was calculated using the Bray-Curtis similarity coefficient. Data were log10(x+1) transformed prior to calculation of the Bray-Curtis coefficient to down weight the contributions of numerically dominant taxa to the similarity measure. We tested if communities at each downstream location were converging on a natural community (i.e. upstream sites) after flows over the weir began. Community similarity was calculated between pairs of sites for three separate comparisons (upstream vs tributary [upper], upstream vs tributary [lower] and upstream vs regulated) on each sampling occasion and for each river (12 comparisons in total for each tributary location and 16 for the regulated location). Each comparison was analysed separately using least squares linear regression to test for temporal patterns in community similarity, i.e. relating community similarity to a continuous fixed factor of days since water began flowing from the weir. *t* – tests were used to determine if the slopes of the relationships were significantly different from zero. A positive slope indicated the community became more similar to upstream reference sites. The regression model was a linear form of a power function using log-transformed values of both similarity and time, because we expected colonisation processes to initially be rapid before slowing or reaching an upper limit over time (Sheldon 1977).

Temporal patterns were next examined using the univariate measure of the total invertebrate density, taxon richness and densities of individual taxa, which were determined at four locations on each river: upstream, tributary (upper), tributary (lower) and regulated. Tests followed regression analyses as described above for temporal changes in community composition. Where there was a non-significant slope, the mean response at each downstream location was compared to upstream using a one-way ANOVA with planned comparisons. A significant positive slope of response variables in downstream locations indicates values of these variables became similar to the upstream reference sites after flows increased. In the absence of a temporal increase, the comparison of the mean of the response variables determined whether invertebrate densities and taxon richness were lower than upstream, potentially indicating a limited response to increased flows.

Finally, we examined whether dispersal via drift from upstream could have contributed to colonisation of the upper-tributary by calculating the proportion of taxa common to both the tributary benthic community and the drift assemblage exiting the weir over time and in each river. Statistical analyses followed the linear regression methods outlined in above. Drift composition can be considered a predictor of benthic community composition because drift was sampled exiting the weir and was upstream of the tributary benthic site. If drift rates were measured at the same site as benthic samples, it would be difficult to separate the effect of drifters entering the site with local movements within the benthos. The logic of this approach has been validated in previous work (Downes and Lancaster 2018).

The above analyses revealed the patterns of change, and next we tested whether specific constraints explained these changes.

Assembly of trophic structure

Temporal patterns in the benthic densities of each feeding group (gatherers, shredders, scrapers, predators, filter-feeders) were tested separately at upstream, tributary (upper), tributary (lower) and regulated sites on each river (Fig. 1), using the linear regression methods outlined in *Patterns of community assembly*. Temporal changes in drift rates of each feeding group were also determined at upstream, tributary (upper) and regulated sites using the same methods.

Evidence of dispersal constraints

We first considered which species were blocked or hindered by the weirs from drifting downstream on each river using published methods (see Brooks et al. 2018). If the weir limited drifting invertebrates, then the similarity between the assemblage entering and exiting the weir will be lower than the similarity between drift assemblages at two sites without an intervening barrier. The effect of the weirs on dispersal was determined by comparing the mean similarity of the drift assemblage between upper and lower drift sites within the upstream location (which reflects assemblage similarity in the absence of a barrier) with the mean similarity between drift the entering and exiting the weirs on each sampling occasion. In this design, there are 12 comparisons upstream (6 occasions x 2 rivers) and 12 comparisons at the weirs (6 occasions x 2 rivers). Similarity was calculated using the Bray-Curtis similarity coefficient on $\log_{10}(x+1)$ transformed data. One-tailed *t*-tests were used to determine if mean similarity values at the weirs were less than mean upstream values; a significant difference would indicate that the weirs reduced downstream drift.

For each feeding group and taxon on each river, a source/sink index (SS) for was calculated for drift rates between the two upstream drift sites (Fig. 1) and for drift through the weir on each sampling occasion, providing 12 comparisons upstream (6 occasions x 2 rivers) and 12 comparisons at the weirs (6 occasions x 2 rivers), following Lancaster et al. (2011). The index ranges between −1 and 1 and is a measure of the proportion of insects that drift between sample sites (i.e. between upstream sample sites, between drift entering and exiting the weir). If $SS < 0$ (i.e. immigration > emigration), then SS represents the proportion of insects that did not drift between upstream sites or through the weir pool. In contrast, the area between the upstream sites or within the weir pool are a source of drifting insects if $SS > 0$ (i.e., emigration > immigration), and SS reflects the proportion of emigrants that originated between paired sample sites. Values of $SS = 0$ indicate comparable immigration and emigration rates. Therefore, drift has been impeded by the weir if the average SS for the weir pools is significantly lower than SS between upstream sites ($SS_{upstream} > SS_{weir}$) and can be considered to be unaffected by the weir if $SS_{weir} = SS_{upstream}$. One-tailed *t* – tests were used to determine whether the mean weir values (SS for feeding groups or taxon) were less than upstream values.

To test whether the weir impeded dispersal and affected dispersal farther downstream, we determined if the drift assemblage in the tributary and regulated locations became more similar to upstream sites after flows overtopped the weir. Specifically, we compared similarity of the drift assemblage at the two upstream drift sampling sites vs tributary (upper) sites, and two upstream drift sampling sites vs regulated sites over time in each river (Fig. 1). For each location, the average of the similarity with the two upstream drift assemblages was used in the analysis. This provided 11 upstream vs tributary comparisons and 13 upstream vs regulated comparisons. We also tested whether drift rates for all invertebrates and for taxon richness increased over time in the tributary and regulated sites. These tests followed the linear regression analysis outlined in *Patterns of community assembly*.

Flying adults may have played a role in recolonisation of the benthos via oviposition, and we examined the numbers of adults trapped at upstream, tributary (upper) and regulated sites, which were plotted against time since flows were released from the weirs. These data were qualitative and unsuitable for statistical analysis because the area sampled by the light trap varied between sites due to variations in amounts of riparian vegetation. However, they were adequate to describe when and where flying adult insects were present and a potential source of colonists.

All statistical analyses were carried out using ‘ggplot’ and base packages within R 3.5.3.

Results

For the majority of statistical analyses examining *Patterns of community assembly* and *Assembly of trophic structure*, the responses were consistent between rivers – that is, there was no significant River x Time interaction for a particular response variable. Exceptions occurred only in the benthos of the lower-tributary site (Online Resource 1), where the responses of total invertebrate densities, taxon richness and densities of gatherers, scrapers, predators and Chironominae and Orthocladiinae differed between the two rivers, so separate analyses were carried out for each river. There were no significant

Location x River interactions in tests for the effect of weirs on drifting invertebrates (*Evidence of dispersal constraints*). These results are discussed in further detail below.

Patterns of community assembly

Over the study, we collected 41 taxa, the most numerous genera belonging to the families of Chironomidae (Diptera), Leptophlebiidae and Baetidae (Ephemeroptera) and Elmidae (Coleoptera).

The benthic community in all downstream locations became similar to upstream sites after flows increased and this pattern was consistent between the rivers (Fig. 2). The assembly of the upper-tributary community was rapid and became similar to upstream by the second sampling occasion – approximately 7 months after flows began (Fig. 2). The development of lower-tributary community was slower and was similar to upstream by the third (~ 11 months) and fourth (~ 16 months) sampling times (Fig. 2). The increased similarity between upstream upper and tributary benthic communities over time was significant, increasing from 10-30% similar within 6 weeks to approximately 80% similarity after 2 years (Fig. 3). The similarity between the existing regulated benthic community and upstream also increased, but more slowly than the tributary, increasing from approximately 50% to 65% similar (Fig. 3, Table 2).

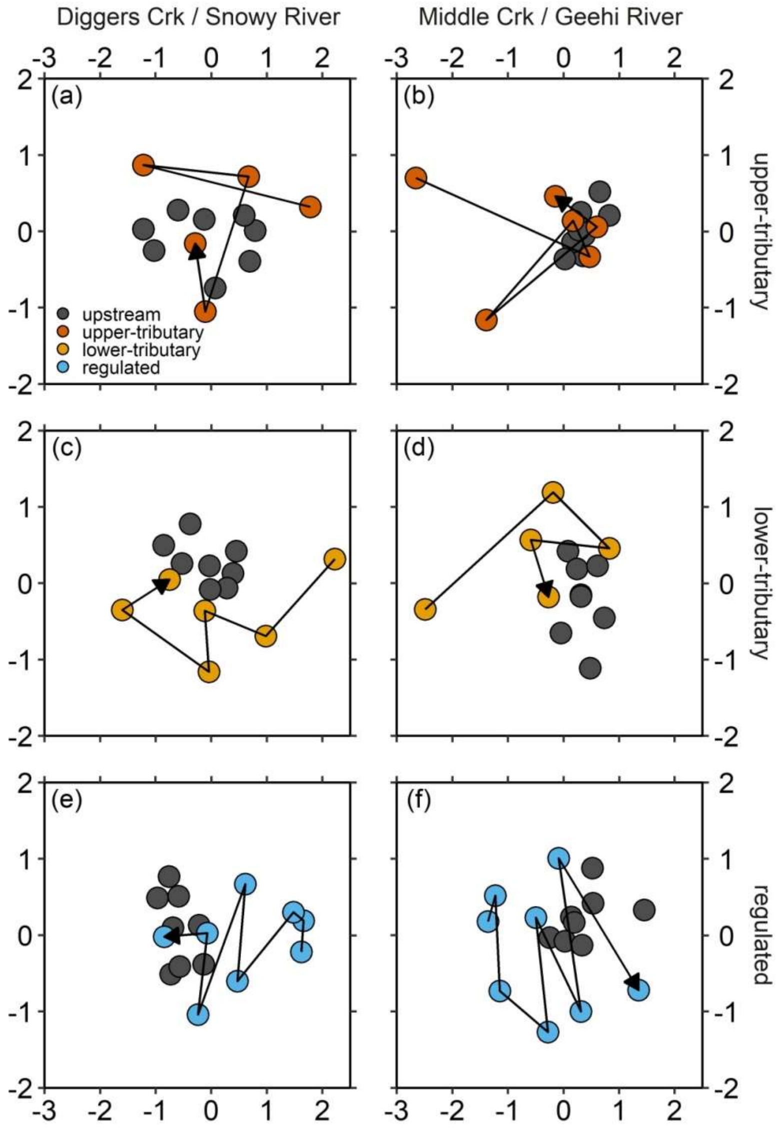

Figure 2. Non-metric multidimensional scaling ordination comparing similarity (Bray-Curtis) of benthic invertebrate communities in upper-tributary (a & b), lower-tributary (c & d) and regulated sites (e & f) with upstream sites over time for each river system. Ordinations were performed separately for each river and location combination. Samples at time 1 from Diggers Creek upper-tributary and Middle Creek lower-tributary were excluded because densities and taxon richness were extremely low, rendering the ordination uninterpretable.

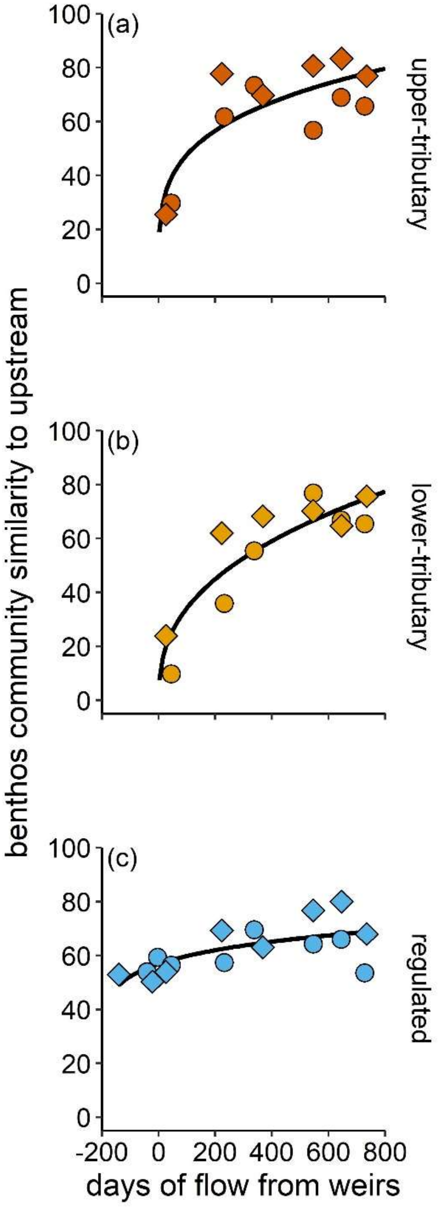

Figure 3. Similarity (Bray-Curtis) between benthic invertebrate communities in (a) upper-tributary, (b) lower-tributary and (c) regulated sites with upstream sites over time. The lines represent significant regression relationships (see Table 2). Circles = Middle Creek / Geehi River, diamonds = Diggers Creek / Snowy River.

These results are further illustrated by the changes in taxon richness, which increased significantly in both tributary locations after flows overtopped the weirs (Fig. 4, Table 2). Benthic densities also increased in the upper-tributary and in the Middle Creek lower-tributary location (Fig. 4, Table 2). Benthic densities at the Diggers Creek lower-tributary were equal to upstream densities, indicating rapid colonisation of some taxa within this river. Benthic taxon richness also increased over time in the regulated river sections, however, benthic densities did not change and were not different to upstream densities, which themselves showed no temporal trends (Fig. 4, Table 2).

Twelve taxa were sufficiently common to undertake meaningful individual statistical analyses. There were no temporal trends in the upstream location for any taxon in either river (Online Resource 2). In the upper-tributary sites, only the caddisfly *Asmicridea* spp. was absent from samples in the first month after flows overtopped the weirs and all taxa were present by the second sampling occasion. Densities of seven taxa significantly increased through time in one or more tributary locations (Online Resource 2). At the lower-tributary site in Diggers Creek, densities of both Chironominae and Orthocladiinae decreased, indicating these taxa initially occupied this location in high numbers, then decreased as other taxa subsequently colonised. Densities of the stonefly, *Austrocercella* spp., mayfly *Offadens* spp. and dipteran, Tanypodinae, did not increase over time in the tributary, but mean densities were not significantly different to upstream, indicating that these taxa colonised quickly (Online Resource 2). For the caddisfly, *Taschorema* complex, densities did not increase over time and were significantly lower than upstream.

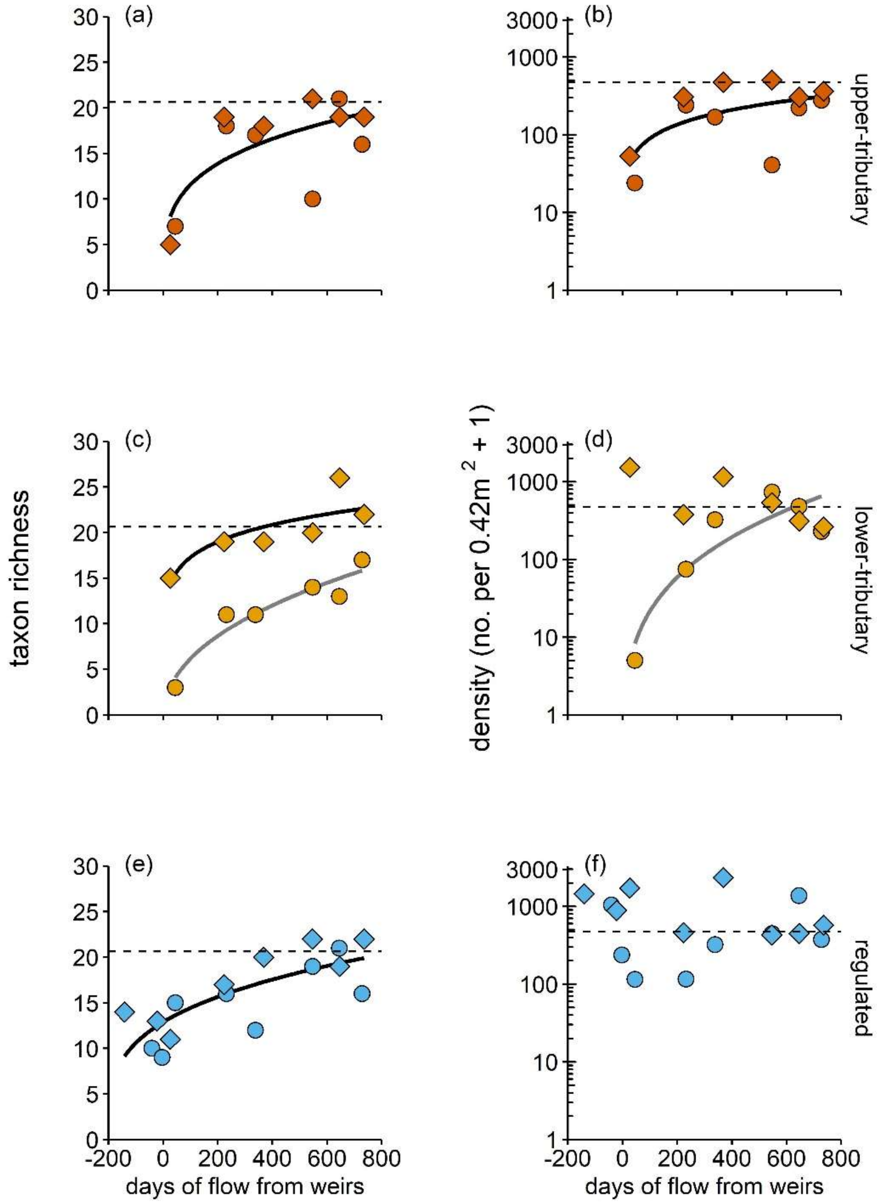

Figure 4. Taxon richness (a, c, e) and benthic densities (b, d, f) at upper-tributary, lower-tributary and regulated sites over time. The lines represent significant regression relationships (see Table 2). For benthic densities in the lower-tributary panel, the grey line represents a significant relationship in Middle Creek only (see Table 2). Dashed lines represent the mean value of upstream sites. Circles = Middle Creek / Geehi River, diamonds = Diggers Creek / Snowy River.

In the regulated sites of both rivers, three taxa significantly increased through time (Online Resource 2). The densities of four taxa did not change over time and were significantly lower than upstream (*Simsonia* spp., *Austrolimnius* spp., *Austrophlebioides* spp., *Taschorema* complex) and the density of one taxon, Tanypodinae, was significantly higher than upstream (Online Resource 2). Mean densities of two chironomid taxa (Chironominae and Orthocladiinae) comprised almost 60% of the total number of invertebrates in the regulated sites.

There was a significant increase in the number of taxa common to both the benthic community and the assemblage drifting through the weir ($F_{1,10} = 10.8$, $p < 0.01$). Initially, there were few taxa common to both the drift and benthos, and this increased to approximately 75% of taxa after 22 months.

Table 2. Summary of linear regression analyses for invertebrate assemblage similarity (Bray-Curtis similarity), taxon richness, total invertebrate density and densities of different feeding groups. Community similarity was calculated between upstream-tributary and upstream-regulated sites on each sampling occasion. The slope of the response – days relationships were compared to zero for each location using t - tests. Where responses differed between rivers, each river was analysed separately. * indicates mean was significantly different from upstream mean.

		benthos					drift				
Response		d.f.	*t*-value	slope coefficient	P	mean density	d.f.	*t*-value	slope coefficient	P	mean drift rate
community similarity	upstream vs upper-tributary	1,10	6.5	0.32	<0.001		1,9	2.6	0.32	<0.03	
	upstream vs lower-tributary	1,10	5.6	0.49	<0.01						
	upstream vs regulated	1,14	3.0	0.08	0.01		1,11	7.0	0.28	<0.01	
total invertebrate density	upstream	1,14	1.5	0.03	0.17	509.2	1,26	1.0	0.04	0.34	1009.5
	upper- tributary	1,10	2.5	0.27	0.03		1,9	0.5	0.09	0.62	1288.2

		benthos					drift				
Response		d.f.	*t*-value	slope coefficient	P	mean density	d.f.	*t*-value	slope coefficient	P	mean drift rate
	lower-tributary (Middle)	1,4	4.2	0.85	0.01						
	lower-tributary (Diggers)	1,4	-2.1	-0.13	0.09	694.9					
	regulated	1,14	-0.6	-0.02	0.57	770.8	1,11	2.7	0.20	0.02	
taxon richness	upstream	1,14	-0.3	-0.02	0.75	20.6	1,26	-0.3	-0.02	0.77	18.5
	upper- tributary	1,10	3.5	0.70	<0.01		1,9	1.4	0.33	0.21	17.1
	lower-tributary (Middle)	1,4	8.4	0.58	<0.01						
	lower-tributary (Diggers)	1,4	3.5	0.12	0.02						
	regulated	1,14	3.7	0.25	<0.01		1,11	5.3	0.39	<0.01	

		benthos					drift				
Response		d.f.	*t*-value	slope coefficient	P	mean density	d.f.	*t*-value	slope coefficient	P	mean drift rate
Densities of Feeding groups											
gatherers	upstream	1,14	1.4	0.09	0.17	88.7	1,26	0.8	0.04	0.41	170.0
	upper- tributary	1,10	1.3	0.28	0.25	59.1	1,9	0.30	0.02	0.77	282.3
	lower-tributary (Middle)	1,4	3.2	1.1	0.03						
	lower-tributary (Diggers)	1,4	-2.3	-0.45	0.08	234.4					
	regulated	1,14	-0.13	0.26	0.26	285.3	1,11	3.4	0.33	<0.01	
scrapers	upstream	1,14	1.1	0.03	0.26	366.6	1,26	0.9	0.02	0.38	680.1
	upper- tributary	1,10	3.0	0.83	0.01		1,9	2.2	0.16	0.11	748.3

		benthos					drift				
Response		d.f.	*t*-value	slope coefficient	P	mean density	d.f.	*t*-value	slope coefficient	P	mean drift rate
	lower-tributary (Middle)	1,4	4.0	1.02	0.02						
	lower-tributary (Diggers)	1,4	-2.3	-0.17	0.09	395.6					
	regulated	1,14	0	0	0.98	387.8	1,11	3.2	0.24	0.03	
predators	upstream	1,14	0.7	0.04	0.48	38.1	1,26	1.1	0.06	0.30	70.7
	upper- tributary	1,10	1.3	0.39	0.23	18	1,9	0.9	0.04	0.37	135.0
	lower-tributary (Middle)	1,4	2.6	1.07	0.06	49.8					
	lower-tributary (Diggers)	1,4	-3.7	-0.37	0.02						
	regulated	1,14	-1.1	-0.11	0.28	74.3	1,11	1.7	0.09	0.12	266.0*

		benthos					drift				
Response		d.f.	*t*-value	slope coefficient	P	mean density	d.f.	*t*-value	slope coefficient	P	mean drift rate
filter feeders	upstream	1,14	-0.5	-0.02	0.65	15.8	1,26	0.7	0.05	0.52	54.9
	upper- tributary	1,10	3.5	0.49	<0.01		1,9	0.8	0.26	0.47	120.8
	lower-tributary	1,10	2.5	0.40	0.03						
	regulated	1,14	6.3	0.36	<0.01		1,11	1.8	0.28	0.11	381.4

Assembly of trophic structure

In upper-tributary sites of both rivers, the benthic densities of gatherers, scrapers, predators and filter feeders were either equal to upstream densities or they increased significantly through time (Table 2, Fig. 5). In the lower-tributary, there were slight differences in assembly between rivers. In Diggers Creek, colonisation of gatherers, scrapers and predators occurred in the first month, with predators and gatherers declining to densities commensurate with upstream (Table 2, Fig. 5). Colonisation of all trophic groups was much slower in the Middle Creek lower-tributary, with densities initially low and then steadily increasing over time (Table 2, Fig. 5). In the regulated sites, only benthic densities of filter feeders increased over time (Table 2, Fig. 5). Densities of the remaining feeding groups did not differ from upstream densities (Table 2, Fig. 5).

Evidence of dispersal constraints

The mean similarity between drift assemblages entering and exiting each weir was significantly lower than between assemblages at the two upstream locations of both rivers (Table 3). Drift rates of gatherers, scrapers and filter-feeders were also significantly reduced by the weir ($SS_{weir} < SS_{upstream}$), but drift of predators were unaffected ($SS_{weir} = SS_{upstream}$, Table 3). Eight taxa were sufficiently abundant for individual statistical analysis. The weir reduced drift rates of five taxa to a greater degree than between upstream sites (Table 3).

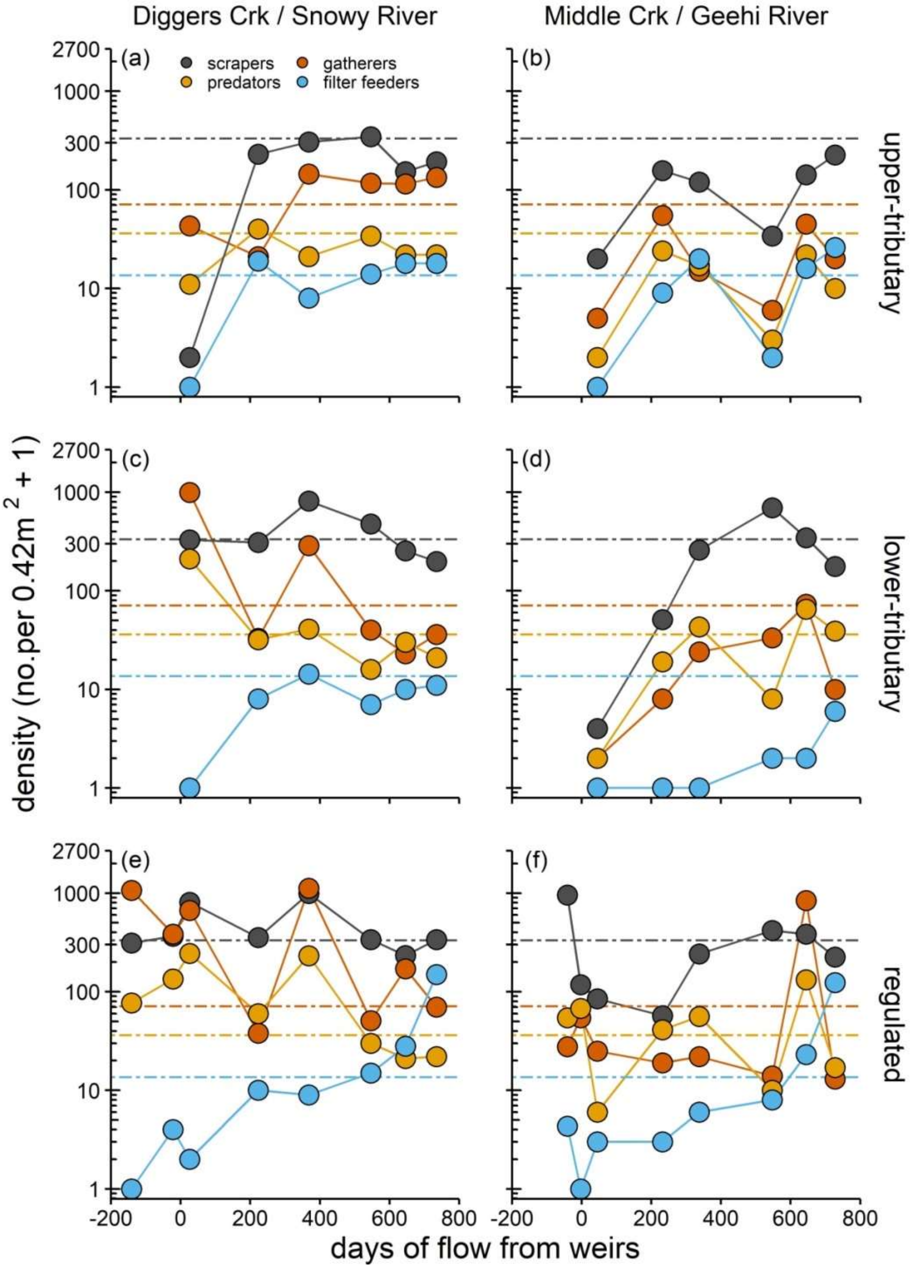

Figure 5. Benthic densities of functional feeding groups over time in upper-tributary (a & b), lower-tributary (c & d) and regulated (e & f), locations in both river systems. See Table 2 for summary of statistical analyses. Dashed lines represent the mean value of upstream sites.

Table 3. Summary of one-tailed *t*-tests of the impact of the weirs on drifting invertebrates. Community similarity *t*-tests were on Bray-Curtis similarity values. Tests on total drift rates, taxon richness and feeding group drift rates were done on SS values. Bold indicate *P* values are less than 0.05.

response	d.f.	*t*-value	*P*	mean upstream	mean weir
				similarity	
community similarity	1,22	3.5	**<0.01**	78.0	60.7
				SS value	
total drift rates	1,22	2.5	**0.01**	0.10	-0.38
taxon richness	1,22	3.3	**>0.01**	0.05	-0.23
feeding groups					
gatherers	1, 22	2.4	**0.01**	0.23	-0.29
scrapers	1, 22	2.3	**0.02**	0.07	-0.43
predators	1, 22	0.7	0.25	0.15	0.02
filter feeders	1, 20	2.6	**0.01**	0.21	-0.45
taxa					
Simsonia spp.	1, 20	0.5	0.30	0.13	-0.02
Offadens spp.	1, 18	1.5	0.07	0.33	-0.06
Austrophlebioides spp.	1, 22	1.9	**0.04**	0.10	-0.34
Trinotoperla spp.	1, 21	2.7	**0.01**	0.12	-0.55
Dinotoperla spp.	1, 21	2.6	**0.01**	0.21	-0.52
Austrocercella spp.	1, 19	2.5	**0.01**	0.19	-0.45
Taschorema complex	1, 22	1.0	0.17	0.09	-0.19
Asmicridea spp.	1, 18	2.6	**0.01**	0.35	-0.38

Composition of the drift assemblage in tributary sites became more similar to upstream sites over time in both rivers (Table 2). In the tributary, there was no increase in taxon richness, total numbers of drifters and drift rates of individual taxa (Table 2, Online Resource 2). The mean values were all equivalent to upstream sites, indicating that substantial numbers of drifting invertebrates were present at tributary sites immediately after the aqueduct was decommissioned and water flowed over the weir.

Similarity of the drift assemblages between upstream vs regulated sites increased over time in both rivers (Table 2). Both taxon richness and total numbers of drifters also increased over time in the regulated sites (Table 2). Drift rates of 5 out of 9 taxa significantly increased in the regulated location (Table 2, Online Resource 2). Mean drift rates of the remaining taxa were not significantly different from upstream drift rates (Table 2, Online Resource 2).

In the tributary locations, drift rates of all feeding groups did not change over time and rates did not differ from upstream (Table 2). Drift rates of gatherers and scrapers increased significantly over time in the regulated sites, predators did not increase and mean drift rates were significantly higher than upstream sites. Drift rates of filter feeders did not increase and did not differ from upstream drift rates (Table 2).

Adults of two mayfly taxa (*Austrophlebioides* spp., *Offadens* spp.) and two caddisfly taxa (*Asmicidea* spp., *Taschorema* complex) were sufficiently abundant to test for temporal and spatial patterns of occurrence. Mayfly adults occurred almost exclusively during summer and early autumn, i.e. between December and April (Fig. 6). Mayfly adults were not present in the tributary locations in the first summer after increased flows, but were trapped in the second summer.

The hydropsychid caddisfly, *Asmicridea* spp., was only collected between December and February in the upstream and regulated locations (Fig. 6). This genus was not present in samples from the tributary location until the second summer (February) following increased flows from the weir. Adult *Taschorema* complex were collected between October and April in all locations, and were present in the tributary locations throughout the first summer after increased flows (Fig. 6).

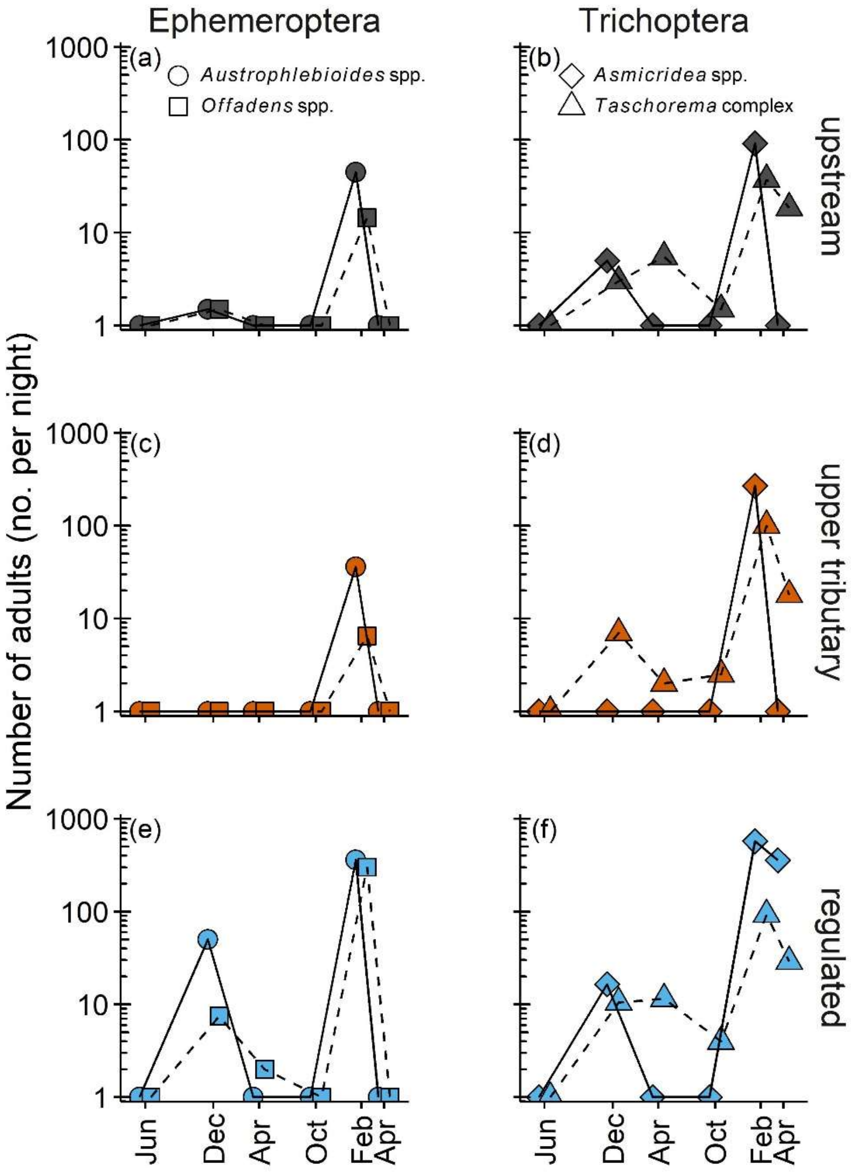

Figure 6. Adult insects collected by light traps in (a & b) upstream, (c & d) upper-tributary and (e & f) regulated locations, after increased flows released from the weirs. Symbols represent the average of the two river systems.

Discussion

Dispersal via drift was central to the colonisation and assembly of stream invertebrate communities in a newly formed habitat (i.e. stream channels that had been dry for 50 years). Even though dispersal constraints created by weirs reduced colonisation rates from source populations, the new communities closely and quickly resembled the upstream unimpacted communities. In areas with an established community (regulated rivers), there were significant increases in discharge and increases in the density and diversity of colonists arriving via drift, but responses in the benthic community were limited to an increase in densities of a single feeding group – filter feeders – rather than causing changes across the whole community. These findings differ from many previous studies that have suggested a strong role for dispersal constraints in community assembly (Steiner and Leibold 2004; Stein et al. 2008; Cornell and Harrison 2013). Such atypical results may be related to several unique aspects of this study. First, we measured natural dispersal rates and evaluated dispersal constraints directly, rather than inferring dispersal limitation indirectly or manipulating dispersal artificially. Second, we examined the impacts of dispersal on assembly of new communities as well as on existing communities. Third, we had two, replicate river systems in different catchments, which largely delivered the same outcomes and increased confidence in the findings. Fourth, our study was undertaken in a protected area with few human impacts (other than flow manipulation and in-stream structures) and over 2 years, which was sufficient time for two different natural colonisation mechanisms: drift in the water and flying adults laying eggs. Much of the community assembly literature has focussed on small-scale laboratory studies of simple organisms (e.g. protists: Jiang and Patel 2008; bacteria: Tan et al. 2012; fungi: Leopold et al. 2017) or outdoor but artificial environments (e.g. pond mesocosms: Chase and Myers 2011; experimental plots: Loughnan and Gilbert 2017). Here, dispersal occurred in natural channels and at landscape scales. Finally, tests of general theory require results from multiple types of ecosystems, but rivers feature only rarely in studies of community assembly. Collectively, we argue that these features make this study a valuable counterpoint to the community assembly literature.

Assembly of new communities

Benthic communities that assembled after the release of water into previously dry stream channels (i.e. tributary stream sections below the weirs) were 80% similar to upstream sites after two years of flow. This successful colonisation of the benthos occurred even though the weirs reduced drift rates of many taxa. So, although there was evidence of dispersal constraints, they had rather little effect on community development. Weirs can be barriers to drifting invertebrates (Brooks et al. 2018) and benthic invertebrate communities can differ upstream and downstream of weirs (Mueller et al. 2011), but our study indicates that impeded dispersal is unlikely to be the cause of differences in the benthos. The presence of unaltered upstream communities providing a pool of colonists was also critical to successful downstream tributary community assembly. Similarly, assembly of invertebrate communities in experimental stream channels is also rapid (<2 years) when potential colonists can drift from upstream (Harris et al. 2007). In contrast, in a study of a new stream channel where upstream source populations were not present, community assembly was much slower, and colonisation of new taxa was still occurring over 40 years after the stream formed (Milner et al. 2008).

Dispersal from upstream intact communities via drift strongly influenced colonisation of the benthos in the tributary. Several lines of evidence support this conclusion. First, the taxonomic composition of the benthos was similar to that of the drifters over the weir. Second, there was little evidence that adults could have contributed to colonisation patterns, particularly in the first year after flows were released. Adults of these groups were present in upstream locations during summer, but were not trapped at the tributary until the second summer after flows were released. This also implies that adults of these taxa do not fly long distances, as adults were present upstream of the weir (≈ 350 m from tributary sites) and the downstream regulated river (≈ 1200 m from tributary sites) over the first summer, and could have presumably flown to the tributary if they had the capability (Graham et al. 2017). Therefore, the presence of adults of these taxa in the second summer was likely due to emergence from local juveniles.

Colonisation patterns of different functional feeding groups indicated no abiotic or resource limitations, or species interactions, that prevented establishment of these groups in the tributary (i.e. environmental or biotic constraints). Benthic algae and biofilms can re-establish rapidly after drying (Robson and Matthews 2004), and may have provided sufficient food for scrapers and gatherers. The filter feeders were predominately caddisflies from the family Hydropsychidae, which use silken nets to capture organic material in faster flowing water (Wallace and Merritt 1980). The new flows were likely to provide suitable micro-habitat for filter feeding, allowing colonisation of filter feeders despite reduced dispersal rates caused by the weirs. There was no discernible delay in predator arrivals, suggesting that potential prey were sufficiently abundant (no biotic constraint). Most predatory freshwater invertebrates are polyphagous (Lancaster and Downes 2013), and the colonisation of diverse taxa may have provided prey for arriving predators.

In summary, our results show that communities can re-assemble afresh very quickly when natural channels that have been dry for decades are re-wetted by flows that deliver drifters from intact locations upstream. Adult flight followed by reproduction played only a secondary role. While the weirs slowed dispersal rates of some taxa, they did not block any species entirely, and thus the effects of dispersal constraints were absent.

Changed dispersal constraints on existing communities

Markedly increased flow (28 to 56-fold increase in discharge) and invertebrate drift into the existing communities of the regulated rivers resulted in gradual changes (i.e. assembly) in benthic community composition, resulting in communities that were approximately 65% similar to upstream sites after 22 months. The drift assemblage in these locations also became more similar to upstream sites, suggesting that new taxa were able to reach locations over 1 km downstream. Although taxon richness of these existing communities increased over time, changes in total invertebrate densities were not detected. Some new taxa clearly established, but were in low densities.

There was little change in the trophic structure of the existing community in response to flows. Densities of benthic gatherers, scrapers and predators did not change and overall densities of these feeding groups were equivalent to upstream. However, many individual taxa within gatherer and scraper feeding groups remained in lower densities than upstream and just a few taxa dominated these groups (scrapers ~ 55% Orthocladiinae, gatherers ~ 88 % Chironominae). Numbers of gatherers and scrapers drifting into the regulated location increased over time (i.e. reduced dispersal constraints), but did not lead to a corresponding benthic response. This finding indicates that environmental or biotic constraints may have prevented the new dispersers establishing in the regulated locations, possibly favouring chironomids. Furthermore, the tributary flows may have been insufficient to change these constraints in the regulated locations. Predator densities also did not alter after flows increased. Invertebrate predators can be limited by the productivity of their prey (i.e. bottom-up effects; Wallace et al. 1999), and prey densities did not change (i.e. no increase in gatherer and scraper densities), so corresponding changes in predator densities in the regulated river would not be expected.

One notable change in trophic structure was an increase in densities of filter feeders, despite no increase in drift rates. One possible explanation is that increased flows reduced environmental constraints. The additional flow is likely to have increased the area of fast-flowing habitat in what was previously a predominantly lentic environment, resulting in more space for filter feeders (Wallace and Merritt 1980; Brooks and Haeusler 2016). The absence of an increase in drift rates suggest that supply rates may have been in excess, or new colonists may have originated from adults. Adults of some hydropsychid filter feeders (*Asmicridea* spp.) were present in the regulated sites throughout the study, and benthic densities could also have increased due to greater recruitment from egg-laying adults. Adults of these taxa can use emergent rocks as oviposition substrates (Reich 2004), and larval densities of stream insects can be controlled by oviposition rates (Encalada and Peckarsky 2012; Lancaster and Downes 2014). The higher flows from the tributary may have increased the amount, quality and availability of oviposition substrates, leading to increases in larval benthic densities. The tributary flows may also have provided a pulse in resources (e.g. nutrients, organic matter), which might allow increased filter feeder numbers or the establishment of new taxa (Kiffney et al. 2006; Holt 2008). In general, these taxa are adversely affected by river regulation (Marchant and Hehir 2002), and their response shows that a small increase in tributary flows may have positive outcomes by increasing habitat availability and providing additional food resources.

In summary, a boost in the numbers and diversity of dispersers had no strong effects on existing communities. Instead, increased discharges effected a reduction in environmental constraints, which altered trophic structure a little. Thus increases in discharge and dispersal produced different outcomes in new versus established communities. Moreover, our expectation that alterations to dispersal would be a major influence on community assembly in both the tributary and regulated locations was not supported by the study.

Possible assembly mechanisms

Our results offer some opportunity for speculation about the mechanisms by which these communities assemble. One obvious difference between this study and many others is that there were no effects of reduced dispersal or order of species arrival in the new habitat (e.g. Chase 2003). We do not know the exact sequence in which species arrived in the tributaries, but we speculate that it had little long term effect given that both tributary communities converged closely on their respective, upstream analogues. In our study, most dispersers were aquatic larvae, and it is probable that drift of most species was sufficiently high that early colonising species did not have time to develop high enough densities to monopolise and preclude colonisation by subsequently arriving species. In many other studies of aquatic systems, dispersal is by adult stages that produce many, new individuals via reproduction (Blaustein and Margalit 1996). Perhaps sequence effects (e.g. priority effects) are more prevalent in the latter type of situation, but the difference highlights the importance of studying diverse ecosystems and at landscape scales.

The relatively small changes seen in existing communities - despite abundant and diverse dispersers - were particularly interesting, and there may be several reasons for this outcome. The existing community may have had the capacity to resist invasion by new species. In effect, the new dispersers from the tributary arrived in an already colonised, densely occupied habitat and failed to become established (see De Meester et al. 2016). Possibly, conditions favoured dominant taxa, such as chironomids, and the increased discharge did not alter environmental or biotic conditions in ways permitting other, functionally similar taxa to invade. In this respect, while the flow increases in the regulated rivers were relatively large, they were still modest compared to natural flows (current flow ~ 5 – 10 % of natural flow). The dams continue to drastically reduce annual snowmelt flows and natural floods, which prevents disturbance events that could scour the benthos, remove existing individuals, and reset community assembly processes. Furthermore, the ability for species to invade an existing community decreases as the period between disturbances increases (Symons and Arnott 2014). Thus, if flows had been greater and more frequent, it is feasible that disturbance could have facilitated colonisation by new taxa. Alternatively, high flows can create a greater diversity of microhabitats, which could then enable establishment by taxa (e.g. torrenticoles) that were unable to exist previously. In this respect, we think an important aspect of this study is that channels were entirely natural – that is, riverbed morphology and particle size distributions had been shaped by river flows for millennia and were undisturbed following the cessation of flow. Consequently, increases in discharge likely spread across more of the original, intact channel and did not have to re-work the existing beds to create diverse flow microhabitats. Thus, it is possible that greater increases in discharge would have produced different outcomes.

Management implications

Freshwater ecosystems are some of the most altered ecosystems worldwide and are experiencing declines in biodiversity far greater than those in terrestrial ecosystems (Vörösmarty et al. 2010). In regulated rivers, environmental flows – water released from dams – are one of the main restoration techniques for ameliorating the ecological effects of river regulation. Environmental flows generally focus on restoring in-stream physical habitat (i.e. environmental constraints) with little thought given to other aspects of community assembly, and assumes that species will return and ecological processes will re-establish (Parkyn and Smith 2011). Our study highlights that environmental flows may rehabilitate communities in some situations (previously dry riverbeds), but not others. Providing there is a source of drifters, successful restoration may require large releases of water from dam structures to provide diverse microhabitats and also create disturbances in regulated systems to initiate a new round of community assembly.

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Electronic Supplementary Material

Online Resource 1. Summary of significant ANCOVA results for total invertebrate density, taxon richness, densities of functional feeding groups and individual taxa in the tributary (lower) location. A significant interaction between days x River, indicates invertebrate responses to increased flows differed between the two rivers. All other tests of a days x River interaction for densities/taxon richness/FFGs/similarity at each location were non-significant.

			benthos		
Response		d.f.	MS	*F*-value	*P*
total invertebrate density	days	1	0.06	8.7	**0.02**
	River	1	0.06	8.1	**0.02**
	days x River	1	0.15	20.4	**0.02**
	Error	8	0.007		
taxon richness	days	1	0.24	32.2	**<0.01**
	River	1	0.25	34.0	**<0.01**
	days x River	1	0.09	11.7	**<0.01**
	Error	8	0.01		
gatherers	days	1	0.04	2.0	0.19
	River	1	0.2	10.5	**0.01**
	days x River	1	0.3	15.7	**<0.01**

				benthos	
Response		d.f.	MS	*F*-value	*P*
	Error	8	0.02		
scrapers	days	1	0.1	12.4	**<0.01**
	River	1	0.06	6.6	**0.03**
	days x River	1	0.14	16.0	**<0.01**
	Error	8	0.01		
predators	days	1	0.05	2.2	0.17
	River	1	0.07	3.3	0.11
	days x River	1	0.26	12.6	**<0.01**
	Error	8	0.02		
Chironominae	days	1	0	0.002	0.96
	River	1	0.07	5.4	0.05
	days x River	1	0.17	14.0	**<0.01**
	Error	8			
Orthocladiinae	days	1	0.004	0.5	0.50

				benthos	
Response		d.f.	MS	*F*-value	*P*
	River	1	0.03	4.1	0.08
	days x River	1	0.16	21.1	**<0.01**
	Error	8	0.01		

Online Resource 2. Summary of linear regression analyses for benthic densities and drift rates of species belonging to different functional feeding groups. The slope of the response – days relationships were compared to zero for each location. Where responses differed between rivers (see Appendix S 1), each river was analysed separately. * indicates mean was significantly different from upstream mean.

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
Coleoptera											
Simsonia spp.	upstream	1,14	2.1	0.23	0.053	18.0	1,26	0.1	0.01	0.90	45.1
(scraper)	tributary (upper)	1,10	2.1	0.38	0.06	8.2	1,9	1.4	0.36	0.18	38.7
	tributary (lower)	1,10	3.1	0.56	**0.01**						
	regulated	1,14	1.9	0.22	0.08	13.7*	1,11	3.6	0.43	**<0.01**	
Austrolimnius spp.											
(scraper)	upstream	1,14	0.5	0.05	0.63	14.3	1,26	-1.2	-0.1	0.23	6.2

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
	tributary (upper)	1,10	2.2	0.37	**0.05**		1,9	0.1	0.03	0.9	3.9
	tributary (lower)	1,10	0.7	0.19	0.50	19.7					
	regulated	1,14	2.0	0.20	0.06	5.9*	1,11	0.7	0.09	0.48	3.5
Ephemeroptera											
Offadens spp.	upstream	1,14	1.0	0.14	0.32	23.8	1,26	-0.2	-0.03	0.80	108.0
(gatherer)	tributary (upper)	1,10	0.6	0.13	0.58	25.4	1,9	0.2	0.06	0.87	236.2
	tributary (lower)	1,10	1.4	0.29	0.19	26.1					
	regulated	1,14	0.04	0.01	0.97	31.0	1,11	1.4	0.25	0.18	297.1

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
Austrophlebioides spp.	upstream	1,14	0.8	0.02	0.46	155.9	1,26	-0.2	-0.01	0.85	144.4
(scraper)	tributary (upper)	1,10	2.8	0.46	**0.02**		1,9	1.6	0.39	0.14	165.2
	tributary (lower)	1,10	2.4	0.47	**0.04**						
	regulated	1,14	1.7	0.11	0.10	91.6*	1,11	1.7	0.15	0.12	317.2
Plecoptera											
Trinotoperla spp.	upstream	1,14	1.0	0.09	0.35	7.3	1,26	1.1	0.09	0.30	193.6
(scraper)	tributary (upper)	1,10	0.5	0.12	0.62	6.1	1,9	1.0	0.33	0.33	159.8
	tributary (lower)	1,10	2.4	0.33	**0.04**						
	regulated	1,14	3.4	0.31	**<0.01**		1,11	4.5	0.41	**<0.01**	

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
Dinotoperla spp.	upstream	1,14	0.7	0.07	0.47	8.5	1,26	0.3	0.03	0.76	68.8
(scraper)	tributary (upper)	1,10	2.8	0.39	**0.02**		1,9	-0.3	-0.08	0.80	88.1
	tributary (lower)	1,10	0.4	0.09	0.67	8.8					
	regulated	1,14	3.3	0.28	**<0.01**		1,11	2.7	0.37	**0.02**	
Austrocercella spp.	upstream	1,14	-0.2	-0.02	0.86	10.9	1,26	1.8	0.17	0.09	62.0
(gatherer)	tributary (upper)	1,10	-0.2	-0.03	0.86	2.5	1,9	1.2	0.30	0.24	46.0
	tributary (lower)	1,10	1.6	0.29	0.14	5.7					
	regulated	1,14	-0.1	-0.01	0.86	2.7	1,11	2.7	0.38	**0.02**	

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
Trichoptera											
Taschorema complex	upstream	1,14	0.5	0.02	0.62	11.9	1,26	0.5	0.03	0.60	20.3
(predator)	tributary (upper)	1,10	2.1	0.26	0.06	5.2*	1,9	1.6	0.46	0.14	39.7
	tributary (lower)	1,10	0.7	0.17	0.51	5.9*					
	regulated	1,14	1.8	0.16	0.09	5.4*	1,11	5.3	0.33	**<0.01**	
Asmicridea spp.	upstream	1,14	0.33	0.03	0.75	8.8	1,26	1.1	0.09	0.27	21.1
(filter-feeder)	tributary (upper)	1,10	2.9	0.44	0.01		1,9	1.0	0.36	0.33	28.1
	tributary (lower)	1,10	2.2	0.33	0.05						

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
	regulated	1,14	3.2	0.30	**<0.01**		1,11	1.6	0.23	0.14	40.1
Diptera											
Chironominae	upstream	1,14	1.0	0.05	0.32	53.0					
(gatherer)	tributary (upper)	1,10	3.1	0.49	**0.01**						
	tributary (lower) - Middle	1,4	2.2	0.6	0.10	15.8*					
	tributary (lower) - Diggers	1,4	-3.7	-0.9	**0.02**						
	regulated	1,14	-1.0	-0.09	0.35	251.0					
Tanypodinae	upstream	1,14	0.2	0.01	0.88	6.4					

		benthos					drift				
Response		d.f.	*t*-value	slope estimate	*P*	mean density	df	*t*-value	slope estimate	*P*	mean drift rate
(predator)	tributary (upper)	1,10	-1.2	-0.26	0.23	5.3					
	tributary (lower)	1,10	-1.2	-0.30	0.24	25.3					
	regulated	1,14	-1.5	-0.16	0.15	44.2*					
Orthocladiinae	upstream	1,14	-0.1	-0.01	0.91	111.1					
(scraper)	tributary (upper)	1,10	1.6	0.30	0.14	17.4*					
	tributary (lower) - Middle	1,4	2.6	0.5	0.06	203.1					
	tributary (lower) - Diggers	1,4	-3.5	-1.1	**0.03**						
	regulated	1,14	-1.9	-0.14	0.08	211.4					

Chapter 5. References

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