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Title

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.

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).

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).

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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Tables

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

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**

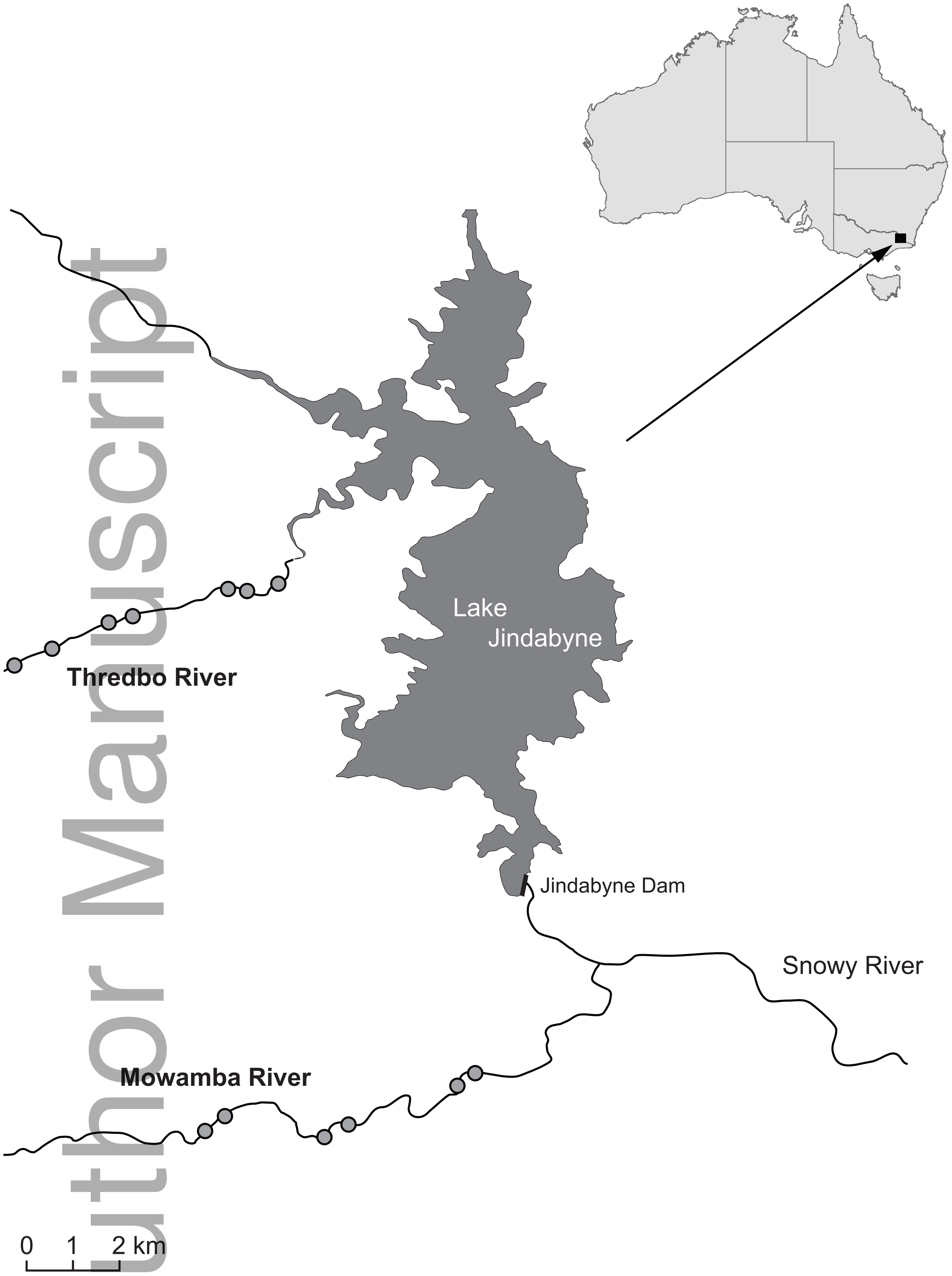
Figure legends

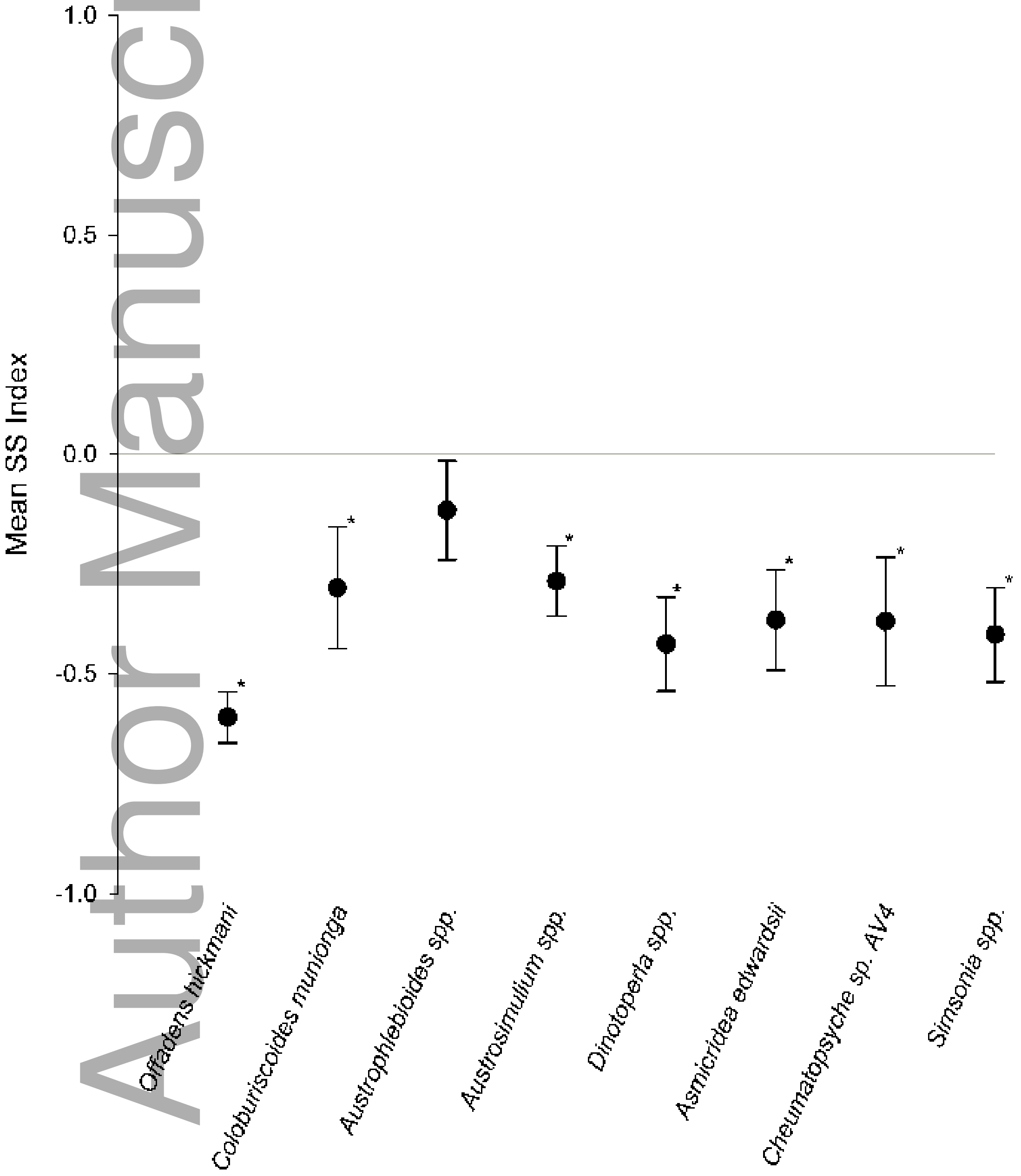
Figure 1. Location of the 13 sampling sites within the Mowamba and Thredbo Rivers.

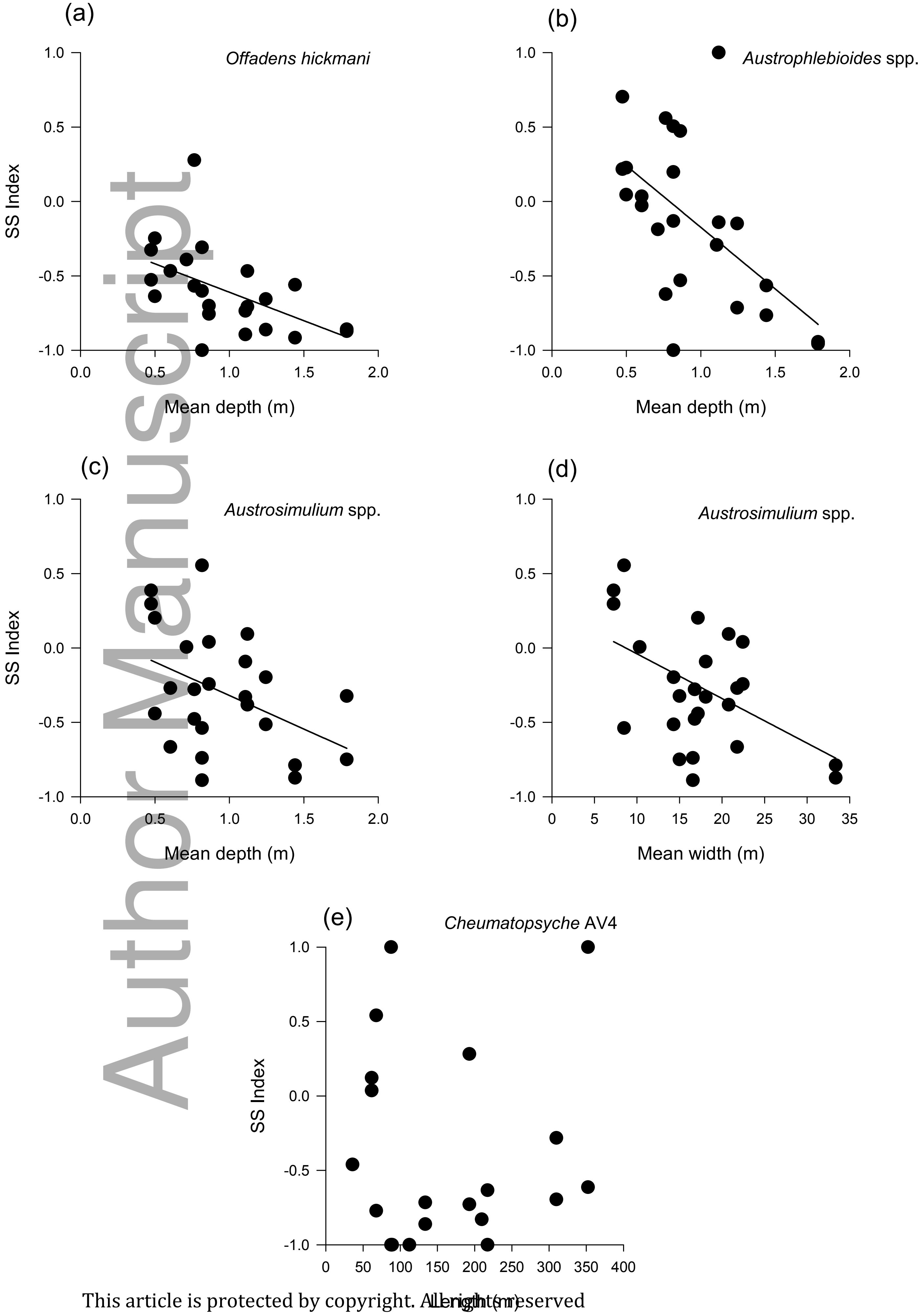
Figure 2. Mean source/sink index (SS) for study taxa. Error bars are standard errors. * indicates mean SS is significantly < 0 (*t*- tests). Grey line shows SS=0.

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.

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.


Lake
Jindabyne
Thredbo River
Jindabyne Dam
Snowy River
Mowamba River
0 1 2 km


Mean SS Index
1.0
0.5
0.0
-0.5
-1.0
*
Offadens hickmani
Coloburiscoides munionga
Austrophlebioides spp.
Austrosimulium spp.
Dinotoperla spp.
Asmicridea edwardsii
Cheumatopsyche sp. AV4
Simsonia spp.


(a)
Offadens hickmani
SS Index
1.0
0.5
0.0
-0.5
-1.0
0.0
0.5
1.0
1.5
2.0
Mean depth (m)
(b)
Austrophlebioides spp.
Mean depth (m)
(c)
Austrosimulium spp.
SS Index
Mean depth (m)
(d)
Austrosimulium spp.
0
5
10
15
20
25
30
35
Mean width (m)
(e)
Cheumatopsyche AV4
SS Index
0
50
100
150
200
250
300
350
400
Length (m)