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Title

Barriers to dispersal: the effect of a weir on stream insect drift

Running title: Effects 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^3s^{-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 (25^{th} % depth), almost twice as deep as the 25^{th} % 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.

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).

The effect of natural pools and the weir pool on the numbers of drifting of 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.

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.

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).

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

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).

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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Tables

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)

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

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**

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**

Figure legends

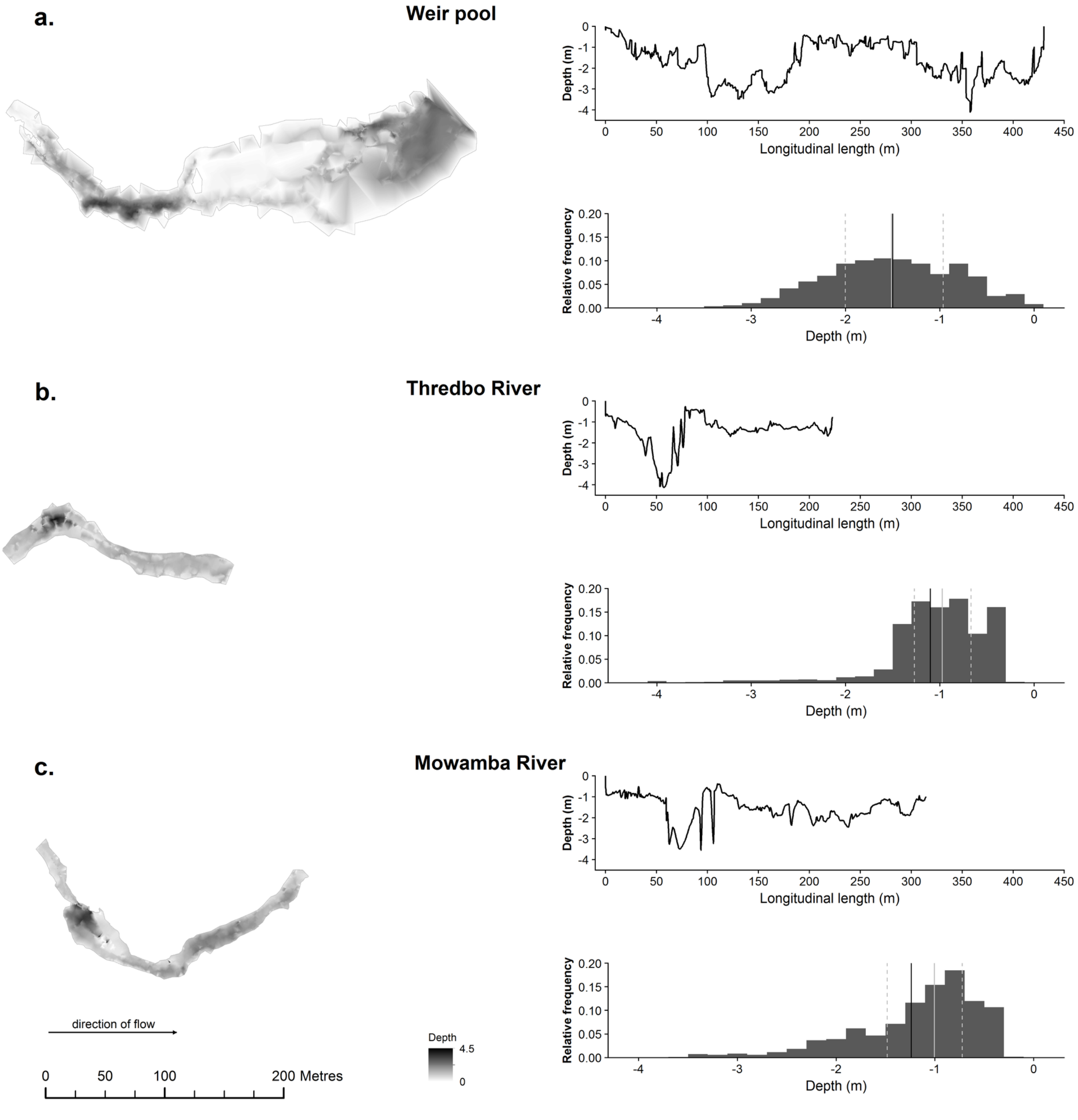
Figure 1. Pool bathymetry and depth frequency distributions of the Mowamba weir (a) and examples of natural pools within the Thredbo (b) and Mowamba (c) rivers. Black line (histograms) = mean, grey line = median and grey dotted lines = 25th percentile and 75th percentile.

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.

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.

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.



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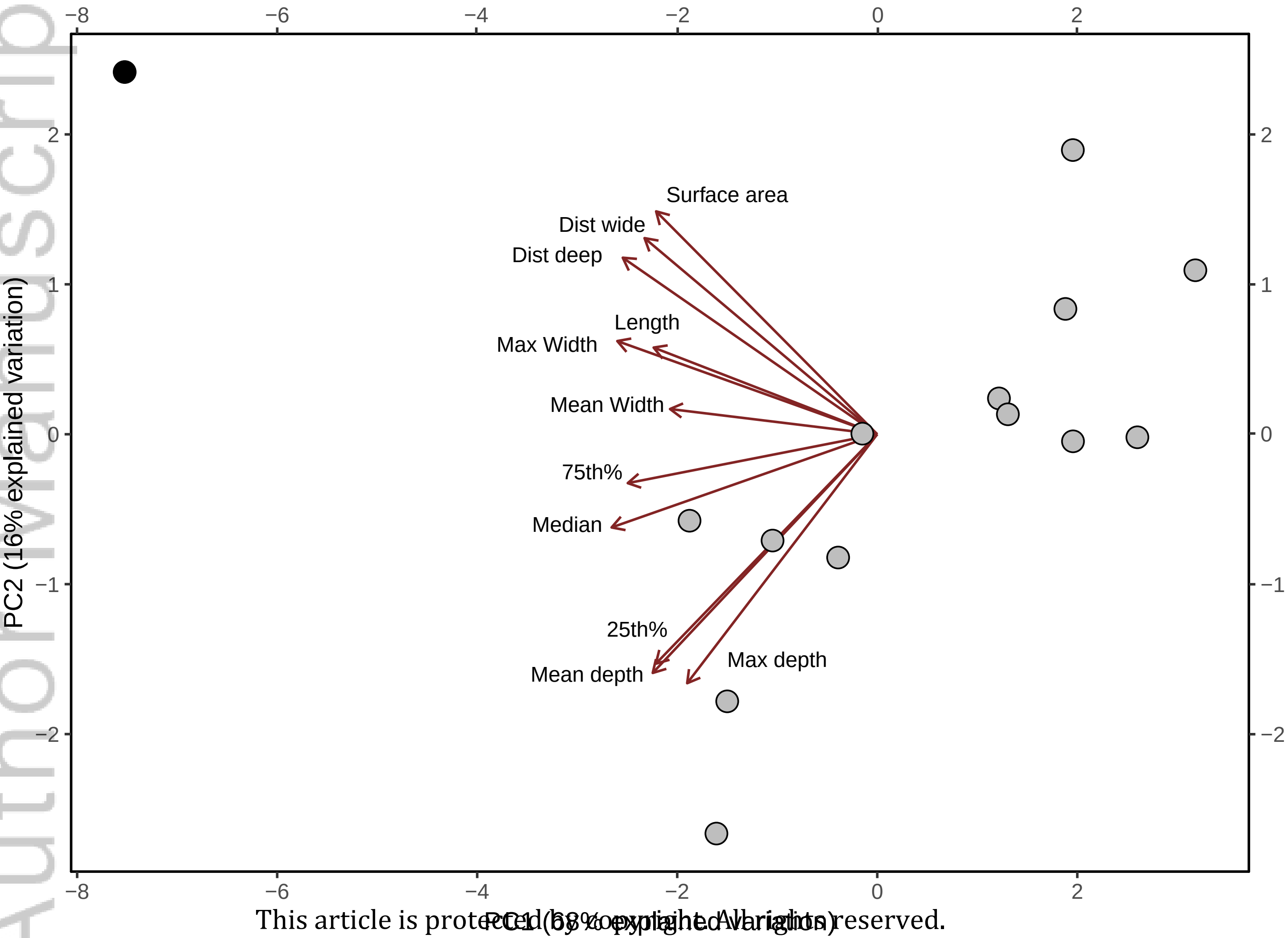
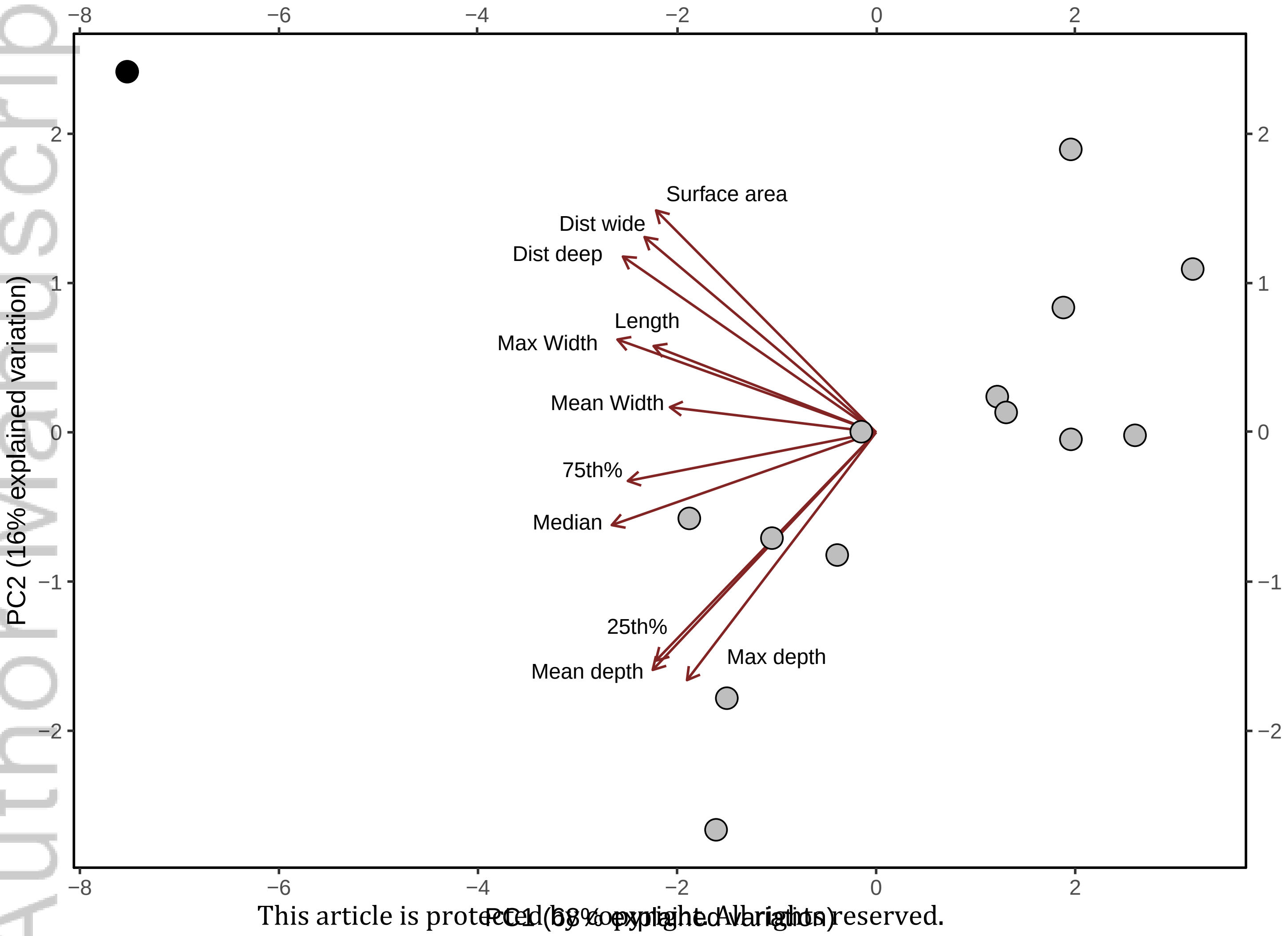

PC2 (16% explained variation)
PC1 (68% explained variation)
−8
−6
−4
−2
0
2
−2
−1
0
1
2
Surface area
Dist wide
Dist deep
Length
Max Width
Mean Width
75th%
Median
25th%
Mean depth
Max depth


−8
−6
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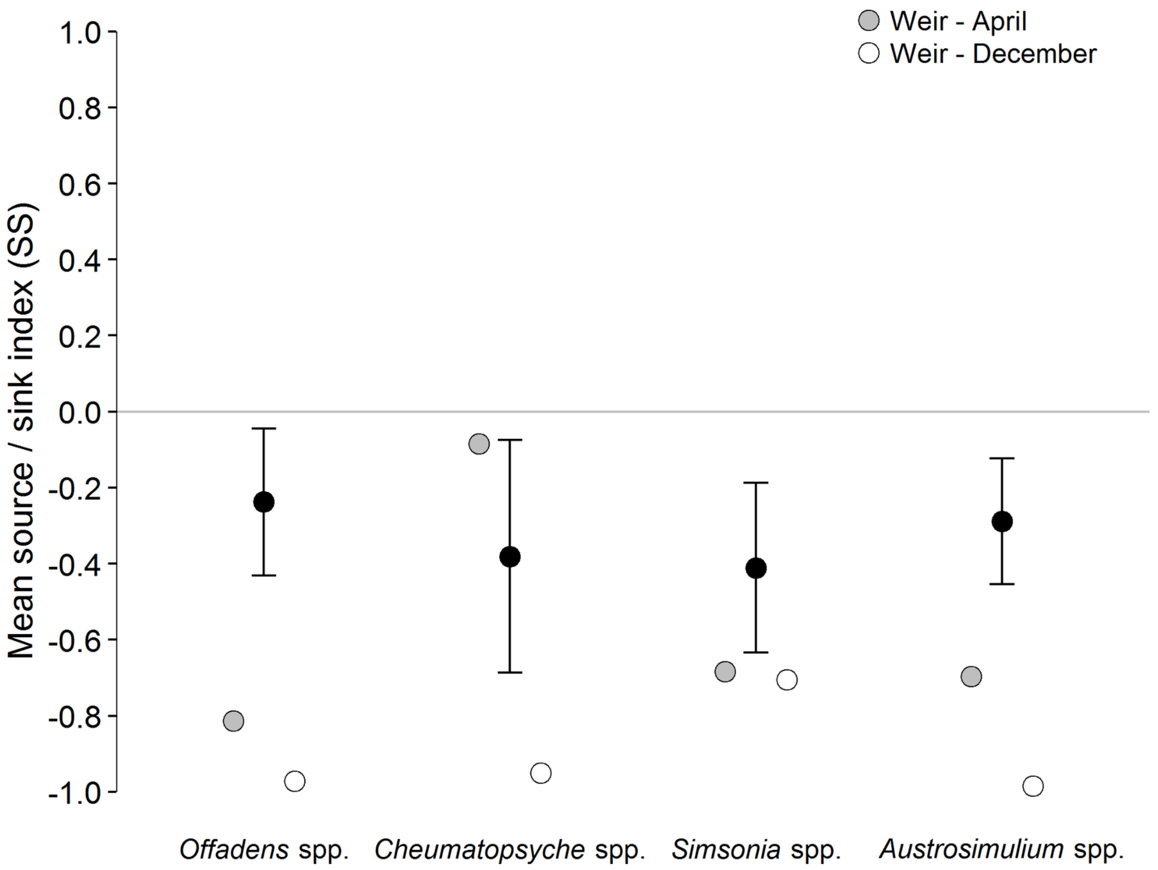
0
2
2
1
0
−1
−2
Surface area
Dist wide
Dist deep
Length
Max Width
Mean Width
75th%
Median
25th%
Mean depth
Max depth
PC2 (16% explained variation)
PC1 (68% explained variation)



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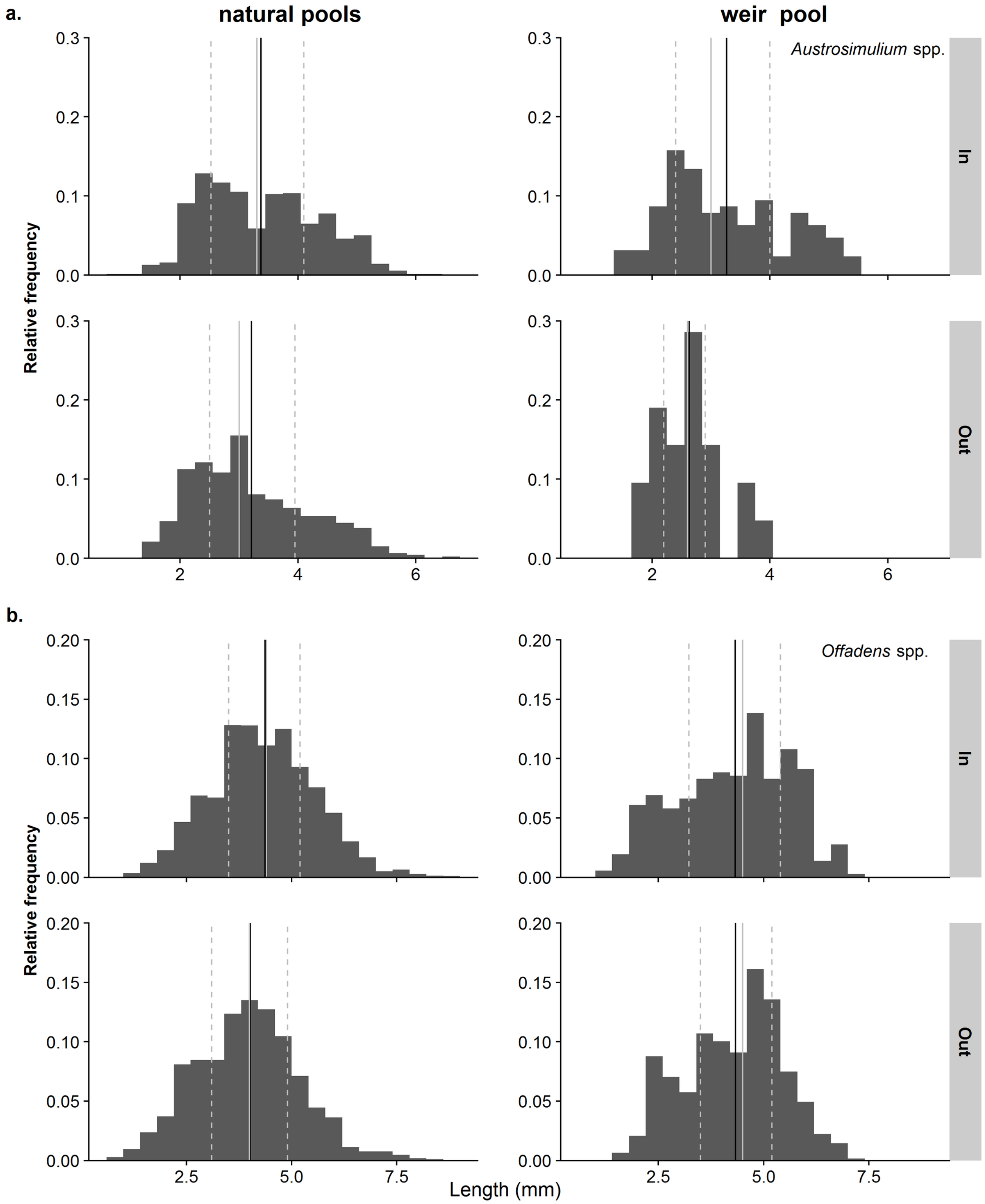

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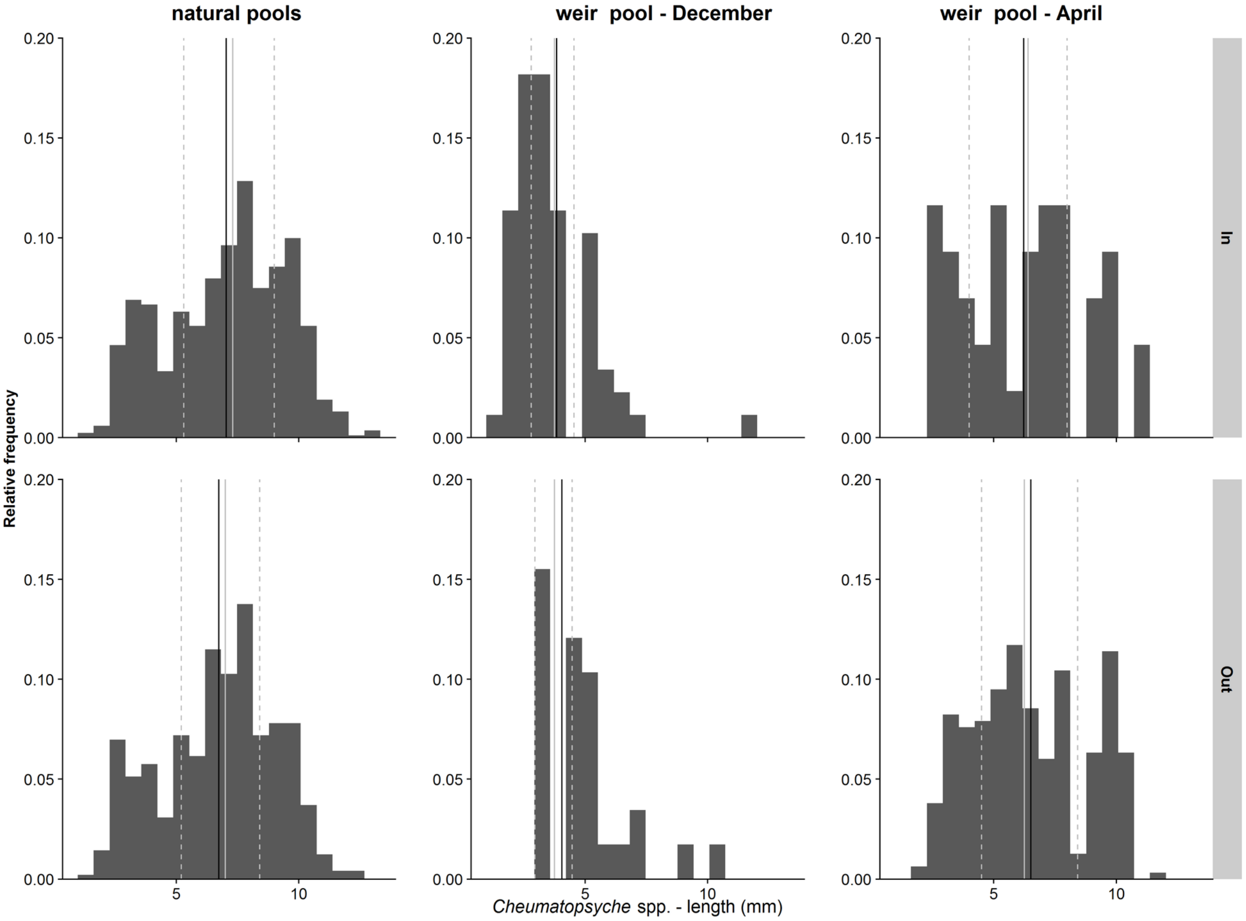

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