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Hydrological controls on oviposition habitat are associated with egg-laying phenology of some caddisflies

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Abstract

1. Seasonal variation in resource availability can have strong effects on life histories and population densities. Emergent rocks (ERs) are an essential oviposition resource for multiple species of stream insects. The availability of ERs depends upon water depth and clast size, which vary with discharge and river geomorphology, respectively. Recruitment success for populations may depend on whether peak egg-laying periods occur at times when ER are also abundant. For multiple species that oviposit on ER, we tested whether seasonal fluctuations in ER abundance were concurrent with oviposition phenology. We also tested whether high discharge drowned ERs for sufficiently long periods to preclude egg laying, and whether this problem varied between rivers differing in channel morphology and particle size distribution.

2. We obtained a continuous timeseries of water level (WL) measured every 30 min for two years at sites on three rivers in south-eastern Australia with similar hydrology but different geomorphology. A relationship between WL and ER numbers was determined empirically at each site and these relationships were used to predict ER availability over the two years. Egg masses of ten species of caddisflies were enumerated each month for a year in one river to establish oviposition phenology.

3. Abundance of ERs was inversely related to discharge in all three rivers. ERs were most abundant during autumn and scarce during spring. Site-specific geomorphology resulted in skewed or multimodal distributions of ER abundance each year. Between years, catchment-scale hydrometeorology mediated patterns of ER availability, despite the close proximity of sites. Temporal variance in ER availability was not consistently correlated with mean WL or WL variance. ER variance increased with WL variance, when WL was below a threshold equivalent to mean annual WL. Above this threshold, most ER were likely to be submerged.

4. Oviposition phenology varied strongly among the ten species of caddisflies, with egg-laying ranging from in 1-2 months to year-round. Temporal variations in ER and egg mass abundance were not correlated for most species. Below a threshold minimum number of ER, egg masses were highly crowded onto the few available ER, which is evidence that ER were in short supply. For five species, high egg mass abundance was positively associated with periods of the year when the time above the threshold number of ERs was high. Unusually, two species laid most egg masses during winter and when the time above this threshold was short. Three species showed no association between egg mass abundance and time above this threshold; two of these species laid eggs year-round.

5. Regional hydrometeorology controlled the availability of ERs, but between-river differences were sufficient to deliver different outcomes in the availability of oviposition sites between years and seasons. Caddisflies were rarely prevented from laying eggs but periods when ERs were in short supply created crowding, which may be associated with negative fitness effects on hatching larvae. Geomorphological controls on availability of oviposition resources may have strong implications for the coexistence of species that overlap temporally in egg-laying.

1. INTRODUCTION

Species' abundances vary in time and space, and short-term temporal patterns (≤1 year) often correspond to seasonal patterns in life cycle events, such as mating, egg-laying, diapause and metamorphosis. The timing of such events is species-specific and the product of complex eco-evolutionary processes (Partridge & Harvey, 1988; Forrest & Miller-Rushing, 2010). Temperature is a central determinant of seasonal patterns because it influences the rates of all biochemical processes, which underpin growth and development, for example (Gillooly *et al.*, 2002). However, life histories reflect requirements across the whole life cycle and temporal variations in abundance may reflect life history trade-offs related to any life stage and to diverse factors, including inter-specific interactions (Tokeshi, 1986; Peckarsky *et al.*, 2001), temporal variations in resources (Wissinger *et al.*, 2004) and physical disturbance (Lytle, 2001; 2002). Ecologically, seasonal variations in densities of individuals are important because they can influence population dynamics and community structure in complex ways.

The outcome of recurring, seasonal biological processes may be influenced by a stochastic abiotic environment such that interannual variations in climate, for example, may underpin variations and trends in populations over multiple generations. Births of new individuals are critical for population persistence and the timing of reproductive recruitment may be the product of selection gradients acting on multiple life stages. In aquatic insects, for example, such selection may act on the survival of adults or neonates, on egg development or diapause, or the availability of oviposition habitat. The number of successful recruits, however, may be contingent also on interannual climate variations. For example, unusually late ice melt resulted in failed adult emergence for some arctic chironomids and dramatically reduced recruitment to the subsequent generation (Welch, 1976). Similarly, a mayfly population with a two-year life cycle had weak recruitment in alternate years owing to poor weather in one year during mating and oviposition; these effects persisted for nearly a decade (Wright, Hiley & Berrie, 1981). For species with specialized oviposition habits, temporal fluctuations in the availability of oviposition habitat can influence recruitment and longer term variability in populations (Peckarsky, Taylor & Caudill, 2000). Spatially, variations in oviposition site abundance can constrain egg supply and densities of subsequent life stages for many aquatic insects, including multiple species of Ephemeroptera and Trichoptera (Lancaster, Downes & Arnold, 2010; Encalada & Peckarsky, 2012; Lancaster & Downes, 2014; Macqueen & Downes, 2015; Lancaster & Downes, 2018) and some Hemiptera and Odonata (Goldstein, Rosenberg & Cheng, 2012; Mellal *et al.*, 2018). If temporal variations in oviposition site abundance also influence populations, then we might expect concurrence between seasonal egg-laying patterns and oviposition site availability. That is the subject of this research.

Extensive research on egg-laying by stream-dwelling caddisflies and mayflies has focused on species that lay their eggs as masses on the underside of emergent rocks (references above), which vary in abundance with temporal variations in water level. Water level, which is typically driven by precipitation–runoff processes, is the primary determinant of emergent rock (ER) availability in rivers, but relations between ER abundance and water level are moderated by local geomorphology and sedimentology. Flows capable of entraining and repositioning ERs, which are typically larger than most bed material clasts, are relatively infrequent, whereas changes in water level driven by hydrology are common to all streams and occur frequently. Therefore, physical movement of ERs is likely to be a less important control of rock exposure or inundation than water level fluctuations. If temporal variations in ER and egg mass abundance are associated, as suggested for some mayflies in a snowmelt system (Peckarsky, Taylor & Caudill, 2000), this might help explain why population sizes differ with interannual variations in precipitation, and between streams that differ in channel morphology and hydrology. Very high discharge is likely to drown most ER and therefore may prevent oviposition, but how often and for how long is oviposition prevented? Brief shortages in ER abundance (days) in response to individual spates or floods may not affect egg supply if adults are sufficiently long-lived that females carrying mature eggs can delay oviposition for short periods. Instead, the longer-term, seasonal or monthly patterns in ER inundation and exposure may be of greater consequence to the annual egg-laying cycle of many stream insects.

If a relationship exists between seasonal variations in oviposition site abundance and egg-laying patterns, it is likely to be a threshold response, i.e. periods of high egg laying are related to some minimum level of resource abundance for a minimum length of time. Close associations are unlikely because species rarely behave optimally (Pierce & Ollason, 1987; Lancaster & Downes, 2010) and, for species that oviposit on ERs, the minimum number of ER required to maintain a viable population may be more critical than the actual number (Peckarsky, Taylor & Caudill, 2000). In addition, life history patterns are typically related to long-term averages in environmental variables (Lytle, 2001) and thus insects may have limited capacity to respond to short-term fluctuations in resources. Spatially, close associations between numbers of ERs and egg masses do occur within and between rivers (Lancaster, Downes & Arnold, 2010) and are likely to arise when females can fly between resource-poor and resource-rich locations, thereby closely tracking resource abundance (Peckarsky, Taylor & Caudill, 2000; Lancaster, Downes & Dwyer, 2020a). Temporally, however, such close tracking of resources is less likely because, at times, there may be no resource-rich locations (e.g. high discharge driven by rainfall may affect all rivers in a region), and gravid females may be too few to respond to a sudden increase in resources. Below a threshold ER abundance, we expect a change in oviposition behaviour that may indicate a potential loss of fitness. For insects that oviposit on emergent rocks, changed behaviour when ERs are scarce could result in egg masses becoming unusually crowded, and fitness costs could be density-dependent mortality for eggs or larvae.

The aim of this paper was to determine whether hydrological controls on ER abundance might limit oviposition potential for insects that lay eggs on ERs, and whether the timing of egg-laying periods (oviposition phenology) corresponds to seasonal patterns of ER abundance, in a system where rainfall–runoff processes drive hydrology. If ERs are scarce or absent at predictable times of year in rivers (e.g. seasons with high rainfall and discharge) that are close together, then we expect oviposition periods of most species to occur at other times. Alternatively, if the effects of discharge on ER abundance are unpredictable or vary between years and nearby rivers, then oviposition periods are less likely to be concurrent with high ER abundance. The study organisms were ten sympatric species of caddisfly from three families that oviposit exclusively or predominantly on ERs, and that overlap in oviposition site preference. For each species, we tested for concurrence between oviposition phenology and annual cycles of ER abundance and variability, e.g. did egg-laying periods coincide with times of high ER abundance? It was not our intention to infer causal mechanisms or the evolutionary drivers of oviposition phenology, but rather to document species-specific oviposition patterns, to test for concurrence with ER abundance and to consider the ecological implications. While it is clear that there will be an inverse relation between water depth and ER availability, the nature of that relation is not theoretically obvious and has never been defined empirically. Peckarsky, Taylor and Caudill (2000) monitored weekly changes in ER availability in relation to discharge over three summers, but we are unaware of any more detailed evaluation of relations between hydrology and ER. Here, for the first time, we identify the nature of the relation between water depth and ER availability, and also describe temporal distributions and time series of ER. The study sites were on three rivers in southeast Australia that were close enough together to have similar species assemblages, climate and hydrology, but that differed geomorphologically. We examined how temporal variations in ER availability were driven by changes in hydrology at 30-minute intervals over a two-year period, and how these relations were moderated by site-specific geomorphology.

To address the aims, we (1) used continuous records of ER availability over two years to describe, quantify and explain monthly, seasonal and interannual variations. We hypothesised that there would be considerable temporal variability in ER numbers across these timescales, that temporal patterns of availability would be relatively consistent (owing to common regional hydroclimatology), but that ER availability would vary in space, between rivers (owing to differences in site geomorphology). (2) For each caddisfly species, we described oviposition phenology by surveying the abundance of egg masses laid on ERs over one year. These data were used to test for associations between temporal patterns of egg mass abundance with ER availability, and also with temperature as a proxy for other seasonal drivers of life histories. Although we did not predict close associations with ER numbers (discussed above), a close association with temperature would indicate that egg-laying patterns may be driven by seasonal processes unrelated to oviposition habitat. (3) Crowding of egg masses onto ER over the year-long survey was calculated and used to identify a threshold, minimum number of ER, below which crowding increased. Complementary tests for changes in oviposition behaviour with ER abundance were carried out on two species pairs known to either avoid or aggregate their egg masses. We then (4), described how often, and for how long, ER abundance fell below this threshold and, for each species, tested whether there was an association between periods of high egg-laying and periods when time above the threshold was high.

2. METHODS

2.1 Study species and study sites

Our ten species of caddisflies were common in the study rivers and all lay their eggs as a single mass attached to a hard substrate. Their egg masses are morphologically distinct and can be identified in the field (Reich, 2004; Lancaster & Glaister, 2019). Eight species oviposit exclusively on ERs: one species of Tasimiidae: *Tasimia palpata* Mosely, and seven species of Hydrobiosidae: *Apsilochorema obliquum* (Mosely), *A. gisbum* (Mosely), *Ulmerochorema rubiconum* (Neboiss), *U. seona* (Mosely), *Ethochorema turbidum* (Neboiss), *Taschorema evansi* (Mosely), *Koetonga clivicola* (Neboiss). Two species of Hydropsychidae (*Austropsyche* CJG sp. AU2, *Cheumatopsyche* sp. AV3) very commonly lay eggs on ERs, but we are uncertain whether they exploit only ERs. Typically, a gravid female in this set of species first lands on the surface of an emergent rock, then walks down the side into the water and lays her eggs in a single gelatinous mass on the side or underside of the rock. The two congeners of *Apsilochorema* (*A. obliquum* and *A. gisbum*) avoid laying egg masses on the same ER. In contrast, the two congeners of *Ulmerochorema* (*U. rubiconum* and *U. seona*) both aggregate their egg masses (many egg masses on a single

ER) and the two species often oviposit on the same ER (Lancaster *et al.*, 2020b). Eggs typically hatch within 2-3 weeks, but this can range from 1 to 4 weeks in summer and winter, respectively. Adult longevity is unknown for these taxa, but likely to be in the order of weeks (Svensson, 1972). Various aspects of oviposition have been described for some of these species (Lancaster, Downes & Reich, 2003; Reich & Downes, 2003; Reich *et al.*, 2011; Bovill, Downes & Lancaster, 2013; Bovill, Downes & Lancaster, 2019; Lancaster *et al.*, 2020b), but this is the first study to examine oviposition phenology and hydrological controls on the availability of oviposition sites.

Our field sites were 1-km reaches on each of three rivers in the Goulburn River catchment, Central Victoria, Australia: Snobs Creek, Little River and Steavenson River (Figure S1). The catchments upstream of these reaches are similar in terms of elevation range, geology and forest vegetation. The three reaches differ in their geomorphology. Steavenson R. is relatively large with an average width of 9.5 m and relatively low mean bed slope of 0.0097 m m^{-1}. Bed materials are organised into a weak pool-riffle sequence with some plane bed sections. The Little R. study reach has an average width of 6.1 m, bed slope is 0.0152 m m^{-1} and bed materials are organised into a distinctive pool-riffle sequence with alternating bars interspersed with occasional plane-bed sections. Snobs Ck is, on average, 5.8 m wide in the study reach, with the steepest slope at 0.0310 m m^{-1}. The bed morphology here is dominated by plane beds of low relative roughness, with short sections of step-pool and immature riffle-pool structures.

The climate of the region is relatively mild, with an annual mean of monthly maximum temperatures of ~20°C. Mean annual rainfall is in the order of 736–849 mm yr^{-1} (State Government of Victoria monitoring sites 088119 and 088023). Annual rainfall varies markedly in these three catchments, ranging from 258–405 mm yr^{-1} in dry years, to over 1000–1401 mm yr^{-1} in wet years. Seasonally, the catchments are characterised by warm, dry summers (mean max. temperature is ~29°C and rainfall is typically <50 mm month^{-1} in Jan and Feb), and relatively cool, wet winters (mean max. temperature is ~12–14 °C and rainfall >90 mm month^{-1} in July and Aug).

The hydrological regime of the three reaches is relatively undisturbed, with no dams and abstraction only from one headwater tributary of the Steavenson R. The highest flows occur in winter (Aug–Sept), and low flows in summer (Feb–Apr). Analysis of the 46 complete (>95%) water years of streamflow between 1974 and 2019 (site 088023) indicates that low flows have been relatively stationary over the past half century. The mean baseflow index is high (mean for 46 years = 0.84) and very stable, with no significant trend over time. The hydrographs are not particularly flashy (mean Richards-Baker Flashiness Index over 46 years is 0.15), which suggests the rivers in this area are likely to be geomorphologically stable (Erskine *et al.*, 1993) compared to flashier rivers in drier regions of Australia (Finlayson & McMahon, 1988).

We obtained a continuous timeseries of water level from which we estimated ER availability between Nov 2016 and Nov 2018 at single riffles on Steavenson R. and Little R. and at a section of plane bed on Snobs Ck. We will call these the indicator riffles, which had areas of 269, 145 and 116 m^2, with median grain sizes of 180, 150 and 160 mm, respectively. The locations were representative of the bed sediment characteristics and morphology in riffle and plane bed sections along their respective study reaches. The differences in geomorphology between the indicator riffles capture a reasonable range of the typical river-bed styles characteristic of rivers on slopes of 1–3 % in the mountains of central Victoria. This allows us to evaluate temporal variations in ER across a meaningful range of geomorphologies. The indicator riffles are representative examples and we do not claim to evaluate the role of geomorphology in a comprehensive manner.

2.2 ER time series

At each indicator riffle, we measured and recorded water level (WL) and then converted WL time series into ER time series using empirical calibrations relating WL to ER counts. At each site, a non-vented, logging pressure transducer (PT: Mini-Diver, Schlumberger Water Services, www.slb.com) was installed vertically at a fixed height close to the substrate by attaching it to a steel bar (star picket) driven into the river bed. A plastic pipe, drilled with holes, enclosed the PT to provide protection and act as a stilling well to dampen surface waves and local turbulence. At Snobs Ck, a logging barometer (Baro-Diver, Schlumberger Water Services, www.slb.com) was fixed to a tree (approx. 2 m from the bank and 0.5 m above ground level) and provided commensurate records of air temperature and pressure for conversion of PT total pressure to submergence depth, using the PT's proprietary software (Diver Office, Schlumberger Water Services, www.slb.com). This single barometer was used to convert all three PT records because the sites are close together and subject to the same synoptic pressure changes (Figure S1). Checks against manual measurements of water depth at each installation confirmed the accuracy of the PT measurements and allowed conversion of submergence depth to total depth above the local river bed (WL).

All three transducers were operational from 10 Nov 2016 with data measured and logged at 30-minute intervals. The PT at Snobs Ck suffered a terminal malfunction on 9 Sept 2018 and was not replaced. The other two PTs were maintained until 28 Nov 2018. There were a few short breaks in the time series, but the small amounts of missing data do not affect our analyses (Supplementary Material A).

To establish relationships between ER numbers and WL, ER were counted manually in each indicator riffle across a range of discharges and WL. Our target species rarely oviposit on small rocks in shallow water (Lancaster, Downes & Reich, 2003; Reich & Downes, 2003) so, consistent with previous research, ER were defined as rocks that were emergent, in at least 50 mm of water and at least 50 mm in b-axis diameter. A total of 17, 23 and 19 counts were made at Snobs Ck, Little R. and Steavenson R., respectively. WL timeseries were smoothed using a 4-hour running mean to remove high-frequency noise (e.g. turbulence in the stilling wells), from which we extracted the WLs corresponding to the times when ER were counted. Curve fitting, using least squares linear regression, determined that exponential models of the form,

$$\mathrm{ER} = a\, e^{-b\,\mathrm{WL}}$$

provided a good description of the decline in ER numbers as WL increased (Figure 1). These models were therefore used to predict ER numbers from measured WL.

Our focus is on ER variability at monthly and annual timescales. In addition to high-frequency noise, each WL time series exhibited a small diel cycle in some months, which we removed by applying a 24-hr running mean. This smoothing slightly reduced the water level associated with flood peaks and slightly raised water levels on the rising and falling limbs of individual flood hydrographs, but had no adverse impact on estimates of ER numbers (Supplementary Material B). To investigate and compare ER time series we extracted various statistics (Table 1), including: percentiles (ER_{10}, ER_{50}, ER_{90}) and moments (mean μ_{ER}, variance σ^2_{ER}, skewness γ_{ER}) from the empirical distributions of ER, for each year and month (subscript "_m" denotes monthly values). In our results, annual statistics are for the period 1 Dec 2016 to 30 Nov 2017 (hereafter 2017) and 1 Dec 2017 to 28 Nov 2018 (hereafter 2018), except for Snobs Ck where the 2018 data runs from 1 Dec 2017 to 31 Aug 2018.

2.3 Oviposition phenology

To describe oviposition phenology of the various caddisfly species, egg masses were surveyed in a 500–600-m stretch of the Little R., which lay within the 1-km study reach. We lacked resources for oviposition surveys in all three rivers or for longer than one year; Little R. was selected because it offered safe access over the widest range of discharge and the caddisfly assemblage is speciose. There were 12 surveys, one per month, at intervals of ~4 weeks from Nov 2017 to Oct 2018. Eggs of the study species typically hatch within 2–3 weeks, so no egg mass could be counted twice. In each survey, we sampled 300 ERs that were >20 cm b-axis and in water depth >10 cm, which are the ERs exploited most often by the study species (Lancaster, Downes & Reich, 2003; Reich & Downes, 2003; Lancaster *et al.*, 2020b). A minority of egg masses do occur on smaller ERs in shallow water, but it was unnecessary to survey ERs of all sizes in order to establish temporal patterns. Different species typically prefer ERs in fast or slow flows (above or below ~35 cm s^{-1}), references above, so half the sampled ERs were selected from slow flows and half from fast flows (flow categories assessed by eye). Sampling was spread over three river sections within the 500–600 m stretch, with 100 ERs in each section (50 fast; 50 slow), and ≥20 m between each section, to ensure that survey results were representative of the entire stretch. In each section, the first 100 ER that satisfied the criteria were examined to avoid potential bias in ER selection. Thus, for each species, in each month we described the total numbers of egg masses on 300 ERs. Each survey started in approximately the same location, but the length of each section and the actual ER examined varied with water level. Once examined, all ER were returned as close as possible to their original placement. Such minor adjustments are unlikely to affect the likelihood of future oviposition (Reich *et al.*, 2011).

2.4 Thresholds and temporal relationships between ER and egg mass abundance

To test for relationships between ER and egg mass abundances, we used ER variables extracted from the timeseries measured in the indicator riffle of the Little R. That riffle was within the stretch used to survey oviposition patterns, although ERs in the indicator riffle were not disturbed during surveys. We assume that temporal patterns in ER abundance in that riffle represented the longer river length; this is a reasonable assumption because oviposition behaviour of these caddisflies is consistent across riffles and rivers, even when ER density varies (Lancaster *et al.*, 2020b). We assume also that patterns were broadly similar among the three rivers, which is also reasonable given site proximity, a common climate and hydrological processes.

Correlation tests were used to determine whether seasonal patterns of egg mass abundance were closely associated with ER availability, and also with air temperature as a proxy for other seasonal drivers of life histories. ER abundance was calculated as the median number of ER in the indicator riffle during the 3 weeks prior to each egg mass survey, i.e. ER_{50_3w} (egg masses were likely to have been laid during the preceding 3 weeks). Although correlation tests do not preserve the temporal structure in the data (i.e. there is a potential for temporal autocorrelation), we consider them adequate for simple data exploration.

A measure of how crowded egg masses were on individual ERs was used to detect changes in female behaviour when oviposition sites were in short supply. Below a minimum threshold number of ERs, egg masses were expected to be unusually crowded onto relatively few ERs. For the entire species assemblage, for each month we calculated how crowded egg masses were on individual ERs using Lloyd's index of mean crowding (Lloyd, 1967; Pielou, 1974). Egg masses are not randomly distributed so crowding is not reflected by a simple change in mean number per ER. Lloyd's index describes the mean crowding experienced by each individual, i.e. a measure of the average number of companions each individual has in a sample unit, in this case, a single ER. This index is density-dependent, so it was divided by density to create a density-independent index of crowding, denoted $\overset{*}{x}/\bar{x}$ for a sample (Pielou, 1974). Following Pielou (1974), we calculated unbiased estimates of $\overset{*}{x}/\bar{x}$ with associated standard errors. Crowding was calculated in two ways: (1) mean individual crowding for individual egg masses, irrespective of which species egg masses belonged to, with $\bar{x}$ calculated as the mean number of egg masses per ER, and (2) mean species crowding, irrespective of the number of egg masses belonging to each species, with $\bar{x}$ calculated as the mean number of species per ER. These measures allowed us to examine all species collectively (crowding per egg mass) and to consider interactions among species (crowding per species). Linear regression was used to test for relationships between the two crowding indices and ER_{50_3w}. Piece-wise linear regression was used to test for a break in slope at some minimum number of ERs, which would indicate an ecologically-meaningful threshold where female behaviour changed. Values of ER_{50_3w} were log-transformed before analyses to ensure homogeneity of variance.

In complementary assessments of female behaviour, we tested whether the strength of avoidance or aggregation behaviour varied with ER abundance for two species pairs, congeners of *Apsilochorema* and *Ulmerochorema*, which were abundant throughout the year. For each species pair and in each month, we used a modified form of Sørenson's coefficient to describe the proportion of egg masses that occurred together (Southwood, 1978). The coefficient ranges from -1 (complete negative association, e.g. avoidance) to +1 (complete positive association, e.g. attraction). As above, regression analyses were used to test for relationships and breaks in slope between Sørenson's coefficient and ER_{50_3w} in the Little R. indicator riffle. For species that typically avoid one another (*Apsilochorema* spp.), values of the coefficient should be <0 and very low values when ER are scarce would indicate increased avoidance and competition. Conversely, if species are attracted to oviposit on the same ER (*Ulmerochorema* spp.), values should be positive, and very high values when ER are scarce would indicate increased co-occurrence.

The ER timeseries from the indicator riffle on the Little R. and the ER crowding threshold, identified above, were used to quantify the number and duration of time periods when ER numbers fell below the threshold (Table 1), i.e. periods when females may be unable to oviposit or risk loss of fitness. The total length of time when crowding was unlikely, was calculated as the proportion of time when ER numbers exceeded this threshold (T_{ovr}, %) and the mean duration of periods when the threshold was exceeded (P_{ovr}, days). Conversely, we considered the number of occasions when ER numbers were below threshold (N_{und}) and the mean duration of those periods (P_{und}, days). To compare rivers in terms of times periods above or below threshold, we first calculated ER density for the threshold number of ER in the Little R. riffle and then calculated the number of ER that corresponded to that density in the other indicator riffles. Thus, we assumed that this threshold density is similar in the three rivers, in order to explore how T_{ovr}, P_{ovr}, N_{und} and P_{und} varied between rivers that differed in geomorphology. These statistics were calculated for each year and month (subscript "_m"), and for the 3 weeks preceding each phenology survey (subscript "_3w").

Finally, for each species, we tested whether periods of high egg-laying corresponded to periods of ER abundance above the crowding threshold. Each month was placed into one of two groups: high ER abundance $T_{ovr\_3w} > 75\%$ ($N = 7$) or low $T_{ovr\_3w} < 55\%$ ($N = 5$). (No months corresponded to T_{ovr_3w} in the range 56–74%, see Results). For each species, we then tested for differences in the number of egg masses laid per month between the two groups using a two-sample *t*-test and log(X+1)-transformed data.

3. RESULTS

3.1 Annual variations in ER availability

Distributions of ER abundance in Steavenson R. and Little R. were positively skewed (Figure S2, Table 2) with minima of 1 or zero, and fewer than ~100 ER available fifty per cent of the time in 2017. ER numbers were generally lower in these riffles in 2018 with fewer than ~50 ER available fifty per cent of the time, but still with strong positive skewness. Despite similar ER_{50} in the two riffles (identical in 2017), variance, σ^2_{ER}, was approximately three to five times greater in Little R. than Steavenson R. Weak bimodality was apparent in both distributions. The sum of ER across each year represents the total number of oviposition opportunities if the riffle was encountered once every 30 minutes by a searching insect: between 2017 and 2018, this was reduced by ~38% and ~22 % in Stevenson R. and Little R., respectively.

At the Snobs Ck riffle, for the full year between Dec 2016 to Nov 2017, the distribution of ER was strongly bimodal (Figure S2, Table 2). Approximately 80 ER were available fifty per cent of the time, less than in the other two riffles, with variability across the year similar to that in Steavenson R. and less than in Little R. Because data from Snobs Ck were only available until August 2018, interannual comparisons are usefully made for periods from Dec to Aug: in 2017, ~110 ER were available fifty per cent of the time, compared with ~150 in the corresponding period in 2018. The sum of available ER increased by 22% between Dec 2016 – Aug 2017 and Dec 2017 – Aug 2018. Distributions for these nine-month periods were bimodal.

These data demonstrate significant interannual variability in the availability of ER on each river. Kolmogorov-Smirnov tests indicate that ER distributions were significantly different between 2017 and 2018 on Steavenson R. and Little R. ($D = 0.24$, $p < 0.01$; $D = 0.18$, $p < 0.01$, respectively) and for the common period between Dec to Aug on Snobs Ck ($D = 0.22$, $p < 0.01$). As expected, there were differences between rivers: the Little R. riffle provided more ER most of the time, and numbers were more temporally variable than at Snobs Ck or Steavenson R.; ER availability on Snobs Ck was strongly bimodal and increased between 2017 and 2018, in contrast to decreased availability on Steavenson R. and Little R.

3.2 Monthly variations in ER availability

Distributions of ER numbers varied considerably between months, with changes in central tendency, spread and skewness between rivers and years (Figure S3; Table S1). ER numbers were not normally distributed in any of the 69 monthly data sets (Shapiro-Wilk W, $857 < n < 1488$, $p < 0.01$) and multimodality, mostly bimodality, was common.

Seasonal patterns in ER availability were consistent between rivers and years (Figure 2a-c). In all cases, numbers were highest in the autumn (Mar–May) and lowest in late winter and spring (Aug–Nov); numbers declined during winter and increased during summer. These patterns were inversely related to the dominant, regional trends in river flow (Figure 2d). Temporal variance, $\sigma^2_{ER\_m}$, was high in the period autumn to early winter, and lower in the period late winter to spring (Figure 3a). ER distributions tended to be negatively skewed in summer and autumn, indicating that most of the time many ER were available, and positively skewed in winter into spring indicating that fewer ER were available (Figure 3b).

We anticipated an association between temporal variance in ER numbers and temporal variability in WL, but higher $\sigma^2_{ER\_m}$ in the Autumn and early Winter (Apr–July, Figure 3a) was not associated with the period of greatest variability in daily discharge (July–Sep, Figure 2d). In addition, $\sigma^2_{ER\_m}$ was not correlated with monthly WL variance measured at the field sites, albeit there was a weak relation at Snobs Ck (Pearson's r = 0.05, 0.06, 0.44, with p = 0.82, 0.76, 0.05 for Steavenson, Little and Snobs, respectively, Figure S4). However, ER variance was highest at times of even modest WL variance, as long as monthly mean WL was below a threshold value approximately equal to annual mean WL (Figure S4). For those months where WL fell below these thresholds there were correlations between $\sigma^2_{ER\_m}$ and monthly WL variance (Pearson's r =

0.74, 0.94, 0.86, with $p < 0.01$ respectively, Figure S4). There were only subtle between-year differences in the general seasonal pattern. In 2018 there was an earlier onset of the autumn-winter decline in ER numbers, which was evident in May, compared with July in 2017 (Figure 2).This shift was accompanied by an earlier switch from high to low temporal variance (Figure 3a) and from negative to positive skewness (Figure 3b) in 2018.

The monthly analysis reveals some additional detail about between-year and between-river differences in absolute ER numbers evident in the annual data. The drop in annual ER availability between 2017 and 2018 on Steavenson R. and Little R. was most pronounced in May and June (Figure 3c). At Snobs Ck, the annual increase in ER availability between 2017 and 2018 was primarily due to increases in availability in Dec–May (Figure 3c). Similarly, the generally higher availability of ERs at the Little R. compared to the other sites, was most pronounced April–July with relatively modest differences in the spring. Also, $\sigma^2_{\mathrm{ER\_m}}$ was notably higher on the Little R. than the other sites in the autumn and was lower in spring (Figure 3a).

3.3 Oviposition phenology

Seasonal patterns of egg laying were species-specific (Figure 4). Oviposition periods of the two species of Hydropsychidae (*Cheumatopsyche* AV3, *Austropsyche* SCG sp. AU2) were short and restricted to spring and early summer. The species of Hydrobiosidae had poorly synchronized cohorts and laid eggs in every month, but the months of maximum and minimum egg production varied between species. *Tasimia palpata* (Tasimiidae) also had a prolonged egg-laying season, but we found no egg masses in the extreme winter months (July, Aug). Egg mass abundance was positively correlated with ER_{50_3w} for two species, *A. obliquum* and *A. gisbum*, and with air temperature for three other species: *U. rubiconum*, *T. palpata* and *Cheumatopsyche* AV3 (Table 3). For two species, *K. clivicola* and *E. turbidum*, egg masses were abundant when air temperature was low, although statistical tests were marginally non-significant. Egg mass abundance of the remaining three species was not associated with either environmental variable.

3.4 Oviposition and ER crowding thresholds

There were negative relationships between ER abundance and the index of mean crowding, $\overset{*}{x}/\bar{x}$, for individual egg masses (regardless of species) and for species (regardless of the number of egg masses) (Figure 5a, 5b). Although these linear relationships were statistically significant, there was a distinct break in slope, suggesting a threshold for increased crowding below $\mathrm{ER}_{50\_3w} \cong 15$ for both measures of crowding. There was a step change in crowding per egg mass in relation to ER abundance, with significantly higher values below the threshold than above (Figure 5a). Mean species crowding increased as ER abundance decreased below the threshold, but remained constant above the threshold (Figure 5b). Oviposition did occur below the threshold, but egg masses and species were crowded onto fewer ERs. High crowding was not concurrent with months when egg masses were very abundant (Figure 5c).

Sørenson's coefficient of inter-specific association was negative for congeners of *Apsilochorema* in all months, and there was a positive relationship with ER_{50_3w}, but no break in slope (Figure 6a). For *Ulmerochorema* spp., however, values ranged from negative to positive but the mean did not differ from zero (*t*-test: $t_{11} = 0.579$, $p = 0.574$) and there was no relationship with ER_{50_3w} (Figure 6b).

Crowding thresholds were exceeded most of the time in both years. T_{ovr} approached 100% in Snobs Ck in both years, with an average duration of periods, P_{ovr}, of ~70 days (Table 2). From Dec 2017 to Aug 2018, there were only two periods below threshold and these lasted less than 2 days. In contrast, critical thresholds were exceeded less of the time in the Steavenson R. and Little R., especially in 2018 when ER were generally fewer. However, even then, ER exceeded crowding thresholds approximately two-thirds of the time (T_{ovr} = 66 and 71%) with P_{ovr} of 15–18 days (Table 2). In this year of lower ER availability, there were 20 periods below threshold on Steavenson R. and 15 on Little R., lasting an average 6–7 days.

Exceedance of crowding thresholds followed similar seasonal patterns in both years with higher proportions of time above threshold in summer and autumn than in winter and spring (Figure 7a, Table S1). This was true of each river but, consistent with the annual analysis, ER numbers rarely dropped below threshold at Snobs Ck (Figure 7a, b). In contrast, T_{ovr_m} fell to 0% in Aug of each year on Little R., and in Aug and Sept 2018 on Steavenson R. Although general seasonal patterns were consistent between years, the onset of reductions in T_{ovr_m} began earlier in 2018 (May 2018 vs July 2017; Figure 7a) and the ER deficit lasted longer. The months Aug–Oct had the most below-threshold events of long duration (Figure 7b) in both years.

There were three different patterns relating monthly egg mass abundance and the time ER numbers were above the threshold (Figure 8). Egg mass abundance was (i) significantly higher in months with the lowest T_{ovr} (*K. clivicola*); (ii) significantly lower in months with the lowest T_{ovr_3w} (*T. palpata, A. obliquum, A. gisbum, U. rubiconum, Cheumatopsyche* AV3), or (iii) did not vary with T_{ovr_3w} (*E. turbidum, U. seona, T. evansi, Austropsyche*). Note that species that laid most egg masses when T_{ovr_3w} was high, could have quite different patterns of egg laying over the year, e.g. compare *Apsilochorema* spp. with *U. rubiconum* in Figures 4 and 8.

4. DISCUSSION

Temporal fluctuations in the abundance of oviposition sites (emergent rocks, ER) were controlled by hydrometeorology and patterns were broadly consistent between rivers and years, but between-river differences in geomorphology and local runoff led to some river-specific patterns. Concurrence between temporal fluctuations in ER abundance and oviposition phenology occurred only for five of the ten caddisfly species. Some ER were available most of the year and periods with no ER were typically short, suggesting that oviposition is prevented infrequently in these systems. Although some eggs were laid when ER were scarce, there was a threshold relationship such that egg masses were unusually crowded onto oviposition sites below a minimum number of ERs, regardless of egg mass abundance. For congeners of *Apsilochorema*, avoidance behaviour increased as ER abundance declined, suggesting that temporal fluctuations in ER abundance does constrain oviposition for some species, and this may have knock-on effects for densities of later life stages. Oviposition patterns of three species were not associated with any measured variable and two species had unexpected patterns with egg masses most abundant in winter when temperatures and ERs were at seasonal lows. This is the first detailed survey of temporal variations in emergent rock abundance and it provides novel insights into which descriptive variables are most pertinent to egg-laying patterns of aquatic insects with this oviposition behaviour. Moreover, our surveys have clarified the nature of the inverse relation between water depth and ER numbers, shown how ER numbers respond to hydrological drivers and geomorphological differences between sites, and revealed unanticipated complexity, for example of ER variability compared to water depth fluctuations. Emergent rocks may be important also for other species and life cycle events, such as emergence and mate location by stoneflies (Alexander & Stewart, 1996; Petersen & Hildrew, 2003), and our survey methods and observations about ER variability may be useful to other ecological studies of aquatic insects.

4.1 Drivers of temporal variations in ER availability

As anticipated, regional precipitation and runoff regimes drove seasonal and interannual variations in the numbers of ER. Seasonal patterns were generally consistent between the three sites because all three rivers were affected by the same regional hydrometeorology. Each river had an annual cycle characterised by drier summer and autumn months with more ER, and wetter winter and spring months with fewer ER. Independent streamflow data confirmed the general pattern of higher winter and spring discharge in both years. They also confirm higher discharges during winter and spring 2018 that are consistent with lower ER abundance at Steavenson R. and Little R. compared with 2017, and the slightly earlier onset of high water in 2018 that was responsible for the earlier drop in ER abundance that year.

Catchment-scale hydrometeorology mediated patterns of ER availability, despite the close proximity of sites. In contrast to the increase in water levels (WL) and drop in ER numbers between 2017 and 2018 on Steavenson R. and Little R., WL were lower and ER numbers increased at Snobs Ck in 2018. The only feasible explanation is that runoff generation was different, with higher flows in the Acheron catchment (Little R., Steavenson R.) in 2018, but lower flows in the Snobs Ck catchment. Several factors that determine catchment runoff could be the cause of this year-to-year difference between catchments, including variations in precipitation or evapotranspiration across the region.

Temporal variance in ER availability was high in autumn to early winter and lower in late winter to spring, but was not correlated with WL variance. Rather, ER variance was highest during periods when WL variance was modest but the absolute WL dropped below thresholds corresponding to the annual mean WL. It is likely that these threshold depths represent a point at which most ER were submerged, above which fluctuations in WL had little or no effect on the number of ER available, but below which modest WL variance has a large effect on ER abundance.

Our investigation of emergent rocks at these three sites in the upper Goulburn River catchment of southeast Australia confirms that ER availability was driven by hydrometeorology, particularly the inverse relation between ER and water level. This relation will dominate in other hydrometeorological regimes and in all rivers, i.e. ER will be more abundant when water levels are low. Catchment-scale hydrology can modify regional and seasonal patterns in water levels and thence ER, so that interannual variations may be different between catchments, as evident here in differences between Snobs Ck and the other two sites.

There were additional contrasts in ER availability between the three field sites that confirm how local geomorphology can add spatial complexity to temporal variations in ER abundance, for example, by determining the absolute number of large rocks that can act as ER. The three indicator riffles contained different densities of ER, independent of flow condition, that reflect differences in the abundance of bed materials >50 mm in diameter and differences in local water depths as determined by bed topography and channel geometry. At Snobs Ck, local topographic variation across the riffle defined two platforms at slightly different elevations which led to strong bimodal distributions of ER. In general, substantial variations in ER abundance are to be expected between riffles, along individual rivers and between rivers (Lancaster, Downes & Arnold, 2010; Lancaster *et al.*, 2020b) as a function of how the delivery, dispersal and spatial sorting of large rocks varies within and between catchments. Geomorphological sorting and arrangement of large rocks varies systematically with bed slope, generating distinctive river-bed types (cascade, step-pool, plane-bed or riffle-pool morphologies) that may have implications for the spatial organisation of ER availability at different points along the river long profile. Moreover, delivery and dispersal of large rocks are dynamic processes affected by episodic sediment delivery (e.g. landslides that reach a channel) and by floods that alter the positions of large rocks, so that geomorphology is expected to also affect the temporal availability of ER on time scales longer than our two-year study.

4.2 Oviposition phenology and crowding thresholds

Life history characteristics, such as the timing of oviposition, can vary enormously between caddisfly species and this was exemplified by our study species. Some species had strongly synchoronized cohorts with short egg-laying periods (1–2 months for *Austropsyche* CSG sp. AU2) whereas others laid eggs in most months (*Tasimia palpata*) or all year round (all seven species of Hydrobiosidae). Studies on the larval stages of some Hydrobiosidae have also indicated poorly synchronized cohorts (Crosby, 1975; Dean & Cartwright, 1987; Bunn, 1988), but we are unaware of studies that document year-round oviposition.

Increased crowding of egg masses below a threshold number of ER is evidence that oviposition sites were in short supply at some times. Females were not especially abundant during periods of crowding (assuming that total egg mass abundance is a proxy for female abundance), indicating that constraints on oviposition depend on the relative, not absolute, abundances of ERs and females. When ER are abundant, females can choose where to lay eggs, but when water levels are high and ER scarce throughout the region, females may have no options other than to oviposit on the few ER available in an aggregative response. In contrast, water levels in a snowmelt system varied strongly between nearby streams and some female mayflies flew from mainstream reaches with no ER to smaller tributaries to locate oviposition sites (Peckarsky, Taylor & Caudill, 2000). Crowding of egg masses in our system occurred in months when the duration of time periods below the threshold number of ER was long (weeks), but not when below-threshold periods were brief (hours–days). This suggests that, although adult caddisflies may be relatively long-lived, females with mature eggs may be unable to delay oviposition for more than a few days.

If periodic crowding of egg masses affects populations, then there may be negative fitness consequences that could affect annual egg production. It was beyond the scope of this study to document population-level impacts, but evidence supports a variety of processes that could increase mortality of offspring. Density-independent mortality is possible if females are forced to oviposit on inappropriate objects, e.g. hatching success may be compromised if the environmental conditions around ER lie outside the species' preferred range (Bovill, Downes & Lancaster, 2013), and may fail completely if water levels drop rapidly and eggs desiccate (Patterson & Vannote, 1979). Density-dependent effects could include increased mortality of eggs (e.g through egg predation, Bovill, Downes & Lancaster, 2015) or mortality of early instar larvae (Hildrew *et al.*, 2004). For the two congeners of *Apsilochorema*, the observed decrease in interspecific association with decreasing ER abundance is consistent with density-dependent effects. Members of this genus avoid conspecifics and congeners during oviposition (Lancaster, Downes & Reich, 2003; Lancaster *et al.*, 2020b) and our observations suggest that competition increases with resource scarcity. This is also consistent with evidence of other forms of competition among larval aquatic insects, which can lead to lower densities or increased spacing of individuals when essential resources are in short supply (Hart, 1985; Lancaster, Hildrew & Townsend, 1988; Kohler, 1992). In contrast, the two congeners of *Ulmerochorema* commonly lay egg masses on the same ER (Lancaster *et al.*, 2020b), but co-occurrence did not vary with ER abundance. This result may appear inconsistent with a crowding response by the multi-species caddisfly assemblage, but changes in the degree of co-occurrence may not occur between species in the assemblage that do not compete and may be difficult to detect for species which typically aggregate their egg masses (Lancaster, Downes & Reich, 2003; Lancaster *et al.*, 2020b).

4.3 Drivers of seasonal oviposition patterns

Consistent with the notion that constraints on reproductive recruitment may influence life histories and hence where species can occur, we found that monthly egg mass abundance coincided with oviposition site availability for five of the ten species. However, the time that ER availability was above the threshold for egg mass crowding was a better predictor of egg mass abundance than ER numbers *per se*. For all five species, high egg mass abundance occurred when time above threshold was also high (>75% vs < 55%), but for only two of these species (*Apsilochorema* spp.) was egg mass abundance also correlated with ER numbers. In spatial surveys, egg mass and ER densities are often correlated (references above) and frequent movements of individuals between resource patches may underpin these close associations (Peckarsky, Taylor & Caudill, 2000; Lancaster, Downes & Dwyer, 2020a). However, monthly fluctuations in ER abundance were largely synchronous across the three rivers, suggesting that females were unlikely to locate many resource-rich patches in this landscape during high discharge. It is noteworthy that time above threshold was typically low when temperatures were cool (winter, early spring) and egg mass abundance was also positively associated with temperature for two of the five species. Thus, although we cannot rule out a role for temperature in driving egg-laying patterns, it is certainly not the only driver and ER availability appears to be important also for some species.

Unexpectedly, monthly egg mass abundance was *negatively* associated with temperature and the time ER abundance was above threshold for two species, *Koetonga clivicola* and *Ethochorema turbidum*. These patterns are unusual for aquatic insects in temperate zones and warrant consideration, even though correlation tests were marginally non-significant ($0.05 < p < 0.10$) for both species, and abundances were statistically significantly higher when time above threshold was low for *K. clivicola* only. Some caddis do overwinter as adults and may be active at sub-zero temperatures, but oviposition by such species does not commence before spring (Ellis, 1978; Berté & Pritchard, 1983). Our observations suggest a great deal of wintertime activity and reproductive recruitment by adults of some species in this system.

Oviposition phenology was not associated with any environmental variable for three species. One hydropsychid, *Austropsyche* CSG AU2, laid eggs for only two months and this precluded meaningful tests of association. The onset of oviposition did not, however, correspond to an obvious seasonal increase in ER numbers, as reported for some mayflies (Peckarsky, Taylor & Caudill, 2000). Two hydrobiosids, *Ulmerochorema seona* and *Taschorema evansi*, laid eggs year-round but egg mass abundance was not associated with any of the measured variables. Egg mass abundances peaked in early spring for both *T. evansi* and *Austropsyche*, whereas egg masses of *U. seona* were least abundant in early spring and there was no obvious peak period. The life history strategies and potential trade-offs associated with these patterns are unclear, but they appear unrelated to oviposition site availability.

4.4 Regional and long-term oviposition patterns

Interannual variations in hydrometeorology produced marked differences in ER abundance between the two years, but it seems unlikely that these differences were large enough to affect reproductive recruitment to populations of the caddisfly species in this study. The greatest variation in ER numbers and the largest between-year differences occurred in summer–autumn, when ER abundance was, on average, well above the threshold for egg mass crowding and any periods below threshold during summer–autumn were short enough that females may have been able to delay egg laying. In this system, perhaps the most significant threat to reproductive recruitment lies in the high-discharge season (winter) when early-onset of winter rains or a prolonged rainy season could increase the duration of periods when ER abundance is below threshold. Of course, flow events capable of moving large rocks could constrain oviposition at any time of year.

The diversity and persistence of caddisfly populations may vary along and between rivers in the same region if variations in catchment runoff or local geomorphology influence differences in ER availability during critical periods. Among our three study sites, Snobs Ck was notably different by having the fewest and shortest periods when ERs were absent or abundances were below threshold. High values of T_{ovr_m} and low values of $P_{und\text{-}m}$ must reflect low relative roughness at Snobs Ck; that is, grain sizes must remain large relative to water depth throughout more of the hydrograph. We do not have the at-a-station hydraulic geometry relations needed to make a proper comparison of this between sites, but lower relative submergence is consistent with Snobs Ck being the steepest and smallest channel, with a plane-bed rather than riffle morphology. In addition, the site at Snobs Ck included a lateral break of slope between a slightly elevated patch closer to the right bank and the remainder of the bed at slightly lower elevation. This caused the strong bimodality in ER distributions at Snobs Ck and may also have contributed to the short time that ER availability was below threshold. During prolonged periods of high water level, such a site could act as a kind of oviposition refuge for insects that oviposit on ERs, in a manner analogous to the snowmelt system where mayflies fly from rivers with no ER to nearby tributaries with ER (Peckarsky, Taylor & Caudill, 2000). In this context, a better understanding of the geomorphological controls of differences in ER availability along and between rivers, would be valuable. Whether such an oviposition refuge affects only the local population or the wider metapopulation depends on the capacity and willingness of females to disperse long distances along or between rivers in search of oviposition sites, or for larvae to travel far from the natal location.

4.5 Implications for communities

One consequence of variations in oviposition phenology is that species-specific pulses of new larvae into the community differ in duration and timing, and such variation in recruitment pulses can affect community structure (Sams & Keough, 2012). It is tempting to speculate that differences in oviposition phenology may facilitate high species diversity and coexistence via temporal resource partitioning (a form of niche differentiation). Although it is fiendishly difficult to test such an hypothesis unequivocally (Butler, 1984; Tokeshi, 1986), differences in phenology could, theoretically, reduce competition for oviposition sites. Egg mass crowding when ER were scarce relative to the number of females seeking to lay eggs does suggest resource limitation and a potential for competition. However, species also differ in the environmental characteristics of preferred ER (Reich, 2004; Lancaster *et al.*, 2020b) which can reduce competition for oviposition sites (a different form of niche differentiation). The strongest evidence of inter-specific competition relates to the behaviour of two species of *Apsilochorema* that avoid one another during oviposition (Lancaster *et al.*, 2020b), and they had the same oviposition phenology with peak egg mass abundance in autumn when ER numbers were at a seasonal high and may not be limiting. Alternatively, species coexistence may be related to temporal variations in recruitment pulses and, hence, variation in the occurrence of similar larval instars and, thus, partitioning of larval resources. This is theoretically possible for the Hydrobiosidae, whose larvae form a guild of free-roaming predators and species can differ in diet composition (Lancaster, 2021). Multiple species of hydrobiosid commonly co-occur in some rivers (Collier *et al.*, 1995; Lancaster, 2021). Coexistence in these guilds may lie in temporal partitioning of prey resources that arises through variations in oviposition phenology and larval development. These are intriguing ideas and this may be a model system for further investigations.

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DATA AVAILABILITY STATEMENT

Data will be made available upon reasonable request to the authors.

CONFLICT OF INTEREST

To the authors' knowledge, there are no conflicts of interest.

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Table 1 – Definitions of descriptive statistics.

Statistic	Description
ER_{min}, ER_{max}	Minimum, maximum number of ER
ER_{10}, ER_{50}, ER_{90}	10th, 50th, 90th percentile of distribution of ER numbers
μ_{ER}	Mean number of ER
σ^2_{ER}	Variance in ER numbers
γ_{ER}	Skewness in ER numbers
T_{ovr}	Proportion of time that ER numbers exceeded the threshold[1]
P_{ovr}	Mean duration of periods that ER numbers exceeded the threshold
N_{und}	Number of occasions that ER numbers were below the threshold
P_{und}	Mean duration of periods that ER numbers were below the threshold
Additional subscripts[2]	
_m	Statistic calculated for each calendar month
_3w	Statistic calculated for 3 weeks preceding a phenology survey

[1] Threshold refers to the number of ER below which egg masses were crowded.

[2] Absence of addition subscripts indicates statistics calculated over a year

Table 2 – Descriptive statistics of annual ER abundance at one site in each of three rivers in each of two years. See Table 1 for description of variables.

River and time period	ER_{min}	ER_{10}	ER_{50}	ER_{90}	ER_{max}	σ^2_{ER}	γ_{ER}	T_{ovr} (%)	P_{ovr} (days)	N_{und}	P_{und} (days)
Steavenson R.											
1 Dec 2016 – 30 Nov 2017	1	20	107	236	275	6517	0.274	83.6	22.7	13	4.2
1 Dec 2017 – 28 Nov 2018	1	6	49	182	232	4222	0.734	65.8	14.9	20	6.1
Little R.											
1 Dec 2016 – 30 Nov 2017	0	3	107	365	501	19398	0.597	76.7	21.5	13	6.3
1 Dec 2017 – 28 Nov 2018	0	2	48	384	588	21386	1.373	71.2	18.4	15	6.7
Snobs Ck											
1 Dec 2016 – 30 Nov 2017	5	28	78	190	239	3828	0.468	98.3	71.8	4	1.4
1 Dec 2016 – 31 Aug 2017	7	35	109	195	239	3740	0.055	98.3	67.4	3	1.3
1 Dec 2017 – 31 Aug 2018	1	33	149	257	335	6772	0.140	98.8	90.2	2	1.6

Table 3 – For each caddisfly species, summary of tests for correlation between numbers of egg masses surveyed each month and two environmental variables. Values significant at α < 0.05 are highlighted in bold; marginally non-significant values (0.05 < α < 0.10) are in italics. d.f. = 10 for each test. See Figure 4 for illustration.

	ER_{50_3w}		Air temperature	
Species	*r*	*p*	*r*	*p*
U. rubiconum	0.123	0.703	**0.900**	**<0.001**
U. seona	0.305	0.335	-0.073	0.822
K. clivicola	-0.297	0.348	*-0.554*	*0.062*
A. obliquum	**0.785**	**0.002**	0.397	0.201
A. gisbum	**0.863**	**0.003**	0.304	0.337
E. turbidum	-0.193	0.547	*-0.536*	*0.072*
T. evansi	-0.264	0.407	-0.117	0.717
T. palpata	0.050	0.877	**0.641**	**0.025**
Austropsyche CSG sp. AU2	-0.162	0.615	0.259	0.416
Cheumatopsyche AV3	-0.092	0.776	**0.628**	**0.029**

Figure legends

Figure 1 For each indicator riffle, relationships between number of ERs (manual counts) and water level above the stream bed (4-hour smoothed average). All model fits were statistically significant: (a) Steavenson R., $F_{(1,\,17)} = 211$, $p < 0.001$, $R^2 = 0.93$; (b) Little R., $F_{(1,\,21)} = 188$ $p < 0.001$, $R^2 = 0.90$; (c) Snobs Ck, $F_{(1,\,15)} = 83.8$, $p < 0.001$, $R^2 = 0.85$.

Figure 2 Monthly variations in ER abundance over two years, showing seasonal patterns and interannual variability at study sites on (a) Steavenson R., (b) Little R. and (c) Snobs Ck. (d) Regional discharge patterns are indicated by daily discharge data from the Acheron R. gauge at Taggerty, which is downstream of both the Little and Steavenson Rivers. × indicates monthly mean.

Figure 3 Monthly statistics for (a) variance of ER, $\sigma^2_{\mathrm{ER\_m}}$, (b) skewness of ER, $\gamma_{\mathrm{ER\_m}}$, and (c) difference in $\mathrm{ER}_{50\_\mathrm{m}}$ between two years (2018-2017). In (a) and (b), solid lines indicate data for 2017, dashed lines 2018. In (b) and (c), dotted lines indicate zero.

Figure 4 Phenology: For ten species of caddisfly, numbers of egg masses laid each month over 300 ERs in the Little R. Top panels are identical show mean daily air temperature (dashed line) and $\mathrm{ER}_{50\_3\mathrm{w}}$ (solid line). Graphs with bars of the same colour show similar patterns with environmental variables, see text for explanation. Air temperature and $\mathrm{ER}_{50\_3\mathrm{w}}$ were not correlated ($r = 0.343$ $p = 0.275$). See Table 3 for summary of correlations between environmental variables and egg mass numbers.

Figure 5 Relationships of an index of mean crowding, $\overset{*}{x}/\bar{x}$, for (a) egg masses and (b) species with $\mathrm{ER}_{50\_3\mathrm{w}}$ in the indicator riffle. (c) Total number of egg masses encountered during each survey in relation to $\mathrm{ER}_{50\_3\mathrm{w}}$. Dashed lines in (a) and (b) are based on linear regression using all data points and are statistically significant: (a) $F_{1,10} = 5.33$, $p = 0.044$, $R^2 = 0.35$ (b) $F_{1,10} = 17.6$, $p = 0.002$, $R^2 = 0.64$. Solid lines indicate relationships above and below a break in slope in the linear regression. In (a) values of $\overset{*}{x}/\bar{x}$ are significantly different between low and high values of ER, shown by solid lines (t-test: $t_5 = 6.51$, $p < 0.001$). In (b) there is a relationship for low values of $\mathrm{ER}_{50\_3\mathrm{w}}$ ($F_{1,3} = 10.3$, $p = 0.049$, $R^2 = 0.78$), but not high values.

Figure 6 Co-occurrence of different species' egg masses on the same ER, as indicated by Sørensons' coefficient of association, in relation to $\mathrm{ER}_{50\_3\mathrm{w}}$ in the indicator riffle. Congeners of (a) *Apsilochorema*: *A. obliquum* and *A. gisbum*; (b) *Ulmerochorema*: *U. rubiconum* and *U. seona*. Dashed line at 0 indicates no association. Values <0 suggest negative association; values >0 suggest positive association. Linear regression indicated a statistically significant relationship in (a) $F_{1,10} = 18.5$, $p = 0.002$, $R^2 = 0.65$, but not (b) $F_{1,10} = 1.32$, $p = 0.277$.

Figure 7 For each river, over two years, (a) percentage of time in each month above threshold, $\mathrm{T}_{\mathrm{ovr\_m}}$, and (b) duration of each below-threshold event, $\mathrm{P}_{\mathrm{und}}$. In (b), Steavenson R. represented by black circles; Little R. by blue crosses, ×; Snobs Ck by green squares, ☐.

Figure 8 For each species, numbers of egg masses (mean ± SE) laid each month in relation to time above threshold, T_{ovr_3w}. Low: T_{ovr_3w} <55%; High: T_{ovr_3w} >75%. *t*-values indicate outcomes of two-sample *t*-tests; d.f. =6 for all tests. Graphs with bars of the same colour show similar patterns, see text for explanation. With egg masses laid in only two months, meaningful statistical analysis was not feasible for *Austropsyche*.

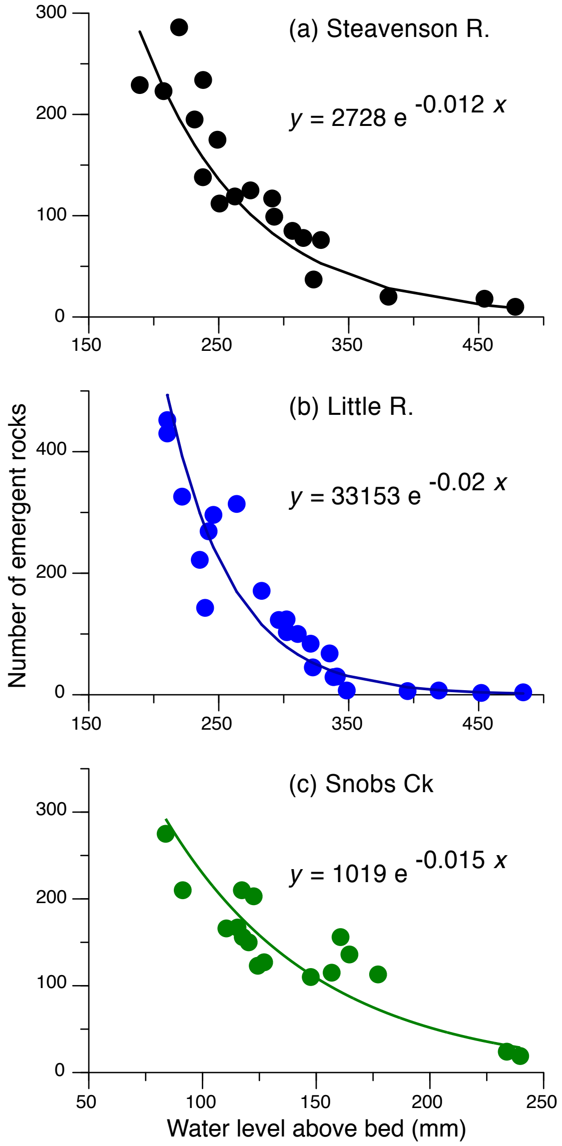

(a) Steavenson R.
$y = 2728\, e^{-0.012\, x}$
300
200
100
0
150
250
350
450
(b) Little R.
$y = 33153\, e^{-0.02\, x}$
Number of emergent rocks
400
200
0
150
250
350
450
(c) Snobs Ck
$y = 1019\, e^{-0.015\, x}$
300
200
100
0
50
100
150
200
250
Water level above bed (mm)

Figure 1

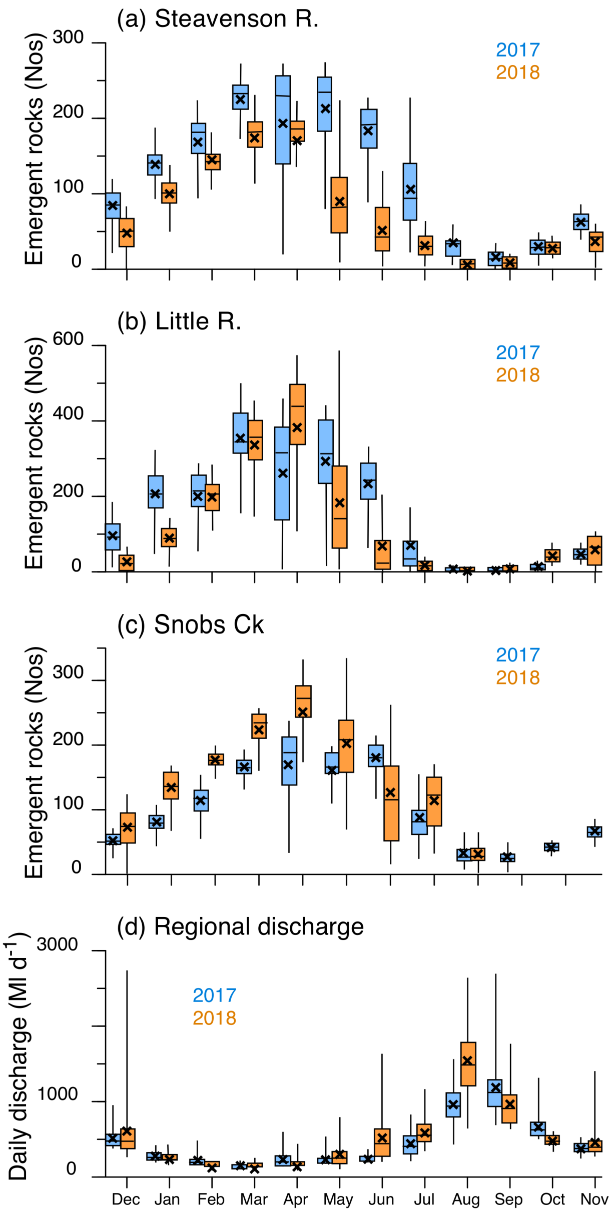

(a) Steavenson R.
Emergent rocks (Nos)
300
200
100
0
2017
2018
(b) Little R.
Emergent rocks (Nos)
600
400
200
0
2017
2018
(c) Snobs Ck
Emergent rocks (Nos)
300
200
100
0
2017
2018
(d) Regional discharge
Daily discharge (Ml d^{-1})
3000
1000
0
2017
2018
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Figure 2

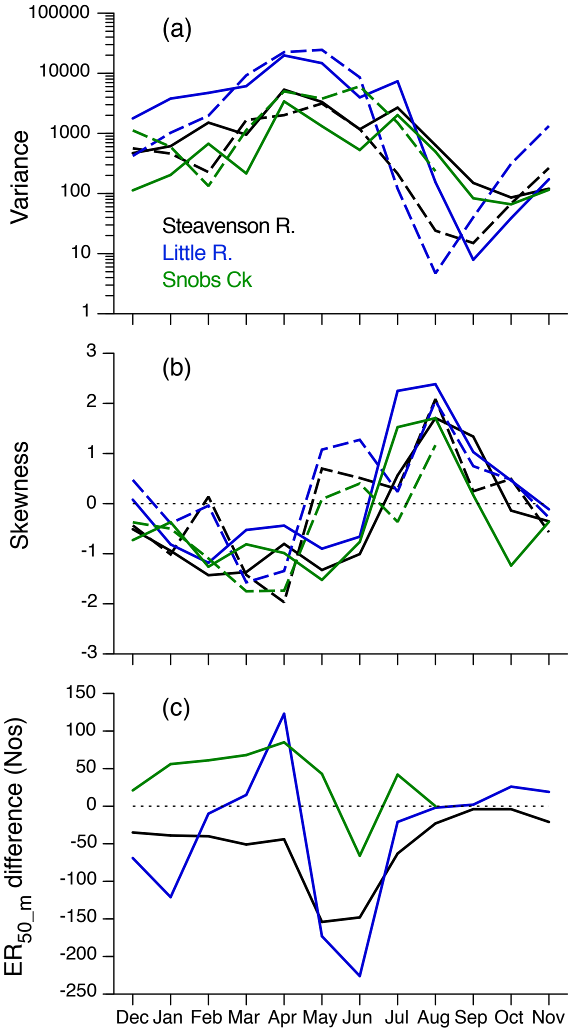
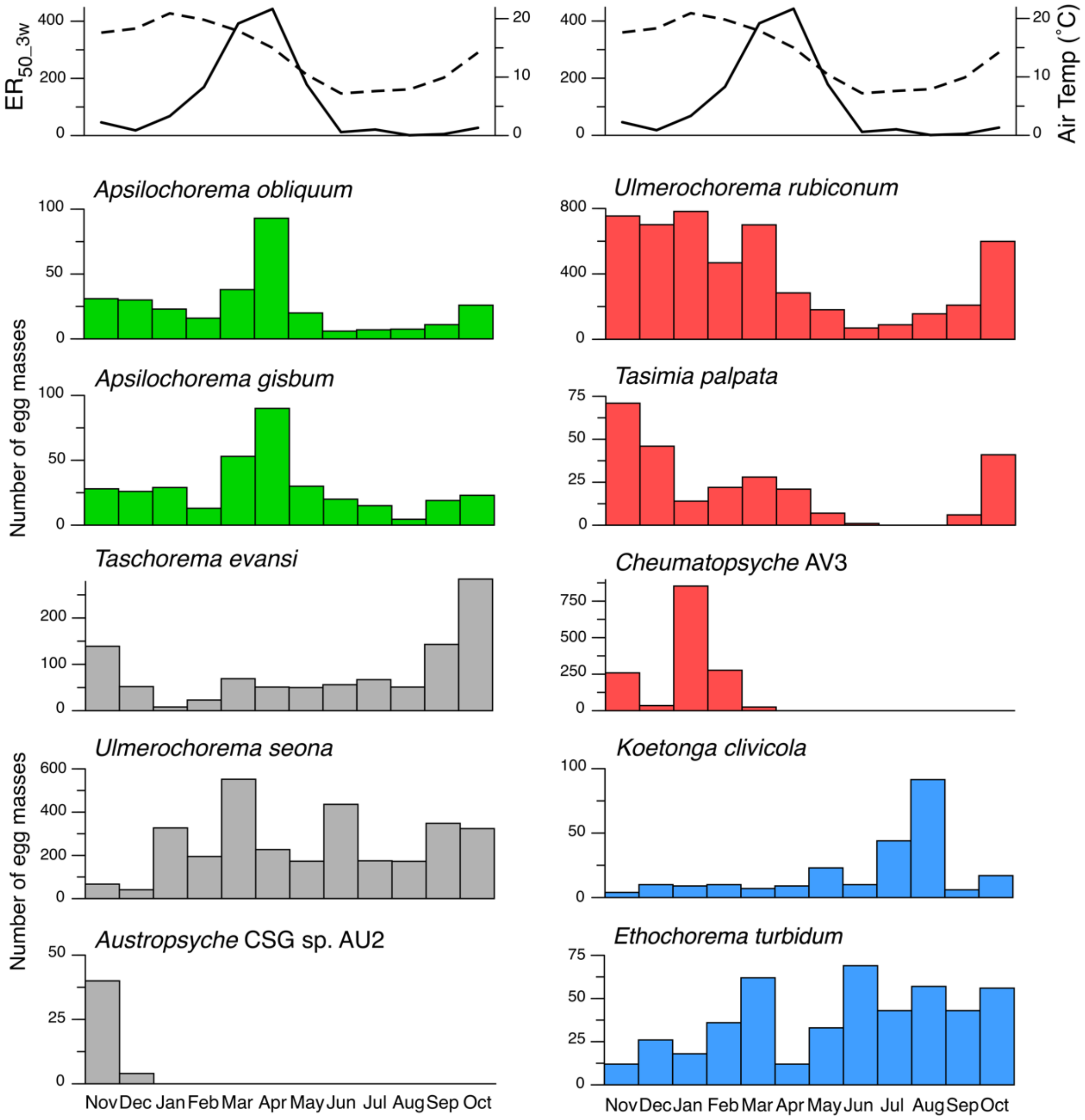

(a)
Variance
100000
10000
1000
100
10
1
Steavenson R.
Little R.
Snobs Ck
(b)
Skewness
3
2
1
0
-1
-2
-3
(c)
ER_{50_m} difference (Nos)
150
100
50
0
-50
-100
-150
-200
-250
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Figure 3



ER_{50_3w}
400
200
0
20
10
0
Air Temp (°C)
Number of egg masses
Apsilochorema obliquum
Apsilochorema gisbum
Taschorema evansi
Ulmerochorema seona
Austropsyche CSG sp. AU2
Ulmerochorema rubiconum
Tasimia palpata
Cheumatopsyche AV3
Koetonga clivicola
Ethochorema turbidum
100
50
800
400
75
25
750
500
250
600
Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct

Figure 4

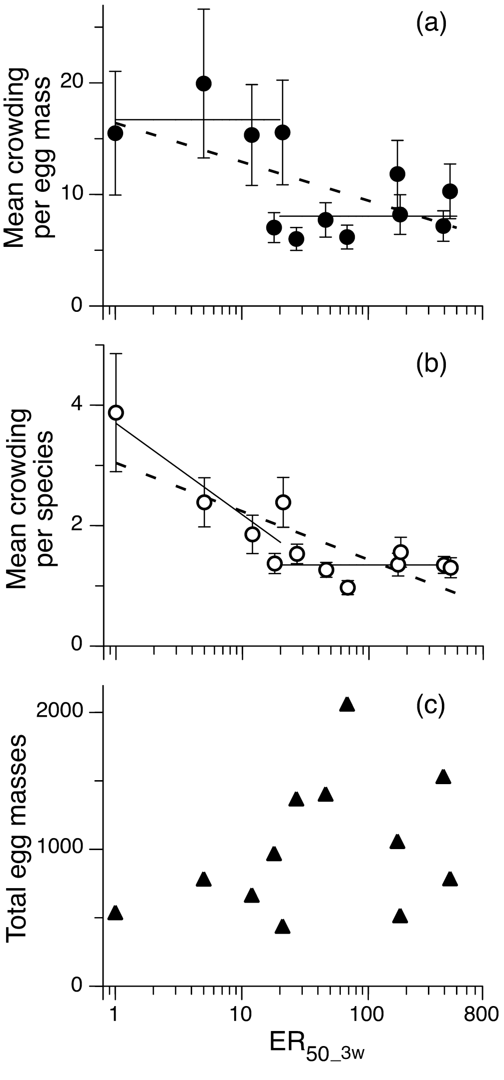

(a)
Mean crowding per egg mass
0
10
20
(b)
Mean crowding per species
0
2
4
(c)
Total egg masses
0
1000
2000
1
10
100
800
ER50_3w

Figure 5

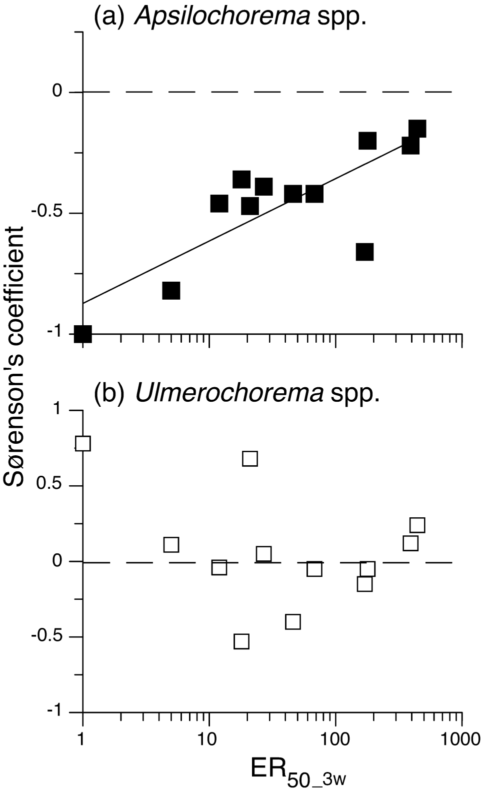

(a) *Apsilochorema* spp.
0
-0.5
-1
(b) *Ulmerochorema* spp.
1
0.5
0
-0.5
-1
Sørenson's coefficient
1
10
100
1000
ER_{50_3w}

Figure 6

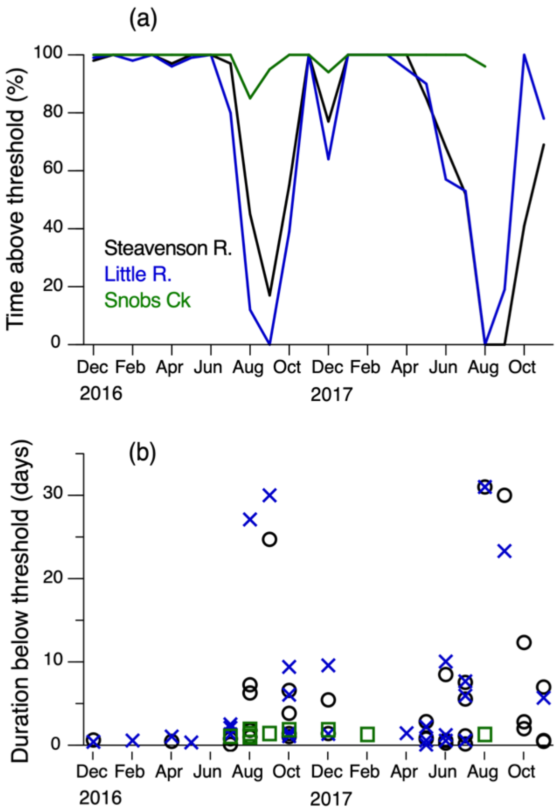

(a)
Time above threshold (%)
100
80
60
40
20
0
Steavenson R.
Little R.
Snobs Ck
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
2016
2017
(b)
Duration below threshold (days)
30
20
10
0
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
2016
2017

Figure 7

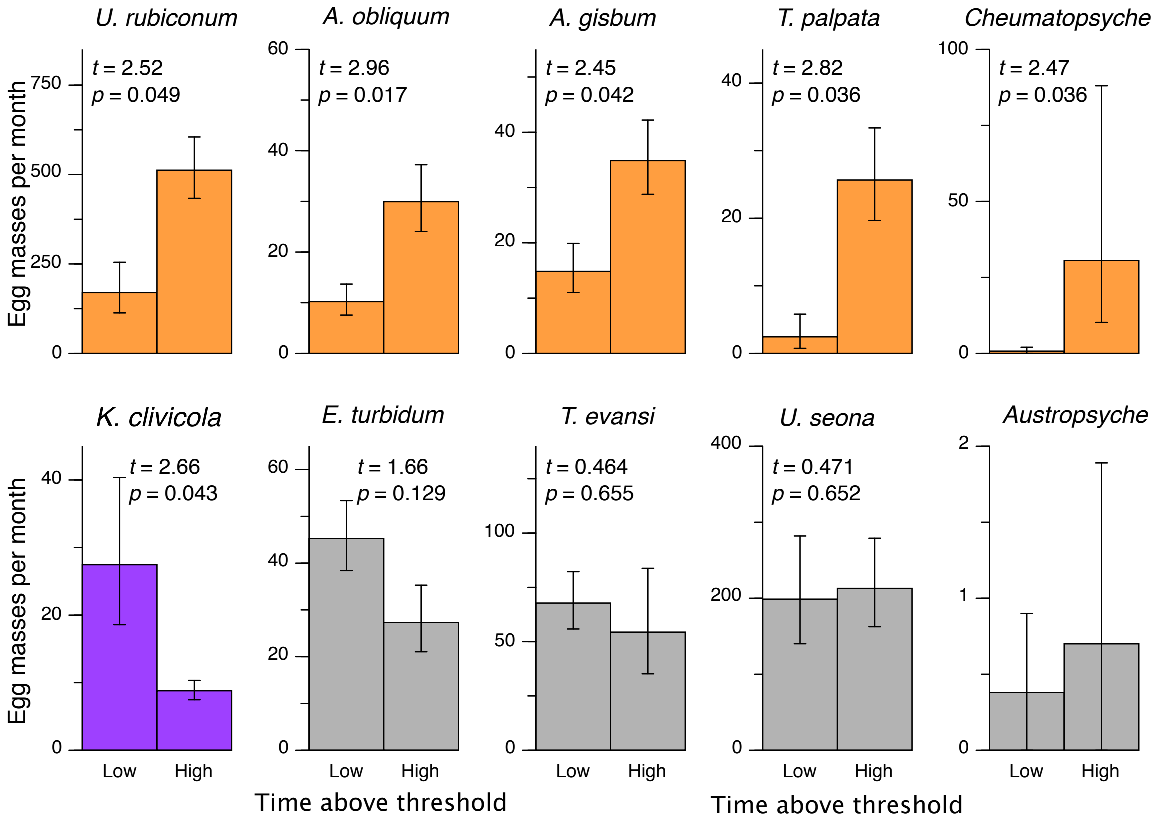
U. rubiconum
t = 2.52
p = 0.049
A. obliquum
t = 2.96
p = 0.017
A. gisbum
t = 2.45
p = 0.042
T. palpata
t = 2.82
p = 0.036
Cheumatopsyche
t = 2.47
p = 0.036
K. clivicola
t = 2.66
p = 0.043
E. turbidum
t = 1.66
p = 0.129
T. evansi
t = 0.464
p = 0.655
U. seona
t = 0.471
p = 0.652
Austropsyche
Egg masses per month
Low
High
Time above threshold
0
250
500
750
20
40
60
50
100
200
400
1
2

Figure 8

Supplementary Material

Jill Lancaster, Stephen P. Rice, Louise Slater, Rebecca E. Lester, Barbara J. Downes

Hydrological controls on oviposition habitat are associated with egg-laying phenology of some caddisflies

Freshwater Biology (2021)

A. Gaps in the ER time series

Data collection was interrupted by instrument problems or physical disturbances on seven occasions, leaving recording gaps of between 4 hours and 13 days, representing 0.10, 0.14 and 1.81% of all measurement intervals on Snobs Ck, Little R. and Steavenson R., respectively. For five gaps of less than 24 hours, missing values were replaced by 24-hour averages and for two gaps of 1.2 days (Little R.) and 13 days (Steavenson R.), the gaps were not filled, representing 0.09 and 1.74% of the respective records. These are small amounts of missing data that do not affect our analysis, except for consideration of monthly water levels statistics at Steavenson R. in Apr 2017, when the 13-day gap occurred.

B. Effects of smoothing on ER time series

We checked the impact of smoothing on ER numbers by comparing distributions of ER derived from WL smoothed using a 24-hr and 4-hr running mean. At each site, percentiles of the monthly ER distributions differed by only small amounts; for example, the use of 24-hr smoothing resulted in a reduction in monthly median ER numbers (ER_{50}) of, on average (i.e. across all months), 0.8, 0.7 and 1.0 ER on Snobs Ck, Little R. and Steavenson R., respectively. These differences in count represent percentage differences of -1.1, -1.3 and -1.6%. Similar differences were apparent in the distribution extremes: average monthly discrepancies for the tenth percentile (ER_{10}) were -1.7, -1.9 and -0.9%, and for the ninetieth percentile (ER_{90}) were -1.3, -2.3 and -2.2% respectively. These differences are small, and we are therefore confident that the 24-hour, running-mean smoothing does not have an adverse effect on estimates of ER numbers. It is notable that in all months at all sites there is tendency for 24-hr smoothing to reduce the estimated number of ER, which confirms that smoothing causes a small net increase in water levels as individual flood hydrographs are slightly flattened and stretched.

Table S1 – Descriptive statistics of monthly ER abundance in one site in each of three rivers in each of two years. See Table 1 for description of variables.

River, month year	ER_{min_m}	ER_{10_m}	ER_{50_m}	ER_{90_m}	ER_{max_m}	$\sigma^2_{ER\_m}$	γ_{ER_m}	T_{ovr_m} (%)	P_{ovr_m} (days)	N_{und_m}	P_{und_m} (days)
Steavenson R.											
Dec 2016	62	85	113	51	84.5	470	-0.511	0.98	15.2	1	0.6
Jan 2017	112	141	172	60	138.9	613	-0.942	1.00	31.0	0	0.0
Feb 2017	113	182	208	95	168.5	1511	-1.429	1.00	28.0	0	0.0
Mar 2017	175	233	258	83	225.0	951	-1.367	1.00	31.0	0	0.0
Apr 2017	72	230	263	191	193.3	5340	-0.804	0.97	8.7	1	0.5
May 2017	108	235	264	156	212.9	3330	-1.325	1.00	31.0	0	0.0
Jun 2017	139	191	221	82	183.5	1170	-1.007	1.00	30.0	0	0.0
Jul 2017	47	93	184	137	105.9	2686	0.564	0.97	10.0	2	0.4
Aug 2017	14	27	87	73	35.0	638	1.708	0.45	2.8	4	4.1
Sep 2017	5	12	37	32	16.1	150	1.338	0.17	5.2	1	24.7
Oct 2017	19	30	42	23	30.0	85.8	-0.139	0.55	4.3	4	3.2
Nov 2017	45	64	75	30	62.3	120	-0.354	1.00	30.0	0	0.0
Dec 2017	11	50	77	66	47.9	563	-0.435	0.77	8.0	2	3.4
Jan 2018	73	102	123	50	100.1	462	-1.014	1.00	31.0	0	0.0
Feb 2018	130	142	167	37	145.0	227	0.138	1.00	28.0	0	0.0
Mar 2018	103	182	217	114	174.0	1664	-1.423	1.00	31.0	0	0.0
Apr 2018	92	186	202	110	170.4	2011	-1.968	1.00	30.0	0	0.0
May 2018	18	81	164	146	89.8	3138	0.699	0.85	6.6	3	1.5
Jun 2018	10	43	103	93	51.4	1178	0.512	0.68	6.8	3	3.1
Jul 2018	12	30	53	41	31.3	214	0.288	0.52	5.4	4	3.6
Aug 2018	2	4	13	11	5.8	24.1	2.086	0.00	0.0	1	31.0
Sep 2018	4	8	14	10	8.6	15.0	0.247	0.00	0.0	1	30.0
Oct 2018	18	26	42	24	27.6	67.9	0.493	0.41	4.2	3	5.7
Nov 2018	11	43	57	46	36.7	266	-0.570	0.69	6.2	3	2.7
Little R.											
Dec 2016	45	93	150	105	95.9	1774	0.078	0.99	15.3	1	0.4
Jan 2017	132	212	275	143	206.8	3792	-0.814	1.00	31.0	0	0.0
Feb 2017	80	219	266	186	199.8	4721	-1.181	0.98	13.7	1	0.6
Mar 2017	274	346	458	184	358.4	6106	-0.526	1.00	30.7	0	0.0
Apr 2017	42	318	401	359	261.5	19811	-0.439	0.96	14.5	1	1.0
May 2017	53	315	421	369	293.0	14724	-0.900	0.99	15.3	1	0.3
Jun 2017	149	247	311	162	233.5	3971	-0.660	1.00	30.0	0	0.0
Jul 2017	7	39	131	124	70.3	7361	2.250	0.80	6.2	3	2.0
Aug 2017	1	3	32	31	7.4	155	2.384	0.12	3.9	1	27.1
Sep 2017	1	3	8	7	3.5	7.9	1.030	0.00	0.0	1	30.0
Oct 2017	8	13	22	14	13.9	38.9	0.461	0.39	2.4	4	4.5
Nov 2017	28	48	62	34	46.5	171	-0.114	1.00	30.0	0	0.0
Dec 2017	1	24	62	61	26.6	422	0.473	0.64	6.6	2	5.5
Jan 2018	44	91	127	83	89.4	1025	-0.393	1.00	31.0	0	0.0
Feb 2018	137	209	245	108	198.1	1970	-0.042	1.00	28.0	0	0.0
Mar 2018	164	361	416	252	336.2	9226	-1.571	1.00	31.0	0	0.0
Apr 2018	94	441	506	412	382.4	22454	-1.345	0.95	14.3	1	1.4
May 2018	16	142	391	375	183.1	24515	1.077	0.90	7.0	3	0.9
Jun 2018	1	21	241	240	68.3	8550	1.273	0.57	4.3	3	3.9
Jul 2018	3	18	34	31	17.0	120	0.236	0.53	8.2	3	4.7
Aug 2018	0	1	5	5	2.0	4.7	2.048	0.00	0.0	1	31.0

Sep 2018	1	5	18	17	7.8	40.2	0.748	0.19	5.7	1	23.3
Oct 2018	23	39	71	48	42.3	312	0.476	1.00	31.0	0	0.0
Nov 2018	5	67	100	95	58.5	1327	-0.280	0.78	10.5	1	5.7
Snobs Ck											
Dec 2016	41	54	64	23	52.2	113	-0.729	1.00	31.0	0	0.0
Jan 2017	64	82	100	36	81.2	204	-0.370	1.00	31.0	0	0.0
Feb 2017	88	119	141	53	114.3	673	-1.260	1.00	28.0	0	0.0
Mar 2017	153	168	187	34	166.2	216	-0.812	1.00	31.0	0	0.0
Apr 2017	72	190	230	158	169.6	3407	-0.987	1.00	30.0	0	0.0
May 2017	96	169	194	98	160.9	1317	-1.523	1.00	31.0	0	0.0
Jun 2017	154	183	207	53	180.5	529	-0.765	1.00	30.0	0	0.0
Jul 2017	38	83	120	82	88.0	2017	1.526	1.00	31.0	0	0.0
Aug 2017	10	28	62	52	33.1	498	1.706	0.85	6.6	3	1.3
Sep 2017	16	27	37	21	27.2	83.3	0.170	0.95	14.2	1	1.4
Oct 2017	30	44	50	20	41.5	66.1	-1.237	1.00	31.0	0	0.0
Nov 2017	50	69	78	28	67.2	115	-0.362	1.00	30.0	0	0.0
Dec 2017	21	75	117	96	73.0	1121	-0.373	0.94	14.5	1	1.9
Jan 2018	99	138	163	64	134.5	599	-0.500	1.00	31.0	0	0.0
Feb 2018	162	180	188	26	177.0	133	-1.094	1.00	28.0	0	0.0
Mar 2018	166	236	252	86	223.5	1133	-1.750	1.00	31.0	0	0.0
Apr 2018	130	275	311	181	251.1	5009	-1.736	1.00	30.0	0	0.0
May 2018	114	211	264	150	202.5	3774	0.090	1.00	31.0	0	0.0
Jun 2018	31	118	253	222	126.7	6071	0.401	1.00	30.0	0	0.0
Jul 2018	59	125	157	98	114.2	1506	-0.364	1.00	31.0	0	0.0
Aug 2018	18	28	49	31	31.6	235	1.166	0.96	14.8	1	1.3

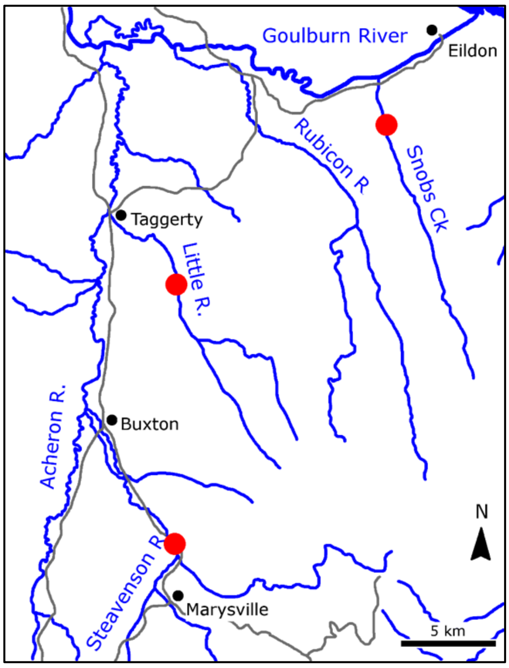


Figure S1 – Map of study sites (red circles) in central Victoria, Australia. Blue lines are rivers, grey lines are roads, black circles are settlements. Latitude and longitude of study sites: Steavenson R. S 37.48801, E 145.75264; Little R. S 37.34839, E 145.75943; Snobs Ck S 37.27715, E. 145.87581. Redrawn from (Lancaster *et al.*, 2020).

References

Lancaster J., Downes B. J., Lester R. E. & Rice S. P. (2020). Avoidance and aggregation create consistent egg distribution patterns of congeneric caddisflies across spatially variable oviposition landscapes. *Oecologia,* 192, 375-389.

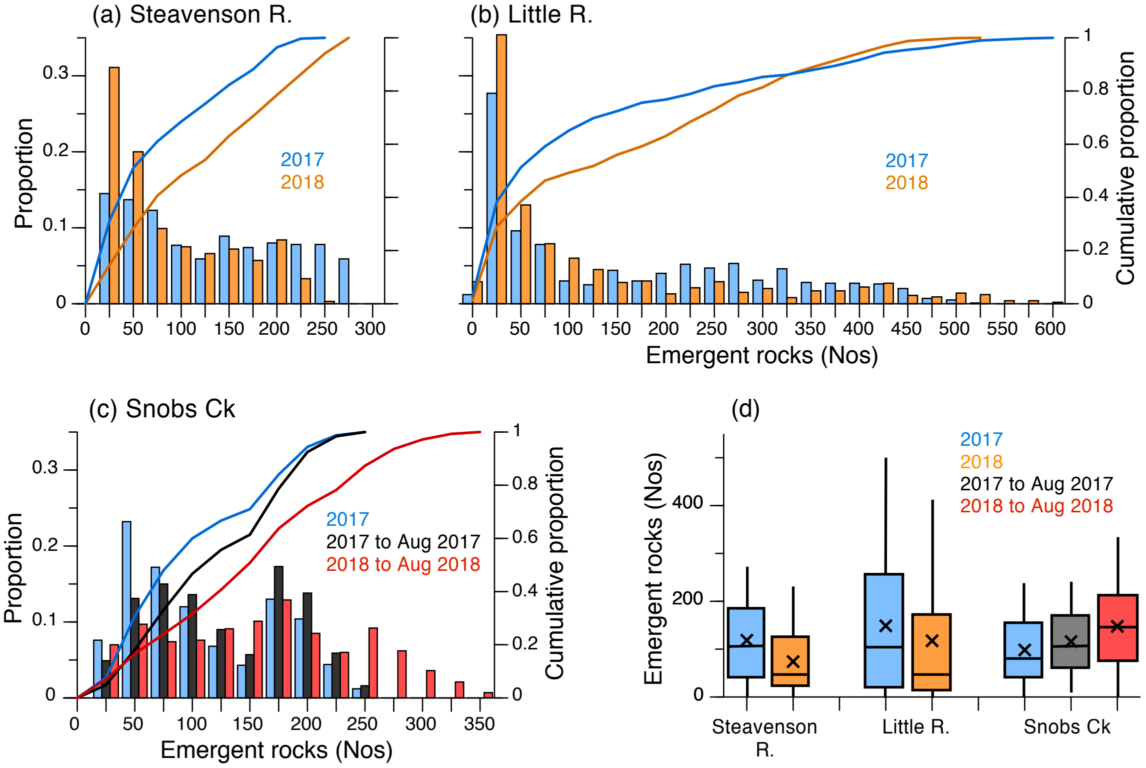


Figure S2 – Annual differences in the frequency distribution and cumulative proportion of ER numbers in (a) Steavenson R., (b) Little R., and (c) Snobs Ck. (a) and (b) show data for two 12-month periods (Dec 2016 – Nov 2017, Dec 2017 – Nov 2018), (c) shows data for one 12-month period, and two shorter periods (Dec 2016 – Aug 2017, Dec 2017 – Aug 2018). (d) Box plots showing variation in ER numbers in each river over the same time periods; × indicates μ_{ER}.

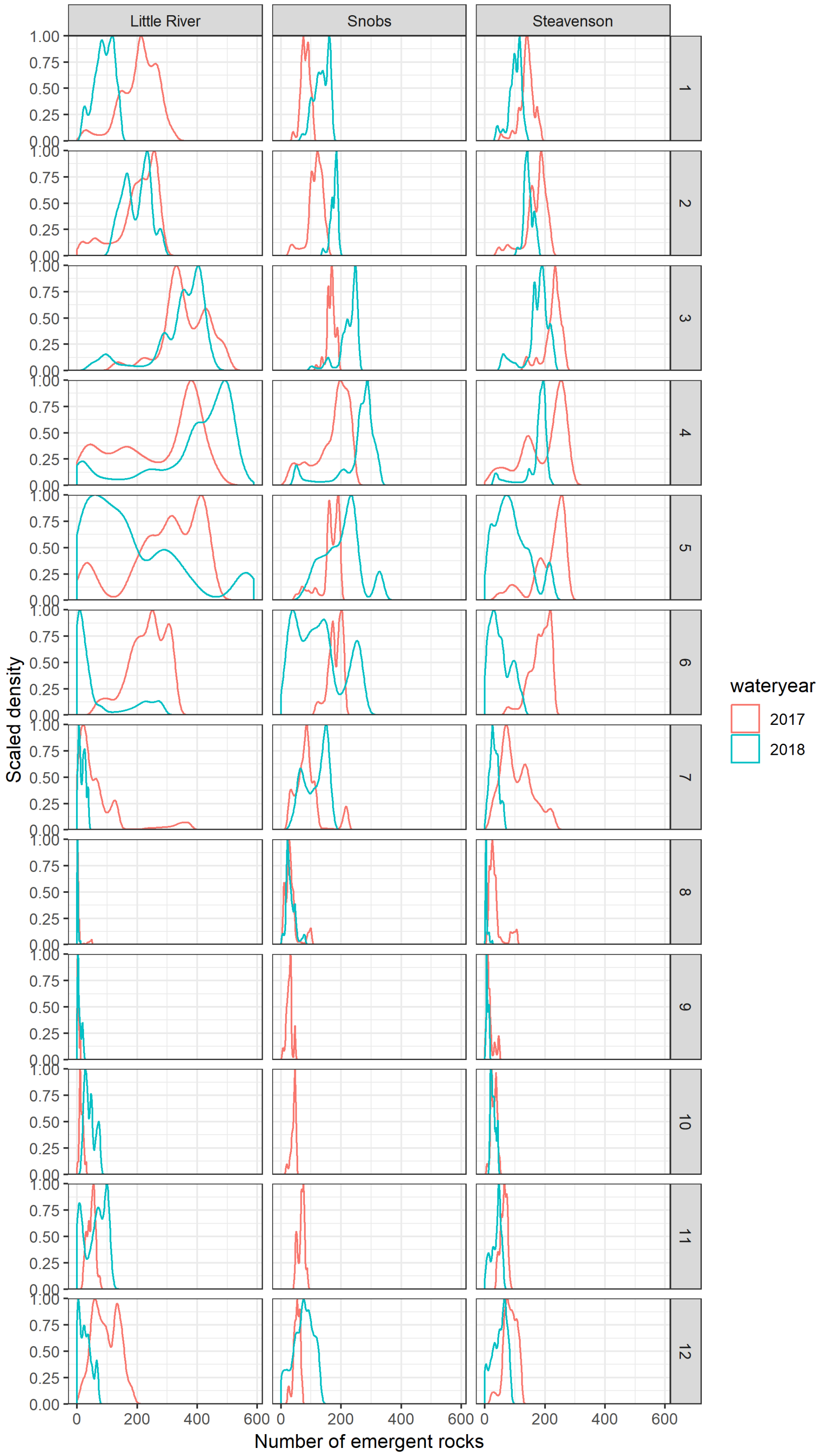


Figure S3 – Frequency distribution of ER in the indicator riffle of each river (columns) in each month (rows) over two water years. Month 1 = January, Month 12 = December.

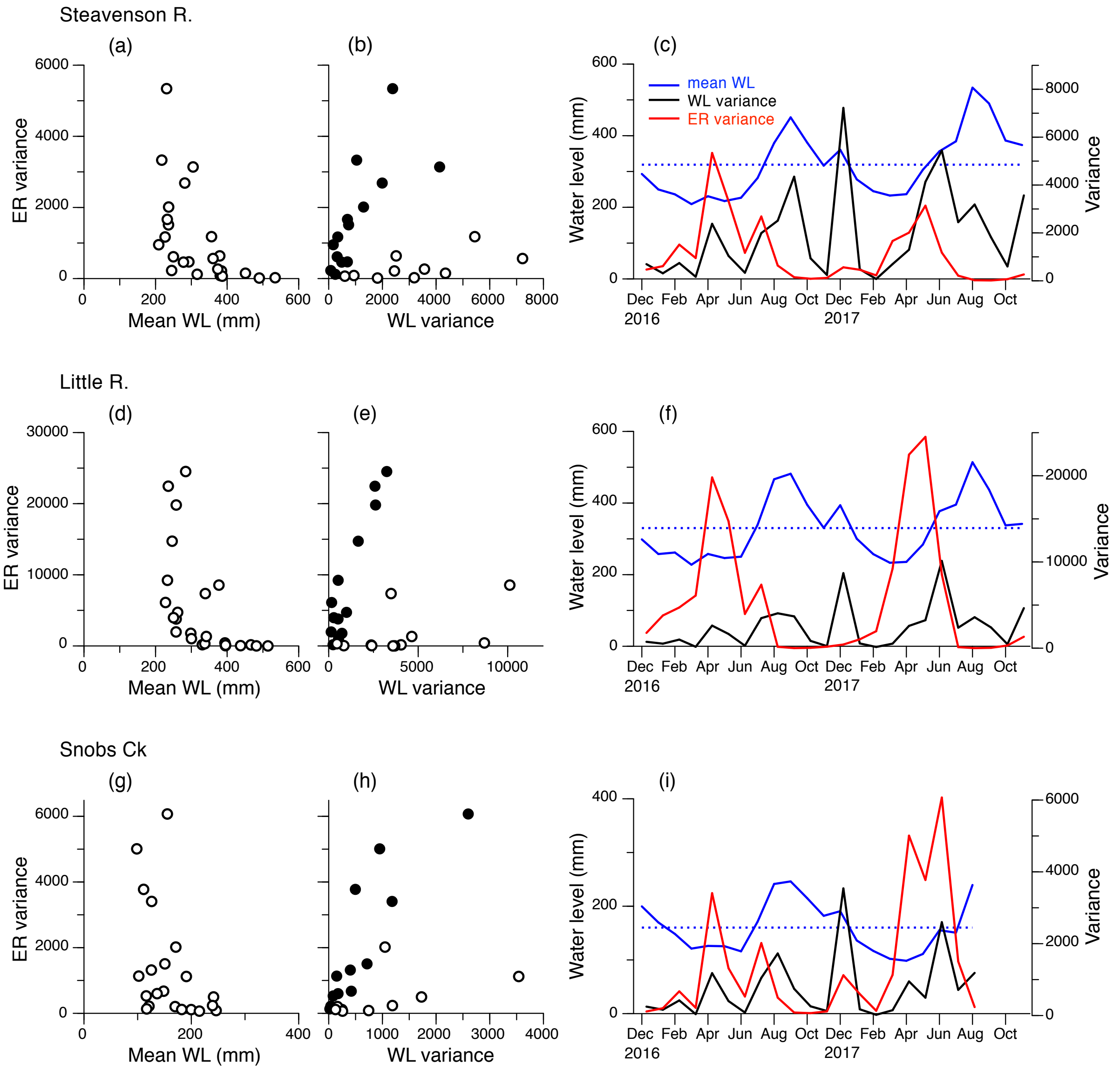


Figure S4 – For three rivers, illustration that high variance in ER numbers is associated with modest water level (WL) variance below a depth threshold equivalent to the annual mean WL. (a), (d), (g): Monthly ER variance, $\sigma^2_{ER\_m}$, with respect to monthly mean WL. (b), (e), (h): Monthly ER variance, $\sigma^2_{ER\_m}$, with respect to monthly WL variance. Closed and open symbols indicate months when WL was below and above the two-year mean, respectively. (c), (f), (i): monthly mean WL, WL variance and ER variance from Dec 2016 to Nov 2018. Dotted blue line represents annual mean WL.