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ORIGINAL ARTICLE

Seasonal differences in amounts of oviposition habitat and egg-laying by caddisflies in rivers with regulated versus unregulated flows

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Abstract

1. Few studies consider spatio-temporal variation in egg-laying for benthic insects in streams. However, such variation can have lasting effects on the numbers and distribution of offspring and subsquent life-cycle stages. For species that require specific egg-laying habitats, such as rocks that protrude from the water surface (emergent rocks, ER), densities of egg-laying habitat can affect densities of benthic eggs and even larvae for some species. For such species, changes in water levels alter the spatio-temporal distribution of ER and can affect densities of eggs and, potentially, larvae. Below dams, modified flow regimes may alter the temporal availability of ER. In this study we tested whether river regulation altered the availability of oviposition habitat and changed the phenology of oviposition compared to unregulated rivers.
2. At multiple sites in two regulated (Murrumbidgee, Tumut) and three unregulated (Goobarragandra, Goodradigbee, Micalong) rivers (south-east Australia), we surveyed densities of ER and egg masses of five species of caddisflies (family Hydrobiosidae) seasonally over 3 years (2019–2021). Samples of adults also were collected during two seasons using light traps.
3. High flows in both regulated rivers submerged all rocks during spring and summer and low-flow releases stranded rocks above the waterline at all (Murrumbidgee River) or most (Tumut River) sites during autumn and winter. No ER or egg masses were observed on any date in the Murrumbidgee River, despite relatively large catches of adults. On the Tumut River, low densities of ER and egg masses were twice observed at one site, during seasons (winter, autumn) when oviposition was low in the unregulated rivers.
4. In unregulated rivers, ER and egg masses (five species, four genera) were present at all sites but with lower densities in winter than in other seasons. During peak oviposition periods, densities of egg masses per site were not strongly related to densities of ER. In summer 2019, ER in two unregulated rivers were blanketed by

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sheets of algae and sediment that appeared to prevent oviposition because no egg masses were observed at this time.

5. In regulated rivers, aseasonal flows precluded egg-laying by submerging (summer, autumn) or stranding (winter, spring) all or most ER. In contrast, ER were available all year in the unregulated rivers and egg-laying occurred all year, except when ER were blanketed by algae and sediment. Within seasons, local densities of egg masses may be limited by numbers of gravid females, rather than numbers of ER, which differs from previous research.
6. Identifying impediments to reproduction is critical to understanding variability in population numbers in natural and altered systems. Our observations of oviposition failure downstream of dams present a new hypothesis for why some insect species are absent from channels where flows are regulated for irrigation. Blankets of algae may similarly preclude reproduction in rivers with low-flow conditions, but this remains untested.

KEYWORDS
flow regulation, habitat-limited oviposition, population dynamics, recruitment, supply-limited oviposition

1 | INTRODUCTION

A central goal in ecology is to understand how and why numbers of organisms differ across time and space (Hixon et al., 2002; Sutherland et al., 2013). However, this understanding is often elusive for organisms with complex life cycles because limits to abundance can be set at any life stage (Marchant, 2021; Piana et al., 2019). For example, some populations of terrestrial plants and benthic marine invertebrates are limited by numbers of propagules or juveniles arriving and recruiting to local populations (Roughgarden et al., 1988; Turnbull et al., 2018), whereas other populations commonly receive excess recruits and are limited by density-dependent processes that follow recruitment (e.g., mortality of older life-stages due to predation, competition: Connolly et al., 2001). Understanding whether populations are primarily limited by recruitment or by post-recruitment processes remains a significant challenge, despite considerable research (e.g., Schiel, 2004).

Nevertheless, this body of research provides a valuable framework for investigating how life-cycle transitions and potential recruitment limitation affect populations of taxa other than plants and marine invertebrates. Many oviparous, mobile animals deposit (settle) egg masses onto substrata. For these taxa, hatching of juveniles (i.e., recruits) follows dispersal and oviposition by mobile adults and is analogous to the dispersal, settlement and recruitment sequence for many terrestrial plant and benthic, marine invertebrates (Downes et al., 2021). In this context, recruitment is defined as the successful life-cycle transition to a particular stage of interest (here from eggs to hatchlings) (e.g., Keough & Downes, 1982) rather than referring to the production of adults per se (e.g., Rothschild, 2000).

Historically, studies of freshwater insects have focused on post-recruitment processes, such as disturbances, environmental gradients and density-dependent effects on densities of relatively late-instar, benthic larvae (e.g., Downes & Reich, 2008; Vinson & Hawkins, 1998). However, numbers of larvae (recruits) also may be limited by constraints on successful oviposition (Encalada & Peckarsky, 2012; Lancaster et al., 2011) and there is evidence that this occurs in other, oviparous taxa as well (Downes et al., 2021). Downes et al. (2021) outlined two overarching factors that limit numbers of eggs laid at any scale of space or time. They are: (1) the amount of ”oviposition habitat” (i.e., the number of suitable places to lay eggs) and; (2) the amount of ”supply” (i.e., the number of gravid females available to lay eggs). At sites or times where the abundance of oviposition habitat is in short supply relative to numbers of gravid females, availability of habitat can limit numbers of oviposited eggs (habitat-limited oviposition). Alternatively, at times or places where habitat is relatively abundant, the supply of gravid females may limit numbers of eggs (supply-limited oviposition). Distinguishing between habitat- and supply-limitation informs whether numbers of eggs are constrained by environmental factors that influence the availability of oviposition habitat (Lancaster et al., 2021; Rodrigues et al., 2019) or by factors that limit the local numbers of gravid females (Blakely et al., 2006). Hypothetically, habitat limitation may be more prevalent among species that require specific oviposition habitat such as plant stems that are free from epiphytic algae (Siva-Jothy et al., 1995), or rocks that protrude from the water in specific flow velocities (emergent rocks or ER; Lancaster et al., 2021) because such places are likely to be rarer than egg-laying habitat that is less specific (habitat limited egg densities [HLED] hypothesis; Downes et al., 2021).

In this study we examine how changes in the natural hydrological regimes of rivers affect the seasonal and spatial abundance of emergent rocks and the knock-on consequences for oviposition.

Emergent rocks are required oviposition habitat for aquatic insects with terrestrial adults that cannot or will not lay eggs on submerged substrata. This phenomena has been demonstrated for a range of taxa, including *Baetis* mayflies in North America (Encalada & Peckarsky, 2006) and the British Isles (Lancaster et al., 2010), some Diptera in North America (Miller et al., 2020), and caddisflies including Rhyacophilidae in the British Isles (Lancaster & Downes, 2014), Tasimiidae and Hydrobiosidae in Australia (Lancaster & Downes, 2018) Hydrobiosidae in New Zealand (Storey et al., 2017) and *Brachycentrus* in North America (Miller et al., 2020). The abundance of ER in a reach or river determines the amount of habitat available for these taxa to lay eggs and is a function of regional hydrometeorology and local geomorphology (Dwyer et al., 2021; Lancaster et al., 2021). Densities of ER depend on clast sizes and riffle-pool structure (Dwyer et al., 2021) and water levels that vary seasonally in response to precipitation, abstraction and other factors (Knighton, 2014). While average water levels vary predictably with discharge, relationships between water level and ER number may not be straightforward across a full range of discharges (Jordt & Taylor, 2021; Miller et al., 2020). Lancaster et al. (2021) compared water levels and ER densities across 2 years in three unregulated rivers. Emergent rock densities were consistently low at the highest water levels but were variable at low water levels, due to differences in local bed topography among sites. Within the lower range of flows, falling water levels that exposed new ER (increased ER densities) also stranded existing ER above the waterline (decreased ER densities). At some sites more rocks were stranded than were exposed, leading to declining numbers of ER at lower water levels. Thus, there was considerable spatial variation in densities of ER during low-flow periods (summer, autumn), but overall densities of ER were higher during these times than during high-flow periods (winter and spring) that submerged most rocks (Lancaster et al., 2021).

Below dams, flows are often regulated for various purposes that may cause unnatural fluctuations in river levels over short (hours to days) or long (months, seasons) timescales. Kennedy et al. (2016) tested the effects on aquatic insect eggs (laying and survival) of short-term fluctuations in river level caused by flow releases for hydropower. To the best of our knowledge, however, no study has tested whether changes to seasonal flow patterns can change seasonal patterns of ER availability and subsequent egg-laying. At monthly or seasonal scales, many dams in temperate rivers withhold water during cooler wet periods (e.g., winter, spring) and release flows during warmer drier times (e.g., summer, autumn; see Shields & Good, 2002). These regulated flows can cause magnitude scale, step-change increases in discharge, and change the seasonal timing of high and low flows (Kondolf & Batalla, 2005). This altered flow regime potentially affects the seasonal availability of ER by submerging rocks when they would otherwise be available to insects, and exposing rocks at times when gravid insects may not be present to lay eggs on them. For aquatic insects that lay eggs in the warmer seasons (many species), high regulated flows at these times may submerge ER and limit the availability of egg-laying habitat at times when gravid females are most abundant, potentially limiting the numbers of eggs (habitat-limited oviposition) and larvae (habitat-limited recruitment) that are delivered to the benthos.

In this study, we ask: does hydrological variability affect densities of ER with consequent effects on seasonal patterns of oviposition phenology for insects and, if so, does the timing and amount of oviposition differ between regulated and unregulated rivers? The study taxa were multiple species of caddisflies from the family Hydrobiosidae that are known to oviposit predominantly on ER in other systems (Lancaster et al., 2020). Hydrobiosids are typically multivoltine, may lay eggs at all times of year, and species using ER vary greatly in oviposition phenology (Lancaster et al., 2021). In an unregulated Victorian river, peak oviposition coincided with high ER densities in late summer and autumn for two taxa, but eight other species either laid egg masses throughout the year or laid most egg masses when ER were scarce (winter, spring). Overall, there were no consistent relations between egg-mass densities and either ER densities or season (Lancaster et al., 2021). However, like other stream taxa that use ER (e.g., Encalada & Peckarsky, 2012; Lancaster & Downes, 2014), some hydrobiosid species exhibit positive spatial relationships between densities of ER and egg masses (e.g., Lancaster & Downes, 2018) at times when gravid females are abundant, which suggests that oviposition may be habitat-limited during peak oviposition periods.

We counted egg mass and ER numbers at multiple sites on replicate regulated and unregulated rivers over 3 years to test four hypotheses. Owing to the altered flow regime in our regulated rivers (see Methods), we predict that (H_1) maximum densities of ER in regulated rivers occur in different seasons than in unregulated streams. If H_1 is correct, we expect that (H_2) seasonal patterns in the densities of egg masses (oviposition phenology) will differ between regulated and unregulated rivers. Following past research (references given above), we expect that (H_3) during peak egg-laying periods oviposition habitat limits egg mass densities such that the highest densities of egg masses occur in sites with the highest densities of ER. Finally, we test whether (H_4) numbers of captured adults (catch per unit effort) differ among seasons and between regulated versus unregulated rivers, to examine whether patterns in the temporal or spatial distribution of egg masses may be influenced by patterns in the supply of adults. Outcomes of these tests, collectively, allow us to examine whether supply or habitat constraints play a stronger role in limiting local densities of egg masses, and whether these outcomes differ between sites, seasons, and regulated versus unregulated rivers.

2 | METHODS

2.1 | Study taxa

Caddisflies of the family Hydrobiosidae are distributed throughout Australia (Neboiss, 2012) but (to our knowledge) oviposition by hydrobiosids has only been studied in a small number of rivers in Victoria, approximately 320 km to the south (see Downes et al., 2021, for review). We therefore conducted pilot studies to test whether keys to identification of egg masses, developed in Victoria, apply to the taxa encountered in the study system. We also conducted a pilot survey to confirm that hydrobiosids in the study system lay eggs predominantly on ER, as they do in Victorian streams. Confirmation of these details were required to validate tests of our hypotheses. Field identification of egg masses to morphotypes is possible because the egg masses of different taxonomic groups have distinct morphologies that are distinguished based on visual and tactile features such as the size and shape of egg masses, arrangement and number of eggs within each mass, and firmness and thickness of the protective layer of spumaline jelly (Lancaster & Glaister, 2019). In the field, we identified egg masses into three morphotypes (A-type, E-type and U-type: see Figure 1) described by Lancaster and Glaister (2019). Species-level identifications were subsequently confirmed using DNA barcoding (Canadian Centre for DNA Barcoding, Guelph) of representative specimens collected from the field, following methodology established in Lancaster and Glaister (2019).

2.2 | Study system

The study system comprises five rivers in New South Wales, Australia: two regulated rivers (Murrumbidgee River, Tumut River) and three unregulated rivers (Goobarragandra River, Goodradigbee River and Micalong Creek) (Figure 2). Sites on regulated rivers were located downstream of major dams that modify flows. The Murrumbidgee River is the third longest river in Australia and drains a total catchment area of 84,000 km^2 (Wen et al., 2011). The Murrumbidgee River flows in a westerly direction through Burrinjuck Reservoir, which drains a total catchment area of 13,100 km^2 (Shields & Good, 2002). The Goodradigbee River flows north into Burrinjuck Reservoir via protected forests within the Brindabella Ranges, without any major impoundments (Chessman et al., 2009). Micalong Creek is an unregulated tributary of the Goodradigbee River (Figure 2) and drains a forested catchment area (Owen & Wyborn, 1979). The Tumut River has a catchment area of 1630 km^2 covered primarily by forested areas, and its discharge is regulated by releases from Blowering Dam (Green et al., 2011). The Goobarragandra River meets the Tumut River approximately 10 km downstream of Blowering Dam (Figure 2). Annual rainfall in the Murrumbidgee catchment is approximately 990 mm and winter-dominant (Hope & Wright, 2003). Agriculture is the greatest user of water from the Tumut and Murrumbidgee rivers, with the majority of flows released from dams for irrigation during summer and impounded for storage in winter (Shields & Good, 2002). This flow regulation can cause sudden large changes in discharge and large differences in the seasonal patterns of flow between the regulated

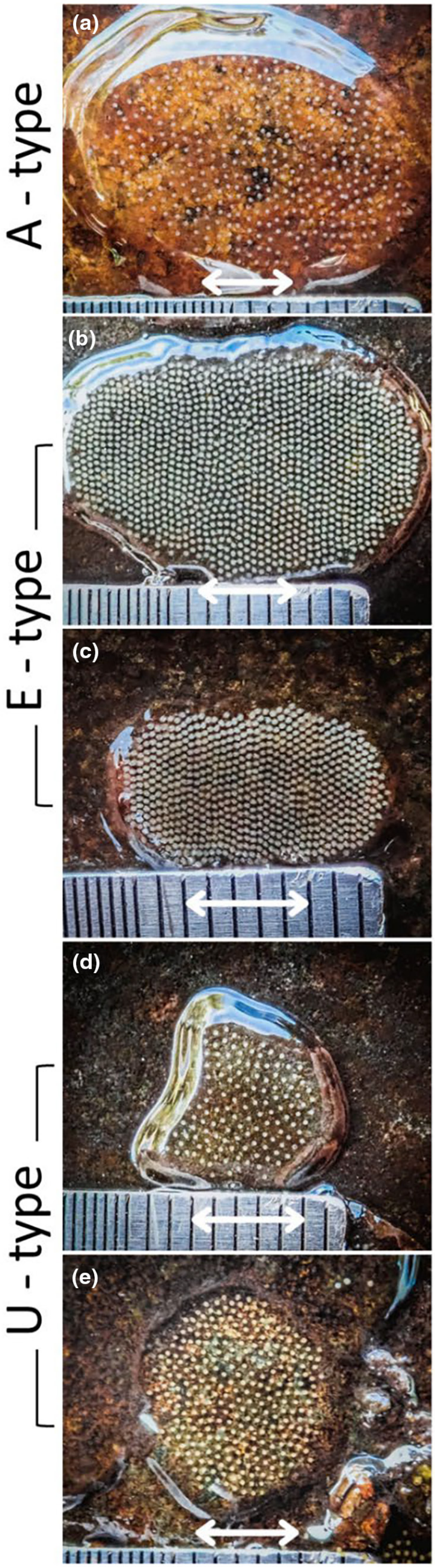
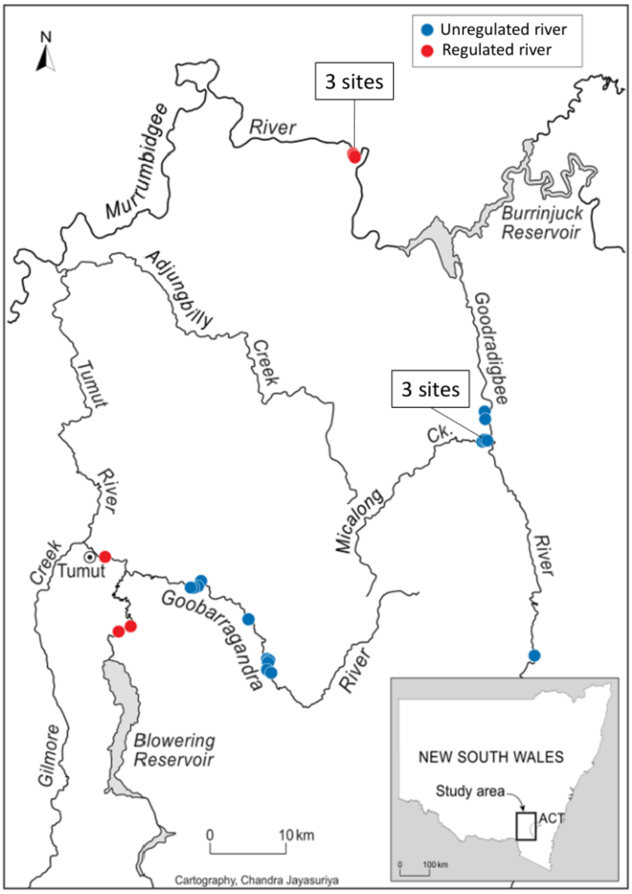


FIGURE 1 Representative examples of Hydrobiosidae egg masses of: A-type (a) *Apsilochorema gisbum*; E-type (b) *Ethochorema brunneum* and (c) *Taschorema evansi*; U-type (d) *Ulmerochorema lentum* and (e) *Ulmerochorema membrum*. Scale bars are approximately 5 mm.



Cartography, Chandra Jayasuriya

FIGURE 2 Map of study system within the Murrumbidgee Catchment, New South Wales, Australia. Sites on regulated rivers were located in the Murrumbidgee River downstream of Burrinjuck Dam (three sites) and Tumut River downstream of Blowering dam (three sites). Unregulated sites were located in Goodradigbee River (three sites), Goobarragandra River (nine sites) and Micalong Creek (three sites). Mean channel width and standard error (SE) for the Murrumbidgee (45.787 m, SE = 0.893), Tumut (39.190 m, SE = 4.559), Goodradigbee (20.580 m, SE = 0.649), Goobarragandra (19.652 m, SE = 1.486) and Micalong (12.640 m, SE = 0.903) were calculated using number of sites.

and unregulated rivers. Historically in our system, discharges in the unregulated rivers have been typically lowest in summer and autumn, and highest in winter and spring (Figure 3a), whereas flows in the regulated rivers have been typically lowest during autumn and winter and highest during spring and summer (Figure 3c). Similar patterns were observed during the study period (2019–2021), with the exceptions that, during winter, flows were below the long-term average in the unregulated rivers (Figure 3b). Variability of median daily flows differed significantly between regulated and unregulated rivers (Figure 4).

Study sites were riffles of broadly similar geomorphological character (see Figure 2 for number of sites and channel widths). Each riffle was a discrete geomorphic unit containing ER that served as potential oviposition sites. Riffles were bounded upstream and downstream by pools with few or no ER and egg masses.

2.3 | Data collection

We conducted a 2-year (2019–2021) programme of field surveys to compare seasonal and spatial differences in the densities of ER, egg masses and terrestrial adults in regulated and unregulated rivers (Table 1). We also conducted pilot surveys in 2019 to confirm whether Hydrobiosidae lay eggs predominantly on ER (not submerged rocks) as has been observed in other systems.

2.3.1 | Pilot survey: Do hydrobiosids lay egg masses on submerged rocks in our system?

Tests of our hypotheses require that hydrobiosid caddisflies lay eggs predominantly on ER. This behaviour is demonstrated for hydrobiosids in Victoria (Reich & Downes, 2003) but had not been tested in our study system. We therefore conducted pilot surveys in autumn and spring 2019 in all study rivers except for Micalong Creek, to examine submerged and emergent rocks for egg masses. In 2019, sites along Micalong Creek ($n = 3$) were yet to be included and hence are absent from the pilot survey. At each site ($n = 18$) we surveyed 100 random submerged rocks for egg masses and compared results with numbers of egg masses surveyed on ER ($n = 63$–198 rocks/site) concurrently. Egg masses were present on ER at all sites where ER were present ($n = 33$–1560 egg masses/site), but no egg masses were found on submerged rocks at any site, confirming that these species lay eggs predominantly on ER.

2.3.2 | Hypotheses 1–3: How do densities of emergent rocks and egg masses vary through time (seasons) in regulated versus unregulated rivers?

Surveys of ER and egg masses were conducted from 2019 to 2021 to ensure two replicate surveys for each season (Table 1). Only ER with a *b*-axis of ≥50 mm, located in water ≥50 mm deep were surveyed because rocks not meeting these criteria are seldom used for oviposition by Hydrobiosidae (Lancaster et al., 2003; Reich & Downes, 2003). Within each riffle, all ER were counted, flipped over and examined for egg masses, then replaced in their original locations and orientations to flow to avoid affecting future oviposition surveys (Reich et al., 2011). All egg masses were identified to morphotype using the identification key in Lancaster and Glaister (2019) and counted. In the rare instances that rocks were too large to be moved, egg-mass morphotypes were identified by touch using the firmness and thickness of the spumaline jelly using the same identification key.

On every sampling occasion, the length and width of each site were measured to determine site area and densities of ER (rocks/m^2) and egg masses (egg masses/m^2). Widths of riffles (wet width) were measured between the wetted margins on each bank at five intervals along the site's length to estimate riffle areas.

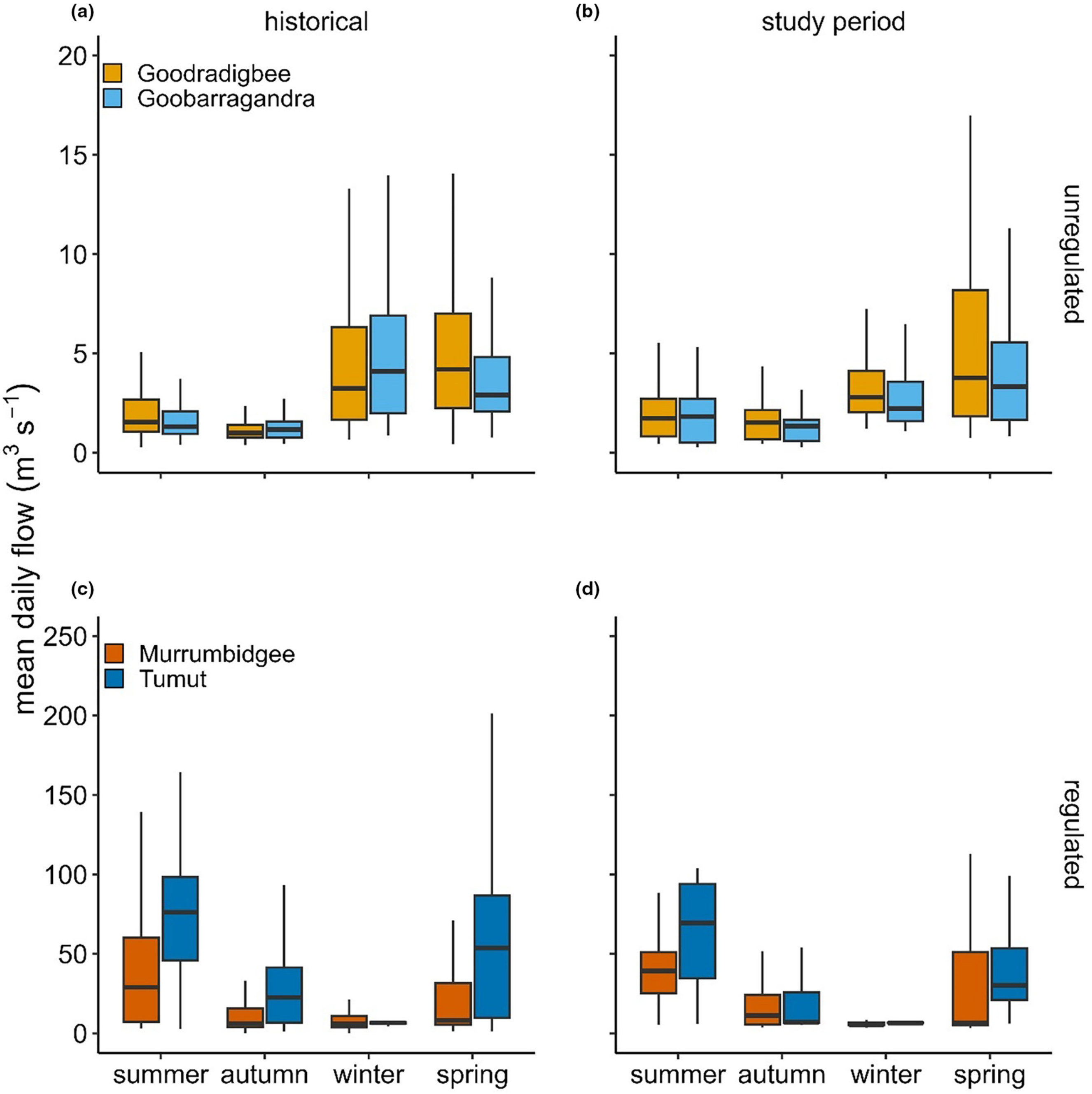


FIGURE 3 (a, c) Historical (2000–2018) median daily flows in each season in the regulated and unregulated study rivers; (b, d) median daily flows recorded in each season during the study period (January 2019–May 2021). Discharge data obtained from the Water Monitoring Network of New South Wales at gauges 4100261, 410088, 410008 and 410073 (WaterNSW, 2021). Mean daily flows are presented in (Figure 4).

2.3.3 | Hypothesis 4: Abundances of terrestrial adults in regulated and unregulated rivers across seasons

Surveys of terrestrial adults were undertaken at all sites in summer and spring 2019 to compare numbers of trapped adults between rivers. Surveys occurred concurrently with oviposition surveys during these periods (Table 1) and were conducted by deploying light traps for two consecutive nights per site, with two traps per site. One trap was placed at either end of each study riffle. Light trapping was only conducted on nights that were relatively warm, dry and calm (as forecast by BOM, 2022).

Each trap (model E701; Australian Entomological Supplies Pty Ltd) comprised a 12-volt battery and ultraviolet fluorescent tube (8-watt, 300 mm long, 320–420 nm wavelength) to attract flying insects. Trapped insects were immobilised within a bucket containing a vial and wick soaked with 90% ethanol. A light-activated switch automatically turned the traps on at sunset and turned them off at dawn. Samples were collected from the traps in the early morning

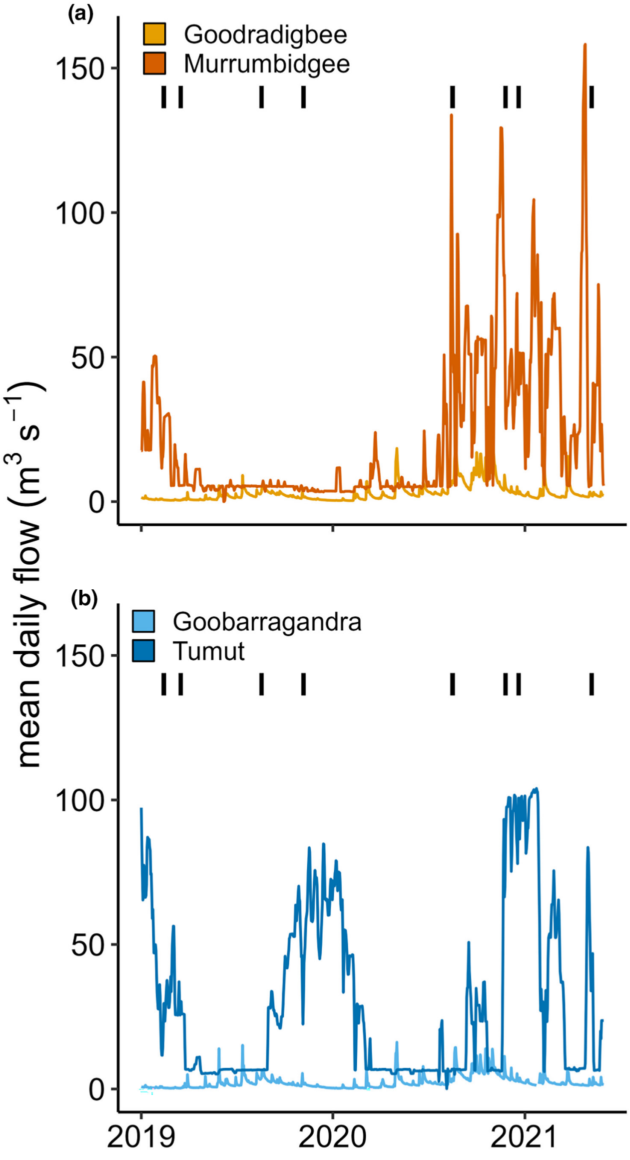


FIGURE 4 Mean daily flows (m^3/s) in the regulated rivers (Murrumbidgee, Tumut) and their unregulated tributaries (Goodradigbee, Goobarragandra) across the study period (January 2019–May 2021). Sampling times are marked with vertical bars.

and specimens were identified to species level with a dissecting microscope following Neboiss (2012).

2.4 | Data analyses

2.4.1 | Hypotheses 1 & 2: Do densities of emergent rocks and egg masses differ between regulated and unregulated rivers and seasons?

In the regulated rivers, ER and egg masses were detected during only two instances (see Results), hence statistical analysis was impossible for these data.

In the unregulated rivers, seasonal variation in densities of ER and egg masses were each analysed using factorial analyses of variance (ANOVA) with three factors: Years (a fixed factor), Seasons (a fixed factor) and Rivers (a random factor), as well as the interactions between these terms. Years was designated as fixed because years were not a random sample from a population of possible years (Quinn & Keough, 2002). At least two replicates for each season are required to identify oviposition differences among summer, autumn, winter and spring. In the unregulated rivers, seasonal replication was fully completed for the Goobarragandra and Goodradigbee rivers but was limited to spring and winter for Micalong Creek (Table 1) due to COVID-19 lockdowns that closed the border between Victoria and NSW. Hence, seasonal variation in both egg mass and ER densities were analysed using two models: without and with the Micalong Creek data (Models 1 and 2, respectively). Note the trade-off between additional temporal and spatial replication between Model 1 (10 sites, two rivers, four seasons) and Model 2 (13 sites, three rivers, two seasons). While oviposition phenology could have been effectively analysed using Model 1 alone, Micalong Creek was included in Model 2 to add context to Model 1's results for spring and winter. Analyses were carried out via Type III sums of squares using SPSS version 26.0 (IBM). Hypotheses regarding seasonal differences in mean ER or numbers of egg masses were specifically tested using Tukey's honestly significant difference (HSD) within the Seasons factor following the main ANOVA. Compared to Tukey's HSD, the use of specific, a priori contrasts within the relevant model term (Seasons) would have been a superior test for differences in ER availability and oviposition among seasons. However, our study species lay egg masses year round in other studies (Lancaster et al., 2021), which means it was not possible to set up specific, a priori predictions. Tukey's HSD provided the necessary test for comparing all pairwise contrasts within the Seasons factor while holding the family error rate at 0.05. Tukey's HSD can be a more powerful test than an *F*-test depending on the arrangement of differences among means (Kirk, 1995). Thus, some pairwise comparisons can be statistically significant even when the *F*-test for the model term does not itself fall below the 0.05 threshold (see Results). We thus conducted Tukey's HSD test when the *F*-value for Season was either statistically significant or close to significant.

2.4.2 | Hypothesis 3: Is egg-laying habitat-limited during peak oviposition periods?

In order to test whether oviposition patterns were consistent with habitat-limitation during peak egg-laying periods, linear regression was used to test for relationships between densities of egg masses and ER for each river. Egg mass and ER density were log ($x+1$)-transformed to satisfy assumptions of homogeneity of variance (Quinn & Keough, 2002).

2.4.3 | Hypothesis 4: Do abundances of terrestrial adults differ between regulated and unregulated rivers?

A nested ANOVA was used to test for summertime differences in numbers of captured adults per unit effort (CPUE) between two

TABLE 1 Temporal replication (coloured cells) of surveys across 3 years and five rivers.

Year	2019				2020		2021	
Seasons	Summer	Autumn	Winter	Spring	Winter	Spring	Summer	Autumn
Goodradigbee R.	🟧🟩	🟧🟦	🟧	🟧🟦	🟧	🟧	🟧	🟧
Goobarragandra R.	🟧🟩	🟧🟦	🟧	🟧🟩🟦	🟧	🟧	🟧	🟧
Micalong Ck			🟧	🟧	🟧	🟧		🟧
Murrumbidgee R.	🟧🟩	🟧🟦	🟧	🟧🟩🟦	🟧	🟧	🟧	🟧
Tumut R.	🟧🟩	🟧🟦	🟧	🟧🟩🟦	🟧	🟧	🟧	🟧

Note: Three sets of attributes were surveyed: 🟧, densities of emergent rocks (ER) and egg masses (EM); 🟩, numbers (CPUE) of terrestrial adults per site; 🟦, densities of egg masses on submerged rocks.

[Correction added on 13 March 2024, after first online publication, due to production error: the shadings in Table 1 are corrected in this version.]

regulated rivers (Tumut and Murrumbidgee rivers) and two unregulated rivers (Goobarragandra and Goodradigbee rivers). River (a random factor) was nested in flow Regulation (a fixed factor) and analyses was carried out for each species using Type III sums of squares. During spring, traps were stolen from Goodradigbee River, thus adult counts for this season were analysed using a one-way ANOVA that tested differences between Rivers (a random factor) across three rivers only.

3 | RESULTS

Genetic identification coupled with morphological examinations of egg masses showed that the following hydrobiosid species were common in the study rivers: *Apsilochorema gisbum* (Mosely) (A-type), *Ethochorema brunneum* (Mosely) (E-type), *Taschorema evansi* (Mosely) (E-type), *Ulmerochorema lentum* (Neboiss) (U-type) and *Ulmerochorema membrum* (Neboiss) (U-type) (Figure 1).

3.1 | Hypotheses 1 & 2: Do densities of emergent rocks and egg masses differ between regulated and unregulated rivers and seasons?

3.1.1 | Emergent rocks

No ER were recorded in the regulated rivers during spring and summer because high-flow releases (Figure 3) caused discharge to be at, or close to, bankfull thereby submerging all potential ER. Unexpectedly, no ER were found in the Murrumbidgee River on any date, because low-flow releases from Burrinjuck dam during autumn and winter (Figure 3) stranded all potential ER above the waterline. Low densities of ER were observed at a single site in the Tumut River during winter 2019 and autumn 2021 (Figure 5), because low-flow releases from Blowering dam (Figure 3) stranded all potential ER at all other sites.

In the unregulated rivers, densities of ER differed significantly among seasons for both models (Supporting information, Table S1; Figure 5) and post hoc tests for Model 1 showed significantly lower densities of ER in winter, when discharges were high, compared with all other seasons (Table 2).

3.1.2 | Egg masses

There were no egg masses found in the regulated Murrumbidgee River during any season in any year. Low densities of egg masses were observed on the Tumut River during winter 2019 and autumn 2021, at the one site where ER were present. Egg masses of U-type were the most abundant on both occasions (Figure 5) and limited to the one site with ER.

In the unregulated rivers, Model 1 showed significantly greater densities of U-type egg masses in summer than winter (Table 2), with 2020 being the main source of difference because egg mass numbers were much lower in 2019 (Figure 5). Otherwise, there were no strong seasonal differences in abundances of U-type egg masses, and there were no seasonal differences at all for the other morphotypes (Table S1). By contrast, Model 2 (which had greater statistical power provided by higher sample sizes) indicated that numbers of all egg mass morphotypes were significantly higher in spring compared to winter (Table S1; Figure 5). Oviposition for all species was observed in unregulated rivers throughout the year, but there was one, unexpected exception: no egg masses were found for any species during late summer 2019, despite the presence of abundant ER (Figure 5: Goobarragandra and Goodradigbee) and presence of adults (see results for H_4). In both rivers, we observed that ubiquitous sheets of algae and sediment had accrued on ER at all sites; these sheets may have inhibited oviposition.

3.2 | Hypotheses 3: Is egg laying habitat-limited during peak oviposition periods?

In order to test whether egg laying is limited by numbers of ER in peak oviposition periods, we needed to identify the periods of highest egg densities in our study system. During the study period, the highest densities of egg masses were laid during autumn ($n = 6625$ egg masses for U-type, $n = 192$ for E-type, $n = 50$ for A-type) and spring to early summer ($n = 33{,}862$ egg masses for U-type, $n = 367$ for E-type, $n = 196$ for A-type). Spring and early summer were combined into a single oviposition period for analysis, because the largest numbers of egg masses during this study were found during the collective

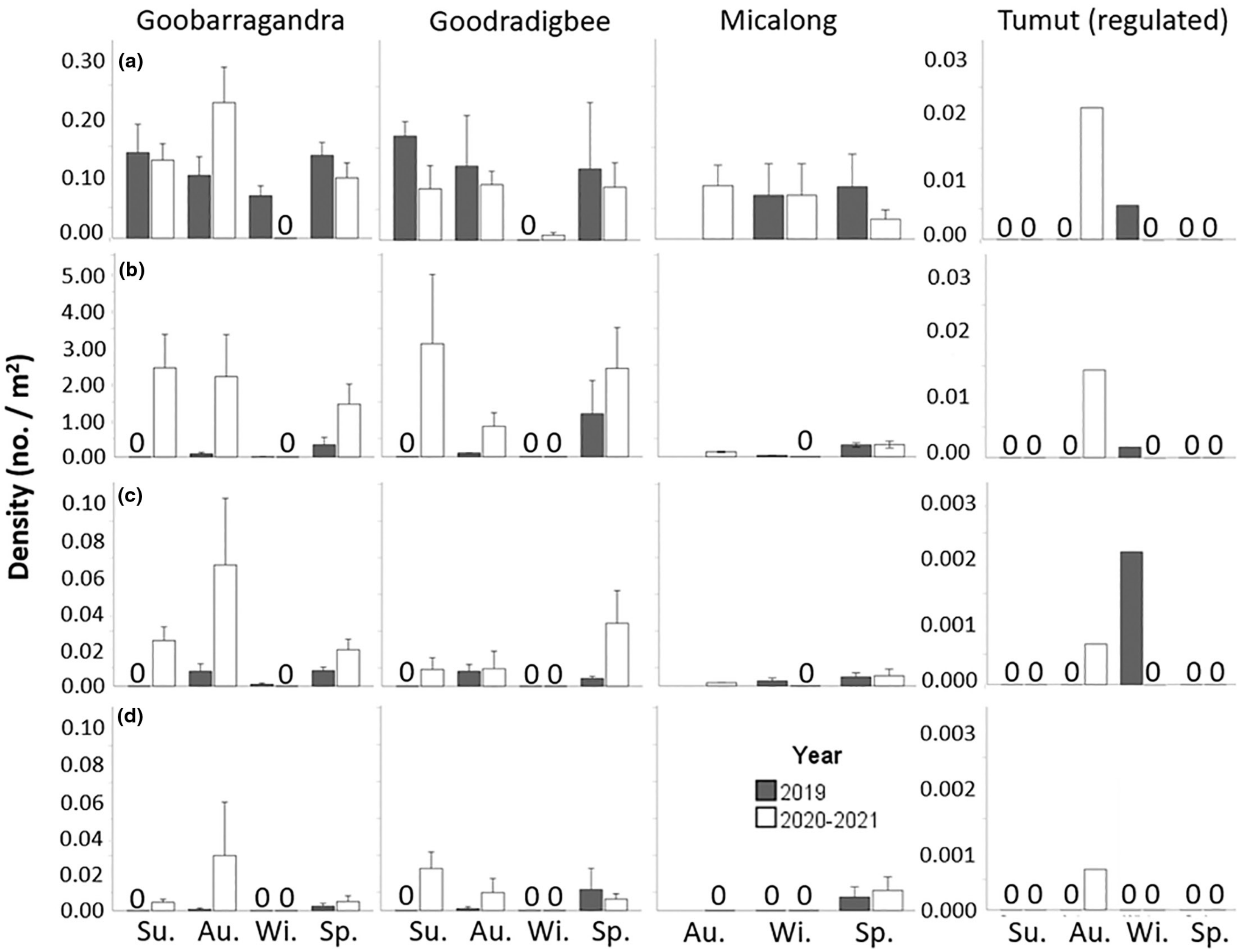


FIGURE 5 For three unregulated rivers and the regulated Tumut River, seasonal variations in densities (no/m^2) of (a) emergent rocks (ER), (b) U-type egg masses, (c) E-type egg masses and (d) A-type egg masses. Note differences in the *y*-axis scale between U-type and other egg mass morphotypes, and between Tumut River and other rivers. Season labels are abbreviated to Su. (summer), Au. (Autumn), Wi. (Winter) and Sp. (Spring). Error bars represent *SE*, and are not present for Tumut River because ER and egg masses were observed at only one site. Zeroes denote seasons when surveys were conducted but no egg masses were observed. Blank spaces denote seasons when no surveys were conducted. Murrumbidgee River is missing from this figure because no ER or egg masses were found at any time.

surveys between spring and early summer 2021 ($n = 30{,}360$ egg masses for U-type, $n = 312$ for E-type, $n = 143$ for A-type).

Linear regression showed marginally non-significant relationships between U-type egg masses and ER densities in the Goobarragandra during spring–early summer ($F_{1,21} = 3.164$, $p = 0.09$), and the Goodradigbee during autumn ($F_{1,10} = 4.522$, $p = 0.062$). During autumn, there were significant relationships between egg mass and ER densities for E- and A-type in the Goobarragandra (Figure 6). However, these relationships were due to the result of strong leverages of single data points with particularly high densities of ER and egg masses. Without these data points, there were no significant relationships between densities of ER and egg masses for E-type ($F_{1,9} = 1.243$, $p = 0.297$) and A-type ($F_{1,9} = 0.416$, $p = 0.537$), and thus H_3 was not convincingly supported. Rather, densities of egg masses were highly variable throughout a wide range of densities of ER (Figure 6).

3.3 | Hypothesis 4: Do numbers of terrestrial adults differ between regulated and unregulated rivers across seasons?

Hydrobiosid adults were trapped at all sites and six species were identified: *Apsilochorema gisbum*, *Ethochorema brunneum*, *Taschorema evansi*, *Ulmerochorema lentum*, *Ulmerochorema membrum* and *Ulmerochorema onychion* (Neboiss). Thus, captured adults matched the identified species for egg masses. There were insufficient numbers of *U. lentum* and *A. gisbum* adults for statistical analysis. *U. membrum*, the most abundant species in all rivers, was trapped at all sites and both seasons (Figure 7). For this species, numbers of adults did not differ between regulated and unregulated rivers but differed significantly between individual rivers within these categories (Table 3). Numbers were highest in the Murrumbidgee River for both seasons. During spring, numbers of adults also significantly differed between rivers for *E. brunneum*, *T. evansi* and *U. onychion* (Table 3) with the regulated Tumut River having consistently highest numbers (Figure 7). Overall, adults were trapped at locations and times when zero egg masses were recorded, including sites in the regulated rivers during spring and summer and unregulated rivers during summer 2019.

TABLE 2 Summary of *p*-values for post hoc, pairwise comparisons (Tukey's HSD) for the unregulated Goobarragandra and Goodradigbee rivers, across all seasons (See Supporting information, Table S1, Model 1 for terms).

	p	*p*
Seasons	**Emergent rocks**	**U-type**
Summer		
Autumn	0.961	0.417
Winter	**0.005**	**0.017**
Spring	0.880	0.809
Autumn		
Winter	**0.001**	0.399
Spring	0.575	0.868
Winter		
Spring	**0.018**	0.083

Note: Dependent variables are densities of emergent rocks (ER/m^2) and *U*-type egg masses (egg masses/m^2). Significant tests at $\alpha < 0.05$ shown in bold.

4 | DISCUSSION

We conducted surveys of ER, egg masses and adults over 2 years in replicate unregulated and regulated rivers to test whether flow regulation reduces densities of ER in specific seasons and whether this has consequences for oviposition phenology relative to that seen in unregulated rivers. Our study species often failed to oviposit in regulated rivers because flow regulation either drowned or stranded ER. In the unregulated rivers, oviposition occurred year round but densities of egg masses were highly variable for a given density of ER, and supply limitation may have been the cause. However, unexpected oviposition failure occurred during late summer 2019 in unregulated rivers despite abundant ER and the presence of adults. We observed significant accrual of algae on ER at this time, which may have inhibited oviposition thereby causing habitat-limitation of oviposition.

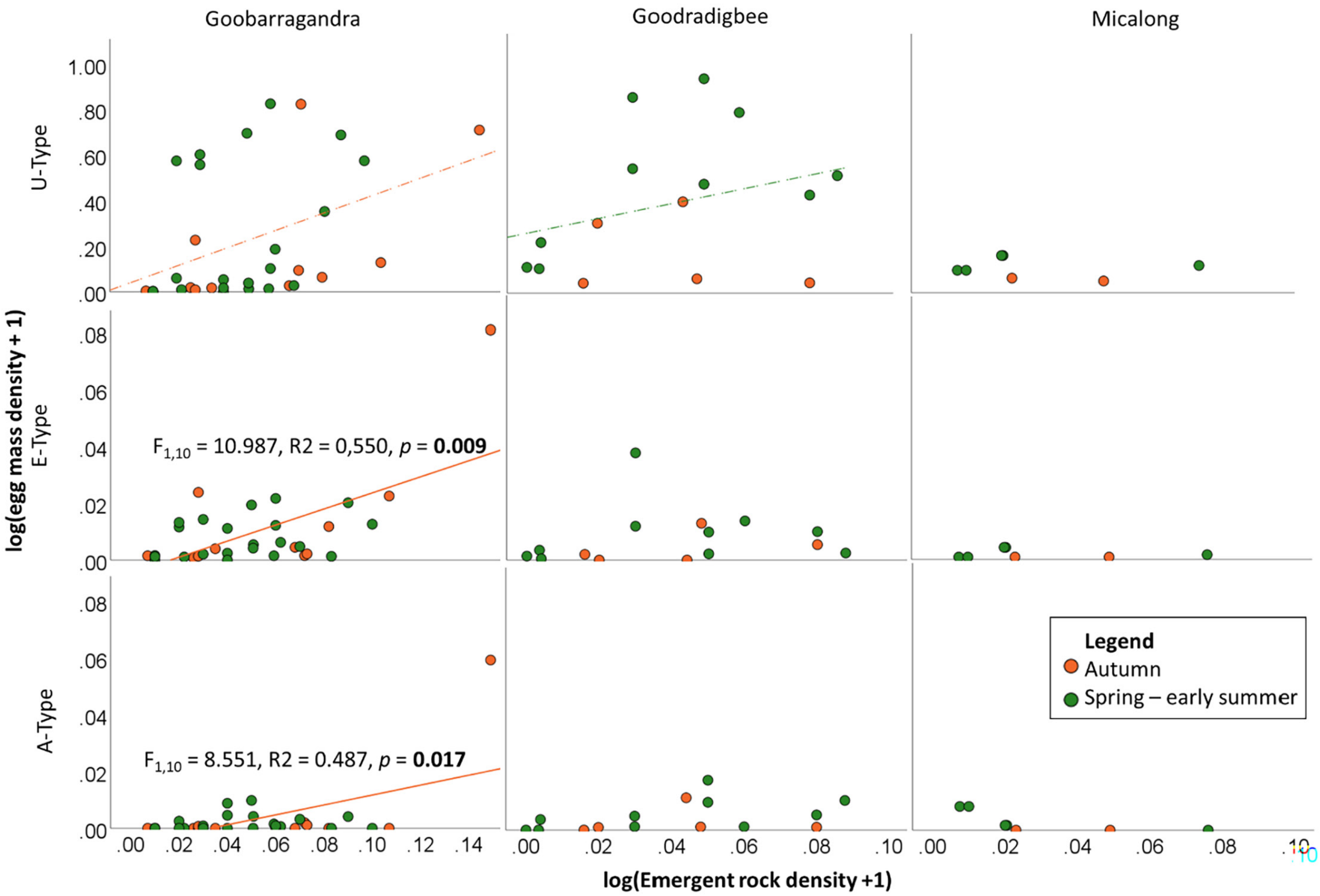


FIGURE 6 Densities of hydrobiosid egg masses (egg masses/m^2) in relation to densities of emergent rocks (ER/m^2) across main oviposition periods (autumn and spring–early summer) within three unregulated rivers. Solid and dotted lines represent significant and marginally non-significant relationships, respectively. Note order of magnitude difference in *y*-axis scale between U-type and other egg mass morphotypes.

To our knowledge, this is the first study showing how high river flows released from dams can restrict oviposition habitat for aquatic insects in some seasons. In the regulated rivers (Tumut and Murrumbidgee), unseasonal high flows submerged all ER during summer, but densities of ER were also unexpectedly low or zero at other times. Only a few ER were observed in one regulated river (Tumut) at a single site, during winter 2019 and autumn 2021, because flow releases from Blowering dam had stranded all large rocks (potential ER) above the waterline at all other sites. No ER were found in the Murrumbidgee River on any date, because flows during autumn and winter were very low and all potential ER were stranded above the waterline.

In contrast, in the unregulated rivers ER were typically available all year and average densities were comparable to previously studied rivers in Victoria (average of 0.10–0.35 ER/m^2; Lancaster et al., 2020). Nevertheless, while numbers of ER were low in the unregulated rivers during winter, they were unexpectedly high in spring despite high discharge levels. This reiterates the conclusions of Lancaster et al. (2021), who showed how difficult it can be to predict densities of ER at low discharges without detailed surveys of rock size and distribution across river beds.

Flow releases in the regulated rivers altered ER availability and had drastic effects on oviposition. In contrast to unregulated rivers, no egg masses of any morphotype were detected during the warmer

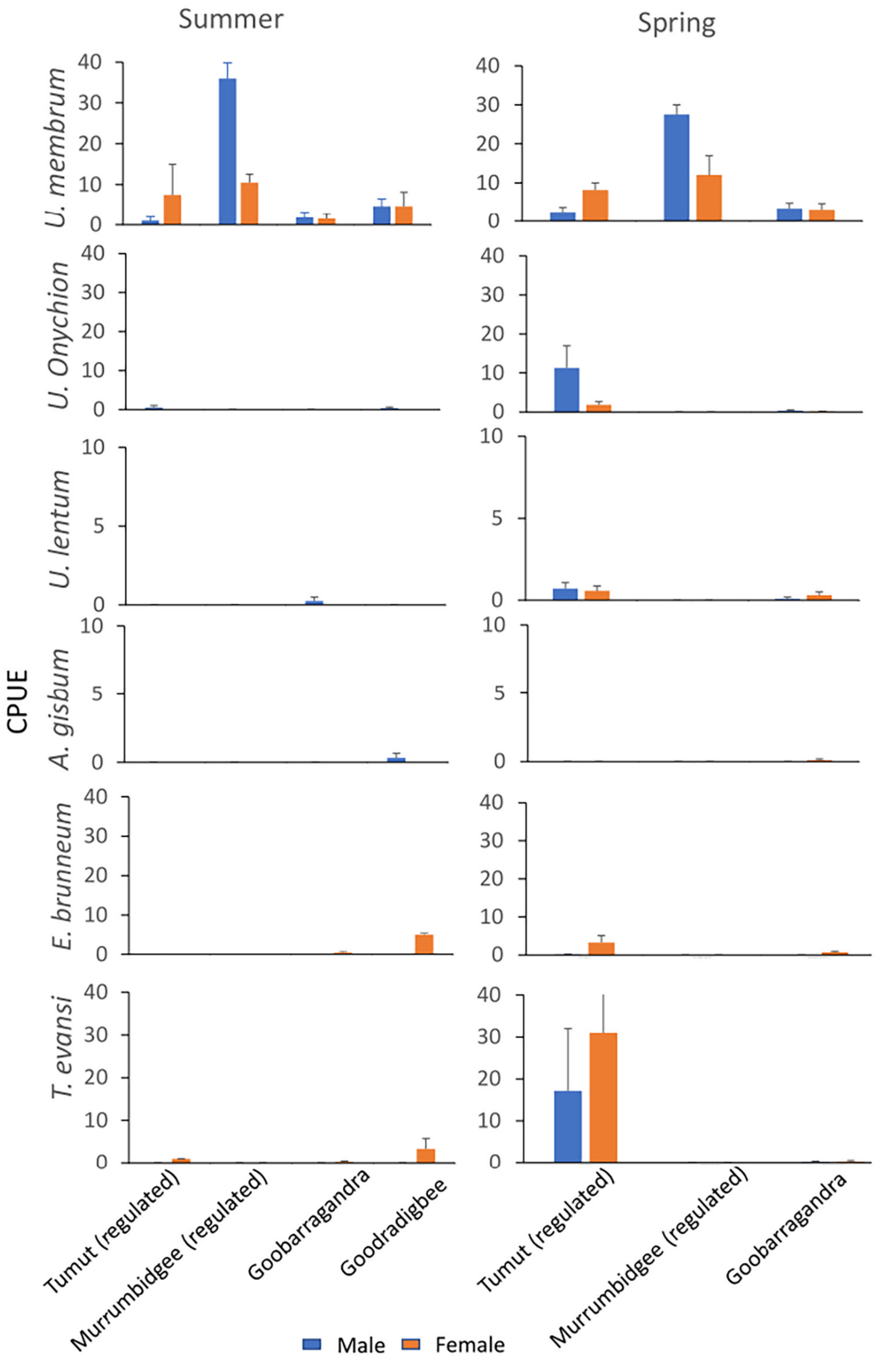


FIGURE 7 Mean numbers of captured hydrobiosid adults (male and female) in summer and spring in 2019. Figure describes catch per unit effort of light trapping (CPUE = 2 nights) for six hydrobiosid species within four rivers. Error bars represent *SE* across sites. Spring data absent for the Goodradigbee.

TABLE 3 ANOVA result for numbers of captured terrestrial adults.

		Summer				Spring			
Species	**Factor**	**df**	**MS**	**F**	***p***	**df**	**MS**	**F**	***p***
U. membrum	Regulation	2	2207.387	2.157	0.317				
	River(Reg.)	2	1023.387	13.408	**0.002**	3	1441.762	13.758	**<0.001**
	Error	9	76.324			16	104.795		
U. onychion	Regulation	2	0.262	1.000	0.500				
	River(Reg.)	2	0.262	2.020	0.188	3	403.581	3.726	**0.033**
	Error	9	0.130			16	108.329		
E. brunneum	Regulation	2	25.929	1.494	0.401				
	River(Reg.)	2	17.357	1.929	0.201	3	29.062	3.326	**0.046**
	Error	9	9.000			16	8.738		
T. evansi	Regulation	2	11.673	1.324	0.430				
	River(Reg.)	2	8.815	2.240	0.162	3	5408.881	6.685	**0.004**
	Error	9	3.935			16	809.085		

Note: Degrees of freedom (df), *F* values (*F*), mean square (MS) and *p*-values (*p*) Summer trapping was completed in the regulated Tumut and Murrumbidgee rivers, and their unregulated tributaries, Goobarragandra and Goodradigbee rivers. Springtime data are unavailable for the Goodradigbee River. Dependent variables are the numbers of hydrobiosid adults for four species that oviposit on emergent rocks (male and female). Significant tests at $\alpha < 0.05$ are shown in bold.

months of summer or late spring in either the Tumut or Murrumbidgee rivers. This pattern was not caused by a lack of adults (except perhaps for *Apsilochorema*). Relatively high numbers of adult *Ulmerochorema* spp. were present along both rivers during summer, and *T. evansi* and *E. brunneum* (both E-type) were present along the Tumut River during spring. The Tumut River gained some egg masses, but this occurred during one autumn and one winter survey, which are at times when oviposition was uncommon in the unregulated rivers. Moreover, oviposition occurred at only one site with ER and overall densities were very low compared to unregulated rivers. Egg masses were never found in the Murrumbidgee River on any date. Our results suggest that oviposition by *Ulmerochorema* spp., *T. evansi* and *E. brunneum* was likely to have been limited by shortages of suitable egg-laying habitat (i.e., habitat-limitation) in regulated rivers.

This oviposition failure is likely to have resulted in either zero (Murrumbidgee River) or low (Tumut River) larval recruitment of some hydrobiosid species downstream of dams. Prior surveys support this finding. Marchant and Hehir (2002) found that hydrobiosid larvae were present in the Tumut River downstream of Blowering Dam but absent from the Murrumbidgee River downstream of Burrinjuck Dam. Additionally, surveys in other regulated rivers in the Upper Murrumbidgee Catchment (e.g., the Cotter River) suggest that downstream larval drift is likely to be limited by dam barriers (Barlow et al., 2005). Interestingly, *Ulmerochorema* sp. (U-type) were less often affected by dams than *Ethochorema* sp. (E-type) (Marchant & Hehir, 2002). It is possible that this variation could reflect differences in the way these taxa lay eggs below dams. In Victoria, some caddisflies (*Ecnomus* spp.) lay eggs on wood when rocks are unavailable (Macqueen & Downes, 2015). Some hydrobiosid species may lay eggs on other hard substrates if emergent rocks are absent, but that requires further investigation.

In the unregulated rivers, constraints on egg mass densities were likely due to a mix of supply- and habitat-limitation depending on season. Egg masses were laid all year but with a noticeable drop in numbers for some taxa during winters. Densities of ER were also low during winters, but adults are commonly fewer during cold periods (Lancaster et al., 2021) so it is unclear whether habitat or supply limit numbers of egg masses during this season. In contrast, zero egg masses were recorded during summer 2019 and egg masses were relatively few during the subsequent autumn, despite abundant ER in both the Goobarragandra and Goodradigbee rivers. This unexpected result was unlikely to have been caused by supply-limitation because adults were present at these sites and times. For example, similar numbers of adult *U. membrum* were trapped in the Goobarragandra River during late summer 2019 (when no egg masses were found) and spring 2019 (when many egg masses were found). Instead, habitat limitation caused by layers of sediment and algae that blanketed ER during late summer 2019 is a more likely cause. Algae can inhibit oviposition in aquatic insects. For example, the damselfly *Calopteryx splendens* avoids laying eggs on encrusted substrate because algae interferes with hatching (Siva-Jothy et al., 1995). If algae inhibit oviposition by caddisflies, then seasonal growth of algae may alter the oviposition phenology for insects reliant on hard substrates, particularly in rivers where pressures from climate change and water abstraction are increasing the frequency and duration of low-flow periods (Gordon et al., 2004), but this hypothesis remains to be tested.

Evidence of habitat-limitation of oviposition in unregulated rivers during peak egg-laying periods was weak. Instead, egg mass densities were highly variable for any given density of ER. This outcome contrasts with past research showing that natural ER densities accounted for 27%–83% of variation in egg mass densities for various aquatic insects that use ER for oviposition (Encalada & Peckarsky, 2006; Lancaster & Downes, 2014, 2018). Consequently, it seems likely that egg mass densities were determined by the supply of gravid females rather than by the density of ER. Numbers of adults trapped along unregulated rivers during summer and spring were fewer than numbers seen along the Murrumbidgee River and Tumut River, respectively; this is consistent with (but not indicative of) supply limitation.

High numbers of adults were recorded along the regulated rivers in summer and spring, with the highest numbers of *Ulmerochorema* adults on the Murrumbidgee River and highest numbers of *T. evansi* on the Tumut River. We were surprised by the high abundances of adults along the regulated rivers because our results suggest that very little oviposition occurred in these systems over a 2-year period. This suggests that relatively few larvae may have been present in the channel to support the local emergence of relatively high numbers of adults. Hydrobiosids are multivoltine and may complete multiple generations within 1 year, so it is improbable that high numbers of adults resulted from larvae recruited during oviposition events before this study. Broadly, there are three potential explanations for the observed high numbers of adults at sites lacking places to lay eggs. Firstly, oviposition may have occurred at these sites during windows of opportunity not captured by our surveys. Although we cannot exclude this possibility entirely, we find it unlikely because very low amounts of oviposition habitat were observed in the regulated rivers at the high and low water levels surveyed, and no windows of opportunity at intermediate water levels are obvious from the hydrographs, which show rapid, step changes in mean, daily flows (Figure 4). Secondly, it is possible that larvae may have dispersed from reaches downstream and emerged at our sites on the regulated rivers. Because hydrobiosids are lotic and do not occur in lakes, it is unreasonable to expect dispersal of larvae from the dammed lakes upstream. The third and most likely explanation is that adults may have dispersed by flight to the regulated reaches from other sites in upstream, downstream or tributary reaches. Limited evidence suggests that caddisflies are able to disperse over distances of kilometres along and between channels (Baker et al., 2003), and other aquatic insects (mayflies, *Baetis* spp.) are known to disperse for kilometres upstream to lay eggs (Peckarsky et al., 2000). Successful dispersal by adults along channels may be a precursor to maintaining population numbers in managed systems, provided that sufficient oviposition habitat can be made available by adjusting the timing and sizes of flow releases (Baker et al., 2003; Peckarsky et al., 2000).

The results of our study illustrate that events that are critical to understanding population numbers occur during oviposition in both natural and altered systems. In our regulated rivers, the effects of river regulation on oviposition habitat presents a new hypothesis for why some species are absent from channels that are downstream of dams (Marchant & Hehir, 2002; Sánchez-Bayo & Wyckhuys, 2019). This hypothesis is yet to be explored. In the unregulated rivers, algal growth may have caused habitat-limitation during one summer. If it is a frequent event, it may restrict oviposition periods to cooler seasons when local supplies of females are typically lower relative to habitat. It is unclear if the algal proliferation we observed was natural or caused by human activities, but it also is a novel hypothesis for explaining variability in population numbers. Ultimately, these mechanisms may help explain the decline of some aquatic insects in systems affected by flow regulation (Sánchez-Bayo & Wyckhuys, 2019) and algae proliferation (Nichols et al., 2006). Certainly, they suggest intriguing models for future research in systems with natural and altered flows.

AUTHOR CONTRIBUTIONS

Conceptualisation: HW, WDB, AJB, BJD. *Developing methods*: HW, WDB, AJB, BJD. *Conducting research*: HW. *Data analysis*: HW, WDB, AJB, BJD. *Data interpretation*: HW, WDB, AJB, BJD. *Preparation of figures and tables*: HW, WDB, AJB, BJD. *Writing*: HW, WDB, AJB, BJD.

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DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding or financial holdings that might be perceived as affecting the objectivity of this review.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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