

A rolling stone gathers no eggs: the importance of stream insect egg laying natural history for stream restoration

SAMANTHA JORDT ¹ AND BRAD W. TAYLOR 

Manuscript received 26 October 2020; revised 11 December 2020; accepted 11 January 2021. Corresponding Editor: John Pastor.

Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695 USA.

¹E-mail: sjordt@ncsu.edu

Citation: Jordt S., and B. W. Taylor. 2021. A rolling stone gathers no eggs: the importance of stream insect egg laying natural history for stream restoration. *Ecology* 00(00):e03331. 10.1002/ecy.3331

Key words: natural channel design; oviposition; particle size; recruitment; substrate stability.

The degradation of waterways has led to the widespread practice of stream restoration aimed at accelerating recovery from damage by land-use change and other disturbances. However, the biological recovery of restored streams often lags behind their physical and chemical recovery (Louhi et al. 2011). Improving stream restoration is important for many reasons, including mitigating the impacts of development and because annually billions of dollars are invested in stream restoration worldwide. Slow biological recovery is not surprising given the emphasis on restoring physical stream features (e.g., riffle-pool sequence, meanders, bank stability) and the expectation that biological recovery will naturally follow (Palmer et al. 2014). Restoration typically improves physical habitats for fish and larval insects (Bernard et al. 2007); yet, habitats for adult aquatic insects are overlooked. Here, we report observations of egg laying in restored and reference streams that reveal how natural history science can be used to enhance stream restoration design, particularly for the recovery of stream insects.

Stream insects have complex life cycles that involve developing in an aquatic habitat, emerging to reproduce terrestrially, then returning to water to lay eggs. Females have various egg-laying strategies; some release their eggs while flying over the water surface, but an estimated

75% of aquatic insect species attach their eggs to objects within the stream such as rocks (Fig. 1A–F) or wood (Statzner and Bêche 2010). For example, mayflies from the widespread genus *Baetis* (Ephemeroptera) select rocks partially extending above the water's surface (hereafter emergent rocks, Fig. 1A–C) to land on, crawl underneath, and attach tombstone-shaped egg masses (Peckarsky et al. 2000). Caddisflies (Trichoptera) lay eggs in much the same way (Fig. 1D; Smith and Storey 2018). Adult waterpenny beetles (Coleoptera) use emergent rocks as both mating sites and access points for females to crawl underwater and lay their bright yellow eggs (Fig. 1E). Gelatinous egg masses of aquatic true flies such as midges (Diptera) are commonly found on emergent rocks (Fig. 1F) and are diverse in structure and attachment mechanisms (Reich 2004).

Egg-laying females can be highly selective (Smith and Storey 2018), often preferring emergent rocks that are large, unembedded, and in fast and constant flow. For many species, egg masses containing hundreds to thousands of eggs are highly aggregated, with a few emergent rocks receiving > 90% of egg masses (Peckarsky et al. 2000). This selective behavior increases egg survival, hatching success (Bovill et al. 2013), and larval recruitment (Encalada and Peckarsky 2012). Moreover, availability of rocks suitable for egg laying can limit stream insect populations (Alp et al. 2013) and determine stream insect community composition (Kennedy et al. 2016). Thus, egg laying on emergent rocks represents a linkage between stream physical characteristics and insect natural history that could have applications for stream conservation and restoration to either maintain or accelerate recovery of stream insect diversity and abundance.

During the summer of 2019, the abundance of rocks suitable for stream insect egg laying and the number of eggs masses they contained was observed throughout the egg-laying period (June to October) in 10 restored and three reference streams in western North Carolina (Appendix S1: Fig. S1). Streams were restored ≥ 7 yr ago, in agriculturally dominated watersheds containing cropland and cattle grazing, and watersheds had <5% impervious surface area (Appendix S1: Table S1). Restoration involved riverbed and bank reconstruction, riparian buffer planting, and cattle exclusion. Restored streams in North Carolina (Tullos et al. 2009) as elsewhere (Louhi et al. 2011) have slow biological recovery and low insect diversity and abundance. Reference streams of similar size with predominantly forested

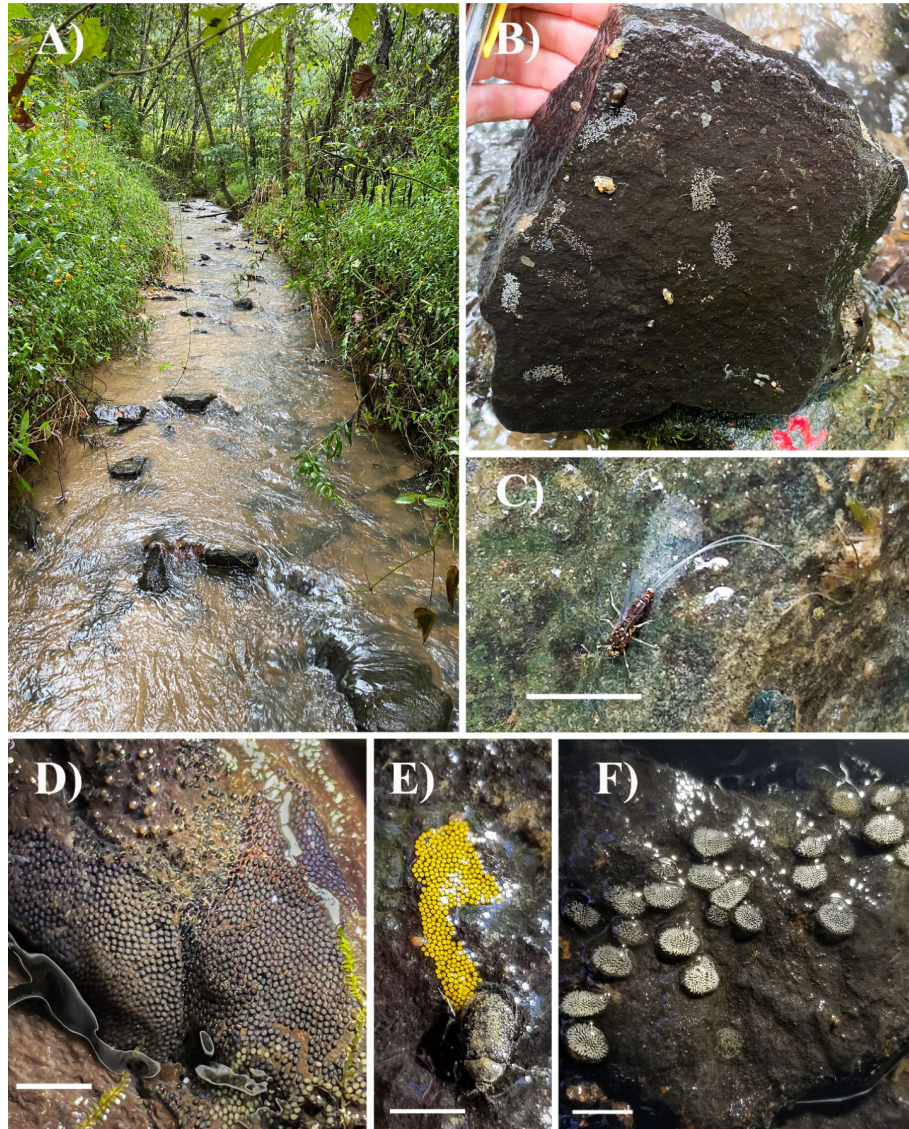


FIG. 1. (A) A restored stream in western North Carolina with examples of emergent rocks. (B) Underside of an emergent rock that female mayflies (Ephemeroptera) and caddisflies (Trichoptera) crawled underneath and attached egg masses. (C) Female mayfly (Ephemeroptera: Baetidae) and egg mass. (D) Egg masses of a caddisfly (Trichoptera: Hydropsychidae) taxon. (E) Female water penny beetle (Coleoptera: Psephenidae) and egg mass. (F) Egg masses of a midge (Diptera: Chironomidae) taxon. Scale bar in panels C–F is 0.5 cm.

watersheds were located nearby (Appendix S1: Fig. S1). Suitable egg-laying habitats were identified as emergent rocks with submerged spaces that adult insects could access along the sides and underneath (i.e., unembedded). Emergent rocks were numbered using a nontoxic paint pen and removed from the water to identify and count egg masses, species or morphotype, and sketch mass locations. New masses were identified by comparing sketches to those made previously. Rocks were replaced in their original location and position. We returned every 1–2 weeks to census these and newly

emergent rocks for egg masses. Mayfly, caddisfly, and true fly taxa constituted ~90 % of the masses in reference and restored streams, with mayflies (45%) dominant in restored streams and mayflies (39%) and caddisflies (36%) codominant in reference streams.

Densities of emergent rocks (number/m² streambed) were 103% greater in reference than restored streams, and as water levels declined emergent rocks increased in reference but not restored streams throughout the summer (repeated-measures ANOVA, time × stream type $F_{1,24,1} = 6.210$, $P = 0.02$; Fig. 2A; Appendix S1:

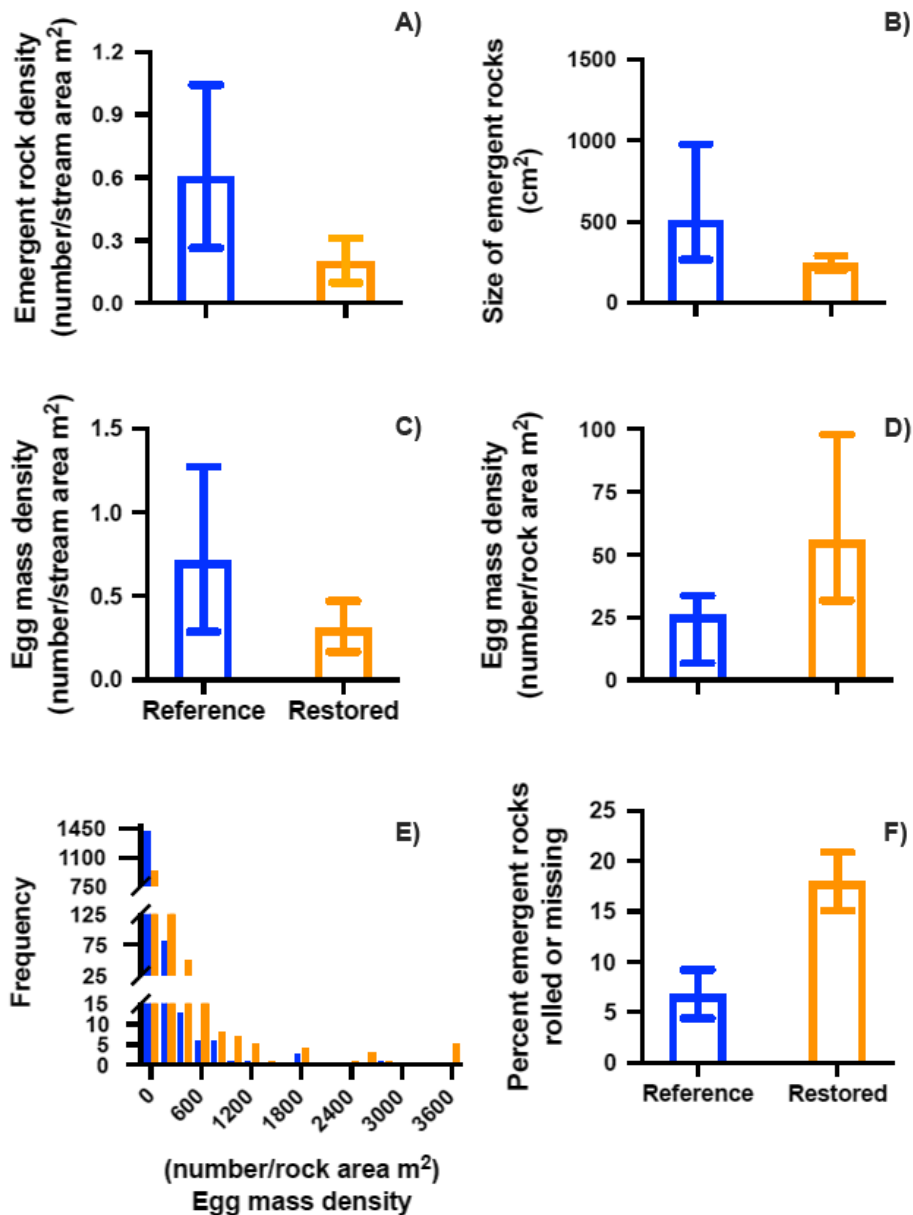


FIG. 2. Reference (blue bars) and restored (orange bars) streams differed in (A) number of emergent rocks, (B) size of emergent rocks, (C) number of egg masses standardized for wetted stream area, (D) number of egg masses standardized for individual rock area, (E) the distribution of egg mass densities among individual emergent rocks (for display purposes, the restored stream distribution is truncated with bin 3,600 including five rocks: three with 3,600, one with 3,900, and one with 7,200 egg masses per rock area), and (F) percentage of emergent rocks that rolled or were not recovered. Means in panels A–D and F are weighted by the number of weeks sampled for each site from 29 May to 13 October 2019. In panels A–D, means are back transformed and asymmetric error bars are 95% confidence intervals back transformed from the natural-log scale. In panels A, B, and D–F, emergent rocks include only those that were unembedded. The histogram bin width is 300.

Fig. S2). Emergent rocks were larger in reference than restored streams (repeated-measures ANOVA, stream type $F_{1,14,1} = 7.907$, $P = 0.01$; Fig. 2B). As a result of more egg-laying habitat, the number of egg masses standardized for streambed area was 78% higher in reference

than restored streams (repeated-measures ANOVA, stream type $F_{1,8,4} = 4.343$, $P = 0.04$; Fig. 2C). However, densities of egg masses on individual rocks (i.e., number masses per m² of individual rocks) were 72% higher in restored than reference streams (repeated-measures

ANOVA, stream type $F_{1,14.6} = 5.867$, $P = 0.04$; Fig. 2D). The distribution of egg masses among rocks was highly aggregated (observed distribution differed from expected Poisson (random) distribution, reference $P < 0.0001$ and restored $P < 0.0001$) and egg masses were more aggregated in restored than reference streams (Kolmogorov-Smirnov test, $D = 0.1597$, $P = 0.0001$), with reference streams containing many rocks with few masses and restored streams containing more rocks with many masses (Fig. 2E). These data suggest sufficient numbers of adults were able to disperse to restored streams but availability of suitable rocks could limit egg laying and thus limit insect recovery. Moreover, greater egg mass densities on emergent rocks in restored streams is notable because the percentage of emergent rocks that rolled or were unrecoverable (rolled out of the study reach or buried in sediment) was 91% higher in restored than in reference streams (generalized linear model, stream type $\chi^2 = 5.36$, $df = 12$, $P = 0.02$; Fig. 2F; Appendix S1: Fig. S2), and differences in emergent rock stability were greater during late summer (generalized linear model, time \times stream type $\chi^2 = 3.90$, $P = 0.04$), when egg laying was high in reference streams. Rolled or missing rocks increased following rainstorms in restored streams and, in one site, no submerged or emergent rocks remained after a storm. We could not determine egg survival on rocks that rolled or went missing because some rocks could not be recovered or were recovered more than 2 weeks later and their eggs could have hatched during this time. However, prior to rolling, 26% (16 of 62) of the rolled and recovered rocks had egg masses ($n = 140$ masses), indicating insects lay eggs on unstable substrates. Although survival of eggs on buried or rolled rocks is unknown, mortality due to desiccation can occur in less than 2 h for some mayflies and caddisflies (Miller et al. 2020) and we observed on multiple occasions that rolling resulted in exposure of the eggs above the water. In reference streams, emergent rocks remained intact, except during heavy rainstorms in early June. These results indicate that, in moderate-gradient, rocky-bottomed, restored streams, insect egg laying is limited by the number of emergent rocks. Further, because emergent rocks in restored streams are unstable, egg mortality may be higher due to emergent rocks rolling or being buried in sediment. Thus, even if adult females can disperse to restored streams and all other habitat conditions are suitable, larval insect populations may fail to establish because adult females lack stable egg-laying habitat.

In small rocky-bottomed streams the characteristics of suitable egg-laying habitat (i.e., large, stable, emergent, unlikely to dry rocks in fast-flowing water) for many stream insects are known and could be readily incorporated into restoration projects to increase stream insect recruitment (Storey et al. 2017). However, to maximize cost-effectiveness and achieve biological recovery,

restoration should consider the site- and taxon-specific natural history and multivariate nature of egg-laying habitat selection. Moreover, restoration projects could be used to test the degree to which insects in restored streams are limited by egg-laying habitat or other factors. For instance, adult dispersal from adjacent reference streams in degraded and disconnected landscapes, or post-recruitment processes such as larval food resources and mortality, factors that may negate the positive effects of restored egg-laying habitat.

One of the most vexing problems in stream restoration is that the return of biological conditions lags behind the return of physical habitat and water quality. Our observations suggest that, in addition to the number of suitable egg-laying sites, the stability of sites may limit insect recruitment and, hence, recovery of insect diversity and abundance in these and similar restored streams. Indeed, many of the taxa that use the underside of emergent rocks as egg-laying habitat are used as indicators of stream health (Ephemeroptera, Plecoptera, and Trichoptera). Thus, considering the natural history of stream insect egg laying during the hydrologic and geomorphologic engineering of restored streams is likely to improve stream restoration and accelerate biological recovery, as the importance of natural history has informed other types of restoration projects (Tewksbury et al. 2014).

ACKNOWLEDGMENTS

This research was supported by the North Carolina Department of Environmental Quality and Division of Mitigation Services. We thank Periann Russell, Barbara Doll, and Eric Fleek for advice selecting sites, Blake Dilworth for assistance with R, Mick Demi and Jared Balik for suggestions that improved early drafts, and the anonymous reviewers for their kind words and valuable insight.

LITERATURE CITED

- Alp, M., L. Indermaur, and C. T. Robinson. 2013. Environmental constraints on oviposition of aquatic invertebrates with contrasting life cycles in two human-modified streams. *Freshwater Biology* 58:1932–1945.
- Bernard, J. M., J. Fripp, and K. Robinson, editors. 2007. Stream restoration design. National Engineering Handbook Part 654 (210-VINEH). U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C.
- Bovill, W. D., B. J. Downes, and J. Lancaster. 2013. A test of the preference-performance hypothesis with stream insects: selective oviposition affects the hatching success of caddisfly eggs. *Freshwater Biology* 58:2287–2298.
- Encalada, A. C., and B. L. Peckarsky. 2012. Large-scale manipulation of mayfly recruitment affects population size. *Oecologia* 168:967–976.
- Kennedy, T. A., J. D. Muehlbauer, C. B. Yackulic, D. A. Lytle, S. W. Miller, K. L. Dibble, E. W. Kortenhoeven, A. N. Metcalfe, and C. V. Baxter. 2016. Flow management for hydro-power extirpates aquatic insects, undermining river food webs. *BioScience* 66:561–575.

- Louhi, P., H. Mykrä, R. Paavola, A. Huusko, T. Vehanen, A. Mäki-Petäys, and T. Muotka. 2011. Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications* 21:1950–1961.
- Miller, S. W., M. Schroer, J. R. Fleri, and T. A. Kennedy. 2020. Macroinvertebrate oviposition habitat selectivity and egg-mass desiccation tolerances: implications for population dynamics in large regulated rivers. *Freshwater Science* 39:584–599.
- Palmer, M. A., K. L. Hondula, and B. J. Koch. 2014. Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics* 45:247–269.
- Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia* 125:186–200.
- Reich, P. 2004. Patterns of composition and abundance in macroinvertebrate egg masses from temperate Australian streams. *Marine and Freshwater Research* 55:39–56.
- Smith, B. J., and R. G. Storey. 2018. Egg characteristics and oviposition behaviour of the aquatic insect orders Ephemeroptera, Plecoptera and Trichoptera in New Zealand: a review. *New Zealand Journal of Zoology* 45:287–325.
- Statzner, B., and L. A. Béche. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology* 55:80–119.
- Storey, R. G., D. R. Reid, and B. J. Smith. 2017. Oviposition site selectivity of some New Zealand aquatic macroinvertebrate taxa and implications for stream restoration. *New Zealand Journal of Marine and Freshwater Research* 51:165–181.
- Tewksbury, J. J., et al. 2014. Natural history's place in science and society. *BioScience* 64:300–310.
- Tullos, D. D., D. L. Penrose, G. D. Jennings, and W. G. Cope. 2009. Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration. *Journal of the North American Benthological Society* 28:80–92.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3331/supinfo>
