

RESEARCH ARTICLE

Water temperature drives variability in salmonfly abundance, emergence timing, and body size

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Abstract

Freshwater organisms are disproportionately impacted by climate change and human disturbance, resulting in shifts in species' distributions and life histories. We coupled contemporary and historical datasets documenting physical and ecological variables over four decades to quantify changes in the abundance, emergence timing, and body size of salmonflies (*Pteronarcys californica*) in the Madison River in southwest Montana. In contemporary surveys, water temperature was the main driver of salmonfly abundance, emergence timing, and body size. Salmonfly densities were negatively correlated with summer water temperature, which explained 60% of variation in larval density among sites, whereas substrate type played a negligible role. Emergence occurred 20 days earlier, and male and female exuvia length were 13.8% and 11.3% shorter, respectively, at the warmest site relative to the coolest site (4°C difference). These patterns were supported by historical data. For example, a 1.2°C increase in mean annual water temperature in the Madison River between 1977 and 2017 coincided with evidence for upstream range contraction. Between 1973 and 2017, emergence timing varied widely among years, occurring up to 41 days earlier in years when spring water temperatures were relatively warm. As climate change progresses, we predict that salmonflies could be extirpated from an additional 28 km of currently occupied habitat, representing a 22.6% reduction in suitable habitat along the Madison River. This study provides evidence of long-term biological change of an aquatic insect and highlights the importance of combining spatial and historical datasets to better understand species' responses to environmental stressors across both space and time.

KEYWORDS

aquatic insect, distribution, long-term, macroinvertebrate, phenology, *Pteronarcys*

1 | INTRODUCTION

Climate change has been linked to observed and predicted changes in species' distribution, phenology, and growth (Parmesan & Yohe, 2003; Sheridan & Bickford, 2011). In aquatic ecosystems, water temperature is a major driver of ecological processes and one of the primary factors influencing aquatic organisms' distributions and life histories (Vannote & Sweeney, 1980). In particular, as water temperatures rise, aquatic

insects are expected to develop faster, transitioning into their adult stage earlier in the year and thus maturing at a smaller adult body size (Dallas & Ross-Gillespie, 2015). Changes to these biological characteristics have important implications at both population and ecosystem levels of organization. Reduced aquatic insect body size can affect multiple aspects of life history, including fecundity and dispersal ability (McCauley & Mabry, 2011; Sweeney, Funk, Camp, Buchwalter, & Jackson, 2018), whereas changes in their phenology can influence

the strength and outcome of predator–prey interactions (Miller-Rushing, Høye, Inouye, & Post, 2010).

The distribution of freshwater macroinvertebrates is also highly temperature dependent as influenced by physiological processes (Dallas & Ross-Gillespie, 2015), niche partitioning (Ward & Stanford, 1982), and biotic processes such as food availability (Sweeney & Vannote, 1986). As climate change progresses, many cold-water obligate species of aquatic insects are experiencing upstream and poleward range shifts or contractions (Giersch et al., 2014; Hassall & Thompson, 2010; Sheldon, 2012). These changes often exceed responses of their terrestrial counterparts (Ricciardi & Rasmussen, 1999; Sala et al., 2000) as most are constrained within river networks, which limits their ability to track suitable habitat.

Negative responses to warming water temperatures can be further amplified when other anthropogenic stressors, such as excessive fine sediment deposition, are present (Piggott, Lange, Townsend, & Matthaei, 2012). Human activities such as agriculture, grazing, forestry, and urbanization can artificially increase fine sediment deposition in rivers and streams (Waters, 1995). Many benthic macroinvertebrates are impaired by increased levels of sedimentation, with negative responses that include habitat loss due to filled interstitial spaces, feeding inhibition, and increased drift among others (Jones et al., 2012).

We examined how changing temperature and substrate conditions influenced the abundance, emergence timing, and body size of a large-bodied aquatic insect, the river stonefly (*Pteronarcys californica*, also known as the salmonfly), in the Madison River in southwest Montana. Salmonflies are iconic insects in the rivers of western North America due to their large size (often exceeding 6 cm in length as adults) and popularity among anglers. Salmonflies spend between 2 and 5 years in their aquatic larval stage depending on the thermal regime of the river they inhabit (DeWalt & Stewart, 1995; Freilich, 1991; Townsend & Pritchard, 1998). In early summer, they emerge in massive, synchronized hatches that draw anglers from around the world and provide a significant nutrient pulse to both aquatic and terrestrial consumers including birds, fish, spiders, and ants (Rockwell & Newell, 2009). Mounting anecdotal evidence suggests that salmonfly populations could be declining throughout the American West (Nehring, Heinhold, & Pomeranz, 2011), including in the Madison River (Stagliano, 2010). Increasing water temperatures and fine sediment additions are a major threat to this charismatic species, as salmonflies have a narrow thermal tolerance and are sensitive to fine sediment deposition that smothers high-quality riffle habitat by filling the interstices between cobbles and gravels (Bryce, Lomnický, & Kaufmann, 2010; Relyea, Minshall, & Danehy, 2012).

We documented physical and ecological parameters to determine how variable water temperature and substrate conditions influence salmonfly abundance, emergence phenology, and body size. We hypothesized that higher water temperatures and proportions of fine bed sediments would lead to lower larval density and that warmer water temperatures would result in earlier emergence timing and smaller body size. Specifically, we predicted that larval density would be lowest at sites with relatively warm water temperatures and/or

relatively high proportions of fine bed sediments. We predicted that salmonfly emergence would occur earlier and body size would be reduced at sites where water temperature was relatively warm. When possible, we paired contemporary surveys with historical datasets to better understand how these responses to variable environmental conditions may vary across space and time. We predicted that as water temperatures increased over time, larval density would decline and emergence timing would advance. Finally, we provided further context for how changes in salmonfly populations in the Madison River may continue throughout the 21st century by using predictive models of water temperature change.

2 | METHODS

2.1 | Study site

This study was conducted on the mainstem of the Madison River in southwest Montana. The Madison River originates in north-western Yellowstone National Park and then flows approximately 210 km northward through broad valleys to join the Jefferson and Gallatin Rivers and form the Missouri River near Three Forks, Montana. The Madison River passes through Hebgen Reservoir and Ennis Reservoir at 177 and 59 km above its mouth. The dams forming Hebgen and Ennis Reservoirs were constructed in 1914 and 1906, respectively. Ennis Reservoir is formed by a small hydroelectric dam that operates under a run-of-the-river configuration with surface water release. Ennis Reservoir is relatively shallow and warms during the summer, which leads to elevated summer water temperatures in the Madison River downstream of the dam (Fraley, 1978). Above Hebgen Reservoir, water temperatures are influenced by geothermal activity in Yellowstone National Park and are therefore much warmer than expected for the location along a typical Rocky Mountain stream continuum. We characterized physical and biological stream parameters at 10 representative 100-m reaches distributed along the length of the river, with two sites upstream of Hebgen Reservoir, six between the two reservoirs, and two downstream of Ennis Reservoir (Figure 1). Historical data were collected at a subset of these sites (Table S1).

2.2 | Environmental conditions

Water temperature was recorded at 30-min intervals from April 1 to September 30, 2017, at all 10 sites using a HOBO pendant temperature logger (Onset Computer, Bourne, Massachusetts) secured to a boulder midchannel and shaded with a UV-safe PVC tube. Particle size and level of embeddedness were determined at 10 sites with a Wolman pebble count (Wolman, 1954) in August 2017 during baseflow when the river was accessible via wading. Percent fine sediment was calculated as the proportion of 200 observations that were recorded as fine sediment (<2 mm). At each site, percent embeddedness was classified as the proportion of particles within the 200 observations where embedded particle height/total particle height > 0 (Sylte & Fischenich, 2002). Water temperature (1977 to

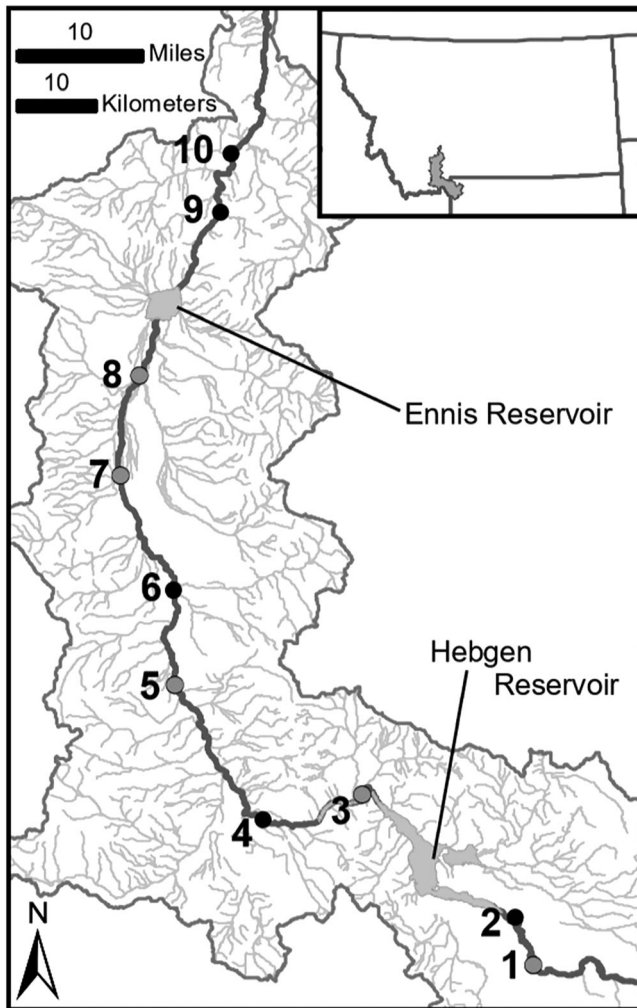


FIGURE 1 Study sites along the Madison River, which flows northwards, in southwest Montana. Site numbers increase in the downstream direction. Water temperature, substrate characterization, and salmonfly larval abundance were quantified at all 10 sites in 2017. Salmonfly exuvia length and emergence timing were quantified at Sites 1, 3, 5, 7, and 8 as denoted by grey dots

2017) and discharge (1939 to 2017) measurements were recorded at 15-min interval by the United States Geological Survey (USGS) at gage #06041000, located in the Madison River approximately three miles below Ennis Reservoir. These data were utilized for analyses through December 31, 2017. Linear regression was used to assess long-term temporal trends in water temperature and discharge.

2.3 | Larval abundance

Benthic macroinvertebrates were collected in riffles at all 10 sites in August 2017 using a 0.75×0.75 m surber sampler. Four individual samples were taken per site and then preserved in 70% ethanol, transported to the laboratory, and stored at 4°C.

We used multiple linear regression to evaluate temperature and substrate factors that could explain variation in salmonfly larval densities among all sites. We limited this analysis to temperature and

substrate variables because increased temperature stress and fine sediment inputs are the two hypothesized mechanisms for the probable decline of salmonflies in the Madison River below Ennis Reservoir (Stagliano, 2010). The full model used the following five explanatory variables that have been shown to represent physically stressful conditions for salmonflies as related to substrate and water temperature: mean summer (June–August) water temperature (Fralely, 1978); maximum weekly maximum temperature, which is the highest 7-day moving average of maximum daily water temperatures (Huff, Hubler, Pan, & Drake, 2006); percent fine sediment (<1 mm; Bryce et al., 2010); percent of particles embedded (McClelland & Brusven, 1980); and mean particle size (Brusven & Prather, 1974). Larval density was log transformed to meet the assumption of normality. A variant of Akaike's Information Criterion corrected (AICc) for small datasets was employed to evaluate all possible combinations of water temperature and substrate metrics explaining variation in salmonfly larval densities between sites in 2017 (Hurvich & Tsai, 1989). The most parsimonious model was selected using the difference (Δ AICc) between their AICc values and minimum AICc, and by their Akaike weight (w_i), which is the probability that any given model is the best in the set of models considered (Burnham & Anderson, 2002). The MuMIn package was utilized for AICc model selection (Barton, 2011). All statistical analyses were performed in R version 3.3.1 (R Core Team, 2013).

Larval densities of salmonflies from our 2017 sampling efforts were compared with historical larval density estimates from 1977. Two 0.25-m^2 benthic samples were collected at Sites 7–10 in August 1977 (Fralely, 1978). In these samples, salmonfly larvae were enumerated in each sample and densities were converted to total larvae per square metre. Differences in salmonfly abundance at Sites 7–10 between 1977 and 2017 were compared using a two-way analysis of variance, with site and year as fixed factors. Larval density was log transformed to meet the assumption of normality. Pairwise comparisons for each site and year were tested using Tukey's Honestly Significant Difference (HSD) test.

2.4 | Emergence timing

During emergence events, salmonfly larvae crawl out of the river and leave their exuvia clinging to features within a short distance (typically 0–2 m) from the water's edge. These large abandoned exuvia are conspicuous along the shoreline, and therefore systematic counts of exuvia are a useful method to quantify salmonfly emergence timing and abundance (Nehring et al., 2011; Walters, Wesner, Zuellig, Kowalski, & Kondratieff, 2018). We recorded first emergence date at five sites (1, 3, 5, 7, and 8) along the Madison River in the summer of 2017 to determine a relationship between water temperature and salmonfly emergence timing. These sites were chosen because they spanned large differences in water temperature (4°C difference among sites) and because salmonflies were abundant (>12 larvae per metre). We chose to represent emergence timing as the first observed exuvia to duplicate methodology used in historical datasets.

At each site, we established a 100-m sample reach along a stream bank adjacent to riffles (typical salmonfly larval habitat). We visually inspected each sample reach at least 5× per week until salmonfly emergence occurred to determine the first emergence date at each site. We defined first emergence date as the first day that salmonfly exuvia were found at any given site. The relationship between first emergence date and mean May water temperature in 2017 was investigated with linear regression. Mean May water temperature was used as the predictor in this model because salmonfly emergence timing is highly correlated with mean water temperature in the month prior to emergence (Gregory, Beesley, & Van Kirk, 2000).

First emergence date was also recorded each year by a citizen scientist at Sites 7 and 10 from 1973 through 2017 (P. E. Farnes, personal communication, January 2017). In this historical dataset, first emergence date was similarly defined as the first date when salmonfly exuvia were found along river banks at each site. Each site was visited at least 2× per week prior to first emergence date. Although this long-term dataset detailing emergence timing was collected by a citizen scientist, any errors associated with emergence dates are likely minor because salmonfly emergence events are brief, generally lasting <1 week at any one location (Sheldon, 1999).

An analysis of covariance (ANCOVA) was used to determine long-term trends in emergence timing at Sites 7 and 10 in the Madison River, with site and year as explanatory variables. The relationship between historical first emergence date and mean May water temperature was investigated with linear regression. Site 7 was excluded from this analysis because there are no long-term water temperature data available above Ennis Reservoir, where this site was located. Historical first emergence dates from Site 10 were paired with historical water temperature data from the same year as recorded by the USGS gage located approximately six miles upstream of the site.

2.5 | Body size

Salmonfly exuvia length was quantified at Sites 1, 3, 5, 7, and 8 in the summer of 2017 to determine a relationship between water temperature and salmonfly body size. Adult female salmonflies can be over 2× larger than males (Walters et al., 2018), so we measured 30 randomly selected salmonfly exuvia of each sex at each site. Total exuvia length, excluding cerci, was measured with digital callipers to the nearest 1/10th of a millimetre.

The relationship between water temperature, sex, and exuvia length among sites was evaluated with an ANCOVA. Mean water temperature from the entire time we had data loggers deployed (April–September) was used in this analysis because salmonflies develop for multiple years before emerging (Townsend & Pritchard, 1998), and their growth rates are therefore influenced by thermal regimes throughout the year. We were unable to deploy temperature loggers throughout the winter months. However, salmonflies have a developmental zero of 3.125°C (Townsend & Pritchard, 2000), so growth in winter months is likely minimal.

2.6 | Future conditions

We evaluated the potential impact of future water warming on salmonfly range by using ArcGIS 10.5.1 to calculate predicted numerical changes in the proportion of thermally suitable habitat for salmonflies in the Madison River. A threshold water temperature (19°C mean August water temperature) above which salmonflies are unable to persist was estimated and used as a proxy for nonsuitable habitat based upon evidence from our survey of salmonfly distributions in the Madison River and from previous estimates of maximum temperatures tolerable for salmonflies throughout the American West (Huff et al., 2006). Future range contraction was estimated based on two potential warming scenarios modelled by NorWeST for the Missouri Headwaters watershed (HUC 100200) for projected changes in August air temperature and stream discharge according to the A1B warming trajectory in the 2080s (Isaak et al., 2017). One NorWeST scenario assumes equal warming in all stream segments, and the other accounts for differential sensitivity to climate change among stream segments. Covariates for the NorWeST model were mean August air temperature, mean August discharge, elevation, slope, percentage of watershed composed of lake or reservoir surfaces, annual precipitation, base-flow index, drainage area, and riparian canopy cover.

3 | RESULTS

3.1 | Environmental conditions

In 2017, sites along the Madison River spanned large differences in water temperature (4°C difference in mean water temperature among sites) and substrate type (0–33% fine sediment; Table S2). Linear regression suggests that water temperatures have warmed in the Madison River since USGS monitoring began in 1977, with mean annual temperature increasing 1.18°C (0.29°C/decade). However, warming was not consistent across seasons. For example, mean August water temperature increased 1°C (0.25°C/decade) in the last 40 years, whereas May water temperature remained consistent (increase of 0.01°C/decade). Flow regimes in the Madison River did not change noticeably since USGS gage records began in 1939; temporal trends for both mean annual discharge (lm: $F_{1, 71} < 0.0001$, $p = .99$) and peak annual discharge (lm: $F_{1, 76} = 0.009$, $p = .92$) were nonsignificant.

3.2 | Larval abundance

Salmonfly larval density varied greatly among sites (0–117 larvae per square metre; Table S2). AICc model selection analysis indicated that mean summer water temperature was the primary constraint on salmonfly population size in the Madison River, explaining 60.0% of variation in salmonfly larval density among sites as the sole variable in the top model (Table 1). In general, salmonfly density was lower at sites with higher summer temperatures (Figure 2). Substrate variables did not improve model fit substantially (Table 1), suggesting that

TABLE 1 Model predictions of salmonfly (*Pteronarcys californica*) larval density using variables related to temperature and substrate quality where $\Delta\text{AICc} < 6$

Model variable	R^2	AICc	ΔAICc	AIC wt.
Mean summer temperature	.60	39.1	0.00	0.65
MWMT	.43	42.5	3.40	0.12
Null model	.00	43.9	4.76	0.06
Mean summer temperature + % Particles embedded	.64	44.0	4.82	0.06
Mean summer temperature + Mean particle size	.62	44.3	5.21	0.05
Mean summer temperature + % Fine sediment	.60	45.0	5.85	0.04
Mean summer temperature + MWMT	.59	45.1	5.96	0.03

Abbreviations: AICc, Akaike's Information Criterion corrected; MWMT, maximum weekly maximum temperature.

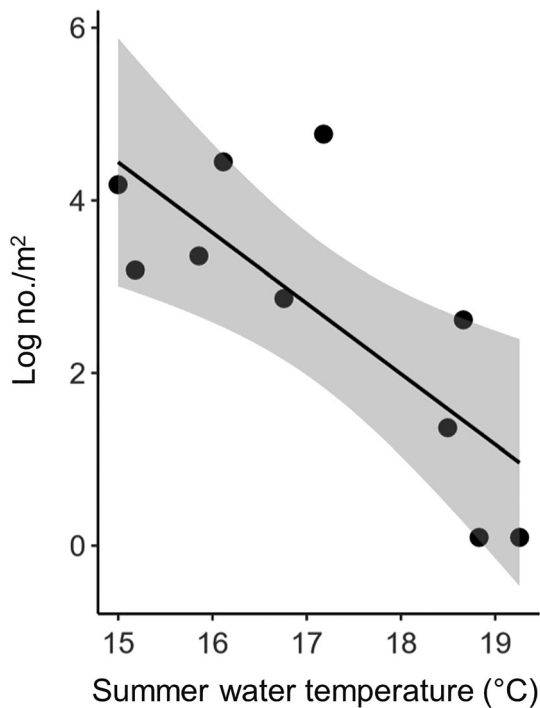


FIGURE 2 In general, salmonfly larval density was lower at sites with higher mean summer (June–August) water temperature. Black dots represent summer water temperature and log salmonfly larval density for each site in 2017

sediment plays a negligible role in regulating salmonfly abundance along the length of the Madison River.

Our results indicated that salmonfly larval densities may have decreased at the most downstream portion of their distribution in the Madison River between 1977 and 2017. Salmonfly larvae were detected at all four sites in August of 1977 but were absent at all sites below Ennis Reservoir (Sites 9 and 10) in 2017. At Site 10, the most

downstream site, salmonfly larval density decreased by 38 larvae per square metre (95% CI [-311.39, -4.55]) from 1977 to 2017 (Tukey's HSD: 0.0004). There was no evidence of a decline in larval density at the three sites farther upstream (Tukey's HSD: Site 7, 0.99; Site 8, 0.73; and Site 9, 0.094).

3.3 | Emergence timing

First emergence date was strongly correlated with mean water temperature in May, the month before emergence, with salmonfly emergence occurring earlier where May water temperatures were warmer (lm: $R^2 = .78$, $F_{1,3} = 15.6$, $p = .029$; Figure 3a). In 2017, first emergence date occurred 20 days earlier at the warmest site (Site 1) relative to the coolest site (Site 3).

Contrary to our prediction, salmonfly emergence timing showed no evidence of advancement between 1973 and 2017 at either site (ANCOVA: $F_{1,72} = 0.13$, $p = .72$; Figure 3b). However, first emergence date was correlated with mean water temperatures in May of the same year (lm: $R^2 = .75$, $F_{1,18} = 57.17$, $p < .001$; Figure 3c), with emergence occurring earlier in years when May water temperatures were relatively warm. Notably, no adult salmonflies were observed—and thus emergence date was not recorded—at Site 10 downstream of Ennis Reservoir for 13 of the last 20 years.

3.4 | Body size

Exuvia length was negatively correlated with mean water temperature from our entire field season (April–September) at each site (lm: $R^2 = .72$, $F_{3,296} = 256.2$, $p < .001$), with no evidence of an interactive effect between sex and water temperature (ANCOVA: $F_{1,296} = 0.11$, $p = .74$). Mean male and female exuvia lengths were 13.8% and 11.3% shorter, respectively, at the warmest site compared with the coolest site (Figure 4).

3.5 | Future conditions

Regional projections of water temperatures in the Madison River based on the A1B climate scenario predicted that 27.9 km of currently occupied habitat on the mainstem of the Madison River will exceed suitable thermal conditions for salmonflies by 2100 if all stream segments warm uniformly, representing a 22.6% reduction in suitable habitat (Figure 5). If stream segments warm differentially, then 36.0 km is predicted to exceed suitable conditions by 2100, for a 29.2% reduction in suitable habitat. Salmonfly populations directly above Ennis Reservoir were the most at risk in both projection scenarios.

4 | DISCUSSION

We found that increasing water temperatures have already affected, and will likely continue to affect, salmonflies in both their larval and adult life stages. Both spatial surveys and historical records suggested

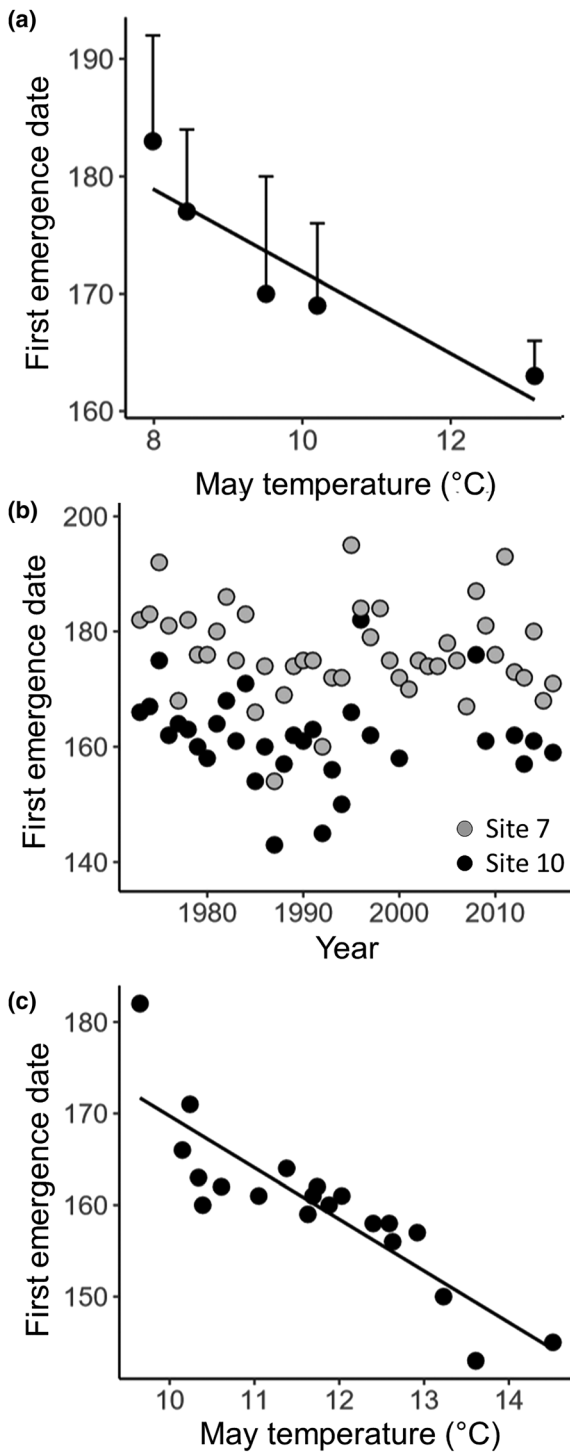


FIGURE 3 (a) Among sites in 2017, first salmonfly emergence date (day of year) was negatively correlated with mean May water temperature, the month prior to emergence. Each dot represents the first emergence date at one site. The vertical bars above each dot represent the entire duration (in days) of salmonfly emergence at each site. (b) From 1973 to 2017, first salmonfly emergence date varied up to 41 days at Site 7 and 39 days at Site 10 among years but did not advance over time. (c) First salmonfly emergence date at Site 10 and mean May water temperature of the corresponding year were strongly correlated. Each dot represents the first emergence date and mean May water temperature for a single year between 1973 and 2017

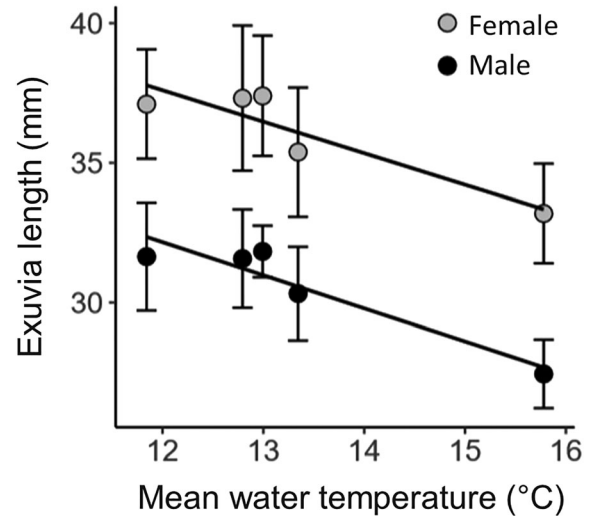


FIGURE 4 Salmonfly exuvia length (mm) was negatively correlated with mean April–September water temperature in 2017. Values are means \pm 1 SD

that water temperature can be a major driver of the variability of salmonfly distribution, emergence timing, and body size. Consistent with previous research (Everall, Johnson, Wilby, & Bennett, 2015), salmonfly emergence occurred earlier and body size was smaller in areas where water temperatures were relatively warm. Salmonfly populations in the Madison River were spatially constrained by summer water temperature, whereas, contrary to our expectations, substrate type and fine sediment played a negligible role in regulating salmonfly larval density. This pattern was supported by historical data available for the Madison River: A 1.2°C increase in mean annual water temperature between 1977 and 2017 coincided with evidence for upstream range contraction of salmonfly populations. These results suggest that this population is vulnerable to climate change and future human disturbance. We suggest river management and restoration efforts focused on reducing summer water temperatures and creating thermal refugia, particularly in the farthest downstream reaches of the Madison River, to help mitigate the effects of climate change and limit future habitat loss for this iconic species.

Our analysis suggests that above-optimal summer water temperatures were a major constraint on salmonfly distribution and abundance in the Madison River. This finding supports previous work indicating that salmonflies are relatively rare in locations where the maximum weekly maximum temperature exceeds 18.6°C (Huff et al., 2006). We cannot state definitively why summer temperature was the best predictor of salmonfly larval abundance in this system; however, we hypothesize that warm summer temperatures may coincide with salmonfly egg or early instar larval stages that may be more susceptible to thermal stress than later life stages. Warmer water temperatures during late summer and early fall can be particularly stressful for many fishes and other aquatic organisms because they often occur in tandem with low-flow conditions and during relatively vulnerable life stages (Leppi, DeLuca, Harrar, & Running, 2012; McCullough, 1999). As demonstrated in a laboratory setting, salmonfly

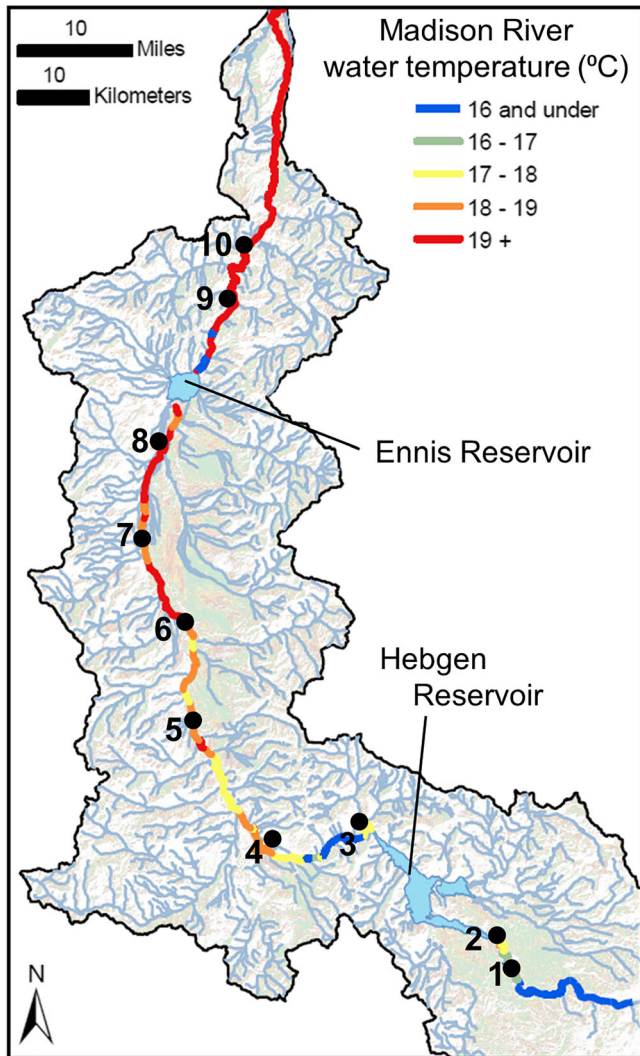


FIGURE 5 Projected mean August water temperature along the Madison River for 2100 assuming the A1B warming trajectory in the 2080s and equal warming in all stream segments (Isaak et al., 2017). 2017 sampling sites are added for context. In 2017, salmonfly larvae were detected at all sites upstream of Ennis Reservoir (Sites 1–8). Red lines indicate areas where mean August water temperature is expected to exceed 19°C and salmonfly populations will likely be unable to persist. This model predicts a loss of 27.9 river kilometres of currently occupied salmonfly habitat [Colour figure can be viewed at wileyonlinelibrary.com]

egg hatching success drops off dramatically at temperatures exceeding 20°C (Townsend & Prichard, 2000). Salmonflies in the Madison River lay their eggs in midsummer, just prior to the warmest time period of the year where water temperatures regularly exceed 20°C. Future work might address how water temperature tolerance thresholds change for salmonflies at different life stages to better understand why summer water temperatures appear to be a limiting factor for salmonflies in the Madison River.

Our findings add to the growing body of evidence that salmonflies have experienced a population decline in the most downstream portion of the Madison River (Stagliano, 2010). In 1977, salmonfly larvae

were found throughout the entire length of the Madison River (Fraleigh, 1978). In 2017, salmonfly larvae were below detection at all sites below Ennis Reservoir despite more rigorous sampling efforts, with twice as many replications per site using a benthic sampler with 2.5× the sampling area compared with 1977. This finding is supported by the long-term emergence timing data collected by a citizen scientist; adult salmonflies have not been observed emerging below Ennis Reservoir for 13 of the last 20 years (P. E. Farnes, personal communication, January 2017). This finding is further corroborated by benthic biomonitoring data collected annually in the Madison River. Salmonfly larvae have not been detected since 2012 at any annual monitoring sites located below Ennis Reservoir (Daniel McGuire, personal communication, April 2016). Salmonflies may persist in portions of the Madison River below Ennis Reservoir at low densities, but they likely no longer fill their functional roles in affecting organic matter processing (Lecerf & Richardson, 2011) or being prey for fish and terrestrial predators (Rockwell & Newell, 2009) to the extent that they likely did when they comprised a larger part of the benthic community.

Experimental and observational studies have found that although species vary in the magnitude of their responses, increased water temperature often results in quicker development and correspondingly earlier emergence for aquatic insects (Harper & Peckarsky, 2006; McCauley, Hammond, Frances, & Mabry, 2015). Similarly, we found that salmonfly emergence was strongly correlated with mean May water temperatures in both spatial and temporal datasets, with salmonflies emerging earlier when water temperatures are warmer. However, contrary to our prediction, salmonfly emergence timing did not advance significantly between 1973 and 2017. Trends towards earlier emergence timing were likely not evident in this system because water temperature in the month preceding emergence, which is a strong cue for emergence timing (Gregory et al., 2000), has remained consistent over the last few decades. This finding does not rule out the potential for advanced emergence timing for salmonflies in rivers with more significant spring warming. The static phenological response of emergent salmonflies in the Madison River could have important ecological implications for aquatic–terrestrial energy flow, as life histories and movement patterns of consumers such as birds (Tarwater & Arcese, 2018), amphibians (Todd, Scott, Pechmann, & Gibbons, 2010), and fish (Kovach, Joyce, Echave, Lindberg, & Tallmon, 2013) are often sensitive to climate change, creating a potential for a mismatch in the timing of resource availability and consumer need.

Laboratory studies have demonstrated that ectothermic organisms, particularly freshwater species, often mature at smaller body sizes when reared at relatively warm temperatures (Forster, Hirst, & Atkinson, 2012). Our field results align with this pattern. We observed a negative relationship between salmonfly body size and water temperature among sites synoptically sampled across a water temperature gradient in 2017. Reduced adult body size can have fitness consequences for at risk populations, because ovariole number and mass are positively correlated with female body size for most insects (Honěk, 1993), and fecundity can even decrease proportionately more than adult female size as water temperatures increase (Sweeney et al., 2018). Additionally, consistent body size reductions could affect entire

ecosystems by modifying the overall size structure and altering size-dependent food web dynamics (Hansen, Bjornsen, & Hansen, 1994; Hildrew, Raffaelli, & Edmonds-Brown, 2007).

Given the exponentially increasing temperatures predicted by climate models (IPCC, 2015), the historically high rate of water temperature increase in the Madison River (Isaak et al., 2017), and evidence of a salmonfly population constrained by above-optimal water temperatures, salmonfly populations in the Madison River are very likely to experience further upstream range contraction into the future. Using climate models for the Pacific Northwest, we predicted that the 2017 range of salmonflies in the Madison River could be reduced by up to 29% by the end of the century. Yet these losses are not inevitable. Water temperatures on the Madison River are potentially influenced by many factors, including damming, water withdrawals for irrigation, and climate change. Because of this complexity, the observed increase in water temperature on the Madison River cannot be explicitly linked to a single proximate cause. Management practices such as restoring floodplain and groundwater connectivity, mimicking more natural stream flow regimes, and regrading incised tributary channels may help mitigate predicted water temperature increases (Beechie et al., 2013) and the associated habitat loss for salmonflies and other cold-water obligate species.

DATA AVAILABILITY STATEMENT

The authors confirm that contemporary data supporting the findings of this study are available within the supplementary materials of this article. Historical data supporting the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

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

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