



# Thermal variability drives synchronicity of an aquatic insect resource pulse

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**Abstract.** Spatial heterogeneity in environmental conditions can prolong food availability by desynchronizing the timing of ephemeral, high-magnitude resource pulses. Spatial patterns of water temperature are highly variable among rivers as determined by both natural and anthropogenic features, but the influence of this variability on freshwater resource pulse phenology is poorly documented. We quantified water temperature and emergence phenology of an aquatic insect (salmonfly, *Pteronarcys californica*) resource pulse in two rivers characterized by differing catchment topography and human impact. Along both rivers, salmonfly emergence occurred earlier where spring temperatures were warmer. Emergence events were brief (4–8 d) at sites in the more human-impacted river, but occurred asynchronously along the entire river, lasting 27 d in total. In contrast, emergence events were more prolonged (6–11 d) at sites on the more natural and topographically complex river, but occurred synchronously along the entire river, lasting 13 d in total. These scale-specific differences in subsidy duration could have opposing consequences for salmonfly consumers depending on their mobility and foraging habits. Asynchronous emergence at a large scale is potentially most important for mobile consumers like birds and fish that can migrate to feed on aquatic insects and track resource waves across a landscape, whereas prolonged emergence duration at a smaller scale may be most important for immobile or opportunistic consumers like spiders and ants. Relating environmental heterogeneity and resource pulse phenology across a gradient of human impact and at multiple spatial scales is needed for a better understanding of how food availability, aquatic–terrestrial linkages, and consumer–resource dynamics may change with climate variability and increasing human activity in the future.

**Key words:** aquatic–terrestrial subsidy; heterogeneity; insect emergence; phenology; resource wave; water temperature.

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## INTRODUCTION

Mounting evidence indicates that spatiotemporal dynamics of food availability affect consumer fitness and behavior. Developmental transitions and movements of prey organisms often result in ephemeral, high-magnitude pulses of high-quality resources that produce

alternating periods of food scarcity and overabundance within an ecosystem (Yang et al. 2008). Consumers are often unable to take full advantage of abundant food resources during pulsed events due to limitations in consumption or assimilation capacity (Darling 1938). However, these temporal constraints can be mitigated when resource pulses occur asynchronously,

which extends the duration of resource availability and thereby increases consumers' seasonal energy intake (Armstrong et al. 2016).

The phenology of organisms, and therefore the timing of resource pulses, is often cued by environmental conditions such as temperature, precipitation, or photoperiod (Polis et al. 1997, Schaubert et al. 2002, Sanz-Pérez et al. 2009). As a result, environmental heterogeneity can result in spatiotemporal variation of resource pulses (Schindler and Smits 2017). Within aquatic systems, organism development and phenology are often driven by water temperature (Vannote and Sweeney 1980, Gillooly et al. 2002), and thus, thermal heterogeneity can be a primary determinant of the timing, pattern, and duration of aquatic resource pulses such as spawning fish (Beechie et al. 2008, Schindler et al. 2013), hatches of aquatic insects (Harper and Peckarsky 2006, McCauley et al. 2015), and phytoplankton blooms (Winder and Schindler 2004). Spatial patterns of water temperature can be highly variable among rivers (Fullerton et al. 2015) and are increasingly altered by human activity through modifications such as impoundments, land-use change, habitat simplification, and water withdrawal (Johnson and Jones 2000, Caissie 2006, Hester and Doyle 2011). However, previous work documenting the phenology of resource pulses in freshwater ecosystems has largely been conducted in relatively pristine watersheds (Armstrong and Schindler 2013, Hagen and Sabo 2014), thus limiting our ability to understand how resource pulse phenology may vary among rivers with differing levels of human activity and natural complexity (Schindler and Smits 2017).

Seasonal pulses of emerging aquatic insects are a globally important subsidy. Adult aquatic insects provide an important food resource to a variety of aquatic and terrestrial consumers, and can increase predator density, growth, and reproductive capacity, thereby supporting the function and stability of both freshwater and terrestrial ecosystems (Sabo and Power 2002, Fukui et al. 2006, Sato et al. 2016). Emergent salmonflies (*Pteronarcys californica*) represent a particularly important aquatic insect resource due to their large size, which often exceeds 6 cm in length, and high abundance in rivers throughout the American West. In early summer, salmonflies are

cued by water temperature to emerge in massive, synchronized hatches that provide a substantial nutrient pulse to a variety of aquatic and terrestrial consumers including birds, fish, frogs, spiders, and ants (Rockwell and Newell 2009). Although emergence events are brief (~1 week at any one location; Sheldon 1999), salmonflies can dominate annual aquatic insect subsidies to terrestrial ecosystems where they are abundant (Walters et al. 2018). Thus, variability in the timing and duration of salmonfly emergence could have important implications for consumers and their ability to prolong access to high-quality foraging opportunities.

We quantified salmonfly emergence phenology and water temperature along neighboring rivers of differing catchment topography and human impact in southwest Montana, USA, to better understand how variability in environmental conditions can alter resource availability and aquatic insect phenology. We hypothesized that spatial patterns of water temperature, as determined by catchment topography and river alteration, would produce differing patterns and duration of salmonfly emergence and that increased thermal variability would yield more diverse and asynchronous emergence phenology. Because salmonflies provide an important resource pulse to both immobile and mobile consumers, we characterized emergence timing and duration at both localized (100 m) and broader (50–100 km) spatial extents along each river.

## METHODS

### Study system

This study was conducted on the Gallatin and Madison rivers in southwest Montana (Fig. 1a). Both rivers originate in northwest Yellowstone National Park and flow northwards, joining to form the Missouri River. Although the rivers run parallel, they are characterized by differing land cover type and levels of human impact throughout our study areas (Appendix S1: Table S1). The Gallatin River is free-flowing and throughout our study area runs almost exclusively through National Forest land. This length is characterized by alternating valley and canyon topography, frequent inputs from large snowmelt tributaries, a stream gradient of 22.6 m/km, and a dense riparian zone consisting primarily of conifer forest

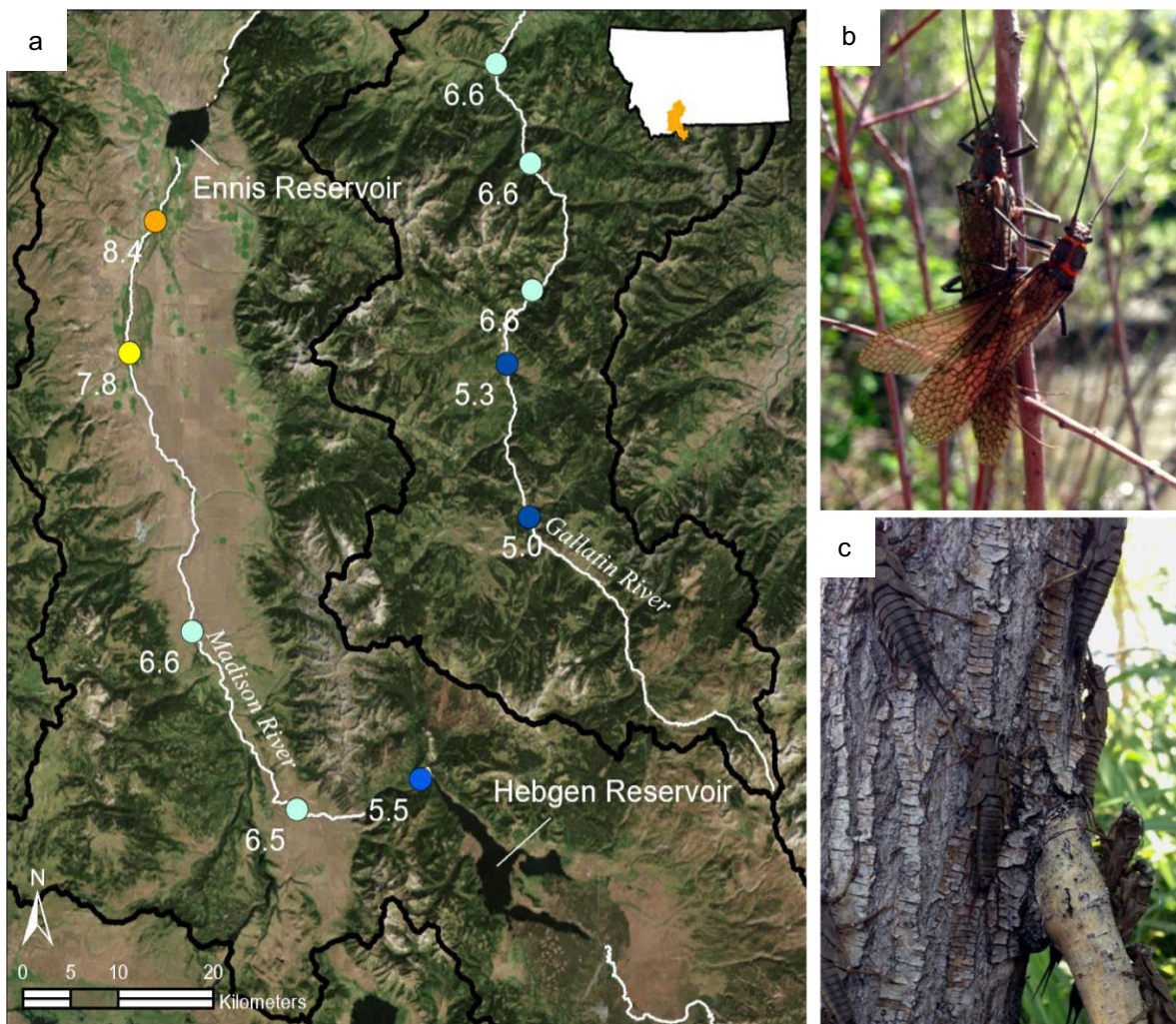


Fig. 1. (a) Study sites along the Madison and Gallatin rivers, which flow northwards. Mean April–May (months preceding salmonfly emergence) water temperatures for 2017 are listed for each site with symbol colors ramping from cool (blue) to warm (orange) to illustrate temperature gradients. White lines denote the main study rivers, and black lines represent their watersheds. Base map is from Google Earth accessed on January 2019. (b) Salmonfly larvae crawl from water to land to complete their metamorphosis and mate, (c) leaving their exuvia clinging to shoreline features (pictured here) or littered along the bank (not pictured). As many as 165 salmonflies/m of riverbank were recorded during emergence.

and willow (*Salix*). Upstream from our most downstream site, the Gallatin River drainage is 2124 km<sup>2</sup>. In contrast, study sites on the Madison River extend between Hebgen and Ennis reservoirs, which were created by dams constructed in 1914 and 1906, respectively. Within this length, the river runs through a broad valley where primary land use consists of livestock grazing with localized dryland and irrigated agriculture and

has a stream gradient of 17.4 m/km. The riparian zone is dominated by grasses (*Gramineae*) and willow (*Salix*). Tributary streams in the most downstream extent of our study area experience dewatering and elevated spring and summer water temperatures due to irrigation withdrawal (Rich and Hagener 2013). Upstream from our most downstream site, the Madison River drainage is 4808 km<sup>2</sup>.

Salmonfly emergence phenology and water temperature were quantified at five sites on both the Madison and Gallatin rivers (Fig. 1). Sites were established so that they were relatively equidistant along the portion of each river where salmonflies are most abundant based on anecdotal evidence from local fishing guides (57.0 km for the Gallatin and 88.7 km for the Madison). Surveys from 2017 confirmed that salmonflies were present at all sites at densities of at least 15 larvae/m<sup>2</sup> (Appendix S1: Table S2).

### *Emergence timing*

We used daily exuvia counts to measure salmonfly emergence phenology at all sites on both rivers during the summers of 2016 and 2017. Salmonflies emerge en masse in early summer to complete their metamorphosis and mate (Fig. 1b). During emergence events, 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 (Fig. 1c). Because salmonflies are so large, these abandoned exuviae are conspicuous along the shoreline, and therefore, systematic counts of exuvia can be a useful method to quantify salmonfly emergence timing and abundance (Walters et al. 2018). At each site, 100-m sample reaches were established along stream banks adjacent to riffles (typical salmonfly larval habitat) and exuviae were collected and removed at the same 10 randomly selected 1-m bank transects within each reach. Two complete passes were made through each entire reach using the same people and effort each pass. Exuvia counts were conducted at least 5 d per week during the entire duration of emergence to minimize exuvia loss due to weather events such as wind, rain, or rising water levels.

Median emergence date and duration (in days) were estimated at each site in 2016 and 2017. We defined site-specific emergence duration as the first day of >5% cumulative emergence (number of exuvia) through the first day of >95% cumulative emergence, and median emergence date as the median day within this emergence window. River-wide duration was defined as the difference between the earliest and latest median salmonfly emergence date for each year and river combination.

### *Water temperature*

Water temperature was recorded at 30-min intervals from 1 April to 31 May 2017, at each site

using a HOBO Pendant water temperature logger (Onset Computer, Bourne, Massachusetts, USA) secured to a boulder mid-channel and shaded with a UV-safe PVC tube. Loggers were lost in peak discharge in 2016, so temperature data for that year are unavailable.

### *Data analysis*

A three-way analysis of covariance (ANCOVA) was used to compare river-scale pattern and duration of salmonfly emergence between rivers and to determine whether this pattern varied between 2016 and 2017. The full model included longitudinal distance, river, and year as fixed factors. Main effects were preserved in the model when associated interaction coefficients were significant ( $P < 0.05$ ). The length of each river where salmonflies were abundant, and therefore the length of river where we quantified emergence timing, was not equivalent for the Madison and Gallatin rivers. We calculated the ratio between slope coefficients of the ANCOVA model to standardize for longitudinal distance. The difference in site-specific emergence duration between the two rivers was determined with a two-way ANCOVA, with river and year as fixed effects.

A two-way ANCOVA was used to evaluate the relationship between water temperature and median salmonfly emergence date among sites in 2017, the year when water temperature data were available, and to determine whether this relationship differed between rivers. The full model included water temperature and river as fixed factors. Salmonfly emergence dates are strongly correlated with spring water temperatures (Gregory et al. 2000). Accordingly, we defined water temperature for all analyses as mean water temperature of the months preceding emergence (April–May) in all analyses. Total water temperature gradients for each river were defined as the difference between the coolest and warmest sites on each river. Statistical analyses were performed in R version 3.3.1 (R Core Team 2013).

## RESULTS

### *Emergence timing*

Salmonfly emergence phenology varied markedly between rivers, but exhibited contrasting patterns at different spatial scales. At a large spatial scale (50–100 km), emergence was relatively

asynchronous along the Madison River (Fig. 2a); the maximum difference in median emergence dates among sites averaged 22.5 d across the two years (21 d in 2016 and 24 d in 2017). In contrast, salmonfly emergence was relatively synchronous along the entire study length of the Gallatin River (Fig. 2b); the maximum difference in median emergence dates among sites averaged 5.25 d across the two years (4 d in 2016 and 6.5 d in 2017). These differences in river-scale emergence duration were also apparent when distance was standardized. Salmonfly emergence lasted 2.26 times longer for an equivalent length of river on the Madison River compared to the Gallatin River (Fig. 3a). The most parsimonious ANCOVA model explaining median emergence date included effects of longitudinal distance (3-way ANCOVA:  $F_{1,14} = 182.5$ ,  $P < 0.0001$ ), river ( $F_{1,14} = 0.035$ ,  $P = 0.85$ ), and an interactive effect between river and distance ( $F_{1,14} = 34.79$ ,  $P = 0.002$ ), with no evidence for an effect of year ( $F_{1,14} = 0.046$ ,  $P = 0.83$ ).

Contrary to patterns of river-scale emergence, site-specific emergence duration was prolonged at sites in the Gallatin River. Emergence lasted 25%, or an average of 2.0 d, longer (standard

error: 0.53,  $P = 0.0016$ ) at sites along the Gallatin River compared to those on the Madison River (Fig. 3b), with no evidence for an effect of year (2-way ANCOVA:  $F_{1,16} = 0.55$ ,  $P = 0.47$ ). In total, emergence lasted 27 d on the Madison River and 13 d on the Gallatin River.

#### Water temperature

We observed differences in the degree of spatial variation in spring water temperature between the Madison and Gallatin rivers during 2017. Sites along the Gallatin River remained relatively cool throughout the spring and exhibited similar seasonal patterns in daily water temperature, with mean spring water temperatures ranging between 5.0°C and 6.6°C among sites (Fig. 1; 1.6°C total water temperature gradient). Water temperatures were more spatially variable among sites on the Madison River, with mean spring water temperatures ranging between 5.5°C and 8.4°C (Fig. 1; 2.9°C total water temperature gradient). Seasonal fluctuations in daily water temperature were muted at the most upstream sites on the Madison River, located just downstream from Hebgen Reservoir (Appendix S1: Fig. S1).

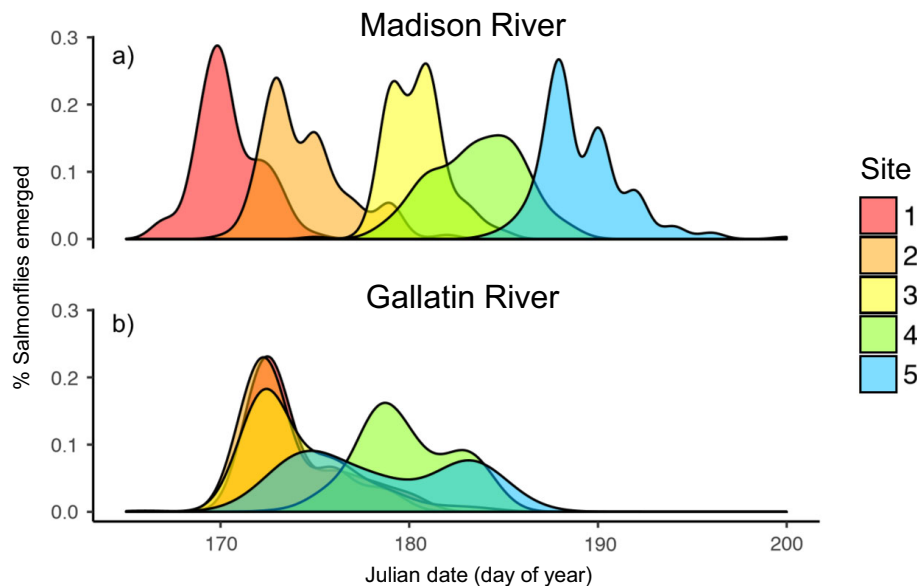


Fig. 2. At the river scale, salmonfly emergence was asynchronous along the (a) Madison River, but relatively synchronous along the (b) Gallatin River. Site numbers increase in the upstream direction, with 1 being most downstream and 5 being most upstream. Data in this figure were pooled across years (2016 and 2017) and grouped by site and river and then smoothed using a kernel density estimator with a bandwidth adjustment of 1.4, which was arbitrarily selected because it highlighted general patterns of emergence.

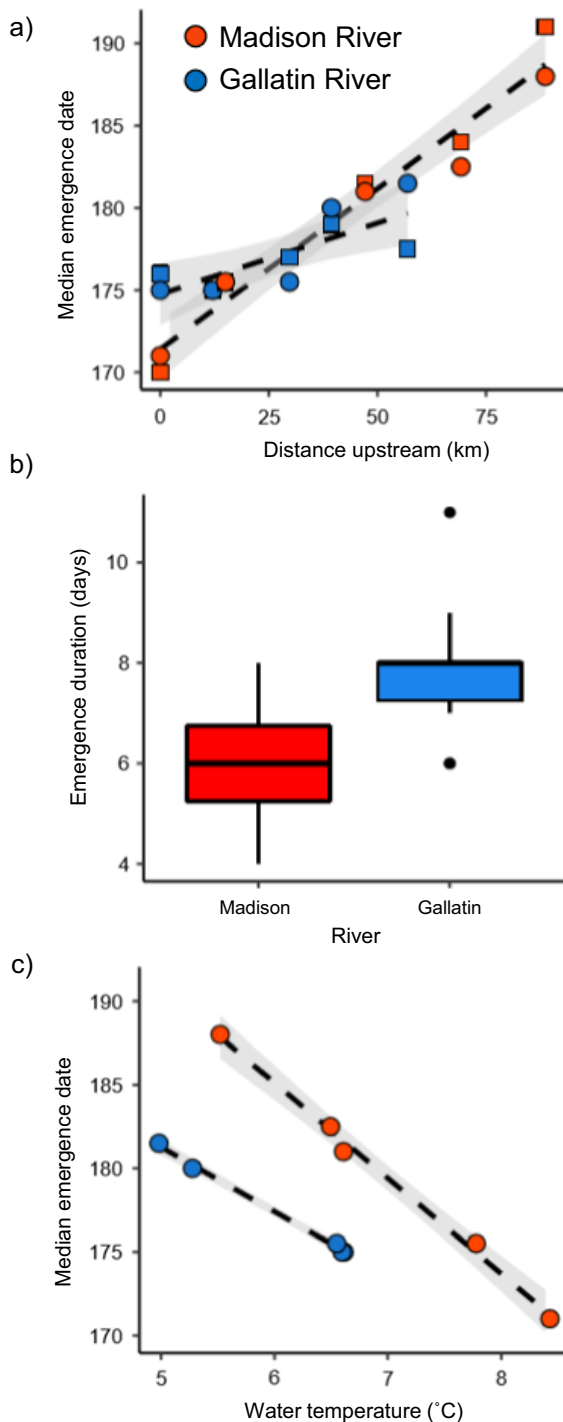


Fig. 3. (a) Emergence moved from downstream to upstream along both the Gallatin (blue) and Madison (red) rivers, but traveled slower along the Madison River ( $F_{1,14} = 34.79$ ,  $P = 0.002$ ), lasting 2.3× longer than for an equivalent river length on the Gallatin

Median salmonfly emergence date was correlated with mean spring water temperature on both rivers (lm:  $R^2 = 0.99$ ,  $F_{3,6} = 469.4$ ,  $P < 0.0001$ , Fig. 3c), with emergence occurring earlier at sites where water temperatures were warmer. The most parsimonious ANCOVA model included main effects of water temperature (2-way ANCOVA:  $F_{1,6} = 750.3$ ,  $P < 0.0001$ ), river ( $F_{1,6} = 619.8$ ,  $P < 0.0001$ ), and an interactive effect between temperature and river ( $F_{1,6} = 37.94$ ,  $P = 0.0008$ ).

## DISCUSSION

In this study, we found evidence that spatial variation in water temperature can desynchronize the timing of an aquatic insect resource pulse. A relatively large water temperature gradient spatially desynchronized the emergence timing of salmonflies along the Madison River; although salmonfly emergence was brief (4–8 d) at any given site, emergence lasted 27 d along the entire extent of the river, moving in a predictable wave from downstream to upstream (Fig. 2). In contrast, a relatively small water temperature gradient led to more synchronized salmonfly emergence along the Gallatin River. Salmonfly emergence was more prolonged (6–11 d) at individual sites, but occurred in relative synchrony at the river scale, lasting only 13 d in

(Fig. 3. *Continued*)

River. Squares represent data points from 2016, and circles represent data points from 2017. (b) In contrast, site-specific emergence duration (100 m) was more prolonged at sites along the Gallatin River, lasting an average of 2 ( $\pm 0.53$  standard error) days longer than at sites on the Madison River. The horizontal line within the box-and-whisker plots represents the sample median, and the outer margins represent the 25th and 75th percentiles. The whiskers extend to the farthest value no further than 1.5× the inter-quartile range from the box. Black circles represent outliers. (c) Median salmonfly emergence date (day of year) was strongly correlated with mean water temperature in the months preceding emergence (April–May) at sites on both the Gallatin and Madison rivers ( $R^2 = 0.99$ ,  $P < 0.0001$ ). Dashed lines represent significant linear fits with gray shading displaying the 95% confidence intervals.

its entirety (Fig. 2). Emergence timing occurred earlier in the season at sites where water temperatures were warmer on both rivers. Our findings are consistent with previous research that demonstrates the importance of spatial thermal variability in mediating the availability of freshwater resources (Ruff et al. 2011, Uno and Power 2015) as well as the potential for human activities to shift the phenology and development of freshwater biota (Zhong and Power 1996, Lessard and Hayes 2003, Wheeler et al. 2015).

Humans can alter the spatial variation of river water temperature in numerous, scale-specific ways. These alterations can lead to both homogenization of temperatures through processes such as channelization, flood suppression, and changes in riparian land use (Poole and Berman 2001) and increased temperature gradients through the creation of large thermal discontinuities such as dams (Ward and Stanford 1983, Olden and Naiman 2010, Ellis and Jones 2013). We found that the synchronicity of an aquatic insect resource pulse varied dramatically between rivers characterized by differing levels of human impact and topographic complexity. Interestingly, spatial water temperature variation was relatively large and salmonfly emergence was correspondingly less spatially synchronized along the relatively human-altered Madison River, leading to longer river-wide duration of emergence. The large temperature variation recorded in the Madison River was likely created in part by the cold-water release at Hebgen dam on the upstream side of our study area and dewatered tributaries due to irrigation withdrawal in the most downstream extent of our study area. However, we did not explicitly link anthropogenic influence to water temperature in this study and are therefore unable to single out how anthropogenic and natural features differentially influenced salmonfly emergence phenology on the Madison and Gallatin rivers.

Natural features such as tributary inputs, riparian shading, and variable hyporheic exchange can also influence spatial patterns of fluvial water temperature in ways that are scale- and river-specific (Poole 2002). Spatial water temperature heterogeneity associated with variable shading and hydraulic features (riffles, pools, sunny, and shaded runs) can desynchronize

aquatic insect emergence and thus prolong emergence events at small spatial scales (0–10 km; Uno 2016). Given the strong correlation between water temperature and salmonfly emergence described in this study, we hypothesize that site-specific emergence duration between the Gallatin and Madison rivers may be due to differences in small-scale physical complexity and corresponding heterogeneity of water temperature at sites on the two rivers. Future work could clarify this point by exploring the influence of habitat and water temperature heterogeneity on aquatic insect subsidy duration at multiple spatial scales.

Ecologists increasingly recognize the importance of asynchronous resource pulses in extending foraging opportunities for both mobile (Schindler et al. 2013) and sessile (Uno 2016) consumers. We documented dramatic and scale-specific differences in the duration of salmonfly emergence between neighboring rivers. These differences in subsidy duration could have opposing implications for consumer populations depending on their mobility. For example, asynchronous salmonfly emergence at a large scale, as documented on the Madison River, is potentially most important for mobile consumers like birds and fish that can migrate to feed on aquatic insects and track resource waves across a landscape (Uesugi and Murakami 2007). In contrast, prolonged emergence duration at a small scale, as documented on the Gallatin River, may be more beneficial to immobile or opportunistic consumers like spiders and ants (Paetzold et al. 2005, Marczak and Richardson 2008) by increasing the duration of high-quality foraging opportunities at a single location. Many resource pulses, including seed masting events, spawning fish, and spring green-up are utilized by consumers characterized by variable mobility or foraging strategies (Ostfeld and Keesing 2000, Willson and Womble 2006, Hebblewhite et al. 2008). However, few studies have investigated how spatial variation in resource pulse timing at multiple spatial scales influences consumer foraging opportunities (but see Deacy et al. 2019). Our findings demonstrate that within-site phenological variability and among-site phenological variability can occur independently and underscore the need to better understand the relative importance of resource pulse duration at multiple spatial scales and the consequent effects for

consumer populations of differing mobility or foraging behaviors.

Prey species can also experience notable effects on their own population dynamics when phenological shifts occur (Yang and Rudolf 2010, Rasmussen and Rudolf 2016). For example, emergence synchrony can benefit prey populations by increasing the probability of finding a mate and through predator satiation, whereby the proportion of adults eaten by predators is inversely related to the number of adults present on any given day (Sweeney and Vannote 1982, Santos et al. 2016). We can therefore expect that the differences we observed in emergence synchrony between the Madison and Gallatin rivers may also affect salmonfly population dynamics and survival. However, the relative strength of these effects on predator and prey populations and the spatial scale at which they are relevant remain unclear.

River water temperature, particularly patterns of warming in spring months, can vary drastically on an annual basis (Arismendi et al. 2013). This study is limited to 1 yr of water temperature data and therefore does not capture variation in water temperature regimes among years. Differences in river flow among years may alter thermal heterogeneity at small spatial scales most notably because features such as pools, side channels, and riparian vegetation can be inundated or masked during high-flow events (Webb et al. 2008). Nevertheless, the shape of river thermal profiles is often parallel from year to year (Fullerton et al. 2015), and thus, we can expect large-scale thermal variability and patterns of emergence phenology to be relatively consistent over time. On the Madison River in particular, a 44-yr record demonstrates that salmonfly emergence date is strongly correlated with spring water temperature over time, with emergence occurring earlier in years when spring water temperatures are relatively warm (Anderson et al. 2019).

Our analysis indicated that at a given spring temperature, salmonfly emergence occurred earlier at sites on the Gallatin River compared to those situated along the Madison River. We cannot definitively state why there was such a clear difference in thermal emergence cues between the two rivers, but it may be due to differing annual thermal regimes in the two rivers. Salmonflies are a multivoltine species and can take

anywhere between 2 and 5 yr to develop in their larval stage depending on the thermal regime of the river they inhabit (Freilich 1991, DeWalt and Stewart 1995, Townsend and Pritchard 1998). Salmonflies may take an additional year to develop in the relatively cool Gallatin River compared to populations in the relatively warm Madison River, resulting in different water temperature cues to emerge in the spring.

## CONCLUSION

Climate variability and ongoing human modification of the natural world are increasingly affecting habitat heterogeneity in ways that can abruptly shift or homogenize environmental conditions (Western 2001). These changes can affect the availability, magnitude, and spatial patterning of resource pulses and subsidies (Schindler and Smits 2017). In particular, the modification of river thermal regimes has the potential to influence ecosystem services important to both human and animal consumers because water temperature cues many economically, ecologically, and culturally important resource pulses that support local economies (Schindler et al. 2010), have broad social importance (Parrella et al. 2006), and benefit consumers ranging from beetles and spiders (Paetzold et al. 2005) to grizzly bears (Deacy et al. 2016). Our findings indicate that human influence may not ubiquitously homogenize environmental conditions and shorten subsidy duration as previously posited, but rather influence water temperature and therefore subsidy duration in ways that can be both river- and scale-specific. Given the widespread alteration of the natural environment and the ubiquity of resource pulses, more work relating environmental heterogeneity and resource pulse phenology among rivers in various regions and across a gradient of human impact is needed for a more complete understanding of how human impact and geographical features influence resource pulse phenology and how food availability, aquatic–terrestrial linkages, and consumer–resource dynamics may change into the future.

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