

ENVIRONMENTAL DRIVERS OF SALMONFLY ECOLOGY
IN SOUTHWEST MONTANA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

August 2018

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ACKNOWLEDGEMENTS

I would first like to extend heartfelt thanks to my advisor Dr. Lindsey Albertson who has kept me enthusiastic and relatively even-keeled throughout my time at Montana State University, and has created a lab setting that that is both social and collaborative. I cannot overstate how lucky I feel to have been placed among my peers in the Ecology Department, particularly those in the Albertson and Cross labs, who have provided me with endless motivation, advice, and distractions. Being a part of this community has kept me curious, elevated my science, and ultimately been a lot of fun: you all have truly been a family to me these past few years.

Thanks also go to the members of my graduate committee Dr. David Walters, Dr. Wyatt Cross, and Dr. Laura Burkle for their valuable feedback and support throughout this process, and to Charlotte Hoover, Niall Clancy, and Cailey Philmon for their help with field and laboratory work. I am grateful to Phillip E. Farnes for collecting and providing data on the timing of historical salmonfly emergence and to Jenny McCarty for building and loaning me the surber sampler used in this study. Site access was granted by Yellowstone National Park (permit 7066) and John Clark at Madison River Ranch. This project was funded by the U.S. Geological Survey Montana Water Center and Montana State University.

TABLE OF CONTENTS

1. INTRODUCTION	1
2. TEMPERATURE-DRIVEN RANGE CONTRACTION AND BODY SIZE REDUCTION OF AN ICONIC AQUATIC INSECT	5
Author Contributions	5
Manuscript Information	6
Abstract	7
Introduction.....	8
Methods.....	11
Study Site	11
Temperature, Substrate, and Discharge	12
Salmonfly Larval Density	14
Salmonfly Body Size and Emergence Timing.....	14
Data Analysis	16
Results.....	19
Historical Conditions	19
Current Conditions.....	22
Future Conditions.....	25
Discussion.....	27
3. LANDSCAPE FEATURES DRIVE SYNCHRONICITY OF AN AQUATIC INSECT RESOURCE PULSE.....	33
Author Contributions	33
Manuscript Information	34
Abstract	35
Introduction.....	35
Methods.....	38
Study Site	38
Emergence Timing.....	39
Water Temperature	41
Data Analysis	41
Results	42
Discussion	45
Conclusion.....	48
4. CONCLUSION.....	49
LITERATURE CITED	51

TABLE OF CONTENTS CONTINUED

APPENDICES	61
APPENDIX A: Summary data from all sites and rivers	62
Table A1. Larval densities	63
Table A2. Exuvia lengths.....	64
Table A3. Adult dry weights.....	65
Table A4. Substrate characteristics.....	66
Table A5. Monthly water temperatures	67
Table A6. Historical emergence dates	68
Table A7. Emergence timing and duration.....	69
APPENDIX B: Supplementary data analyses for the Gallatin River	70
Table B1. AICc model predictions of environmental variables constraining larval densities	71
Figure B1. Exuvia length versus water temperature	72

LIST OF TABLES

Table	Page
1. Water temperature at sites on the Madison River	12
2. Model predictions of salmonfly (<i>Pteronarcys californica</i>) larval density.....	25
3. Larval densities on the Madison and Gallatin Rivers	40

LIST OF FIGURES

Figure	Page
1. Chapter 2 study sites	13
2. Historical and current larval densities.....	21
3. Historical and current adult dry weight	21
4a. Temporal trends of first emergence dates, 1973 - 1977	23
b. Historical emergence date versus water temperature	23
5a. Current exuviae lengths versus water temperature.....	24
b. Current emergence date versus water temperature.....	24
6. Projected August water temperature for 2100	26
7a. Photograph of salmonflies mating.....	40
b. Photograph of abandoned exuvia	40
8a. Emergence synchronicity along the Madison River.....	43
b. Emergence synchronicity along the Gallatin River.....	43
9a. Longitudinal patterns of emergence	43
b. Water temperature cues emergence timing	43

ABSTRACT

Aquatic insects have ecological, cultural, and economic value throughout the American West. They can control the processing of in-stream nutrients, are a vital component of both aquatic and terrestrial food webs, and support economically important species such as trout and the eco-tourism industries structured around these fisheries. Salmonflies (*Pteronarcys californica*) are one of the most well-known aquatic insects in the American West due to their large size and popularity among fly-fishers. However, mounting anecdotal evidence suggests that salmonfly populations could be in decline. We conducted surveys and compiled historical datasets that quantified salmonfly abundance, body size, and emergence timing along the Gallatin and Madison Rivers in southwest Montana to determine the status of salmonfly populations in these rivers, understand environmental drivers that are constraining their distribution and driving their development, and initiate long-term monitoring. Most notably, we found evidence for temperature-driven changes in salmonfly distribution and body size along the Madison River in the last four decades and observed marked differences in salmonfly emergence phenology and duration at multiple spatial scales between the Madison and Gallatin Rivers. Above-optimal summer water temperatures appear to be the major constraint on salmonfly populations in the Madison River, but only play a minimal role in dictating salmonfly distribution along the Gallatin River. This research provides rare empirical evidence of long-term biological change of an aquatic insect and highlights the importance of combining temporal and spatial datasets to explicitly address species' responses to environmental stressors across multiple spatial and temporal scales. Freshwater habitats are increasingly imperiled by climate change and human-induced habitat alteration, which will invariably continue to impact the ecology of aquatic insects like salmonflies. This work contributes to the understanding of how these ongoing changes will influence the structure of aquatic communities, the flow and transfer of energy and nutrients, consumer-resource dynamics, and stream-riparian food web linkages.

CHAPTER ONE

INTRODUCTION

Fluvial ecosystems are increasingly altered by various factors including climate, land use change, impoundment, and water extraction (Carpenter et al. 2011). Human-induced changes to the physical structure of rivers and streams have resulted in widespread alteration of river organismal assemblages and modified how energy is transferred between aquatic and terrestrial ecosystems (Poff et al. 2007, Deacy et al. 2017). Although a considerable amount of research has studied the impacts of these changes on fish (e.g. Isaak et al. 2012, Schindler et al. 2013), the impacts on aquatic insects remain relatively under-studied (Jackson and Füreder 2006, Strayer and Dudgeon 2010). Addressing this knowledge gap is critical because aquatic insects support aquatic and riparian food webs (Baxter et al. 2005), are sentinels of river health (Lenat 1988), and provide economic and cultural value by supporting fisheries popular among anglers (Lewis and King 2014).

Salmonflies (*Pteronarcys californica*) 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 fly-fishers. Salmonflies spend 2-5 years as larvae living among gravels in the riverbed, and then in early summer are cued by water temperature to emerge in spectacular, synchronized hatches that draw anglers from around the world (e.g. Santella 2013, Willoughby 2015) and provide a significant carbon pulse to over twenty species of aquatic and terrestrial consumers including birds, fish, spiders, and ants (Muttkowski

1925, Rockwell and Newell 2009). Mounting evidence suggests that salmonfly populations could be declining throughout the American West (Stagliano 2010, Nehring et al. 2011). These losses have the potential to alter in-stream and aquatic-terrestrial energy fluxes since salmonflies can control processing of detritus (Lecerf and Richardson 2011), dominate aquatic subsidies to terrestrial ecosystems (Walters et al. 2018), and provide an important resource pulse for a variety of terrestrial and aquatic consumers (Rockwell and Newell 2009). In my research, I use salmonfly populations to ask how changing water resources related to temperature, substrate, and flow are driving shifts in aquatic insect ecology and productivity in the Gallatin and Madison Rivers in southwest Montana.

Increasing water temperature 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 et al. 2010, Relyea et al. 2012). A large body of experimental and predictive research has demonstrated the potential negative effects of these stressors on aquatic insects, with responses that include range contraction, signs of physiological stress such as reduced body size, and phenological advancement (Dallas and Ross-Gillespie 2015). However, few studies have documented natural long-term responses of aquatic insects in parallel with recorded increases in water temperature or human disturbance. In chapter two, I compare current surveys with several long-term datasets documenting physical (water temperature, discharge, substrate characterization) and ecological (larval density, adult body size, emergence timing) parameters to

determine how environmental change has impacted salmonfly distribution, abundance, body size, and emergence phenology in the Madison River in the last four decades. I then provide further context for how these changes in salmonfly populations may continue throughout the 21st century within this watershed with predictive models of temperature change and extrapolated historic water temperature trends.

Although warming water temperatures pose a serious threat to salmonflies and other cold-water obligate species, their ecology will likely also be altered by changes to spatial patterns of water temperature. For example, thermal heterogeneity can determine the phenology and availability of resource pulses that are cued by water temperature (Lisi et al. 2013), including salmonfly emergence (Gregory et al. 2000). Changes to resource phenology have potentially important implications for consumers, because asynchronous resource pulse phenology can extend the duration of resource availability, and thereby stabilize and boost consumers' seasonal energy intake (Armstrong et al. 2016). Spatial patterns of water temperature are increasingly altered by human activity through modifications such as impoundments, land-use change, habitat simplification, and water withdrawal (Caissie 2006), but previous work exploring the link between resource pulse phenology and water temperature has largely been conducted in relatively complex and pristine watersheds, thus limiting our ability to understand how resource pulse phenology may vary among rivers with differing natural features and levels of human activity. In the third chapter, I quantify how spatiotemporal patterns of water temperature and salmonfly emergence phenology vary between the Gallatin and Madison Rivers in order to better understand how anthropogenic and natural features in rivers can influence the duration,

magnitude, and spatial patterning of a resource pulse cued by water temperature. In the fourth chapter I summarize my findings and provide suggestions for future research.

CHAPTER TWO

TEMPERATURE-DRIVEN RANGE CONTRACTION AND BODY SIZE

REDUCTION OF AN ICONIC AQUATIC INSECT

Contribution of Authors and Co-Authors

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Contributions: HEA helped design the study, conducted the research, analyzed the data, and wrote the manuscript

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Manuscript Information

Heidi E. Anderson, Lindsey K. Albertson, and David M. Walters

Freshwater Science

University of Chicago Press

Status of Manuscript: Officially submitted to a peer-reviewed journal June 7th, 2018

Abstract

Freshwater ecosystems are disproportionately impacted by climate change and human disturbance, yet few studies have documented long-term changes for freshwater species. We coupled historical datasets with current surveys documenting physical and ecological variables over four decades to quantify changes in the abundance, body size, and emergence timing of the river stonefly, *Pteronarcys californica*, (common name: salmonfly) in the Madison River in southwest Montana USA. Since 1977, salmonflies in the Madison River have experienced a 34.0% upstream range contraction and 11.8% reduction in adult dry mass at the most downstream extent of their current distribution. These changes are paralleled by an observed 1.2°C increase in mean annual water temperature. Emergence timing did not advance between 1973 and 2017, likely because spring water temperatures that cue emergence remained consistent over time. Salmonfly abundance, body size, and emergence timing were negatively correlated with water temperature across a spatial temperature gradient. Current salmonfly populations on the Madison River are spatially constrained by August water temperature, suggesting that this population is vulnerable to climate change and future human disturbance. If warming trends continue, we predict that salmonflies could be extirpated from an additional 30 river kilometers of current habitat by 2100, culminating in a total range contraction of 50% on the Madison River since 1977. This study provides rare empirical evidence of long-term biological change of an aquatic insect and highlights the importance of combining historical and spatial datasets to explicitly address species' responses to environmental stressors across both space and time.

Introduction

Freshwater ecosystems are highly vulnerable to climate change and human disturbance, and as a result are experiencing negative interactive effects of warming water temperatures, habitat fragmentation, and habitat degradation that often exceed observed changes in terrestrial ecosystems (Sala et al. 2000). Freshwater species are also more sensitive to these stressors than their terrestrial counterparts (Ricciardi and Rasmussen 1999) because most are ectothermic and constrained within river networks, which limits their ability to track suitable habitat. Despite the increasingly altered nature of freshwater systems and disproportionate sensitivity of freshwater species to shifting environmental conditions, long-term studies tracking changes to aquatic insect populations are generally lacking (Jackson and Füreder 2006). Addressing this knowledge gap is critical because aquatic insects support aquatic and riparian food webs (Baxter et al. 2005), are sentinels of river health (Lenat 1988), and provide economic and cultural value by supporting fisheries popular among anglers (Lewis and King 2014).

Increasing water temperatures and excessive fine sediment inputs are two of the most pervasive threats to freshwater species (Woodward et al. 2010, Jones et al. 2012). A large body of research has demonstrated the negative effects of these stressors on aquatic insects in particular, with responses that include range contraction, signs of physiological stress such as reduced body size, and phenological advancement among others (Dallas and Ross-Gillespie 2015). Despite this extensive research, few studies have documented natural long-term responses of aquatic insects in parallel with recorded increases in water temperature or human disturbance. For example, much of the relevant literature regarding

distributional shifts for freshwater macroinvertebrates is predictive, using current conditions, emission scenarios, and bioclimatic models to forecast future conditions (Hering et al. 2009, Markovic et al. 2014, Shah et al. 2014, but see Giersch et al. 2014). Similarly, most evidence of reduced aquatic insect body size and advanced emergence timing at warmer temperatures comes from experimental studies or field studies utilizing a current spatial gradient of water temperatures (McCauley et al. 2015, Zeuss et al. 2017). Examples of biological change in natural settings coincident with long-term records of shifting environmental conditions could help better understand the realized impacts of climate change and human disturbance on freshwater organisms.

We examined the influence of shifting environmental conditions over 4 decades on a large-bodied aquatic insect, the salmonfly (*Pteronarcys californica*), in the Madison River in southwest Montana. Salmonflies are iconic aquatic insects of the American West that serve important ecological and economic rolls. They provide a significant food resource to both aquatic and terrestrial consumers and draw anglers from around the world when they emerge en masse over the course of several days in early summer (Walters et al. 2018). 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 et al. 2010, Relyea et al. 2012). Mounting anecdotal evidence suggests that salmonfly populations could be declining throughout the American West (Stagliano 2010, Nehring et al. 2011). These losses have the potential to alter in-stream and aquatic-terrestrial energy fluxes, since salmonflies can

control processing of detritus (Lecerf and Richardson 2011), dominate aquatic subsidies to terrestrial ecosystems (Walters et al. 2018), and provide an important resource pulse for a variety of terrestrial and aquatic consumers (Rockwell and Newell 2009).

Additionally, the extirpation of salmonflies from certain waterways may have negative economic impacts on local communities that are based around eco-tourism and fishing industries.

We compared current surveys with several long-term datasets documenting physical (water temperature, discharge, substrate characterization) and ecological (salmonfly larval density, salmonfly adult body size, salmonfly emergence timing) parameters to determine how environmental change has impacted salmonfly distribution, abundance, body size, and emergence phenology. We hypothesized that increased water temperatures and deposition of fine sediment would correspond with lower salmonfly abundance over time and space, predicting that current abundances will be lower than historical abundances and lower at sites with relatively warm water temperatures or relatively high proportions of fine bed sediments. We also predicted that water temperatures would be the primary control on salmonfly body size and emergence timing, with body size negatively correlated with water temperatures and emergence occurring earlier where water temperatures are warmer across both space and time. We provide further context for how these changes in salmonfly populations may continue throughout the 21st century by using predictive models of temperature change and extrapolated historic water temperature trends.

Methods

Study Site

This study was conducted on the mainstem of the Madison River, a blue-ribbon trout stream in southwest Montana. The Madison River originates in northwestern Yellowstone National Park, Wyoming at an elevation of 2,074 m, flowing approximately 210 km northward through broad valleys and joining the Jefferson and Gallatin Rivers to form the Missouri River near Three Forks, Montana at an elevation of 1,235 m. The riparian zone is dominated by willow (*Salix*), grasses (*Gramineae*), cottonwood (*Populus*), and alder (*Alnus*). Primary land use within the Madison River valley is livestock grazing, with localized dryland and irrigated agriculture and natural vegetation of sagebrush steppe. The river is gravel-bedded along its length and supports populations of brown, rainbow, and cutthroat trout. The Madison River passes through Hebgen Reservoir, Earthquake Lake, and Ennis Reservoir at 177, 149, and 59 km above its mouth. The dams forming Hebgen and Ennis Reservoirs were constructed in 1914 and 1906, respectively. 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. Water temperatures are relatively cool between the Hebgen and Ennis Reservoirs but warm significantly below Ennis Reservoir (Table 1). We characterized physical and biological stream parameters at eleven representative 100 m reaches distributed along the entire length of the river, with 2 sites upstream of Hebgen Reservoir, 6 between Ennis and Hebgen Reservoirs, and 3 downstream of Ennis Reservoir (Figure 1).

Table 1. Water temperature (°C) at sites on the mainstem Madison River from April – September 2017. Site numbers increase in the upstream direction. Dotted lines represent dams: Ennis Reservoir is located between sites 3 and 4 and Hebgen Reservoir is located between sites 9 and 10 (Figure 1)

Site	Mean	Maximum	Minimum
1	15.92	23.27	7.70
2	15.52	24.99	6.91
3	15.02	23.50	6.22
4	13.34	23.29	1.87
5	12.79	21.80	1.50
6	12.47	22.81	1.00
7	11.84	22.73	0.74
8	11.94	21.85	2.00
9	12.99	22.30	2.40
10	15.63	25.50	6.50
11	15.78	25.74	6.59

Temperature, Substrate, and Discharge

Water temperature was recorded at 30-minute intervals from April 1st – September 30th, 2017 at each site using a HOBO pendant temperature logger (Onset Computer, Bourne, Massachusetts) secured to a boulder mid-channel and shaded with a UV-safe PVC tube. Particle size and level of embeddedness were determined at each site with a modified 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 (<1mm). Low and high embeddedness were classified as the proportion of representative gravels where embedded height/total height > 0 and embedded height/total height > 25%, respectively (Wolman 1954). These thresholds of embeddedness were used to account for the fact that

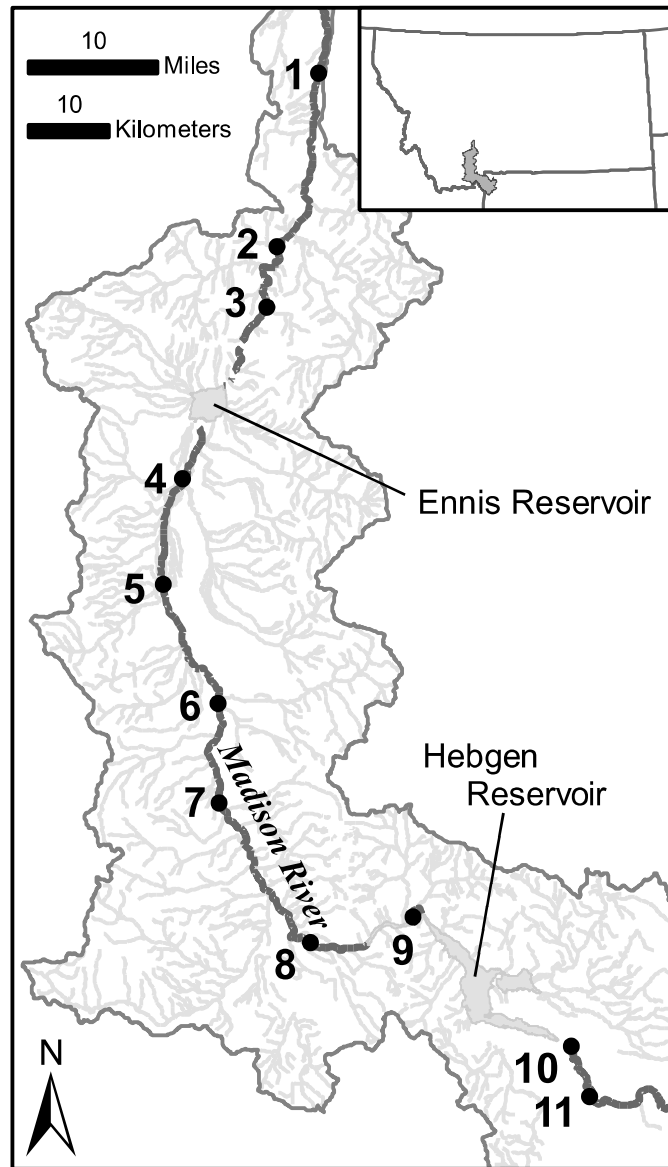


Figure 1. Study sites along the Madison River, which flows northwards, in southwest Montana

we only characterized substrate during low flow, and thus gravels that were slightly embedded when we sampled may be unembedded and provide habitat for salmonflies at other times of year when higher discharge potentially flushes fine sediments. Continuous water temperature (1977 to present) and discharge (1939 to present) measurements for the Madison River are available from the United States Geological Survey (USGS) gage #06041000 directly below Ennis Reservoir and were utilized for analyses through December 31st, 2017.

Salmonfly Larval Density

Benthic macroinvertebrates were collected in riffles at all sites in July, August, and September 2017 using a 0.75 x 0.75 m surber sampler. Four individual samples were taken per site in each of the 3 months for a total of $n = 12$ per site. Samples were preserved in 70% ethanol, transported to the laboratory, and stored at 4°C. Salmonfly larvae in each sample were enumerated to calculate their densities (larvae/m²). Current datasets were compared to historic macroinvertebrate samples. Two 0.25 m² benthic samples were collected each month at sites 1 - 5 in February, March, and August 1977, for a total of $n = 6$ samples per site (Fraley 1978). Density was converted to total larvae/m².

Salmonfly Body Size and Emergence Timing

Adult salmonflies were collected to compare body sizes between historical and current populations. In 1977, 100 adult salmonflies of each sex were collected at sites 2 and 4 within the first 2 days of emergence to determine differences in body size above and below Ennis Reservoir (Fraley 1978). The insects were killed with chloroform fumes

in the field, randomly pooled into 4 groups of 25 for each sex, and oven dried to a constant weight in the laboratory (Fraley 1978). In 2017, 35 adult salmonflies of each sex were collected at site 4 above Ennis Reservoir within the first 2 days of emergence. No adult salmonflies or exuviae were found at site 2. Adult salmonflies were frozen at the field site, then oven-dried at 55°C for 48 hours and weighed individually (Mettler Toledo AB304-S Analytical Balance).

First date of salmonfly emergence was recorded via visual inspection for salmonfly exuviae by a citizen scientist at sites 2 and 5 from 1973 through 2017 (P.E. Farnes, personal communication, January 2017). We recorded salmonfly emergence at 5 sites (4, 5, 7, 9, and 11) in the summer of 2017. These sites were chosen because they span a wide temperature gradient (4°C mean April – September water temperature) and because salmonflies are relatively abundant (>12 larvae/m²). At each site, 100 m sample reaches were established along uninterrupted stream banks adjacent to riffles, which represents typical salmonfly larvae habitat. Exuviae were collected at the same ten randomly selected one-meter sections of bank within each reach at least 5 times per week during the entire duration of emergence. To determine a relationship between water temperature and salmonfly body size among sites, thirty salmonfly exuviae of each sex were collected on the first date of mass emergence in 2017, defined as the first day with $>25\%$ cumulative emergence at each site. Total exuviae length, excluding cerci, was measured with digital calipers to the nearest 1/10th of a millimeter. Salmonfly exuviae length rather than adult dry mass was used to estimate spatial differences in body size because predation on adult salmonflies was extensive at one of our sites (site 11) and we

were therefore unable to collect sufficient numbers of adults despite there being large numbers of exuviae along the shoreline.

Data analysis

Statistical analyses were performed in R version 3.3.1 (R Core Team 2013). Differences in salmonfly density at sites 1-5 between 1977 and 2017 were compared using a linear mixed effects model with site and year as fixed effects and month alone and month nested within site as a random effects. This model accounted for the non-independence of repeated monthly samples taken at each site. Larval density was log transformed to meet the assumption of normality. The model was fit with the lme4 package (Bates et al. 2014) and significance was tested using a Kenward-Roger denominator degrees of freedom approximation (Kenward and Roger 1997). Post-hoc comparisons of least squares means and confidence intervals for each site and year were calculated using the lsmeans function (Lenth and Herve 2015). We used raw data to create figures illustrating differences in larval densities between current and historical datasets.

A 2-way ANOVA with year and sex as fixed effects was used to compare differences in adult salmonfly dry mass at site 4 between 1977 and 2017. Long-term temporal trends in water temperature and discharge were assessed with linear models. An analysis of covariance (ANCOVA) was used to determine long-term trends in emergence timing at sites 2 and 5 on the Madison River. Both historical and current emergence timing were regressed against mean May water temperature from equivalent sites and years with a linear model. 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 et al. 2000). The relationship between water temperature, sex, and exuviae length among sites was evaluated with an ANCOVA. Mean water temperature from our entire field season (April – September) was used in this analysis, as salmonflies develop for multiple years before emerging (Townsend and Pritchard 1998), and their growth rates are therefore influenced by thermal regimes throughout the year. Salmonflies have a developmental zero of 3.125°C (Townsend and Pritchard 2000), so growth in winter months is likely minimal.

We used multiple linear regression to evaluate temperature and substrate factors that could explain variation in current salmonfly larval densities among all eleven sites. Larval density was log transformed to meet the assumption of normality. The full model used the following 6 explanatory variables that represent stressful physical conditions: mean August water temperature, maximum weekly maximum temperature (MWM), highest 7-day moving average of maximum daily water temperatures, mean July water temperature, percent fine sediment (<1mm), percent of particles embedded, and percent of particles highly embedded (>25% embedded height/total height). A variant of Akaike's Information Criterion corrected for small datasets (AICc) was employed to evaluate all possible combinations of water temperature and substrate metrics explaining variation in current salmonfly larval densities between sites (Hurvich and Tsai 1989). The most parsimonious model was selected based off the difference ($\Delta AICc$) 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 and

Anderson 2002). The MuMIn package was utilized for AICc model selection (Barton 2011).

We evaluated the potential impact of continued water warming on salmonfly range by using ArcGIS 10.5.1 to map water temperature along the Madison River and calculate numerical changes in the proportion of thermally suitable habitat for salmonflies. 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 non-suitable habitat based upon evidence from our current survey of salmonfly distributions on the Madison River and from previous estimations of maximum temperatures tolerable for salmonflies throughout the American West (Huff et al. 2006). Future range contraction was estimated based on 3 potential warming scenarios. The first scenario was based on a linear extrapolation of historic mean August water temperature trends (as recorded by a USGS gage #06041000 located directly below Ennis Reservoir) to the year 2100. The other 2 warming scenarios were 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 (Isaak et al. 2017). 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 (Isaak et al. 2017). Maps were created using NorWest ArcMap

shapefiles (Isaak et al. 2016). Estimated change in salmonfly distribution over the last 4 decades was based on comparison of current surveys and historical datasets (Fraley 1978). Total range contraction was estimated by summing the estimated change in salmonfly distribution over the last 4 decades with the projected additional range loss through 2100 derived from the linear extrapolation of historic mean August water temperatures.

Results

Historical Conditions

Salmonflies experienced range contraction and body size reduction between 1977 and 2017. Salmonfly larvae were detected at all 5 sites in 1977 but were absent during all sampling events at sites below Ennis Reservoir (sites 1-3) in 2017 (Figure 2). We detected significant effects of year (Kenward-Roger ANOVA: $F_{1, 14} = 80.27$, $p < 0.001$), site ($F_{4, 15} = 106.06$, $p < 0.001$), and an interaction between year and site ($F_{4, 47} = 14.22$, $p < 0.001$) on salmonfly larval density. Declines in larval density were statistically significant at all sites below Ennis Reservoir: salmonfly larval density decreased by 1.21 larvae/m² (SE: 0.29) at site 1 (lsmeans: $t = 2.53$, $p = 0.014$), 24.00 larvae/m² (SE: 0.29) at site 2 ($t = 10.42$, $p < 0.001$), and 5.08 larvae/m² (SE: 0.29) at site 3 ($t = 5.84$, $p < 0.001$). There was no evidence of a decline in larval density at the 2 sites upstream of Ennis Reservoir (lsmeans: site 4: $t = 1.63$, $p = 0.11$, site 5: $t = 0.122$, $p = 0.23$). Adult male and female salmonfly dry mass decreased 14.5% and 10.6%, respectively, between 1977 and 2017 at site 4, the only site for which we had both historical and current body size records

(2-way ANOVA: $F_{1,74} = 4.19$, $p = 0.044$, Figure 3). We found no evidence of an interactive effect between sex and year ($F_{1,74} = 0.24$, $p = 0.62$).

Upstream shifts in salmonfly distribution and decreased adult salmonfly body size were coincident with recorded changes in physical stream conditions from 1977 to 2017. Mean August water temperature at the output of Ennis Reservoir increased 1°C (0.25°C/decade) between 1977 and 2017. Mean annual temperature at the same site increased 1.18°C (0.29°C/decade). In contrast to shifting temperature and sediment regimes, flow regime on the Madison River did not change noticeably since USGS gage records began in 1939; temporal trends for both mean annual discharge (lm: $F_{1,71} < 0.0001$, $p = 0.99$) and peak annual discharge (lm: $F_{1,76} = 0.009$, $p = 0.92$) were non-significant.

For the 2 sites where emergence timing data was available, salmonfly emergence timing showed no evidence of advancement between 1973 and 2017 (ANCOVA: $F_{1,72} = 0.13$, $p = 0.72$), but varied widely across years, ranging over 39 days at site 2 and over 41 days at sites 5 (Figure 4a). Notably, no adult salmonflies were observed—and thus emergence date was not recorded—at site 2 below Ennis Reservoir for 13 of the last 20 years. First emergence date was correlated with mean water temperatures in May, the month before emergence, of the same year (lm: $R^2 = 0.75$, $F_{1,18} = 57.17$, $p < 0.001$, Figure 4b). In contrast to increasing mean August and annual water temperatures, May water temperatures have remained consistent since water temperature monitoring began in 1977 (increase of 0.01°C/decade).

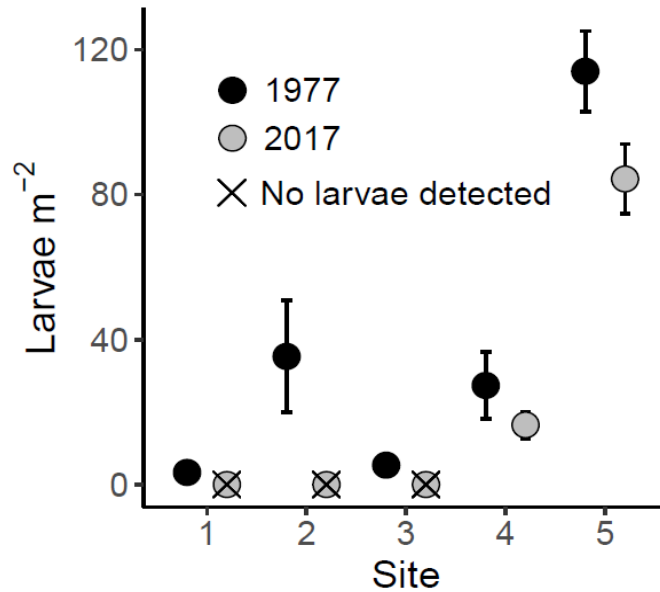


Figure 2. Salmonfly larval densities for 5 sites along the Madison River. Salmonfly larvae were present at all sites in 1977 but were not detected at sites 1-3 in 2017. Values are means \pm 1 SE of $n = 6$ in 1977 and $n = 12$ in 2017. Black and grey circles indicate sampling in 1977 and 2017, respectively. An X overlaying these circles represents a site where no larvae were detected

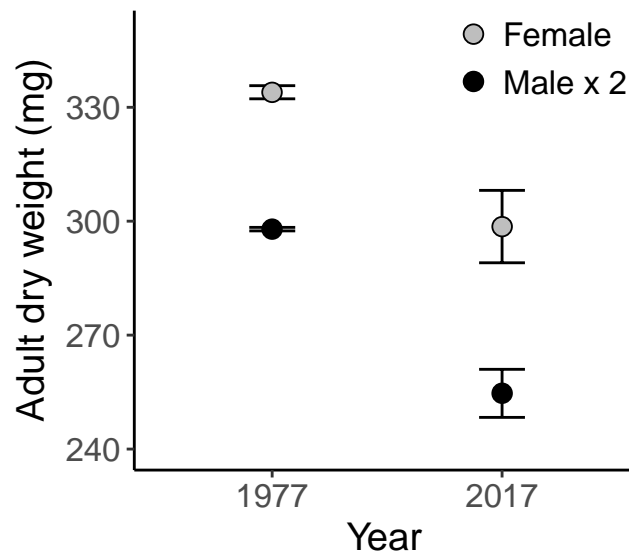


Figure 3. Adult salmonfly dry weight (mg) at site 4 in 1977 and 2017. Mean dry mass across both sexes was 11.8 % smaller in 2017 compared to at the same location 40 years previous (2-way ANOVA: $p = 0.044$). Male dry mass was doubled for ease of graphical viewing. Values are means \pm 1 SE

Current Conditions

Sites within the Madison River spanned large gradients of mean August water temperature (3.7°C), fine sediment (0-33%), and salmonfly larval densities (0 – 117 larvae/m²). AICc model selection analysis indicated that mean August water temperature was the primary constraint on salmonfly population size on the Madison River, explaining 65.0% of variation in salmonfly larval density as the sole variable in the top model (Table 2). Other top models in the AICc output included variables related to fine sediment inputs (Table 2), suggesting that sediment may also play a role in regulating salmonfly abundance in the Madison River.

Salmonfly body size and emergence timing were affected by site-specific thermal regimes. Exuviae length was negatively correlated with mean water temperature from our entire field season (April – September) at each site (lm: $R^2 = 0.72$, $F_{3, 296} = 256.2$, $p < 0.001$), with no evidence of an interactive effect between sex and water temperature (ANCOVA: $F_{1, 296} = 0.11$, $p = 0.74$). Mean male and female exuviae length was 13.8% and 11.3% shorter, respectively, at the warmest site compared to the coolest site (Figure 5a). Median salmonfly emergence date was correlated with mean May water temperature across sites, with emergence occurring earlier where May water temperatures were warmer (lm: $R^2 = 0.85$, $F_{1, 3} = 24.19$, $p = 0.016$, Figure 5b). Median emergence date occurred 24 days earlier at the warmest site relative to the coolest site.

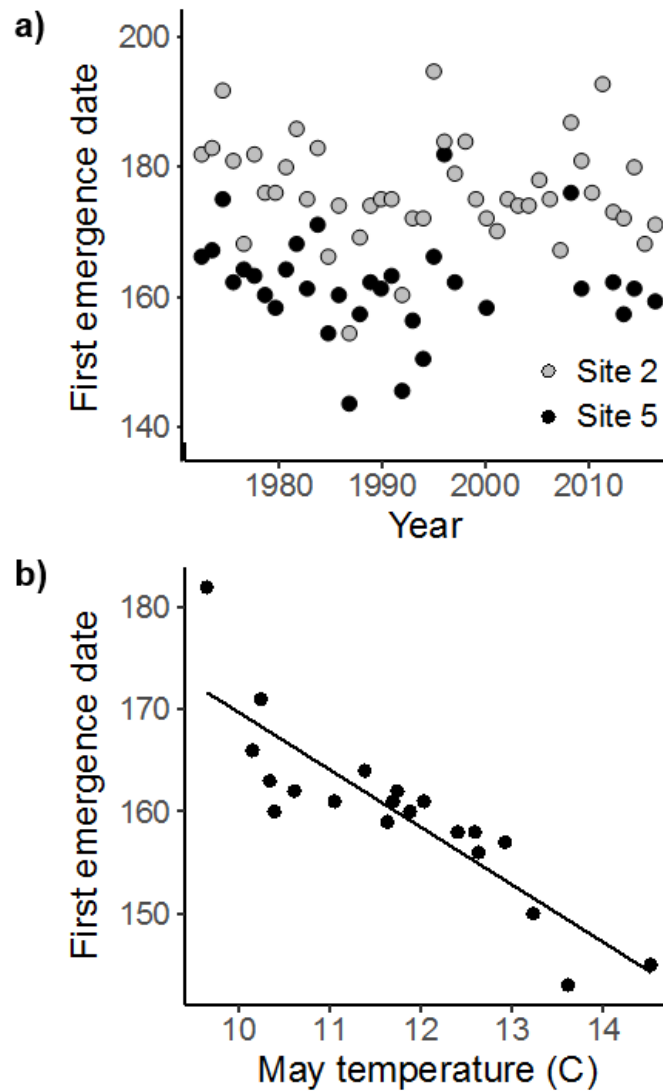


Figure 4. (a) First salmonfly emergence date (day of year) from 1973 to 2017. Emergence timing varied up to 39 days at site 2 and 41 days at site 5 among years. Emergence date did not change over time (ANCOVA: $p = 0.72$). (b) First salmonfly emergence date and mean May water temperature of the corresponding year were strongly correlated (lm: $p < 0.001$, $R^2 = 0.75$)

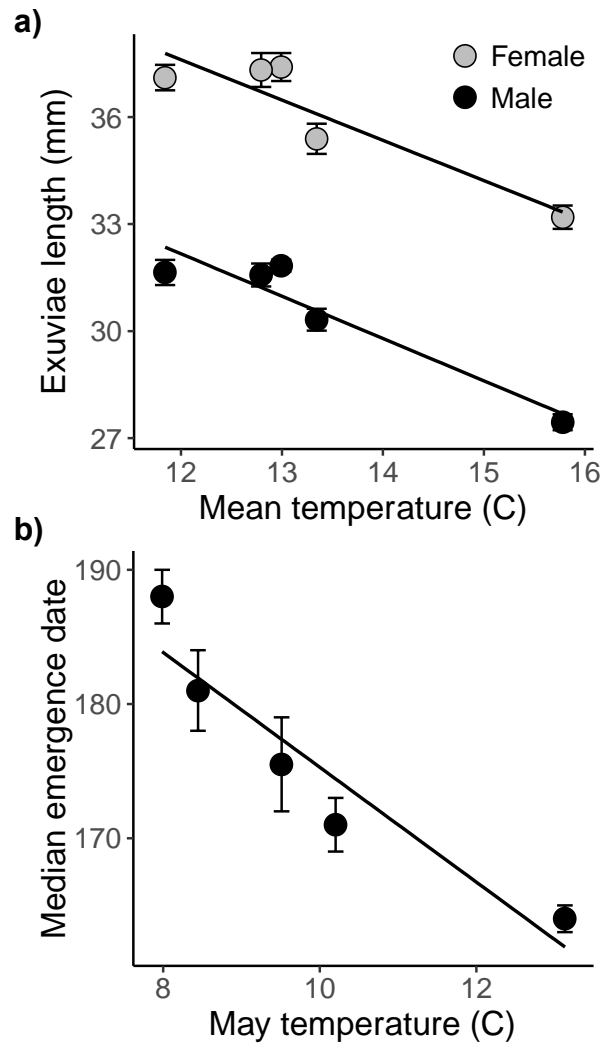


Figure 5. (a) Salmonfly exuviae length (mm) was negatively correlated with mean April – September water temperature (ANCOVA: $p < 0.001$, $R^2 = 0.72$). Values are means \pm 1 SE. (b) Median salmonfly emergence date (day of year) was negatively correlated with mean May water temperature, the month prior to emergence (lm: $p = 0.016$, $R^2 = 0.85$). Error bars represent emergence duration, defined as the first day of > 5% cumulative emergence through the first day of > 95% cumulative emergence

Table 2. Model predictions of salmonfly (*Pteronarcys californica*) larval density using variables related to temperature and substrate quality where $\Delta AICc < 5$

Model variables	R^2	AICc	$\Delta AICc$	AIC wt.
Mean August Temperature	0.65	41.2	0.00	0.40
Mean July Temperature	0.63	41.8	0.52	0.31
Mean August Temperature + % Particles embedded	0.69	45.2	3.92	0.06
Mean July Temperature + % Particles embedded	0.69	45.3	4.02	0.05
Mean July Temperature + % Particles highly embedded	0.68	45.4	4.13	0.05
Mean August Temperature + % fine sediment	0.68	45.4	4.16	0.05
Mean August Temperature + % Particles highly embedded	0.68	45.4	4.20	0.05
Mean August Temperature + MWMT [‡]	0.66	46.0	4.75	0.04

[‡]Maximum weekly maximum temperature

Future Conditions

Future range contraction was estimated based on 3 potential warming scenarios. The first scenario was based on a linear extrapolation of observed mean August water temperatures on the Madison River between 1917 and 2018 (USGS 2017). In this scenario, assuming observed warming trends continue linearly, mean August water temperatures will increase approximately 2°C by 2100. A warming of this magnitude will result in a further loss of 29.9 km of suitable salmonfly habitat, for a total of 50.1% habitat loss on the Madison River since 1977 (Figure 6). Regional projections of water temperatures in the Madison River based on the A1B climate scenario (Isaak et al. 2017) similarly 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, and 36.0 will exceed suitable conditions by 2100 if stream segments warm differentially. Salmonfly populations directly above Ennis Reservoir were the most at-risk in all projection scenarios.

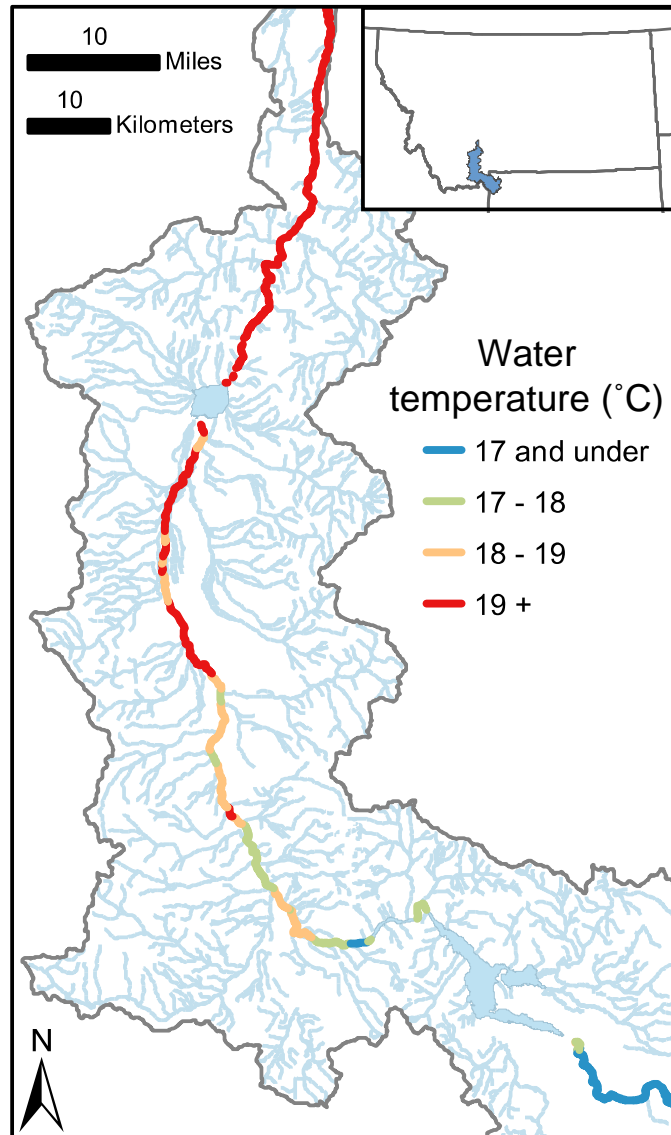


Figure 6. Projected mean August water temperature along the Madison River for 2100, assuming an increase of 2°C from present. This increase is based linear extrapolations of observed warming trends from 1977 to 2017 to 2100 (USGS 2017). Red lines indicate areas where mean August water temperature is expected to exceed 19°C and salmonfly populations will likely be unable to persist. This model predicts a loss of 30 river kilometers of currently occupied salmonfly habitat

Discussion

We coupled rare long-term records with current surveys to provide empirical evidence of temperature-driven changes in the distribution, body size, and emergence timing of a large aquatic insect in the Madison River. Upstream range contraction and decreased body size for salmonflies coincided with a 1.2°C increase in mean annual water temperature, but emergence timing did not advance between 1973 and 2017, likely due to non-uniform warming throughout the year. Salmonfly abundance, body size, and emergence timing were all negatively correlated with water temperature across a spatial gradient of water temperatures. Our approach highlights the usefulness of combining historical datasets with spatial datasets to explicitly address species' responses to environmental stressors across both space and time.

As climate change continues to accelerate, geographical shifts of species distributions towards higher latitudes and elevations are accelerating and becoming more widespread (Chen et al. 2011). These rates of distributional change can be particularly pronounced for cold-water obligate freshwater species (Comte and Grenouillet 2013). In this study, we provide evidence of upstream range contraction for a sensitive freshwater species. We documented the loss of salmonflies from the 64 river kilometers below Ennis Reservoir. In 1977, salmonflies were found throughout the entire length of the Madison River. 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 2.5x the sampling area in 2017 compared to 1977. Further, salmonfly larvae were relatively abundant at site 2 below Ennis Reservoir in 1977 (35.3

larvae/m²), but have not been observed emerging at this site in 13 of the last 20 years. Our findings are corroborated by biomonitoring data collected on the Madison River by Northwestern Energy; salmonflies have not been detected since 2012 at their 3 annual monitoring sites below Ennis Reservoir (Northwestern Energy 1997 - 2016). Thus, while salmonflies may persist in portions of the Madison River below Ennis Reservoir at very low densities, they no longer fill the functional, ecological roles (e.g., organic matter processing or prey for fish and terrestrial predators; Rockwell and Newell 2009, Lecerf and Richardson 2011) that they likely did when they comprised a larger part of the benthic community.

The negative effects of water temperature warming for cold-water obligate species are exacerbated by other anthropogenic stressors such as increased fine sediment deposition (Schindler 2001). Our results suggest that in the Madison River salmonfly populations are primarily constrained by above-optimal water temperatures, whereas fine sediment only exerts a secondary control on current salmonfly distribution and abundance. This analysis could potentially downplay the importance of fine sediment in controlling salmonfly distribution at the most downstream extent of this river, as sites 1 and 2 were characterized by both water temperature and fine sediment values that exceed previously determined optima for the *Pteronarcys* genus (Huff et al. 2006). Qualitative comparisons of field site descriptions from 1977 (Fraley 1978) and 2017 indicate that fine sediment and embeddedness have likely increased below Ennis Reservoir. Interactions between increased water temperature and fine sediment inputs are common in freshwater ecosystems, and can have severe synergistic responses at the population,

community, and ecosystem scales, altering nutrient flow and decreasing abundance and diversity of freshwater taxa (Piggott et al. 2012). To establish how species will respond to climate change and increasing water temperatures throughout their range, future work might address how water temperature tolerance thresholds change where multiple stressors are operating.

Reduced body size has been suggested as a universal response to global warming and has been documented across a variety of ecosystems and trophic levels (Daufresne et al. 2009, Gardner et al. 2011). This temperature-driven response is particularly pervasive for freshwater species (Forster et al. 2012). Aquatic ectotherms that experience water temperatures exceeding their thermal optimum are predicted to be smaller and less fecund (Vannote and Sweeney 1980, Angilletta et al. 2004). Previous work supports this prediction for salmonflies, with salmonfly egg hatching success dropping off at temperatures exceeding 17.5°C in a laboratory setting (Townsend et al. 2000). Our results also align with theoretical predictions, displaying a negative relationship between salmonfly body size and water temperature observed both spatially, among sites synoptically sampled across a water temperature gradient in 2017, as well as temporally, with reduction of adult body size coincident with warming water temperatures since 1977. Reduced adult body size can have fitness consequences for at-risk populations, since ovariole number and mass is positively correlated with female body size for most insects (Honěk 1993). Consistent body size reductions could affect entire ecosystems by modifying the overall size structure and altering size-dependent food web dynamics (Hansen et al. 1994, Hildrew et al. 2007).

Experimental and observational studies have established that although species vary in the magnitude of their responses, increased water temperature predictably results in quicker development and correspondingly earlier emergence for aquatic insects (Harper and Peckarsky 2006). Similarly, we found that salmonfly emergence was strongly correlated with mean May water temperatures in both spatial and temporal datasets; salmonflies emerge earlier when water temperatures are warmer. However, despite an observed increase in mean annual water temperature over the last 4 decades, salmonfly emergence timing did not advance significantly between 1973 and 2017. Trends towards earlier emergence timing were likely not evident in this system because of non-uniform warming throughout the year. Increases in water temperature were negligible in the spring and early summer months, when water temperatures cue salmonflies to emerge, and were more pronounced in late summer and early fall. 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 nevertheless have important ecological implications for aquatic-terrestrial energy flow, as life histories and movement patterns of consumers such as birds (Tarwater and Arcese 2018), amphibians (Todd et al. 2010), and fish (Kovach et al. 2013) are often sensitive to climate change, creating a potential for a mismatch in the timing of resource availability and consumer need.

Given the exponentially increasing temperatures predicted by climate models (IPCC 2014), the historically high rate of water temperature increase on the Madison River (Isaak et al. 2017), and evidence of a salmonfly population primarily constrained

by above-optimal water temperatures, salmonfly populations on the Madison River are very likely to experience further upstream range contraction and reduced body size into the future. We predict that the historic range of salmonflies on the Madison River could be halved by the end of the century. A loss of this magnitude has the potential to alter aquatic-terrestrial energy flow and consumer foraging behavior, as salmonflies often make up the majority of benthic biomass when present (Nehring et al. 2011) and are an important food resource for terrestrial and aquatic consumers (Rockwell and Newell 2009). Species throughout the world are being lost at accelerating and undefined rates (Ceballos et al. 2015). Many current conservation efforts focus on large, charismatic species, but it is equally critical to document change for less-studied taxa like aquatic insects that form the base of the food web and to further understanding of how their loss will affect ecosystem dynamics into the future.

Ecologists overwhelmingly recognize that multi-site, long-term research is critical for both advancing ecological theory and understanding the impact of processes like global change which play out over many years (Kuebbing et al. 2018). Freshwater ecosystems are increasingly altered by a variety of factors including climate change, land use change, impoundment, and water extraction (Carpenter et al. 2011), but documenting the effects of these alterations has proven challenging due to a lack of historical datasets and consistent monitoring efforts, particularly at the historical boundaries of species' distributions where signs of physiological stress, altered life history patterns, and range contraction will necessarily first appear (Tingley and Beissinger 2009). This study contributes to the limited list of studies displaying empirical evidence of temperature-

driven range contraction and body size reduction using long-term datasets. Biological evidence of long-term change is necessary to further understanding of how predicted experimental and modeling impacts compare to observed change, and to inform effective conservation efforts into the future.

CHAPTER THREE

LANDSCAPE FEATURES DRIVE SYNCHRONICITY OF AN AQUATIC INSECT
RESOURCE PULSE

Contribution of Authors and Co-Authors

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Contributions: HEA helped design the study, conducted the research, analyzed the data, and wrote the manuscript.

Co-Author: Lindsey K. Albertson

Contributions: LKA originally formulated the idea and helped write the manuscript.

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Contributions: DMW helped design the study, and contributed critical revisions to later drafts and data analysis.

Manuscript Information

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Ecological Applications

Ecological Society of America

Status of Manuscript: Prepared for submission to a peer-reviewed journal

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 resource pulse phenology is poorly documented. We quantified water temperature and emergence phenology of an aquatic insect (*Pteronarcys californica*) resource pulse in neighboring rivers characterized by differing catchment topography and human impact. Water temperature cued emergence timing, with emergence occurring earlier where temperatures were warmer. Emergence was brief (4-8 days) at sites on the more human impacted river, but occurred asynchronously along the entire extent of the river, lasting 27 days in total. In contrast, emergence was more prolonged (6-11 days) at sites on the more natural, topographically complex river, but occurred in relative synchrony along the entire river, lasting only 13 days in total. Scale-specific differences in subsidy duration could have opposing implications for consumer populations depending on their mobility and foraging habits. Relating environmental heterogeneity and resource pulse phenology across a gradient of human impact is needed for a better understanding of how food availability, aquatic-terrestrial linkages, and consumer-resource dynamics may change in the future.

Introduction

Mounting evidence suggests 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 resources that produce alternating periods of scarcity and overabundance within an ecosystem (Yang et al. 2008). Consumers are often unable to take full advantage of abundant 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 can extend the duration of resource availability and thereby increase consumers' seasonal energy intake (Armstrong et al. 2016). Although the benefit of asynchronous resource pulses to consumers has been well documented in a variety of ecosystems and at multiple trophic levels (Bronstein et al. 1990, Schindler et al. 2013, Searle et al. 2015), variation in resource pulse phenology among locations is not well described.

The phenology of organisms, and therefore the timing of resource pulses, is often cued by environmental conditions such as temperature, precipitation, or photoperiod (Yang et al. 2008). As a result, environmental heterogeneity can result in spatiotemporal variation of resource pulses (Schindler and Smits 2017). Within aquatic systems, organism development and phenology is often driven by water temperature (Allan and Castillo 2007), and thus thermal heterogeneity is a primary determinant of the timing, pattern, and duration of aquatic resource pulses such as spawning fish (Beechie et al. 2008), hatches of aquatic insects (Harper and Peckarsky 2006), 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 (Caissie 2006). However, previous work documenting the phenology of resource pulses in freshwater ecosystems has largely been conducted in relatively complex, pristine watersheds, thus limiting our ability to understand how resource pulse phenology may vary among rivers with differing levels of natural complexity and human activity.

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 (Baxter et al. 2005). Emergent salmonflies (*Pteronarcys californica*) represent a particularly high-quality 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 spectacular, synchronized hatches that provide a significant 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 subsidies to terrestrial ecosystems when abundant (Walters et al. 2018). Thus, variation 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 small (100 m) and large (50 – 100 km) spatial scales along each river.

Methods

Study System

This study was conducted on the Gallatin and Madison Rivers in southwest Montana. Both rivers originate in northwest Yellowstone National Park and flow northwards, joining to form the Missouri River. The Gallatin River is free-flowing, and throughout our study area runs through the Gallatin National Forest. This length is characterized by alternating valley and canyon topography, frequent inputs from large snowmelt tributaries, and a dense riparian zone consisting primarily of conifer forest, willow (*Salix*), and cottonwood (*Populus*). Study sites on the Madison River extend between two reservoirs. Within this length, primary land use consists of livestock grazing with localized dryland and irrigated agriculture, and the riparian zone is dominated by grasses (*Gramineae*) and willow (*Salix*). Tributary streams in the most downstream extent experience dewatering and elevated spring and summer water temperatures due to irrigation withdrawal (Rich and Hagener 2013).

We quantified salmonfly emergence phenology and water temperature at five sites on both the Madison and Gallatin Rivers. 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, 88.7 km for the Madison). Surveys from 2017 confirmed that salmonflies were present at all sites at densities of at least 15 larvae/m² (Table 3).

Emergence timing

We used daily exuvia counts to measure salmonfly emergence phenology at all sites during the summers of 2016 and 2017. Salmonflies emerge en masse in early summer to complete their metamorphosis and mate (Figure 7a). During emergence events, larvae crawl out of the river, leaving their exuvia clinging to shoreline features within a short distance (0-2m) from the water's edge (Figure 7b). Because salmonflies are so large, these abandoned exuvia are conspicuous along the shoreline, and therefore systematic counts of exuvia are a useful method to quantify salmonfly emergence timing and abundance (Walters et al. 2018). At each site, we established 100 m sample reaches along uninterrupted stream banks adjacent to riffles (typical salmonfly larval habitat), and collected and removed exuvia at the same ten randomly-selected one-meter bank transects within each reach at least 5x per week during the entire duration of emergence.

Median emergence date and duration (in days) were estimated for each unique site and year combination. We defined site-specific emergence duration as the first day of > 5% cumulative emergence through the first day of > 95% cumulative emergence, and median emergence date as the median day within this emergence window. River-wide

River	Site	Larvae/m ²	SD
Gallatin	1	15.41	17.51
Gallatin	2	65.78	44.85
Gallatin	3	116.15	96.23
Gallatin	4	69.93	51.28
Gallatin	5	112.59	59.86
Madison	1	16.44	12.76
Madison	2	84.30	33.31
Madison	3	64.44	34.44
Madison	4	23.26	23.86
Madison	5	116.74	80.36

Table 3. Mean salmonfly (*Pteronarcys californica*) density (larvae/m²) at each study site on the Gallatin and Madison Rivers. Aquatic benthic macroinvertebrates were collected in riffles at all sites in July, August, and September 2017 using a 0.75 x 0.75 m surber sampler. Salmonflies were isolated from the bulk sample and enumerated. Four individual samples were taken per site in each of the three months for a total of $n = 12$ per site. Densities were converted to larvae/m². SD is one standard deviation from the mean. Site numbers increase in the upstream direction.

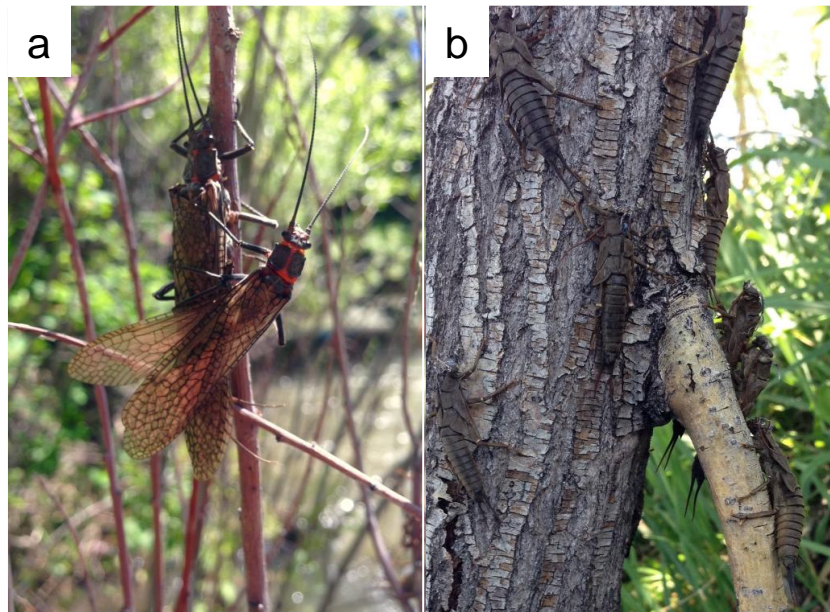


Figure 7. a) Salmonfly larvae crawl from water to land to complete metamorphosis and mate, b) leaving their exuvia clinging to shoreline features (pictured here) or littered along the bank (not pictured). We recorded as many as 165 salmonflies per meter of river bank during emergence events.

duration was defined as the difference between the earliest and latest median salmonfly emergence date for each year and river combination. River-wide emergence was considered asynchronous when emergence timing did not overlap among sites on the same river and synchronous when emergence occurred simultaneously at multiple sites on the same river.

Water temperature

Water temperature was recorded at 30-minute intervals from April 1st – May 31st, 2017 at each site using a HOBO[®] Pendant water temperature logger (Onset Computer, Bourne, Massachusetts) to assess the influence of water temperature on salmonfly emergence timing. Loggers were lost in peak discharge in 2016, so temperature data for that year is 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. 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 was available, and to determine if 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 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 site on each river. Statistical analyses were performed in R version 3.3.1 (R Core Team 2013).

Results

Salmonfly emergence phenology varied markedly between rivers, but exhibited contrasting patterns at different spatial scales. At the river scale, emergence was relatively asynchronous along the Madison River (Figure 8a); the maximum difference in median emergence dates among sites averaged 22.5 days across the two years (21 days in 2016 and 24 days in 2017). In contrast, salmonfly emergence was relatively synchronous along the entire study length of the Gallatin River (Figure 8b); the maximum difference in median emergence dates among sites averaged 5.25 days across the two years (4 days in 2016 and 6.5 days 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 (Figure 9a). 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 on the Gallatin River, lasting an average of 2.0 days longer (SE: 0.53, $P = 0.0016$) than sites on the Madison River, with no evidence for an effect by year (2-way ANCOVA: $F_{1,16} = 0.55$, $P = 0.47$). In total, emergence lasted 27 days on the Madison River and 13 days on the Gallatin River.

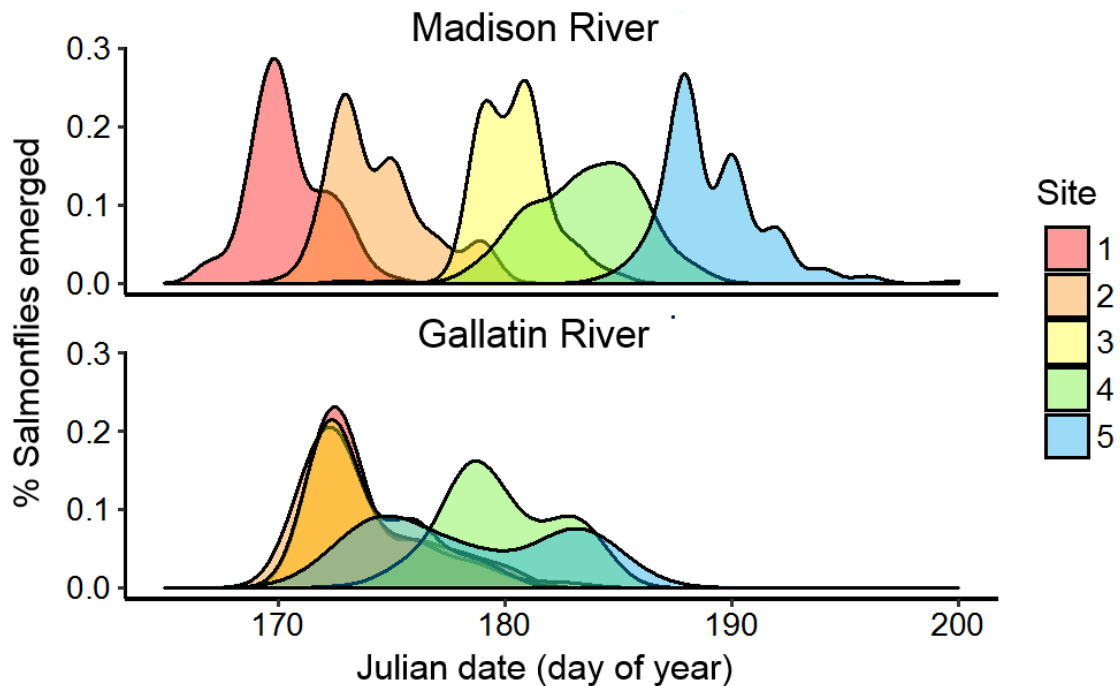


Figure 8. At the river scale, salmonfly emergence was asynchronous along the **a)** Madison River, but relatively synchronous along the **b)** Gallatin River. Site numbers increase in the upstream direction. The area under each curve is equivalent to 1. Emergence data in this figure were pooled across years and grouped by site and river. Data were smoothed using a kernel density estimator with a bandwidth adjustment of 1.4, which was arbitrarily selected because it highlighted general patterns of emergence.

Median salmonfly emergence date was strongly correlated with mean spring water temperature on both rivers (lm: $R^2=0.99$, $F_{3,6} = 469.4$, $P < 0.0001$, Figure 9b), 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 ($F_{1,6} = 37.94$, $P = 0.0008$). Spring water temperatures ranged from 5.0 – 6.6°C at sites along the Gallatin River (1.6°C total water temperature gradient) and from 5.5 – 8.4°C at sites along the Madison River (2.9°C total water temperature gradient).

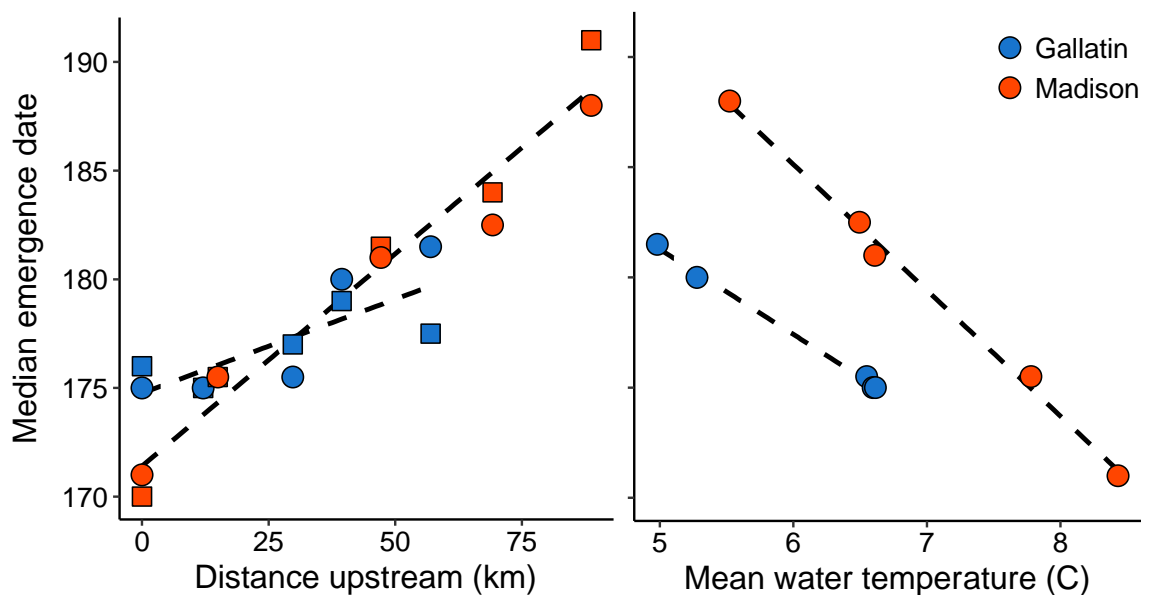


Figure 9. a) Emergence moved from downstream to upstream along both the Gallatin (blue) and Madison (red) Rivers, but traveled slower along the Madison River ($F_{1,14} = 34.79$, $P = 0.002$), lasting 2.26x longer than an equivalent length on the Gallatin River. **b)** Median salmonfly emergence date was strongly correlated with mean water temperature in the months preceding emergence (April – May) at sites on both the Gallatin and Madison Rivers ($R^2=0.99$, $P < 0.0001$). Squares represent data points from 2016 and circles represent data points from 2017. Dashed lines represent significant linear fits with grey shading displaying the 95% CIs.

Discussion

Spatial heterogeneity in water temperature can influence the duration and spatial patterning of aquatic resource pulses (Schindler and Smits 2017). Thermal regimes are highly variable among rivers (Fullerton et al. 2015), but the influence of this variability on resource pulse phenology has been poorly documented. We provide evidence that the availability of an aquatic insect resource pulse varied dramatically in rivers characterized by differing levels of human impact and topographic complexity, and thus differing thermal regimes. Although salmonfly emergence was brief (4-8 days) at any given site on the more human-impacted Madison River, emergence lasted 27 days along the entire extent of the river, moving in a predictable wave from downstream to upstream. In contrast, salmonfly emergence was more prolonged (6-11 days) at individual sites on the more natural, topographically complex Gallatin River, but occurred in relative synchrony at the river scale, lasting only 13 days in its entirety. Emergence timing was cued by spring water temperatures, occurring earlier in the season at sites where water temperatures were warmer. Our findings highlight the importance of spatial thermal variability in mediating how an aquatic insect resource pulse is propagated across a landscape and demonstrate that resource pulse phenology can vary dramatically among locations, though these patterns may be scale-dependent.

Ecologists increasingly recognize the importance of spatially asynchronous resource pulses in extending foraging opportunities for consumers. Model simulations demonstrate that phenological homogenization can result in dramatic reductions in resource availability (Fryxell et al. 2005, Schindler et al. 2010, Armstrong et al. 2016),

but the degree to which resource pulse synchronicity varies among locations with varying natural and anthropogenic features has not been well described in the field. We documented dramatic and scale-specific differences in the duration of salmonfly emergence between neighboring rivers of similar stream order characterized by differing catchment topography and levels of human impact. These differences in subsidy duration could have opposing implications for consumer populations depending on their mobility and foraging habits. 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 smaller scale, as documented on the Gallatin River, may be most important for immobile or opportunistic consumers like spiders and ants (Uno 2016). 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). Our findings underscore the need to understand the relative importance of resource pulse duration at multiple spatial scales for the entire recipient consumer population.

Homogenization of biotic and abiotic conditions is one of the most prevalent and well-studied consequences of an increasingly human-dominated world (Western 2001, Olden et al. 2004). However, although human activity is often associated with environmental homogenization and more natural ecosystems are associated with environmental heterogeneity, these generalizations may depend on scale and the

environmental attribute of interest. For example, humans can alter the thermal regimes of rivers in numerous, scale-specific ways that can lead to both homogenization of temperatures through processes such as channelization, flood suppression, and changes in riparian land use (Poole and Berman 2001) as well as increased temperature gradients through the creation of large thermal discontinuities such as dams (Ward and Stanford 1983). Similarly, natural features such as tributary inputs, riparian shading, and variable hyporheic exchange can influence spatial patterns of fluvial water temperature ways that are scale and river specific (Poole 2002). We found that sites on the more human-impacted Madison River spanned a relatively large spring water temperature gradient, thereby desynchronizing thermal emergence cues and prolonging subsidy duration at the river scale compared to a relatively small water temperature gradient and shortened subsidy duration along the more natural Gallatin River. These findings illustrate that human-induced alteration of environmental conditions can dramatically alter resource pulse phenology, but suggest that human influence may not ubiquitously homogenize environmental conditions and shorten subsidy duration as has been previously posited (Schindler and Smits 2017).

As shown in this and previous studies, habitat heterogeneity can spatially desynchronize the timing of resource pulses cued by environmental conditions, and thus prolong resource availability for consumers (Coogan et al. 2012, Lisi et al. 2013). However, environmental variability can also result in phenotypic and genotypic divergence within prey populations that can influence the magnitude and quality of resource pulses. For example, water temperature is the primary determinant of aquatic

insect body size and emergence timing (Sweeney and Vannote 1978), which have the potential to influence consumer density and behavior (Yang et al. 2010). Further work is needed to parse apart the differential effects of environmental heterogeneity on subsidy duration, magnitude, and quality, and the relative importance of each for consumer populations, in order to better predict how the relationship between consumers and subsidies may change with climate change and increasing human activity in the future.

Conclusion

Climate change 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 significance (Parrella et al. 2006), and benefit consumers ranging from beetles and spiders (Paetzold et al. 2005) to grizzly bears (Deacy et al. 2016). Given the widespread alteration of the natural environment and the ubiquity of resource pulses, more work linking environmental heterogeneity and resource pulse phenology across a gradient of human impact is needed to better understand ongoing changes to resource availability, consumer-resource dynamics, and cross-ecosystem subsidies.

CHAPTER FOUR

CONCLUSION

In this thesis, I quantified spatial and temporal variation of salmonfly abundance, body size, and emergence timing between the Gallatin and Madison Rivers in southwest Montana, as well as among sites on each river, and then related observed variation with differences in environmental conditions. Most notably, I found evidence for temperature-driven changes in salmonfly distribution and body size along the Madison River in the last four decades and observed marked differences in emergence phenology and duration at multiple spatial scales between the Madison and Gallatin Rivers. Given the declines in salmonfly abundance as demonstrated in this and other studies (Stagliano 2010, Nehring et al. 2011), it is critical to further understand how salmonfly populations influence broader ecosystem dynamics to be able to predict the impact of ongoing and potential future declines. Future work could address to what extent consumers track ephemeral pulses of emergent salmonflies, the contribution of this resource pulse to consumer physiology and population dynamics, how consumer community composition may vary in rivers displaying marked differences in emergence phenology, and the economic value of salmonfly hatches to local fishing-based businesses.

Although this research focused solely on salmonfly populations in the Madison and Gallatin Rivers, our findings have implications that extend beyond this species and these watersheds. Changes in the ecology of key aquatic insects such as salmonflies in response to altered water resources may result in major changes to river productivity,

aquatic-terrestrial linkages, consumer fitness and behavior, and the continued success of fishing and eco-tourism industries in rivers throughout the American West.

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APPENDICES

APPENDIX A

SUMMARY DATA FROM ALL SITES AND RIVERS

Table A1. Mean salmonfly larval density per m² at each site. Benthic macroinvertebrates were collected in riffles at all sites in on day in July, August, and September 2017 using a modified 0.75 x 0.75 m surber sampler. Four individual samples were taken per site in each of the three months for a total of N = 12 per site. Densities were converted to larvae per m².

River	Site	Mean larval density per m²	SD
Gallatin	1	1.48	4.07
Gallatin	2	4.30	6.76
Gallatin	3	15.41	17.51
Gallatin	4	65.78	44.85
Gallatin	5	116.15	96.23
Gallatin	6	69.93	51.28
Gallatin	7	112.59	59.86
Gallatin	8	11.41	14.17
Madison	1	0.00	0.00
Madison	2	0.00	0.00
Madison	3	0.00	0.00
Madison	4	16.44	12.76
Madison	5	84.30	33.31
Madison	6	27.56	26.83
Madison	7	64.44	34.44
Madison	8	23.26	23.86
Madison	9	116.74	80.36
Madison	10	2.81	6.58
Madison	11	12.59	12.07

Table A2. Salmonfly exuviae length (mm) on the date of peak emergence in 2017 for all sites where emergence was quantified and exuviae were abundant (Site 3 on the Gallatin River and site 8 on the Madison River were excluded because not enough exuviae were present in sample reaches). N = 30 for each unique sex and site combination and SD is 1 standard deviation.

River	Site	Female		Male	
		Mean length (mm)	SD	Mean length (mm)	SD
Gallatin	4	40.07	1.98	32.55	1.60
Gallatin	5	39.95	2.08	32.24	1.10
Gallatin	6	38.53	1.58	32.85	1.41
Gallatin	7	38.63	1.74	32.01	1.69
Madison	4	35.39	2.31	30.32	1.68
Madison	5	37.32	2.60	31.57	1.76
Madison	7	37.11	1.96	31.64	1.93
Madison	9	37.40	2.15	31.83	0.93
Madison	11	33.19	1.78	27.45	1.23

Table A3. Salmonfly dry weight (mg) for adults on the date of peak emergence in 2017 for all sites where emergence was quantified and adults were abundant (excluded sites 3 and 6 on the Gallatin River and site 11 on the Madison River). N = 30 for each unique sex and site combination. SD is 1 standard deviation.

River	Site	Female		Male	
		Mean dry weight (mg)	SD	Mean dry weight (mg)	SD
Gallatin	4	352.71	44.78	148.81	15.43
Gallatin	5	382.36	41.75	159.25	12.50
Gallatin	7	250.40	59.66	131.17	19.14
Madison	4	298.62	52.17	127.36	17.35
Madison	5	346.94	54.94	146.80	15.01
Madison	6	318.16	50.35	138.50	13.48
Madison	8	329.52	71.96	133.70	26.91
Madison	9	337.44	57.34	132.92	12.00

Table A4. Substrate characteristics for each site as determined by a Wolman's pebble count in August 2017. N=200 for each site. D₅₀ is the particle size that 50% of the particles are equal to or smaller than. Percent particles embedded was classified as the proportion of particles > 1mm that where embedded height/total height > 0. Percent fine sediment is the proportion of particles < 1 mm.

River	Site	D₅₀	% Fine sediment	% Particles embedded
Gallatin	1	11.79	10	37
Gallatin	2	9.80	2	28
Gallatin	3	16.89	3	64
Gallatin	4	17.19	1	34
Gallatin	5	14.80	1	26
Gallatin	6	16.18	0	59
Gallatin	7	19.75	0	54
Gallatin	8	14.00	0	41
Madison	1	6.09	19	54
Madison	2	12.60	7	61
Madison	3	14.12	1	44
Madison	4	6.70	6	21
Madison	5	11.74	0	29
Madison	6	15.13	2	47
Madison	7	12.10	1	38
Madison	8	24.43	2	52
Madison	9	14.41	3	34
Madison	10	2.65	33	30
Madison	11	9.58	0	55

Table A5. Mean monthly water temperatures at each site. Temperature was continuously recorded every 30 minutes.

River	Site	April	May	June	July	August	September
Gallatin	1	8.24	10.27	12.21	18.95	19.12	13.35
Gallatin	2	6.83	8.02	9.88	15.43	15.24	10.77
Gallatin	3	6.06	7.17	8.89	14.01	13.88	9.91
Gallatin	4	6.13	7.06	9.06	14.17	14.00	10.00
Gallatin	5	6.31	6.78	8.68	13.81	13.75	10.14
Gallatin	6	4.39	6.17	8.50	13.40	13.30	8.98
Gallatin	7	4.56	5.41	7.69	12.20	11.84	8.37
Gallatin	8	5.75	6.41	8.20	11.72	11.44	8.76
Madison	1	9.28	13.02	16.59	21.62	20.17	14.83
Madison	2	8.56	12.49	16.23	21.45	20.10	14.29
Madison	3	7.92	11.92	15.75	21.10	19.64	13.81
Madison	4	6.66	10.20	13.50	18.93	17.84	12.93
Madison	5	6.05	9.51	12.82	18.19	17.33	12.86
Madison	6	5.50	8.96	12.55	17.96	17.06	12.77
Madison	7	4.77	8.44	11.33	16.98	16.68	12.84
Madison	8	4.69	8.30	11.92	17.13	16.49	13.12
Madison	9	3.06	7.99	13.40	19.61	18.53	15.37
Madison	10	10.76	12.98	16.42	20.51	18.56	14.54
Madison	11	10.89	13.13	16.58	20.67	18.73	14.68

Table A6. First date (day of year) of salmonfly emergence from 1973 to 2016 for two sites along the Madison River as recorded by P.E. Farnes of Snowpack Hydrology. First emergence date was recorded via visual inspection for salmonfly exuviae along the shoreline at each site. NAs represent years where exuviae were looked for but not found.

- First emergence date -			- First emergence date -		
Year	Site 2	Site 5	Year	Site 2	Site 5
1973	166	182	1995	166	195
1974	167	183	1996	182	184
1975	175	192	1997	162	179
1976	162	181	1998	NA	184
1977	164	168	1999	NA	175
1978	163	182	2000	158	172
1979	160	176	2001	NA	170
1980	158	176	2002	NA	175
1981	164	180	2003	NA	174
1982	168	186	2004	NA	174
1983	161	175	2005	NA	178
1984	171	183	2006	NA	175
1985	154	166	2007	NA	167
1986	160	174	2008	176	187
1987	143	154	2009	161	181
1988	157	169	2010	NA	176
1989	162	174	2011	NA	193
1990	161	175	2012	162	173
1991	163	175	2013	157	172
1992	145	160	2014	161	180
1993	156	172	2015	NA	168
1994	150	172	2016	159	171

Table A7. Salmonfly emergence timing and duration at five sites on the Gallatin River and five sites on the Madison River in both 2016 and 2017 as determined by daily exuviae counts during the entire emergence event at each site. An additional site on the Madison River (site 11) was added in 2017. These sites were chosen because they spanned a wide temperature gradient (4°C mean April – September water temperature) and because salmonflies were relatively abundant (>12 larvae per m²). Site-specific emergence duration was defined as the first day of > 5% cumulative emergence through the first day of > 95% cumulative emergence. Peak emergence date was defined as the single date when the most exuviae were collected within our transects. Dates are represented as Julian dates (day of year).

Year	River	Site	First day > 95%	Peak emergence date	First day > 5%	Duration
2016	Gallatin	3	180	172	172	8
2016	Gallatin	4	179	172	171	8
2016	Gallatin	5	182	172	172	11
2016	Gallatin	6	183	180	175	8
2016	Gallatin	7	182	175	173	9
2016	Madison	4	173	170	167	6
2016	Madison	5	179	175	172	7
2016	Madison	7	184	181	179	5
2016	Madison	8	188	185	180	8
2016	Madison	9	194	190	188	6
2017	Gallatin	3	178	176	172	6
2017	Gallatin	4	179	172	171	7
2017	Gallatin	5	179	176	172	8
2017	Gallatin	6	184	178	176	8
2017	Gallatin	7	185	183	178	6
2017	Madison	4	173	170	169	4
2017	Madison	5	179	173	172	7
2017	Madison	7	183	179	179	6
2017	Madison	8	186	181	179	6
2017	Madison	9	190	188	186	4
2017	Madison	11	165	163	163	2

APPENDIX B

SUPPLEMENTARY DATA ANALYSES FOR THE GALLATIN RIVER

Table B1. Top model predictions of salmonfly (*Pteronarcys californica*) larval density in the Gallatin River using variables related to temperature and substrate quality (equivalent methods used for Madison River and described in full in chapter 1). Covariates were inconsistent among the top models, and the intercept-only model was the second best model, suggesting that salmonfly abundance may not be constrained by the temperature and substrate metrics included in this analysis. Further, percent fine sediment and maximum water temperatures at all sites in the Gallatin River were within suitable ranges as defined by previous, region-wide field surveys (Bryce et al. 2010, Relyea et al. 2012).

Model variables	R ²	AICc	ΔAICc	AIC wt.
% Fine sediment	0.53	33.8	0.00	0.341
Intercept only	0.00	34.2	0.44	0.274
Mean July temperature	0.46	34.9	1.17	0.190
Mean August temperature	0.43	35.4	1.59	0.154
% Particles embedded > 25%	0.07	39.3	5.49	0.022
% Particles embedded	0.04	39.5	5.75	0.019

Figure B1. The relationship between water temperature, exuviae length, and sex between the Gallatin and Madison Rivers was evaluated with a three-way ANCOVA. Mean water temperature from our entire field season (April – September) was used in this analysis as salmonflies develop for multiple years before emerging (Townsend and Pritchard 1998), and their growth rates are therefore influenced by thermal regimes throughout the year. Salmonflies have a developmental zero of 3.125°C (Townsend and Pritchard 2000), so growth in winter months is likely minimal. The most parsimonious model included interactive effects of sex, river, and water temperature (ANCOVA: exuviae length ~ water temperature * sex * river, $F_{7, 532} = 281$, $p < 0.001$). As described in Chapter 2, exuviae length was negatively correlated with water temperature for both males and females in the Madison River. These patterns did not hold true among sites in the Gallatin River.

