Reduced Flow and Macroinvertebrate Emergence: How Climate Change in the Eastern Sierra Nevada Threatens Emergence Patterns of Aquatic Insects

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ABSTRACT

At high elevations, climate change will cause extended low flows in mountain streams. In the Sierra Nevada, low flow is predicted to occur two months earlier by 2080 as a result of climate change impacts. Aquatic insects may be especially vulnerable to low flow, which may decrease cross-ecosystem resource subsidies to terrestrial food webs. This thesis aims to understand how extended low flow will affect aquatic insect emergence. The experiment, conducted at the Sierra Nevada Aquatic Research Laboratory (SNARL) in Mono County, California, divided nine experimental stream channels into three treatment groups that simulated different climate change scenarios–unmitigated, mitigated, and current. I examined how early onset summer low flows influence the timing and duration of emergence in aquatic macroinvertebrates. Specifically, I determined how early low flows alter: 1) the abundance of emergent insects; 2) the size of emergent insects, and; 3) the community composition of emergent insects. Seasonality drove most of the variation in size and abundance, however, Chironominae's peak emergence significantly advanced in an unmitigated climate change scenario ($p=2.67 \times 10^{-3}$). Flow timing also explained variation in community composition ($p=0.001$). The impact of low flows on emergence patterns is important to consider as changes in the phenology, biomass, and composition of aquatic insect emergence could benefit some terrestrial consumers at the expense of others.

KEYWORDS

Climate change, benthic invertebrates, freshwater stream ecology, life history, aquatic-terrestrial interactions

INTRODUCTION

Climate change is threatening balanced hydrological systems by shifting natural precipitation, snowmelt, and ice melt patterns (Steel et al. 2018). At high elevations, increased temperatures elevate freezing lines, intensify albedo feedbacks, reduce snowfall, and accelerate snowmelt, all of which alter seasonal flows of snowmelt driven streams (Berg and Hall 2017, Farjad et al. 2017). The Sierra Nevada is a vulnerable area of particular concern due to California's reliance on Sierra Nevada snowpack to act as a natural reservoir for the state's freshwater supply (Reich et al. 2018). Under a "business as usual" scenario, the Sierra Nevada is predicted to experience a 7°C rise in temperature, a 64% reduction in springtime snowpack volume, and an average runoff of snowmelt into streams up to 50 days earlier by the end of the 21st century (Reich et al. 2018). Growing demand for freshwater threatens to further alter streams and to exacerbate the damage to freshwater systems (Hart and Finelli 1999). Although these projections are of valid concern for California residents, early onset low flow environments resulting from shifts in springtime streamflow may impact emergent aquatic macroinvertebrate communities and the aquatic and terrestrial food webs they support (Steel et al. 2018).

Behavioral and compositional characteristics of aquatic macroinvertebrate communities are heavily dependent on the physical conditions of freshwater streams (Dewson et al. 2007, Steel et al. 2017). Flow drives abiotic environmental conditions, thereby triggering responses in macroinvertebrate communities both directly and indirectly based on macroinvertebrates sensitivity to differing habitat conditions (Hart and Finelli 1999). Reduced flows may cause water temperatures to rise, dissolved oxygen availability and nutrient content to shift, the physical structure of streams to be disturbed, and declines in habitat area and heterogeneity (Cowx et al. 1984, Dewson et al. 2007, Steel et al. 2017). Although macroinvertebrate communities have adapted over evolutionary timescales to seasonal flow variability, rapidly altered flow regimes can outstrip adaptive capacity. Reduced density and richness of macroinvertebrates has been associated with reduced flow, but the mechanisms behind these changes are disputed as a result of the complexity of stream systems and the interconnectedness of many environmental variables (Dewson et al. 2007, Rolls et al. 2012). One mechanism likely to explain variation is changing emergence patterns of adult aquatic insects (Jonsson et al. 201).

Emergent insects are a proxy for aquatic insect productivity and play a key role in carrying subsidies from aquatic to terrestrial food webs (Castro-Rebolledo et al. 2013, Salvarina et al. 2016). Aquatic insects emerge from the water, cued by changing environmental conditions, as they transition from pupae to adults (Castro-Rebolledo et al. 2013). Shifts in flow may harm these consumer-resource systems by altering macroinvertebrate life histories (Harper and Peckarsky, 2006). Consequences of early onset low flow includes early emergence and reduced size structure, mating potential, and reproductive success of adults (Peckarsky et al. 2001, Brown et al. 2012). In addition to threatening the stability of macroinvertebrate communities, shifts in emergence threaten terrestrial food webs by destabilizing a reliable source of adult insects for terrestrial consumers, such as spiders, lizards, bats, and some birds (Salvarina et al. 2016). Therefore, it is important to gain a broader understanding of how low flow advancement up to two months earlier in the Sierra Nevada may reshape both aquatic and terrestrial ecosystems. Whereas the impact of low flow has documented changes in macroinvertebrate larvae community composition and abundance, few studies consider how low flow impacts life histories of aquatic insects and their emergence phenology.

In this study, I examine how early onset summer low flows influence the emergence of aquatic macroinvertebrates. Specifically, I seek to understand how the abundance, size structure, and community composition of emerging aquatic insects responds to early low flows. The experimental design involved nine artificial stream channels fed by a natural creek located in the Sierra Nevada. I collected emergence samples throughout the summer as I manipulated flows across the nine channels based on three treatments: 1) low flow 6 weeks earlier than normal (unmitigated climate change scenario); 2) low flow 3 weeks earlier than normal (mitigated climate change scenario); and 3) flow following the stream's current flow regime. I hypothesized that low flows will result in advanced insect emergence, reduced insect size, and shifted community composition.

METHODS

Study system

To understand the change in emergence patterns of aquatic insects under different climate change scenarios, I collected samples of emergent insects during a three-month summer period at an experimental stream complex in the Sherwin Range of the eastern Sierra Nevada mountains. The facilities are managed by The Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California reserve located in Mono County, California at an elevation of 7,200 feet. I used SNARL's nine identical, artificial stream channels to run the experiment. The nine channels, made of concrete, measure 50m in length and 1m in width with identical patterns of riffles and pools. Each channel contains sediment and rocks to match natural streambed characteristics. Stream flow patterns of the nine artificial channels naturally follow that of Convict Creek (lat. 37°37'N, long. 118°50'W), a snowmelt fed creek that feeds directly into the channels. Gates at the head of each channel manually open and close to control the amount of water entering from Convict Creek, and mesh barriers exclude fish from the channels.

The nine channels were randomly assigned into three treatment groups, with three channels (i.e. replicates) per treatment. The natural hydrography of the Sierra Nevada is marked by spring snowmelt that contributes to stream flows throughout the summer (Reich et al. 2018). Historically, peak runoff occurs in late April and early May and drops off around July and August.

I also used 15 year mean annual discharge data for Convict Creek as a baseline to determine each treatment's flow regime (Figure 1). I controlled stream flow at each channel based on treatment group: 1) low flow 6 weeks early to simulate an unmitigated climate change scenario; 2) low flow 3 weeks early to simulate a mitigated climate change scenario; and 3) current low flow timing. The experiment was run from May 1st to August 21st with 6 week early low flow channels reaching low flow July 13th, 3 week early low flow channels reaching low flow August 3rd, and current low flow channels reaching low flows August 21st.
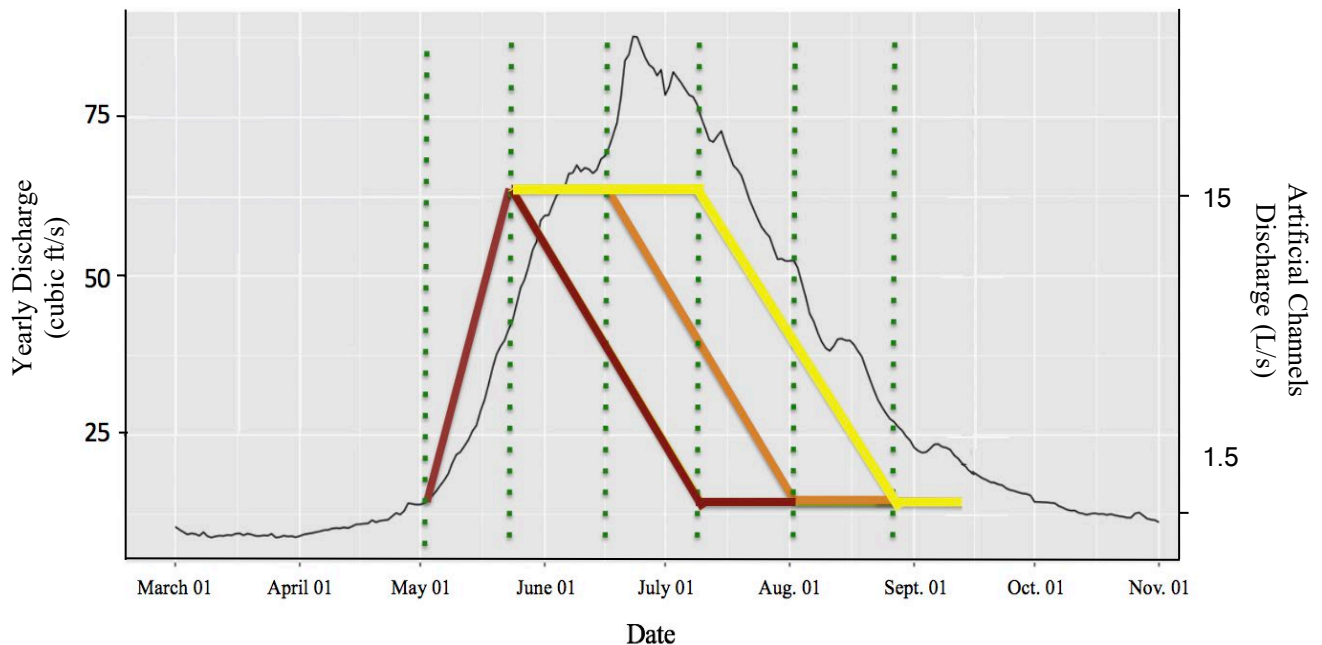
Figure 1. Simulating flow regimes using historical yearly discharge of Convict Creek. The y-axis on the left corresponds to historical yearly discharge, measured in cubic feet per second. Discharge in Convict Creek is much greater than that going into the artificial channels. The y-axis on the right corresponds to controlled discharge in the artificial channels and ranges from 1.5 to 15 liters per second. The colors represent the three flow regimes (red = 6 week early flows, orange = 3 week early flows, yellow = current flow). The vertical dotted green lines represent sampling dates.

Habitat sampling

Beginning mid-April and lasting throughout the duration of the experiment, I collected measurements of habitat conditions. These measurements included dissolved oxygen (mg/L) (Hobo U26), light (lux) and temperature (°C) (Onset MX2202), conductivity (µS/cm) (Hobo U24-001 Freshwater logger), and depth (m) (Hobo U20). These loggers, attached to concrete blocks alongside channels and deployed in channel pools, logged data continuously throughout the experiment in each of the nine stream channels. I also measured primary production using the light and dark bottle method six times throughout the summer, in tandem with macroinvertebrate sampling. I also measured flow discharge at irregular intervals using a flow velocity meter to generate rating curves and adjust flows when necessary.

Aquatic insect sampling and identification

Emergence trap design and deployment

To determine how early onset periods of low flow impacted insect communities over the summer, I sampled emergent macroinvertebrates every 21 days between May 11th and August 21st (May 11, June 1 and 22, July 13, August 2 and 21), resulting in 6 sample times by the end of the experiment. I collected insect samples from each of the nine channels at each sample time, so that over the course of the summer, 54 insect samples were collected in total. I caught emergent insects using emergence traps that were designed and constructed using templates from Malison et al. (2010) and Cadmus et al. (2016).

I deployed traps between the same riffle and pool site across the 9 channels for a period of 72 hours beginning at 4:00 pm on the first day of sampling. I designed the traps in a rectangular pyramid shape covered in 250μm mesh to funnel emerging insects to the top of the traps and into a Nalgene bottle filled with ½ inch of ethanol. At the end of the 72-hour period, I removed the traps from the channels one at a time and emptied the contents of the Nalgene bottle into a tray. I removed insects from the tray and placed them into a small vial filled with ethanol that was labeled by sample and channel number. After transferring the insects from the Nalgene into the vial, I used a pair of forceps to collect insects that were still alive and trapped under the mesh. I also put these insects into the vial.

Insect identification:

To identify collected insects, I used a stereomicroscope in the Ruhi Freshwater Ecology and Conservation Lab at UC Berkeley. I primarily used the 4th edition of *An Introduction to the Aquatic Insects of North America* to identify aquatic specimens (Merritt et al. 2007). In addition, I used various online expert photo identification platforms to identify the insects (Beuk 2018, Iowa State University 2020). I identified insects to the lowest feasible taxonomic level. I also measured the size of the insects in millimeters using the stereomicroscope, and I determined the sex of Chironomids and Ephemeropterans when possible using visible morphological structures of the genitalia.

Data analysis

I used R (R Core Team 2019) and RStudio (R Studio Team 2016) to analyze my data. To determine the differences in abundance and size of emergent macroinvertebrates between the three treatments, I used a repeated measures analysis of variance (ANOVA) test. To meet the assumptions of normality, I log transformed the average abundance and size data within treatments prior to performing the repeated measures ANOVA, and I produced figures using the package ggplot2 (Wickam 2016)

To visualize changes in the composition of emergent communities, I ran a nonmetric multidimensional scaling (NMDS) ordination using the package vegan (Oksanen et al. 2019). I distinguished NMDS samples based on whether they were collected before (high flow) or after (low flow) the channel's flow was reduced. I also used permutational analysis of variance (PERMANOVA) with the package vegan (Oksanen et al. 2019) to test for significant differences in the community composition and variance between high and low flow samples.

RESULTS

Environmental conditions

Environmental conditions, including maximum hourly temperature and mean daily discharge, varied over time within treatment group in the summer 2019. Rising temperatures were correlated with low flow timing. Maximum hourly stream temperatures from the 6 week treatment channels rose beginning in early-mid June (Figure 2a). The 3 week treatment channels' temperatures rose at the beginning of July (Figure 2a). The temperature in treatment 3 channels rose steadily throughout the summer, reaching an hourly maximum of 25°C and matching 6 and 3 week treatment temperatures in early-August (Figure 2a).

As designed, discharge measurements reflected the three climate change scenarios, with flows dropping first in 6 week early low flow, then 3 week early low flow, and lastly current low flow treatments (Figure 2c). In early July, 6 week treatment channels were at low flow, 3 week treatment channels were at mid flow, and the current treatment channels remained at high flow (Figure 2d). At this time, hourly temperature maximums and minimums varied the most (Figure 2b).
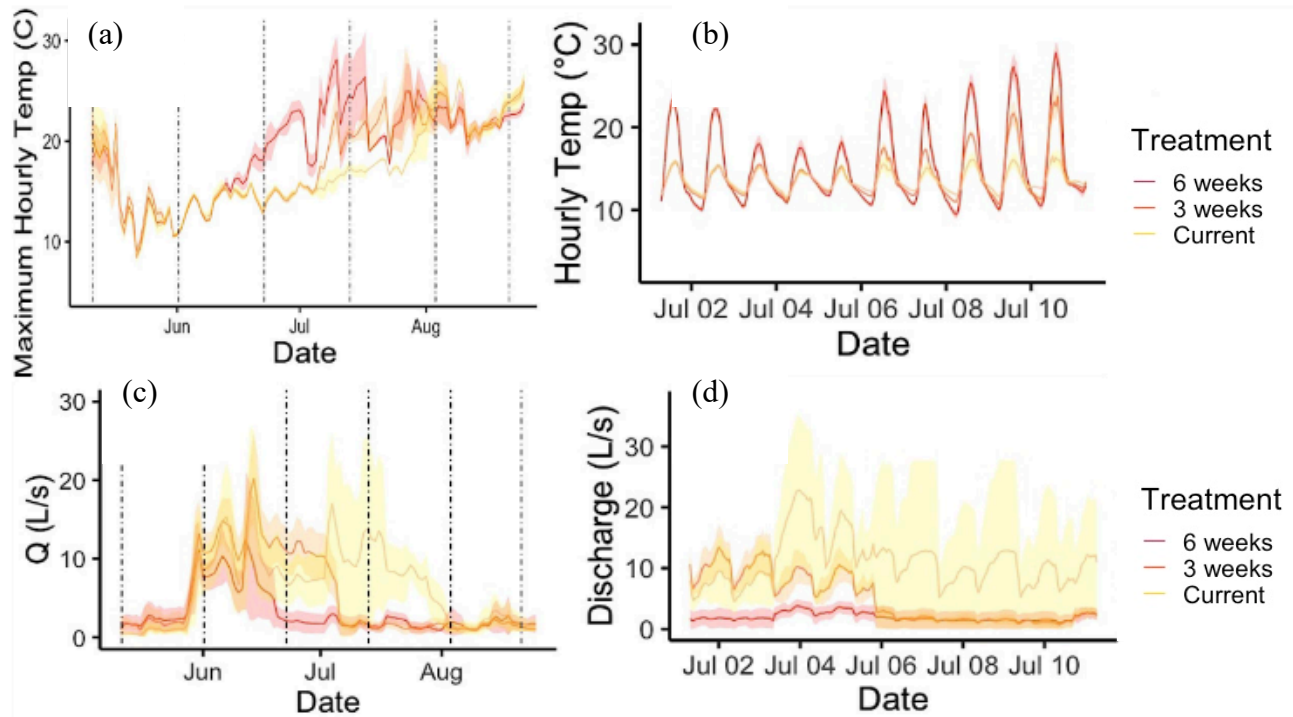
Figure 2. Variations in abiotic conditions across channel treatments over the summer 2019. The red, orange and yellow lines represent the 6 week early, 3 week early, and current early low flow trwatments respectively. Standard deviations in temperature and discharge are shown by the shaded regions with colors representing the same treatment as line color. The dotted vertical lines indicate sampling dates. (a) Maximum hourly temperature (°C) over the summer. (b) Hourly temperature range (°C) in early July. (c) Mean daily discharge (L/s) over the summer. (d) Hourly discharge (L/s) in early July.

Macroinvertebrate emergence

In total, I collected 4,150 aquatic organisms across the six samples (Table 1). Of these, 3,853 belonged to the order Diptera, making it the most abundant order in the study area. Of the Diptera, 3,781 were members of the family Chironomid, with the most abundant subfamilies being Chironominae (2,928 individuals) and Orthocladiinae (672 individuals). Ephemeroptera made up the next most abundant order, with 179 individuals collected. 93 Trichoptera and 13 Plecoptera were collected. I identified 4 aquatic Hemiptera and 1 aquatic Coleoptera. Some terrestrial insects belonging to the orders Aranea, Coleoptera, Hemiptera, Orthoptera, Hymenoptera and Thysanoptera were collected and identified, however I did not include terrestrial insects in the data set for analysis.

Table 1. Summary of identified aquatic insects within samples, counted by order, family, and some select subfamilies. Additional subfamilies and genera of Diptera, Ephemeroptera and Trichoptera, as well as terrestrial insects, are not included.

Species	11-May	1-Jun	22-Jun	13-Jul	2-Aug	21-Aug	Total
Diptera	**102**	**84**	**649**	**979**	**996**	**1043**	**3853**
Chironomid	98	78	631	963	974	1037	3781
Chironominae	38	45	419	768	688	970	2928
Orthocladiinae	93	29	134	139	261	16	672
Prodiamesinae	2	2	42	51	6	16	119
Muscidae		4	10		13	4	31
Ceratopogonidae		1		2	3		6
Culicidae	3						3
Ephydridae	1	1	1				3
Mythicomyiidae			2				2
Phoridae			1	1			2
NA			4	13	6	2	25
Ephemeroptera		**3**	**86**	**67**	**23**		**179**
Baetidae		2	6	54	18		80
Leptophlebiidae			63	7	1		71
Ephemerellidae			9	1			10
Heptageniidae		1		3	1		5
Procleon				1			1
NA			8	1	3		12
Trichoptera			**3**	**24**	**36**	**30**	**93**
Hydroptilidae			1	12	32	26	71
Lepidostomatidae			1	10			11
NA			1	2	4	4	11
Plecoptera			**12**		**1**		**13**
Chloroperlidae			12				12
NA					1		1
Hemiptera		**1**	**3**				**4**
Saldidae			1				1
NA		1	2				3
Coleoptera		**1**					**1**
Curculionidae		1					1
NA					**2**	**5**	**7**
Total	**337**	**252**	**2100**	**3096**	**3063**	**3144**	**4150**

Abundance

The average total abundance of emerging insects increased over time within all three treatments (Figure 3). Average total abundance of emerging insects did not vary significantly between the treatments, but did vary significantly by time, with more insects emerging as the summer progressed based on a repeated measures ANOVA (p=3.98e-0.5, Figure 3a). Analyzing individual taxa alone shows that both time and treatment were significant explanatory variables of differences in Chironominae abundance (p=2.67 x10^{-3}, p=6.12 x10^{-5}, Figure 3b). Furthermore, low flow timing, the interaction between time and treatment, was a significant explanatory variable of differences in Chironominae abundance (p=2.67 x10^{-3}, Figure 3b).
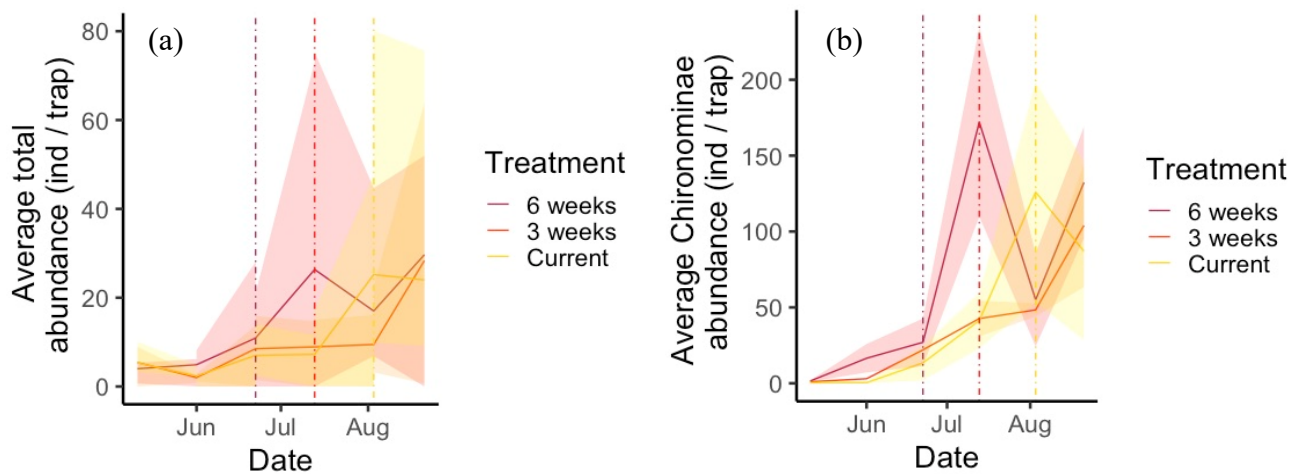
Figure 3. Comparing average abundance of emergent insects over time between treatments. (a) Average total abundance (b) Average Chironominae abundance.

Size

The average sizes of insects in the 6 week, 3 week, and current flow treatments were 2.17 mm, 2.64 mm, and 2.27 mm respectively. The average size across all treatments was 2.36 mm. Low flow timing did not explain the variation in average community size, but time of year did (p=0.0263, Figure 4a). Average community size increased until June 22 under the 6 week early low flow and current low flow treatments, and until July 13 under the 3 week early low flow treatment, before decreasing again. The average size of insects within each treatment was smaller

at the end of the experiment in late August than at the beginning of the experiment in mid May. Neither time nor low flow timing could explain the variation in average size of Chironominae and Orthocladiinae (Figure 4b and 4c).
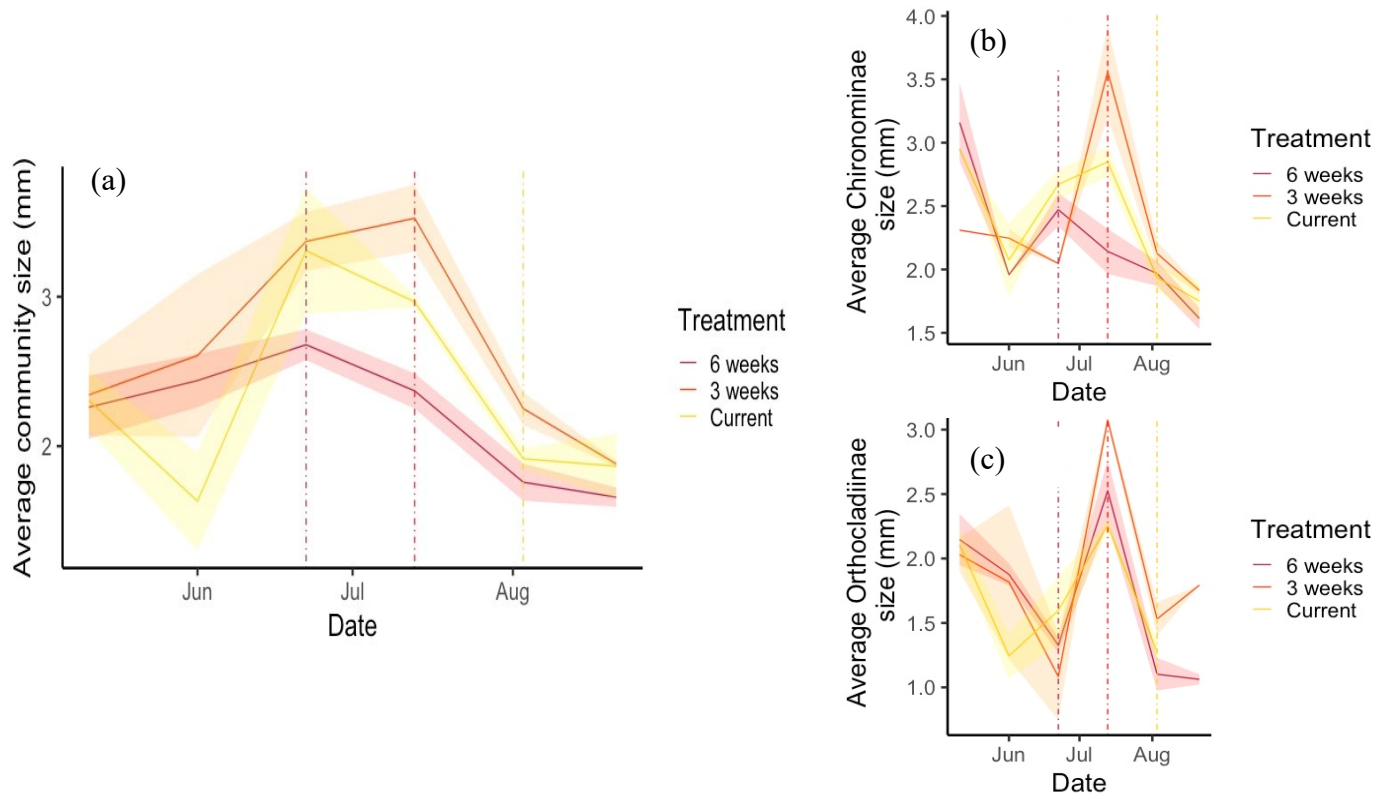

Figure 4. Comparing average size of emergent insects over time between treatments. (a) Average community size (mm) (b) Average Chironominae size (mm) (c) Average Orthocladiinae size (mm).

Community composition

Communities of benthic macroinvertebrates emerging from 6 week and 3 week early low flows treatments did not vary significantly from the communities emergening from streams following current flow regimes, as visualized by a 2-dimensions using NMDS (k=2, stress=0.119, R^2=0.986, Figure 5a). Coordinates included sites and species. Time was a significant explanatory variable of differences in community composition in samples (p=0.001, Figure 5b). I also found that low flow timing explained variation in community composition (p=0.001, Figure 5d). Culicidae was most influential in structuring the ordination at the beginning of the season, while Trichoptera and different species of Diptera were most important later in the season (Figure 5c).
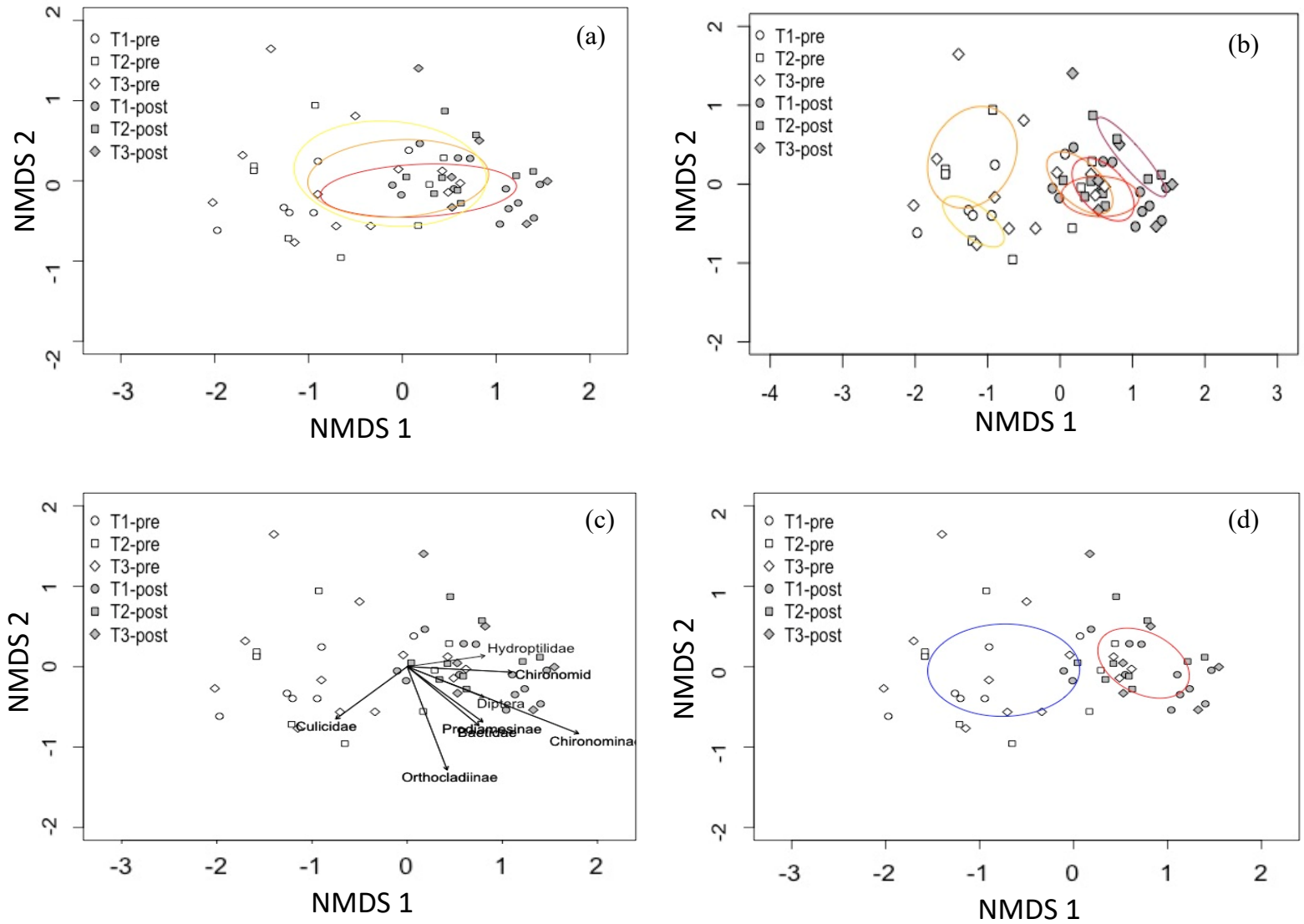
Figure 5. Nonmetric multidimensional scaling (NMDS) ordination of all time and treatments. Symbols represent treatment type (T1 = 6 week early low flow, T2 = 3 week early low flow, T3 = current flow). Shading represents when samples were taken (pre = high flow, post = low flow). (a) Ellipses represent standard deviations around the centroids for the 3 treatments. (b) Ellipses represent standard deviations around the centroids for the 6 sample times. The color gradient from light to dark represents sample times from early to late in the season. (c) Species most influential in structuring the ordination. (d) Ellipses represent standard deviations around the centroids for pre and post low flow samples.

I found that there was a significant variation between low and high flow community variability based on a PERMANOVA analysis (p=0.001, Figure 6). However, the test did not meet the assumption of homogeneity of variance.
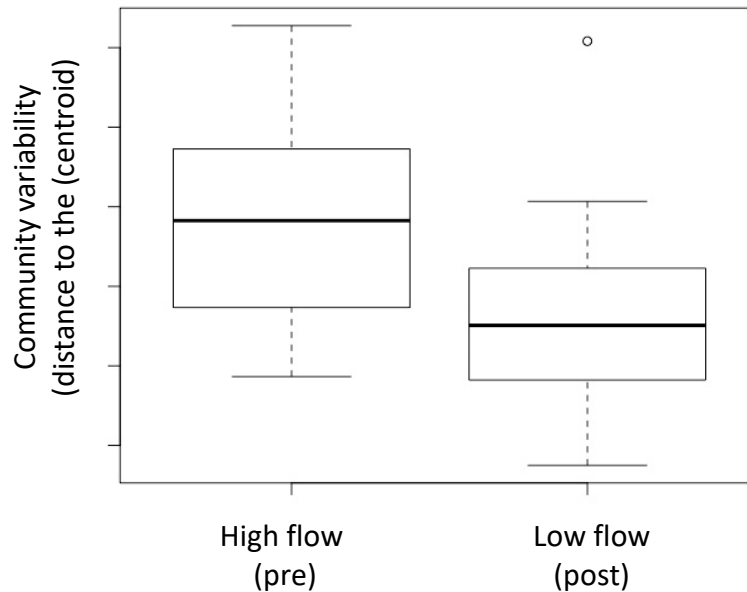

Figure 6. Permutational analysis of variance (PERMANOVA) boxplot. Low flow samples have less variability in community than high flow samples. The assumption of homogeneity was not met.

DISCUSSION

Flow regime alteration is one of the most consequential anthropogenic impacts on streams (Hart and Finelli 1999). Environmental conditions greatly impact aquatic insects' life histories, with advanced low flow threatening to alter aquatic insect phenology and development (Reich et al. 2018, Steel et al. 2018, Harper and Peckarsky 2006). Studies on adult insects and their emergence patterns are important because of adult insects' role as carriers of energy and nutrients from aquatic to terrestrial systems (Ballinger and Lake 2006, Jonsson et al. 2015) and their capacity to alter terrestrial food webs. I found that emergence abundance, size and community composition were significantly influenced by seasonality. Advanced low flow also impacted the emergence timing of specific taxa and altered the community composition of emerging insects. This suggests that low flows are likely to impact ecosystems, with a range of effects on terrestrial consumers depending on their feeding behavior and diet preferences.

Low flow vs. seasonality on abundance and size

Life histories of aquatic insects often adapt to a streams natural flow regime and seasonal variation (Brown et al. 2012, Castro-Rebolledo and Donato Rondan 2015, Closs and Lake 1994, Cowx et al. 1984). Despite their different treatments, the 9 channels all experienced decreased flows, increased temperatures, and similarities in sedimentation based on personal observation. Therefore, it is unsurprising that our analysis supports previous findings that seasonality explains changes in emergence abundance and size (Closs and Lake 1994). Regardless of when flows were reduced, smaller insects emerged in greater abundances later in the season. This finding is consistent with the widespread acknowledgement that changing flows and temperatures, both characteristic conditions of Sierra Nevada summers, induce changes in emergence timing (Brown et al. 2012, Greig et al. 2012, Schulz et al. 2019) and insect size (Brown et al. 2012).

Abundance and size varied throughout the sampling time period, but low flow timing did not significantly influence the abundance or size structure of emerging insect communities as a whole. Terrestrial consumers can be size selective (Jonsson et al. 2015) and can have opportunistic and/or specialized feeding behaviors (Ballinger and Lake 2006). Their consumption patterns may already be adapted so that they primarily feed when insects are emerging more frequently and at larger sizes. Chironominae was the most abundant taxa observed, making up about 71% of all individuals observed, and the abundance of only Chironominae was significantly altered as a result of low flow timing. Chironominae's response to low flow timing suggests that some taxa are more sensitive to low flow than others and that terrestrial consumers will be impacted disproportionately depending on their primary prey source. Other factors linked to low flow timing (e.g. predator density and interactions, resource availability, dissolved oxygen, photoperiod, etc.) can alter emergence patterns (Connolly et al. 2004, Brown et al. 2012, Hansen et al. 1991), and may have influenced why I did not find that more insects were affected by low flow timing. The small sample size of many taxa may also have limited power in detecting changes in emergence for rheophilous or rare taxa.

Low flow and community composition

This thesis' findings support my hypothesis that low flows result in significantly different community compositions of emerging insects, as low flow timing was a significant predictor of community composition in addition to seasonality, a variable that is already linked to changes in the community composition of emergent aquatic insects (Closs and Lake 1994, Wesner 2010). I also found that the communities in low flow conditions were less variable than those in high conditions. The difference in variability between flow levels is interesting in itself because reduced community variability during low flow suggests a potential reduction in beta diversity. However, the failure of the PERMANOVA to meet the assumption of homogeneity of variance undermines these results and raises the concern that the variability in communities impacts our understanding of how different the communities really are.

My experiment suggests that seasonality and low flow timing are likely to affect emergence in aquatic insect communities. Insects may respond to early low flows by emerging earlier, thereby shifting food availability for terrestrial consumers. Earlier emergence could also alter the community compositions of emerging insects, changes that may actually be more important than within-taxa responses (Jonsson et al. 2015). Because adult macroinvertebrates can occupy different trophic levels in terrestrial food webs based on whether or not they feed as adults, changes in community composition can alter terrestrial food webs regardless of stable insect biomass (Greig et al. 2012, Wesner 2010). Furthermore, changes in community composition can impact terrestrial consumers by disproportionately favor terrestrial consumers that feed primarily on midges, like bats, who benefit from feeding on Diptera during certain times of their lives (Clare et al. 2011).

Limitations and Future Directions

Changes in taxa phenology and biomass could have been missed in the analysis because of the small sample size of some taxa. Processing additional samples taken June 11th, July 2nd and 23rd, and August 13th would increase the power of my analysis and might reveal significant differences in the phenology and biomass of other taxa. Future studies spanning multiple summer seasons would also allow for a better understanding of the compounding effects of low flow on emergent insects and terrestrial food webs over multiple years. Larval communities of macroinvertebrates respond differently to changes in flow depending on whether they inhabit riffle or pool sites (Herbst 2018), and comparing the response of emerging insect to low flow from riffles and pools could be a valuable comparative study in the future. Furthermore, examining potential

abiotic mechanisms of change in emergence (e.g. temperature, sedimentation, DO, water velocity, habitat area, etc.) would also be helpful so that the appropriate steps can be taken by management to mitigate changes to freshwater ecosystems from low flows. Lastly, future analysis with larval samples collected from the same study system may be used to see if altered growth in larvae result in shifts in taxa emergence timing.

Broader Implications

Climate change is a global threat to ecological systems. Accelerated snowmelt and altered stream flow may be the greatest climate change threat in the Sierra Nevada (Reigh et al. 2018). Chirinominae, the most abundant taxa, showed advanced emergence during low flow, and the community composition of emergent insects may also differ under early low flow conditions. However, the impact of low flow timing and changing emergence patterns cannot be generalized across all terrestrial consumers. By altering when food is available, what type of food is available, and the amount of food available to terrestrial consumers, low flows could benefit some terrestrial consumers at the expense of others. The consequences of low flow on aquatic insects may have cascading impacts within terrestrial food webs and will be compounded during supraseasonal drought (Wesner 2010). Therefore, emergent macroinvertebrates have the potential to inform how low flows will damage freshwater and terrestrial ecosystems alike due to their important subsidies to terrestrial food webs and sensitivity to changing environmental conditions.

build emergence traps, and prepare the experiment. Thank you also to Guillermo de Mendoza for providing identification support. Access to the site was granted by the Sierra Nevada Aquatic Research Laboratory. Funding was provided by Sequoia Science Learning Center Research Grant and Valentine Eastern Sierra Reserve Graduate Student Award.

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