Annual Report Vol. 43 (2020)

Understanding food web structure in high-elevation streams of the Teton Range

Lusha M. Tronstad[1,3], Scott Hotaling[2], Karen Jorgenson[3], Taylor Price[4], Shannon Weld[5], Sarah Collins[3], Trinity Hamilton[4], Rebecca J. Bixby[5], Debra S. Finn[6]

1 Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY
2 School of Biological Sciences, Washington State University, Pullman, WA
3 Department of Zoology and Physiology, University of Wyoming, Laramie, WY
4 Department of Plant and Microbial Biology, University of Minnesota, Minneapolis, MN
5 Department of Biology, University of New Mexico, Albuquerque, NM
6 Department of Biology, Missouri State University, Springfield, MO
* Author for correspondence: tronstad@uwyo.edu

Abstract Climate change is dramatically altering high-elevation streams around the world through the recession of glaciers and other meltwater sources. Rapidly changing hydrological regimes imperil entire communities of mountain stream biodiversity. We have monitored high-elevation streams in the Teton Range since 2015, with a specific focus on understanding how hydrological source variation affects the susceptibility of downstream communities, and the stoneflies *Zapada glacier* and *Lednia tetonica*, to climate-induced impacts. We monitor streams fed by three sources – glaciers, snowfields, and subterranean ice (primarily rock glaciers). Streams fed by subterranean ice – "icy seeps" – are predicted to persist on the landscape longer than their surface counterparts due to the inherent thermal buffering of their source ice provided by debris cover. We hypothesize that icy seep communities will be buffered against climate-induced environmental changes and will act as key refugia for cold-adapted communities. In late 2019, the conservation implications of our work were escalated by the listing of one of the key species we study, the stonefly *Zapada glacier*, under the US Endangered Species Act due to climate-induced habitat loss. In 2020, our first objective was to collect a 6th year of continuous data for core sites and continue investigating longer term signals in the data. For our second objective, we addressed another large gap in contemporary knowledge of high-elevation stream ecology: food web structure. Despite imminent threats to biodiversity in headwater streams, little is known of the basic quantity and quality of basal resources in mountain streams, how these resources vary with stream type, and linkages between feeding groups. Additionally, little is known about the diet or trophic position of *Zapada glacier*. We will use an array of modern approaches, including stable isotopes and nutrient content analyses, to generate a high-resolution view of food web structure in the high Teton Range. Our results will inform management in the Teton Range while also shedding new light on a standing challenge in mountain stream ecology worldwide.

Introduction

Alpine streams and the biotic communities they contain are imperiled worldwide due to climate warming and the rapid decline of glaciers and other permanent ice features (Hotaling et al., 2017). Directional change in environmental conditions can drive extirpation of local populations, especially for organisms with narrow habitat tolerances. High elevation animal populations may have 'no place to run', such that local extirpations could result in regional extirpations or even global extinctions, given the high degree of endemism common in mountain taxa (Giersch et al., 2015, 2017; Jordan et al., 2016). However, little is known of how climate change will alter species distributions, communities, and ecosystems on a stream-by-stream basis because no long-term study of alpine streams has been conducted. Instead, studies typically rely on space-for-time (SFT) approaches in which catchments with different degrees of glacial influence are compared. While SFT studies provide valuable snapshot assessments that can generate mechanistic hypotheses, they are unable to capture or predict actual change within a catchment. Furthermore, the history of individual locations can have unexpected effects on present-day conditions (Pickett, 1989). Specific to alpine streams, SFT approaches may overlook how hydrological sources feeding streams might change with decreasing influence of surface glaciers. For example, alpine streams with a heavy contribution from subterranean ice (icy seeps) are likely to be more resistant to climate change than streams with no such hydrological buffer to shrinking surface ice sources. This hypothesis is central to our long-term research effort developed with the support of UW-NPS funding.

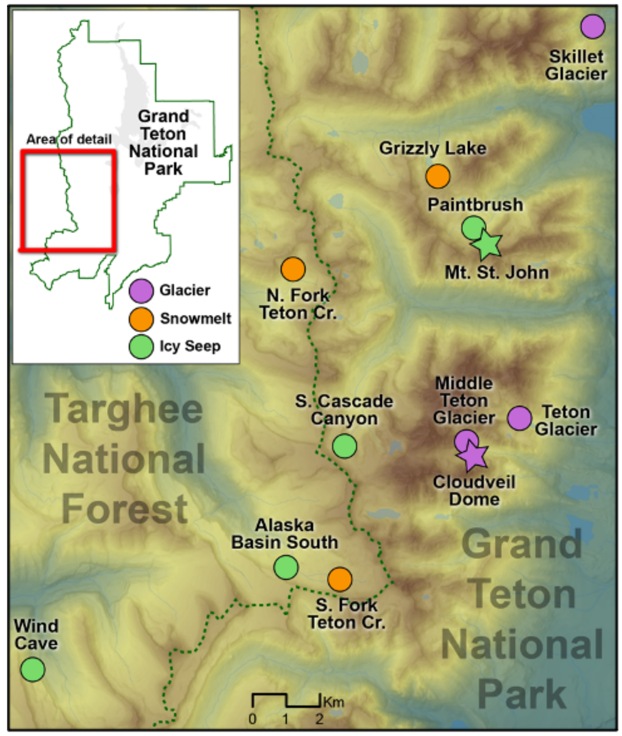

Figure 1. The twelve long-term study sites that make up the Teton Alpine Stream Research (TASR) project. New sites added in 2020 are denoted with stars.

In 2015, we established the Teton Alpine Stream Research (TASR) project to use long-term ecological monitoring to understand how alpine stream biodiversity is structured at present and how it may change in the future. We are using the Teton Range in Wyoming as a surrogate for many mid-latitude mountain ranges around the world that are seeing rapid declines of mountain glaciers and snowpack. Instead of a space-for-time approach where conditions in one drainage (e.g., minimal glaciation) are used as a proxy for future conditions in another drainage (e.g., with extensive present-day glaciation), we are employing long-term, annual monitoring. For the first 5 years of the project, we focused on annually monitoring 10 sites. In 2020, we added two new sites [Mt. St. John (icy seep) and Cloudveil Dome (glacier-fed)] that are easily accessible to improve the robustness of our data set (Fig. 1). This research framework provides a powerful means for disentangling how complex processes are affecting Teton Range alpine streams on decadal timescales while also providing an important space for student training. Our efforts have already yielded many valuable results. We have shown that population genetic differentiation varies across species (Hotaling et al., 2019*a*), microbial communities reflect their hydrological sources (also the first formal description of "icy seeps"; Hotaling et al., 2019*b*), and that macroinvertebrate communities also differ with hydrological source but not to the degree that microbes do (Tronstad et al., 2020). Two of our recent physiology-focused studies are also now published. We used organismal physiology and gene expression to show that our focal stoneflies—including *Zapada glacier*—may be more tolerant of short-term warming than expected (Hotaling et al., 2020). We also showed that our focal stoneflies are not as cold tolerant as expected, further highlighting a potential mismatch between their environmental conditions and physiological needs (Hotaling et al., in review). Thus, it appears likely that other interacting factors (e.g., resource availability, competition) may limit the distributions of these 'meltwater' insects more than environmental conditions alone.

Overall, our most striking result has been the characterization of a new alpine stream type – the icy seep – that is fed by subterranean ice (Hotaling et al., 2019*b*; Tronstad et al., 2020). Historically, alpine streams have been classified into three main types that reflect the diversity of hydrological sources in mountain ecosystems: glacier-fed streams, snowmelt-fed streams, and groundwater-fed springs (Ward, 1994; Hotaling et al., 2017). The unique icy seep stream type had not been formally recognized until we began our work in the Tetons. Rock glaciers and other "cold rocky landforms" (CRLs) are the sources for icy seeps and are broadly important to mountain biodiversity worldwide because they are predicted to persist longer than glaciers and snowfields due to the insulating nature of their debris cover (Anderson et al., 2018) and they are common in mountain ranges worldwide. For instance, in the American West there are ∼5,000 glaciers and perennial snowfields of which around one-fourth are surface glaciers (Fountain et al., 2017). There are more than 10,000 rock glaciers across the same area (Johnson et al., 2021) and a similar story likely exists for other regions (e.g., Scotti et al., 2013; Lilleoren and Etzelmuller, 2011; Charbonneau and Smith, 2018). A major accomplishment associated with our 2020 research has been the submission of a synthesis paper detailing the potential for rock glaciers and other CRLs to serve as climate refugia for not only stream biodiversity (our focus) but also terrestrial and lake/pond biodiversity (Brighenti et al., In review).

For 2020, our UW-NPS funded research had three objectives: (1) continue our long-term monitoring of core sites, (2) collect data on alpine stream food web structure, and (3) collect data to assess longitudinal microbial diversity—from headwaters to lower elevations—in our focal streams. Here, we focus on the results of our first objective—long-term monitoring—as the continuing pandemic has limited the laboratory data processing and analysis for our other two objectives.

Methods

Long-term monitoring

Each year, we collect the same suite of abiotic and biotic data from our core sites. Abiotic data include hourly temperature data from *in situ* temperature loggers, conductivity, dissolved oxygen, and other variables that vary substantially among glacier-fed, snowmelt-fed, and icy seep (Hotaling et al., 2019*b*) stream types and that we expect to respond to changing climate. Our primary biotic data are the macroinvertebrates and algae, which we collect quantitatively. We collected data from our 10 long-term sites (pre-2020) and two new sites that will be included going forward. Our full, 12-site data set includes three snowmelt-fed streams, four glacier-fed streams, and five icy seeps (Figure 1). We aim to prepare a grant proposal for the NSF LTREB program following a 7th year (2021) – both to fill gaps that exist due to a subset of missing core sites in early years, and to include additional biological data in 2021 that are not included as part of our core annual data collection procedures. Of the 10 core sample streams, we currently have four sites with six years of data (2015-2020), three sites with five years of data (2016-2020), and three sites with four years of data (2017-2020). As such, the 2022 field season will mark a completion of 6+ years of continuous data collection at all 10 sites and 71 total site-years of data.

Preliminary results

Abiotic data trends across multiple years

A major driver for the need of long-term ecological data in mountain ecosystems is the interannual variability in snowpack. The first six years of our project highlight this well. During the two years of the project, we collected data during low snow years (Figure 2A). Among the abiotic data shown, year-to-year patterns have been surprisingly consistent. Even specific conductivity (SPC)—a variable known to be influenced by snowmelt —appears largely unresponsive to seasonal snowpack trends (Figure 2B). Our data confirm that SPC is relatively high in icy seeps due to their subterranean source, something we have noted

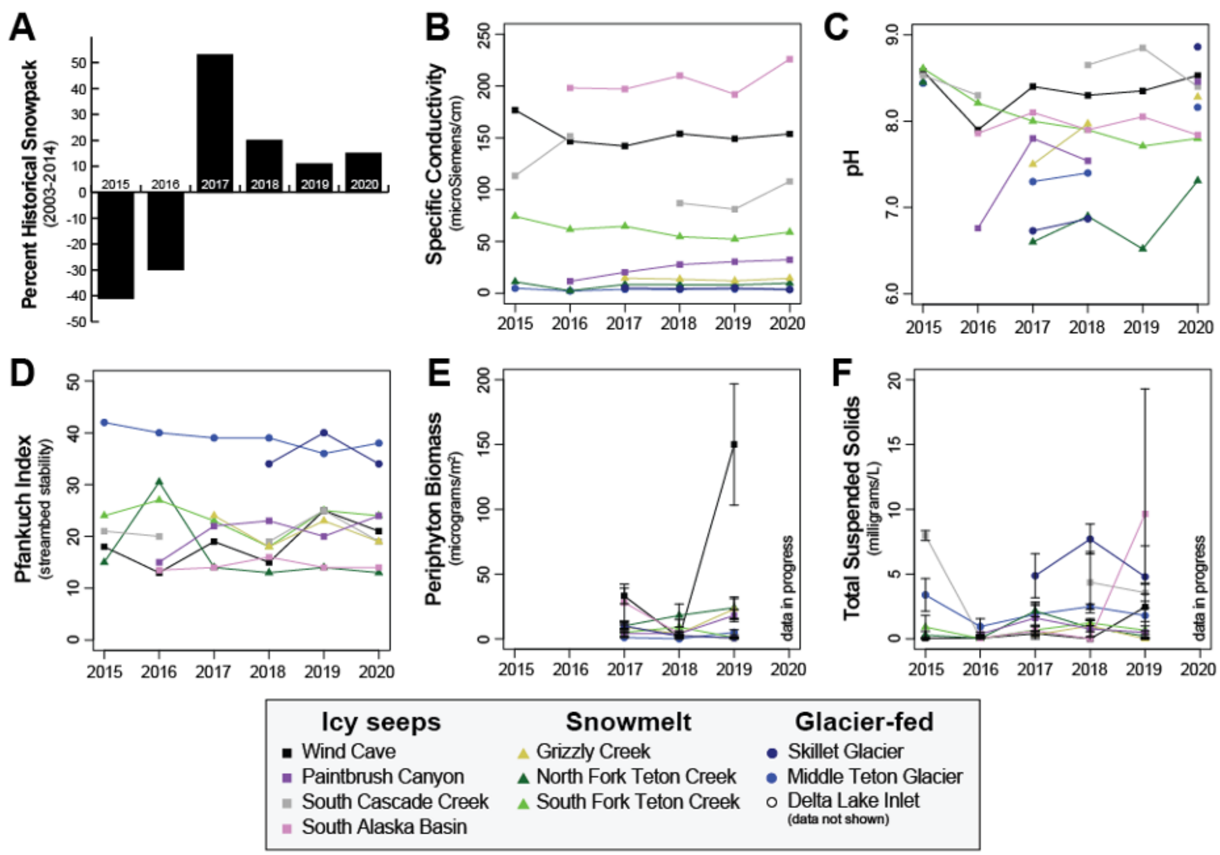

Figure 2. Long-term monitoring data for 10 core sites. (A) Percentage of snowpack versus historical average for each year at a representative SNOTEL site in the Teton Range. (B-F) Five variables collected annually for all sites. Gaps indicate missing data. In (E) and (F), 2020 data are currently in-process. Similarly, some data for the Delta Lake Inlet site below the Teton Glacier are being processed and thus are not shown. A major factor of interest that is not shown here is trends in stream temperature. We are analyzing those data now and will report in 2021.

previously (Hotaling et al., 2019*b*). We began collecting periphyton biomass (algal growth on streambed rocks) in 2017 (Figure 2E). While we don't have enough data to consider longer term trends, we documented much higher periphyton biomass in 2019 at Wind Cave. Wind Cave is fed by subterranean ice and tends to retain little to no snow year-round (Tronstad et al., 2020). The 2019 spike in biomass corresponds to the lowest snow year in the study, perhaps indicating that less snow (and thus more light on the exposed streambed) led to an unusually high amount of biomass that year. These are the types of data points that we are excited to link to other metrics we are collecting (e.g., invertebrate biomass) to better understand how environmental processes such as snowpack influence stream productivity and ultimately resident species. This is particularly interesting given that Wind Cave is the original site where a stonefly of conservation concern, *Lednia tetonica*, was originally described (Baumann et al., 2012).

We measured concentrations of specific ions at our core sites in 2019 and identified intriguing patterns. Several cations (e.g., calcium, magnesium) were an order of magnitude greater in icy seeps than other stream types (Figure 3), likely due to leaching from bedrock. Sulfate concentrations were greatest in glacier-fed streams, likely because glaciers act as larger long-term "collectors" of atmospheric deposition, a major source of sulfate. We observed relatively high concentrations of nitrate (1-3 mg/L) across all stream types (Figure 3A) but only nitrite—an inter-

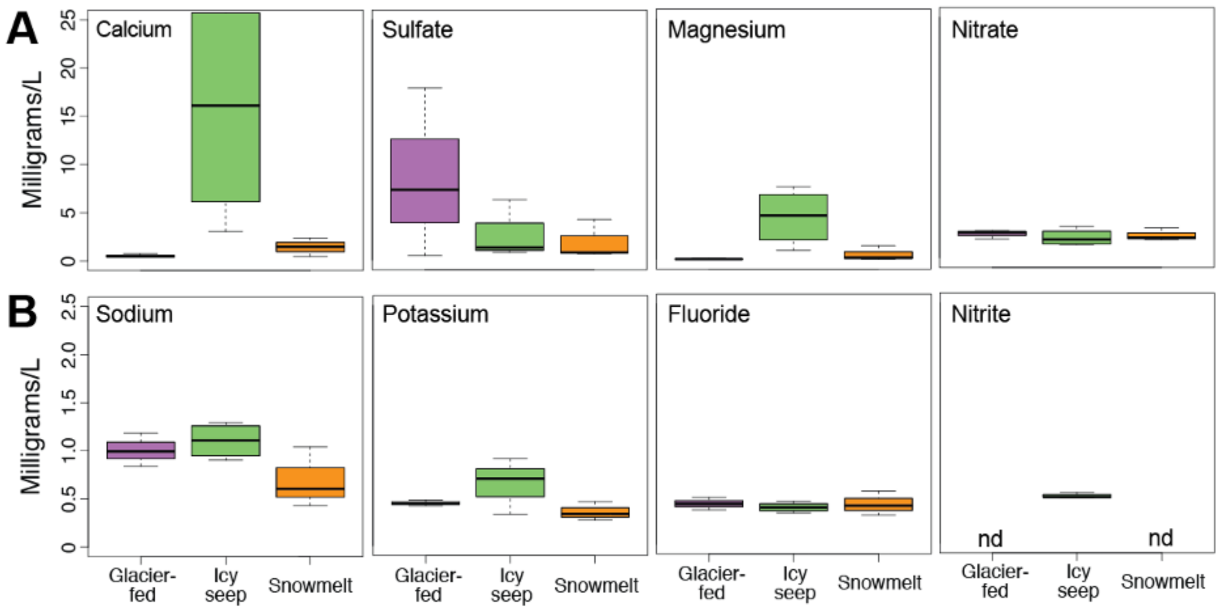

Figure 3. Ion data averaged across our 10 core sites (3 glacier-fed, 4 icy seeps, 3 snowmelt). Note that the y-axis is an order of magnitude for (A) versus (B). nd = not detectable.

mediate between nitrate and ammonium—remained above detectable limits in icy seeps (~0.5 mg/L). We think this is due to higher levels of microbial activity in these habitats. Sodium and fluoride were largely similar across stream types; however, potassium was highest in icy seeps (Figure 3B).

Conclusions

Since beginning this project in 2015, we have made considerable progress. In 2020, three graduate students from three universities joined us in the field. Each student is conducting an independent project within the larger project framework, and are authors on this report (KJ, TP, SW). By integrating students into the work, we are not only adding new biological understanding of Teton alpine streams in a global change context but also providing an environment for student training and success. In 2020, we added two new sites to our project that will increase the robustness of our conclusions in the years and decades to come. With six years of data collection, we continue to move closer to our two long-term goals: (1) testing long-term trends in habitat change in Teton Range across multiple stream types including icy seeps, the stream type that we expect to be most resistant to climate change and (2) establishing the necessary baseline of long-term data to obtain large-scale federal funding from the NSF.

Future work

2021 UW-NPS research

We plan to submit a UW-NPS grant proposal in 2021. Given the listing of *Zapada glacier* and *Lednia tumana* under the US Endangered Species Act in 2019, our monitoring efforts are more pressing than ever. Our proposal will be centered around two goals: (1) Continuing our long-term monitoring of alpine streams and ESA listed species (e.g., *Z. glacier*) in the Teton Range and (2) clarifying the true scale of invertebrate biodiversity in these habitats through the use of molecular metabarcoding. To the first goal, 2021 will mark our 7th year of continuous monitoring. This additional year will raise the number of sites with 6+ years of continuous data from four to seven, an important threshold for our long-term efforts and for the NSF LTREB proposal effort. We will also be able to add an additional year of microbial sampling (2021) to the LTREB proposal. To the second goal, we have historically used morphology to identify sampled invertebrates. While a powerful technique that allows us to readily compare patterns across years, it is well-established that the use of morphology alone leads to underestimation of total diversity due to the presence of "cryptic diversity" (Balint et al., 2011). Cryptic species are those that look morphologically similar to one another yet are genetically distinct. We will use metabarcoding—the bulk extraction and sequencing of DNA from our invertebrate samples—to generate estimates of species richness from both morphology and molecular data for the same samples. This will allow us to estimate the degree to which cryptic diversity is present in alpine streams of the Teton Range and whether or not genetically, but not morphologically, distinct species represent an area of overlooked conservation concern for Grand Teton National Park managers.

Through the remainder of 2020 and into 2021, we will also continue to make progress on three existing projects which will yield manuscripts in 2021: (1) a long-term analysis of stream temperatures to address the question of whether Teton alpine streams warming at a similarly alarming rate to those in the Alps (e.g., Niedrist and Fureder, 2020), (2) clarifying the food-web structure in Teton alpine streams (led by MS student Karen Jorgenson, U. of Wyoming), (3) clarifying microbial community structure among and within drainages (led by PhD student Taylor Price, U. of Minnesota).

Manuscripts published and in preparation

In 2020, we published or submitted four manuscripts from our project: (1) a study linking thermal tolerance and gene expression for alpine stoneflies (Hotaling et al., 2020, *Global Change Biology*) and (2) a related study focused on cold tolerance of the same taxa (Hotaling et al., in review, *Western North American Naturalist*). (3) We also published the results of our initial efforts to assess macroinvertebrate diversity in the Teton Range, highlighting that icy seeps may act as biological intermediaries between glacier- and snowmelt-fed streams (Tronstad et al., 2020, *Western North American Naturalist*). Finally, we organized an international team to write an overarching opinion piece detailing the importance of rock glaciers and other "cold rocky landforms" to terrestrial and aquatic biodiversity in mountain ecosystems worldwide. This manuscript is currently in revision at *Global Change Biology* (Brighenti et al., In review, in revision).

A number of manuscripts are currently in preparation. The first, led by Dr. Tronstad, is focused on the biological diversity of icy seeps specifically and stems from our summer 2016 fieldwork. The second, led by PhD student Matthew Green (UC Irvine), will be a review of the *Lednia* genus in North America with a focus on distribution, ecology, and climate change threats. The third, led by PhD student Taylor Price (U. of Minnesota), details the microbial diversity of our focal streams and stems from fieldwork conducted in 2018 and 2019. The fourth, led by MS student Karen Jorgenson details (U. of Wyoming), will focus on food-web structure in our focal alpine streams and will stem from fieldwork Karen performed with our group in 2020. And, finally, a fifth study, led by Dr. Hotaling, will focus exclusively on long-term trends in temperature across Teton alpine streams and will explicitly compare our North American results to a related study from the Alps (Niedrist and Fureder, 2020).

Acknowledgements

We thank the UW-NPS Research Station for continued grant and staff support and park staff for logistical assistance.

References

Anderson, R. S., L. S. Anderson, W. H. Armstrong, M. W. Rossi, and S. E. Crump. 2018. Glaciation of alpine valleys: The glacier - debris-covered glacier - rock glacier continuum. Geomorphology **311**:127–142. ⟨GotoISI⟩://WOS:000432759400011.

Balint, M., S. Domisch, C. Englehardt, P. Haase, S. Lehrian, J. R. Sauer, K. Ttheissinger, S. Pauls, and C. Nowak. 2011. Cryptic biodiversity loss linkted to global climate change. Nature Climate Change **1**:313–318.

Baumann, R. W., R. G. Call, and M. L. Bean. 2012. Lednia tetonica, a new species of stonefly from Wyoming (Plecoptera: Nemouridae). Illiesia **8**:104–110.

Brighenti, S., S. Hotaling, D. S. Finn, A. G. Fountain, M. Hayashi, D. Herbst, J. Saros, L. M. Tronstad, and C. Millar. In review. Rock glaciers and related landforms: Overlooked climate refugia for mountain biodiversity. Global Change Biology .

Charbonneau, A. A., and D. J. Smith. 2018. An inventory of rock glaciers in the central British Columbia Coast Mountains, Canada, from high resolution Google Earth imagery. Arctic Antarctic and Alpine Research **50**. ⟨GotoISI⟩://WOS: 000440275100001.

Fountain, A. G., B. Glenn, and H. J. Basagic. 2017. The geography of glaciers and perennial snowfields in the American West. Arctic Antarctic and Alpine Research **49**:391–410. ⟨GotoISI⟩://WOS:000407837100004.

Giersch, J. J., S. Hotaling, R. P. Kovach, L. A. Jones, and C. C. Muhlfeld. 2017. Climate-induced glacier and snow loss imperils alpine stream insects. Global Change Biology **23**:2577–2589. ⟨GotoISI⟩://WOS:000402514900006.

Giersch, J. J., S. Jordan, G. Luikart, L. A. Jones, F. R. Hauer, and C. C. Muhlfeld. 2015. Climate-induced range contraction of a rare alpine aquatic invertebrate. Freshwater Science **34**:53–65. ⟨GotoISI⟩://WOS:000349995000005.

Hotaling, S., D. S. Finn, J. J. Giersch, D. W. Weisrock, and D. Jacobsen. 2017. Climate change and alpine stream biology: Progress, challenges, and opportunities for the future. Biological Reviews **92**:2024–2045. ⟨GotoISI⟩://WOS: 000412314400009.

Hotaling, S., M. E. Foley, L. H. Zeglin, D. S. Finn, L. M. Tronstad, J. J. Giersch, C. C. Muhlfeld, and D. W. Weisrock. 2019*a*. Microbial assemblages reflect environmental heterogeneity in alpine streams. Global Change Biology **25**:2576–2590. ⟨GotoISI⟩://WOS:000497502700007.

Hotaling, S., J. J. Giersch, D. S. Finn, L. M. Tronstad, S. P. Jordan, L. E. Serpa, R. G. Call, C. C. Muhlfeld, and D. W. Weisrock. 2019*b*. Congruent population genetic structure but differing depths of divergence for three alpine stoneflies with similar ecology and geographic distributions. Freshwater Biology **64**:335–347.

Hotaling, S., A. A. Shah, M. E. Dillon, J. J. Giersch, L. M. Tronstad, D. S. Finn, and J. L. Kelley. in review. Cold physiology of mountain stoneflies (Plecoptera: Nemouridae): Insights from the high Rocky Mountains. Western North American Naturalist .

Hotaling, S., A. A. Shah, K. L. McGowan, L. M. Tronstad, J. J. Giersch, D. S. Finn, H. A. Woods, M. E. Dillon, and J. L. Kelley. 2020. Mountain stoneflies may tolerate warming streams: Evidence from organismal physiology and gene expression. Global Change Biology **26**:5524–5538.

Johnson, G., H. Chang, and A. Fountain. 2021. Active rock glaciers of the contiguous United States: Geographic information system inventory and spatial distribution patterns. Earth System Science Data **13**:3979–3994.

Jordan, S., J. J. Giersch, C. C. Muhlfeld, S. Hotaling, L. Fanning, T. H. Tappenbeck, and G. Luikart. 2016. Loss of genetic diversity and increased subdivision in an endemic alpine stonefly threatened by climate change. Plos One **11**. ⟨GotoISI⟩://WOS:000378801200009.

Lilleoren, K. S., and B. Etzelmuller. 2011. A regional inventory of rock glaciers and ice-cored moraines in Norway. Geografiska Annaler Series a-Physical Geography **93A**:175–191. ⟨GotoISI⟩://WOS:000294724200003.

Niedrist, G., and L. Fureder. 2020. Real-time warming of alpine streams: (Re)defining invertebrates' temperature preferences. River Research and Application .

Pickett, S., 1989. Space-for-time substitution as an alternative to long-term studies, Pages 110–135 . Springer, New York, NY.

Scotti, R., F. Brardinoni, S. Alberti, P. Frattini, and G. B. Crosta. 2013. A regional inventory of rock glaciers and protalus ramparts in the central Italian Alps. Geomorphology **186**:136–149. ⟨GotoISI⟩://WOS:000315974400010.

Tronstad, L. M., S. Hotaling, J. J. Giersch, O. Wilmot, and D. S. Finn. 2020. Headwaters fed by subterranean ice: Potential climate refugia for alpine stream communities? Western North American Naturalist **80**:395–407.

Ward, J. V. 1994. Ecology of alpine streams. Freshwater Biology **32**:277–294. ⟨GotoISI⟩://WOS:A1994PQ02700004.