8-2024

The Drivers and Ecological Importance of Streamflow Permanence for Native Salmonids: Evaluated at Multiple Spatio-Temporal Scales

Skylar Rousseau
Utah State University

Recommended Citation

Rousseau, Skylar, "The Drivers and Ecological Importance of Streamflow Permanence for Native Salmonids: Evaluated at Multiple Spatio-Temporal Scales" (2024). *All Graduate Theses and Dissertations, Fall 2023 to Present*. 262.
https://digitalcommons.usu.edu/etd2023/262

THE DRIVERS AND ECOLOGICAL IMPORTANCE OF STREAMFLOW PERMANENCE FOR NATIVE SALMONIDS: EVALUATED AT MULTIPLE SPATIO-TEMPORAL SCALES

by

Skylar Rousseau

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

of

MASTER OF SCIENCE

in

Ecology

Approved:

Timothy E. Walsworth, Ph.D. Major Professor	Sarah E. Null, Ph.D. Committee Member
William C. Saunders, Ph.D. Committee Member	D. Richard Cutler, Ph.D. Vice Provost of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2024

ABSTRACT

The Drivers and Ecological Importance of Streamflow Permanence for Native Salmonids: Evaluated at Multiple Spatio-Temporal Scales

by

Skylar Rousseau, Master of Science

Utah State University, 2024

Major Professor: Dr. Timothy Walsworth
Department: Watershed Sciences

Cycles of drying and rewetting that characterize non-permanent waterbodies help shape the form and function of freshwater systems. Though non-permanent flow is common and increasing with climate change, there exists significant uncertainty regarding the set of local conditions that make a watershed resilient or vulnerable to stream drying. As such, we are equipped with an inadequate mapping of the spatio-temporal distribution of non-permanent flow and a limited understanding of how accelerated, climate-induced drying may impact the availability of habitats that support native stream fish. Additionally, though these streams represent a substantial portion of aquatic habitat available to spring spawning salmonids in snow fed watersheds in the northern Rocky Mountains, non-permanent stream contributions to early life history remains unclear. I identified the dominant climatic and landscape controls on flow permanence across the Northern Rocky Mountains and conducted a sensitivity analysis to simulate how habitat availability responds to changes in baseline climate and landcover conditions. Accelerated climate warming will increase the amount of habitat lost to drying, particularly in small, arid catchments that support cutthroat trout (*Oncorhynchus* *clarkii*). While summer habitat loss may increase, it is important to understand whether non-permanent streams provide suitable conditions for native stream fish when they are inundated. For one snowmelt fed watershed in Northern Utah, I characterized variability in the distribution of viable spawning habitat and documented the use of these habitats by spawning Bonneville cutthroat trout (*O. c. utah*; hereafter, “BCT”). The mosaic of suitable spawning habitat shifted in response to snowpack, with colder permanent streams providing more spawning habitat in a drought year, and warmer non-permanent streams becoming more suitable in a year with a large snowpack. Response diversity among streams to snowpack changes meant that basin wide spawning opportunities were conserved across years and acute climate conditions. Additionally, BCT successfully spawned in streams whose flow period varied substantially across years. These results provide a framework for land-use and climate adaptation plans to consider how even though changing flow regimes may reduce summer habitat availability for native, cold-water salmonids, increasingly common non-permanent streams can also provide seasonally amenable conditions that support diverse life history expressions and sensitive life stages.

(126 pages)

PUBLIC ABSTRACT

The Drivers and Ecological Importance of Streamflow Permanence for Native Salmonids: Evaluated at Multiple Spatio-Temporal Scales

Skylar Rousseau

In freshwater ecosystems, aquatic resources are distributed patchily across both space and time. Non-permanent streams, which go through periodic episodes of drying and rewetting, account for more than half of all streams in North America and help create much of the diversity that defines aquatic ecosystem form and function. While non-permanent streams have become increasingly common under climate change, we have a poor understanding of both their distribution across the landscape as well as how native stream fishes make use of them when they are flowing. I analyzed a large data set that spanned multiple decades across the northern Rocky Mountains to describe the dominant climate and landscape conditions that make a stream and its watershed vulnerable to summer drying. Additionally, I examined the sensitivity of habitat supporting native salmonids to changes in climate and landcover. Accelerated climate warming will increase the amount of habitat lost to drying, particularly in small, arid catchments that support cutthroat trout. While summer habitat may decline under anticipated climate futures, it is important to understand if non-permanent streams are useful when they are flowing. As such, I described the spatio-temporal variability in annual spawning suitability for a native salmonid species that occupies streams with different flow classes in an Intermountain West river basin. I then characterized how suitability is impacted by watershed physical and annual climatic conditions. In the low snowpack year, suitable spawning habitat was concentrated in permanent tributaries, as non-permanent streams did not support sufficient surface flows. In a high snowpack year, non-permanent tributaries provided extensive suitable spawning habitat, while permanent tributaries demonstrated reduced suitability due to cold temperatures. Importantly, aggregate, basin-wide spawning opportunities remained relatively constant between years, as suitability gains in non-permanent tributaries balanced the losses in permanent ones. Additionally, salmonids spawned successfully in streams with highly variable surface flows. This research can inform land-use and climate adaptation plans to consider how even though changing flow regimes may reduce summer habitat availability for native, cold-water salmonids, increasingly common non-permanent streams can also provide seasonally amenable conditions that support diverse life history expressions and sensitive life stages.

ACKNOWLEDGMENTS

I want to thank my advisor, Dr. Timothy E. Walsworth, for all his support and contributions toward this research. The time, effort, and sincere interest he showed in both this project and my development as a scientist will make me forever grateful and inspired to understand the nooks and crannies of the natural world. This work was funded in large part by the United States Forest Service (USFS), and I would like to thank them for making this research possible. I would also like to thank Dr. Brett Roper at the USFS for all his help getting this project off the ground and supporting me throughout the research process. I would also like to thank the Utah State University Office of Research for providing a catalyst grant that enabled a thorough field effort.

I would also like to thank my committee members, Dr. Sarah Null and Dr. William Saunders for their help conceptualizing and improving this work. I want to extend a deep thank you to everyone in the Quantitative Fisheries and Aquatic Ecology Laboratory for their friendship and support. My experience at USU would not have been nearly as fun or memorable without them. I am also indebted to Kevin Landom, who helped me navigate everything graduate school related: from where to find fry traps in the storage yard to the intricacies of our lab's printer. I also appreciate Kevin's guidance and sense of humor. Thank you to everyone in the Fish Ecology Lab for the camaraderie, and to Dr. Phaedra Budy, Dr. Casey Pennock, and Gary Theide for mentorship. Additionally, I am grateful to Erline Vendredi, Thad Nicholls, and Brian Bailey for shepherding me through graduate school logistics.

I would also like to thank all the field help I received during this project, the folks who volunteered their time to collect samples and measure rocks. I'd like to extend a big

thank you to Tom Doolittle and Kolton Kerr, in particular, for spending lots of time with me staring at barely flowing creeks. Finally, I would like to thank my family, my dog, Hank 4, and Kimiko Smith for their continued love and support.

Skylar Rousseau

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The distribution of heterogeneous habitat patches is a primary control on the physical and biological processes that define ecosystem form and function. In dynamic freshwater systems, patterns of surface flow dictate levels of connectivity and the interaction between spatially distinct patches, drive biogeochemical processes, and facilitate material and nutrient transport through the river basin (Dunning et al., 1992; Stanley et al., 1997; Larned et al., 2010; Datry et al., 2014). These physical processes create a diverse mosaic of habitats that provide unique and complementary resource opportunities to the aquatic species that occupy them. As such, patterns of surface flow influence community assemblages (Poff & Ward, 1989; Datry et al., 2014; Moidu et al., 2023), species distributions (Kominoski et al., 2018; Rogosch et al., 2019), and population vital rates (Erman & Hawthorne, 1976; Labbe & Fausch, 2000).

Contemporary research has established that the matrix of available, suitable habitats is also temporally dynamic, as climate and landscape factors interact to drive plasticity in habitat conditions across different time scales. As such, habitats patches that are often unproductive may become available and suitable during a particular season (Armstrong et al., 2021), or in certain years with amenable conditions (Schindler et al., 2010; Brennan et al., 2019; Walsworth et al., 2020). Non-permanent waterways, which are streams and rivers that sometimes go dry, account for over half of the global stream network (Larned et al., 2010; Datry et al., 2014). At the water shed scale, cycles of drying and rewetting create an ever-shifting landscape composed of heterogenous habitats. The location and timing of surface flows drives the expansion and contraction of total habitat available to aquatic species and regulates connectivity among distinct habitat patches. The heterogeneity created by a dynamic stream network contributes to ecosystem portfolio effects (Schindler et al., 2015). When external conditions change, some parts of the portfolio respond positively, others negatively, but overall, the portfolio is stable so long as it's diversified. In ecosystems, response diversity among habitat patches decouples local conditions from shared regional drivers of those conditions which reduces the impact of climate change and stochastic disturbances on aquatic habitat and occupying species (Schindler et al., 2015).

Though the expansion and contraction of river networks is a pervasive and natural phenomenon, the frequency and duration of no-flow events has increased under climate change (Stewart et al., 2005; Döll & Schmied, 2012; Zipper et al., 2021). In the Intermountain West where spring snowmelt drives hydrologic cycles, warmer winter and spring temperatures not only cause earlier and accelerated melt, but also cause a greater fraction of winter and spring precipitation to fall as rain (Stewart et al., 2005). As a result, peak streamflow occurs 1-4 weeks earlier, subjecting non-permanent streams to earlier and longer periods of drying (Stewart et al., 2005). Additionally, historically permanent streams are subject to greater variability in minimum flows which increases their risk of flow discontinuity (Döll & Schmied, 2012; Reynolds et al., 2015). Despite the ubiquity of non-permanent streams across the landscape we are equipped with an inadequate understanding of the actual distribution of non-permanent streams. The most spatially consistent dataset mapping flow classifications across the United States is the National Hydrography Dataset Plus – High Resolution, which can have a flow permanence misclassification of up to 50% in headwater streams (Fritz et al., 2013; Hafen et al., 2020). A lack of knowledge regarding the distribution of non-permanent streams also means that we don’t yet understand how accelerated climate induced drying will affect the availability of suitable habitat for stream fishes, and cold-water salmonids in particular, who rely on a series of connected habitat patches to fulfill their life history.

In snowmelt driven watersheds characteristic of the Intermountain West, non-permanent streams typically flow in the spring following snowmelt runoff and dry in the summer or fall. These predictable windows of inundation align with the spring spawning season of native salmonids in the region. Though there exists significant uncertainty regarding the ability of non-permanent streams to support salmonid life history, recent research has shown that when temporary aquatic habitat availability predictably aligns with life history needs, total habitat availability is expanded (Heim et al., 2019). Populations that exploit non-permanent resource opportunities, often distinct from those available in permanent habitats, can find improved rates of spawning, growth, refuge, and dispersal (Labbe & Fausch, 2000; Boughton et al., 2009; Colvin et al., 2019; Tsuboi et al., 2022). In this thesis, I seek to identify the climatic and landscape controls of streamflow permanence for watersheds across the northern Rocky Mountains and characterize the potential and realized ability of non-permanent streams to support spawning and early life history of cutthroat trout (*Oncorhynchus clarkii*).

In Chapter II, I leverage a multi-decadal dataset to 1) identify the dominant climatic and landscape drivers of streamflow permanence for watersheds in the Columbia River and upper Missouri River basins and 2) conduct a sensitivity analysis of simulated climate and management scenarios to predict loss of habitat for native bull trout (*Salvelinus confluentus*) and cutthroat trout. I apply machine learning to a multi-decadal dataset describing climate, landscape, and flow conditions on federally owned land in the northern Rockies between 2004 and 2021. The spatial extent of the dataset was selected prior to the initiation of the monitoring program to cover the distribution of target salmonid species. This allowed me to conduct a risk assessment for species most vulnerable to habitat loss as a result of climate or landcover induced stream drying. I found that that interactions between topography and local climate conditions strongly predict flow permanence classes, with smaller, warmer catchments that accumulate less snow and support little riparian vegetation cover being the most vulnerable to drying. Reductions in spring snowpack that result from either low precipitation or warmer spring air temperatures accelerate drying and initiate strong changes in upstream habitat accessibility and quantity, particularly in catchments that have historically supported cutthroat trout. Additionally, I found that flow permanence classification is sensitive to changes in riparian vegetation cover, suggesting that management actions affecting vegetation in the riparian zone should account for increasing variability in flow permanence patterns.

In Chapter III, I conduct a two-year field study in one watershed in northern Utah to 1) characterize the spatio-temporal distribution of viable spawning habitat for native Bonneville cutthroat trout (*O. clarkii utah*; hereafter, “BCT”), 2) identify physiographic and climatic controls on the probability that tributary habitats support early life history, and 3) document the timing and use of these temporary habitats by BCT across years and conditions. Non-permanent streams can support spawning if they flow long enough and warm enough for offspring to develop and move to permanent habitat. I assess the spawning suitability of 23 tributary streams whose flow permanence varies substantially in response to changing climate conditions. Suitability is calculated as the window of days during which eggs of spawning individuals would be able to accumulate sufficient degree days to hatch and emerge before the stream dries or the growing season ends. I found that in a drought year, high elevation, permanent streams provided more suitable spawning habitat as most non-permanent streams supported inadequate surface flow. However, in a year with a large snowpack, non-permanent streams provided extensive suitable spawning habitat as suitability in high elevation, permanent streams were diminished due to cold temperatures. Interestingly, aggregate spawning opportunities across the basin were relatively constant, as suitability gains in non-permanent streams balanced the losses in permanent tributaries. Additionally, I found that BCT successfully spawn in streams whose flow permanence patterns vary substantially across years and conditions. Response diversity among streams with variable flow permanence patterns buffers total habitat availability against climate changes, which allows BCT spawn across a wide range of conditions so long as connectivity is maintained.

In Chapter IV, I synthesize the findings of my two research chapters into general conclusions regarding the controls on non-permanent streamflow and their ecological function in the context of salmonid life history. Though contemporary hydrologic research has characterized long term trends in stream drying across a range of spatial and temporal extents (Döll & Schmied, 2012; Sando et al., 2015a; 2022b; Messager et al., 2021), few studies illustrate how this will initiate changes in habitat availability for mobile aquatic species (Jaeger et al., 2014). Additionally, much research has evaluated the risk of habitat loss for cold-water salmonid species in the context of man-made barriers, invasive species, and warming stream temperatures (Reiman et al., 2001;

Peterson et al., 2008; Isaak et al., 2016), though little research has considered how changing flow permanence regimes may impede access to habitats that are anticipated serve as refugia under climate warming. My results contend that changing streamflow permanence patterns need to be considered in tandem with these other factors in species management and land use plans mitigating threats to the persistence of fluvial species and the habitats that support them. However, while anticipated climate futures may limit summer habitat availability, my Chapter III results are in line with other research suggesting that habitat importance is not always synonymous with habitat permanence (Wiggington et al., 2006; Heim et al., 2019). When non-permanent stream availability aligns with salmonid life history timing, these streams can provide unique conditions distinct from their permanent counterparts that support the early life history of BCT. My results suggest that conservation efforts seeking to maximize spawning opportunities should leverage existing ecological mechanisms whereby habitat diversity stabilizes habitat availability across years and acute conditions.

References

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., ... & Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, *11*(4), 354-361.

Boughton, D. A., Fish, H., Pope, J., & Holt, G. (2009). Spatial patterning of habitat for Oncorhynchus mykiss in a system of intermittent and perennial streams. *Ecology of Freshwater Fish*, *18*(1), 92-105.

Brennan, S. R., Schindler, D. E., Cline, T. J., Walsworth, T. E., Buck, G., & Fernandez, D. P. (2019). Shifting habitat mosaics and fish production across river basins. *Science*, *364*(6442), 783-786.

Brooks, P. D., Gelderloos, A., Wolf, M. A., Jamison, L. R., Strong, C., Solomon, D. K., ... & Stewart, J. (2021). Groundwater-mediated memory of past climate controls water yield in snowmelt-dominated catchments. *Water Resources Research*, *57*(10), e2021WR030605.

Colvin, S. A., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., ... & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries*, *44*(2), 73-91.

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: a challenge for freshwater ecology. *BioScience*, *64*(3), 229-235.

Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, *7*(1), 014037.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175.

Erman, D. C., & Hawthorne, V. M. (1976). The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Transactions of the American Fisheries Society*, *105*(6), 675-681.

Fritz, K. M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington Jr, P. J., Leibowitz, S. G., ... & Nadeau, T. L. (2013). Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. *JAWRA Journal of the American Water Resources Association*, *49*(4), 867-882.

Hafen, K. C., Blasch, K. W., Rea, A., Sando, R., & Gessler, P. E. (2020). The influence of climate variability on the accuracy of NHD perennial and nonperennial stream classifications. *JAWRA Journal of the American Water Resources Association*, *56*(5), 903-916.

Heim, K. C., McMahon, T. E., Calle, L., Wipfli, M. S., & Falke, J. A. (2019). A general model of temporary aquatic habitat use: water phenology as a life history filter. *Fish and Fisheries*, *20*(4), 802-816.

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., ... & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374-4379.

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894-13899.

Kominoski, J. S., Ruhí, A., Hagler, M. M., Petersen, K., Sabo, J. L., Sinha, T., ... & Olden, J. D. (2018). Patterns and drivers of fish extirpations in rivers of the American Southwest and Southeast. *Global Change Biology*, *24*(3), 1175-1185.

Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774-1791.

Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, *55*(4), 717-738.

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., ... & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391-397.

Moidu, H., Rodríguez-Lozano, P., Leidy, R. A., Bogan, M. T., Grantham, T. E., & Carlson, S. M. (2023). Ecological consequences of shifting habitat mosaics within and across years in an intermittent stream. *Freshwater Biology*, *68*(7), 1161-1175.

Peterson, D. P., Rieman, B. E., Dunham, J. B., Fausch, K. D., & Young, M. K. (2008). Analysis of trade-offs between threats of invasion by nonnative brook trout (Salvelinus fontinalis) and intentional isolation for native westslope cutthroat trout (Oncorhynchus clarkii lewisi). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 557-573.

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian journal of fisheries and aquatic sciences*, *46*(10), 1805-1818.

Reynolds, L. V., Shafroth, P. B., & Poff, N. L. (2015). Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change. *Journal of Hydrology*, *523*, 768-780.

Rieman, B., Peterson, J. T., Clayton, J., Howell, P., Thurow, R., Thompson, W., & Lee, D. (2001). Evaluation of potential effects of federal land management alternatives on trends of salmonids and their habitats in the interior Columbia River basin. *Forest ecology and management*, *153*(1-3), 43-62.

Rogosch, J. S., Tonkin, J. D., Lytle, D. A., Merritt, D. M., Reynolds, L. V., & Olden, J. D. (2019). Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere*, *10*(4), e02681.

Sando, R., & Blasch, K. W. (2015). Predicting alpine headwater stream intermittency: A case study in the northern Rocky Mountains. *Ecohydrology & Hydrobiology*, *15*(2), 68-80.

Sando, R., Jaeger, K. L., Farmer, W. H., Barnhart, T. B., McShane, R. R., Welborn, T. L., ... & Shallcross, A. (2022). Predictions and drivers of sub-reach-scale annual streamflow permanence for the upper Missouri River basin: 1989–2018. *Journal of Hydrology X*, *17*, 100138.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609-612.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257-263.

Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, *47*(7), 427-435.

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of climate*, *18*(8), 1136-1155.

Tsuboi, J. I., Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D., ... & Kanno, Y. (2022). Small giants: Tributaries rescue spatially structured populations from extirpation in a highly fragmented stream. *Journal of Applied Ecology*, *59*(8), 1997-2009.

Walsworth, T. E., Baldock, J. R., Zimmerman, C. E., & Schindler, D. E. (2020). Interaction between watershed features and climate forcing affects habitat profitability for juvenile salmon. *Ecosphere*, *11*(10), e03266.

Wigington Jr, P. J., Ebersole, J. L., Colvin, M. E., Leibowitz, S. G., Miller, B., Hansen, B., ... & Compton, J. E. (2006). Coho salmon dependence on intermittent streams. *Frontiers in Ecology and the Environment*, *4*(10), 513-518.

Zipper, S. C., Hammond, J. C., Shanafield, M., Zimmer, M., Datry, T., Jones, C. N., ... & Allen, D. C. (2021). Pervasive changes in stream intermittency across the United States. *Environmental Research Letters*, *16*(8), 084033.

CHAPTER II

CLIMATE AND LANDCOVER INDUCED SHIFTS IN STREAMFLOW PERMANENCE INITIATE CHANGES IN HABITAT AVAILABILITY FOR NATIVE SALMONIDS

Abstract

Cycles of drying and rewetting that characterize non-permanent waterbodies help shape the form and function of freshwater systems. Though non-permanent flow patterns are common and increasing with climate change, there exists significant uncertainty about the local landscape and climatic conditions that make a watershed resilient or vulnerable to drying. As such, we are equipped with an inadequate mapping of the spatio-temporal distribution of non-permanent flow and a limited understanding of how accelerated, climate-induced drying may impact the availability of habitats that support native stream fishes. We used a multi-decadal dataset characterizing habitat and streamflow on public lands to train a random forest model that classified wet or dry summer flow in watersheds across the Northern Rocky Mountains. We identified the dominant landscape and climatic controls on streamflow permanence and predicted the amount of wetted stream habitat lost to seasonal drying for bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) across a range of simulated climate and management scenarios. Results suggest that interactions between topography and local climate conditions strongly predict flow permanence classes, with smaller, warmer catchments that accumulate less snow and support little riparian vegetation cover being the most vulnerable to drying. As climate change warms air temperatures and reduces spring snowpack, accelerated drying may initiate strong changes in upstream

habitat accessibility and quantity, particularly in catchments that have historically supported cutthroat trout. Additionally, flow permanence is sensitive to changes in riparian vegetation cover, and management actions should account for increasing variability in flow permanence patterns. Climate adaptation plans should incorporate changing streamflow permanence patterns into analyses and strategies considering threats to the persistence of cold-water species and the habitats that support them.

Introduction

Streamflow permanence is a primary control on the physical and biological processes that define aquatic ecosystem form and function. Patterns of surface flow mediate connectivity between diverse habitat patches (Dunning et al., 1982; Larned et al., 2010), drive biogeochemical processes and nutrient transport (Stanley et al., 1997; Datry et al., 2014), impact community assemblages (Poff & Ward, 1989; Datry et al., 2014; Moidu et al., 2023), species distributions (Kominoski et al., 2018; Rogosch et al., 2019), and population vital rates (Erman & Hawthorne, 1976; Labbe & Fausch, 2000). Non-permanent rivers and streams, which encompass both intermittent and ephemeral classifications, are streams that sometimes cease to flow. Non-permanent waterways are common, accounting for over half of the global stream network (Larned et al., 2010; Datry et al., 2014). Though expansion and contraction of river networks is a natural and pervasive hydrologic phenomenon (Moidu et al., 2021), the frequency and duration of no-flow periods has increased as climate change shifts temperature and precipitation regimes (Stewart et al., 2005; Döll & Schmied, 2012; Zipper et al., 2021). In addition to climate-induced changes in historical patterns of flow, consumptive water use will continue to increase the prevalence of low and no-flow conditions (Chiu et al., 2017;

Falke et al., 2011; Zipper et al., 2021). Despite the ubiquity of this stream type across the landscape, our understanding of the spatio-temporal distribution of non-permanent streams, as well as the drivers and ecological ramifications of accelerated drying remains poorly understood (Messager et al., 2021).

Within the United States, the National Hydrography Dataset Plus – High Resolution (hereafter; “NHD”) represents the most comprehensive, spatially consistent data source for streamflow permanence classifications (The NHD was retired October 1, 2023, to be replaced by the 3D Hydrography Program, though data is not yet available for this active remapping effort). However, streamflow permanence classifications contained in the NHD, and its many versions, are based on field surveys and interviews that occurred between 1881 and 2000 (Beaman, 1928; Guptill, 1990; Hafen et al., 2020). Subsequent comparisons of NHD flow classifications to field observations indicate flow permanence misclassification rates of up to 50% in headwater streams (Fritz et al., 2013; Hafen et al., 2020). NHD classifications do not account for the increasing variability in streamflow permanence patterns that have been observed in the last two decades (Eng et al., 2016; Zipper et al., 2021), and as drying accelerates, NHD will be increasingly inaccurate. Still, policymakers rely on explicit definitions of stream classes to delegate protection status (Meridian, 2024). Protections afforded to non-permanent waterways are regularly in flux as frequent revisions to the Clean Water Act often exclude temporary streams (Fesenmyer et al., 2021). The current mapping of flow classes that inform delineation of streams qualified for protection is largely inadequate (Sando et al., 2022). This presents significant challenges for climate adaptation and land use plans attempting to manage natural resources for sustainable human benefit and conserve critical habitat for aquatic species of concern.

These challenges are particularly evident in the interior Columbia River Basin (hereafter; “CRB”) where further network contraction may exacerbate existing habitat fragmentation that currently threatens the persistence of multiple cold-water salmonid species, including bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) (Dunham & Rieman, 1999; Rieman et al., 2007; Al-Chokhachy et al., 2015). Much work has evaluated the effect of climate warming on the distribution of suitable refuge habitats for cold water species and their subsequent persistence (Keleher & Rahel, 1996; Isaak et al., 2015a; 2016b). A narrow thermal tolerance for bull and cutthroat trout species is expected to restrict their range to high elevation, headwater streams where in-stream conditions are more resilient to warming (Isaak et al., 2016). However, increased fragmentation from drying may limit dispersal into these refuge habitats, and there exists an urgent need for research evaluating how seasonal expansion and contraction of river networks will mediate the availability of viable, connected habitat in streams with reduced climate velocities (Isaak et al., 2016; Colvin et al., 2019).

Research leveraging long-term monitoring data to evaluate the effect of active land-management practices on the abundance of suitable habitat for cold-water salmonids has demonstrated the sensitivity of both critical habitat and population vital rates to improved management practices (Reiman et al., 2001; Roper et al., 2019). However, few of these studies attempt to link land use to the streamflow permanence patterns that exert a primary control on total habitat availability and dispersal among quality patches (Moidu et al., 2023). Furthermore, while the importance of non-permanent streams for ecosystem function is increasingly recognized and accounted for in large scale forest management plans, riparian zones around non-permanent streams are still subject to fewer management regulations (USFS 2003; Kershner et al., 2004). As such, it is important to investigate the direct and indirect relationships between land-use practices, the landscape attributes they affect, and streamflow permanence patterns that shape the mosaic of viable habitat available to native salmonid populations.

Though fisheries researchers often overlook the importance of streamflow permanence in regulating the abundance and distribution of aquatic populations (Heim et al., 2019), hydrologic research has used physical and statistical modeling frameworks to map the spatio-temporal distribution of non-permanent streams and characterize the climatic and landscape controls on flow permanence across global (Doll & Schmied, 2012; Messager et al., 2021), regional (Jaeger et al., 2014a; 2019b; Sando et al., 2015a; 2022b), and local (Kaplan et al., 2020; Moidu et al., 2021) extents. For watersheds in the CRB whose hydrograph is driven primarily by snowmelt, temperature and snowpack persistence are consistently strong predictors of streamflow permanence class (Stewart et al., 2005; Sando & Blasch, 2015; Jaeger et al., 2019). However, watersheds do not display homogenous responses to climate conditions, as a stream network's particular resilience or vulnerability to drying is also mediated by a suite of local landscape and physiographic attributes (Reynolds et al., 2015; Belmar et al., 2016; Kaplan et al., 2020; Thurber, 2022). While much work has characterized long term trends in accelerated drying, few studies illustrate how this will initiate changes in habitat availability for mobile aquatic species (Jaeger et al., 2014).

As the consequences of climate change become increasingly evident in the physical and biological processes that define riverscapes in the CRB, there exists a significant need to better evaluate the drivers of streamflow permanence patterns in the context of their ecological ramifications for native, cold-water species of concern. Furthermore, much of the research on climate change in the CRB focuses on impacts rather than potential mitigation strategies (Marshall et al., 2020). As such, there also exists a need to identify direct and indirect relationships between land use practices, streamflow permanence, and habitat availability to guide climate adaptation and land management plans more effectively.

Here, we apply machine learning to a multi-decadal dataset that characterizes climate, landscape, and flow observations on federally owned land in the CRB and parts of the upper Missouri River Basin, the spatial extent of which was selected a priori to cover much of the distribution of target native salmonid species (USFS, 1995a; 1995b; Kershner et al., 2004). Initially, all sites within our study area were selected based on a perennial flow classification in the 1990's (Kershner et al., 2004). However, since the initiation of the monitoring program, many of the streams demonstrated interannual variation in flow permanence. The overall objectives of this paper are to 1) identify the dominant climatic and landscape drivers of streamflow permanence for watersheds in the CRB and upper Missouri River Basin and 2) conduct a sensitivity analysis to determine how habitat availability for bull trout and cutthroat responds to changes in simulated climate and management conditions. This work will allow us to better understand the factors that make watersheds more vulnerable or resilient to drying, as well as how specific management actions may affect these relationships in streams that support bull trout and cutthroat. Results provide pragmatic suggestions for improved land use practices and inform priority conservation and restoration efforts for sensitive species.

Methods

Study Area

Much of the data used to model streamflow permanence were collected as part of the PacFish/InFish Biological Opinion Monitoring program (hereafter; "PIBO"), a large-scale stream and riparian habitat monitoring program that covers the interior CRB and parts of the upper Missouri River Basin. The program was implemented at the turn of the 21st century to monitor how riparian and aquatic habitats critical to native, anadromous, and inland salmonid species persistence change over time as a function of land management practices (USFS, 1995a; 1995b; Kershner et al., 2004) At its inception, the program identified 4300 sub-basins (12 digit Hydrologic Unit Codes (HUC)) throughout the interior CRB and upper Missouri River Basins that were comprised of federal land ownership and were historically accessed by anadromous and inland salmonids (Kershner et al., 2004). Monitoring sites were established by PIBO during 2000-2005 in approximately one third of the identified watersheds to fit specific site establishment criteria: 1) low-gradient portions of each watershed (stream gradient ≤ 3%), and 2) ≥50% of the upstream contributing watershed was comprised of federally managed lands. The spatial extent of our study area covers 22 national forests in eastern Washington and Oregon, most of Idaho, western Montana and small parts of northern Nevada, Utah, and eastern Montana (Figure 1). Additionally, selected sites are subject to a gradient of land use practices and potential ecosystem stressors which helps our model distinguish the importance of impacted land cover for predicting streamflow.

Physiography in the study area varies dramatically and includes steep mountain ranges, broad valleys, plateaus, steppes, and plains. Ecoregions include the Cascade and Rocky Mountain ranges, the Idaho Batholith, the Columbia Plateau, parts of the Snake River Plain and the Northwestern Great Plains (Griffith, 2010). While the range of elevations present in our sites varies from roughly sea level to nearly 3000 meters at the mouth of catchments, the lower and upper quartiles of elevation data are between 1150 and 1800 meters (Table 1). Climate also varies substantially, from minimal precipitation and high air temperatures in arid lowland areas to steep mountainous watersheds where cold, wet winters give way to warm, dry summers and a melting snowpack drives hydrology.

Streamflow Data

Streamflow was recorded as observational, binary data (wet or dry) during sampling events that occurred roughly every 5 years for each site between 2001 and 2021. Stream reaches were coded as non-permanent in a given year if any portion of the reach was dry. While the highly dynamic nature of stream network expansion and contraction cycles makes explicit definitions of flow class difficult (Zipper et al., 2021), we opted for flow class definitions relevant to the life history of migratory fish species. As watersheds were sampled at the most downstream point that occurred on federal land, a dry observation means that even if the upstream portion of the stream network is still flowing, downstream drying bars access for fluvial populations. Data from the initial 4300 sites were filtered to just those sites that contained streamflow observations and consistently available landscape and climate data. A total of 5561 streamflow observations (5236 wet, 325 dry) across 1941 sites were included in model development.

We also included day of year of streamflow observations as a numerical variable (Julian date) to account for the fact that streams sampled later in the summer would have a higher probability of being observed dry than streams sampled closer to peak runoff.

Climatic and Landscape Data

To characterize the factors driving streamflow permanence across our study extent, we selected a total of 6 climatic and 29 landscape variables for inclusion in model development (Table 1). We use the term "landscape" to broadly describe all non-climatic predictor variables that include both topographic and physiographic attributes. The bulk of this site-specific attribute data comes from the PIBO monitoring program, which summarizes catchment specific metrics on topology, geomorphology, land use, terrestrial and riparian conditions across large spatio-temporal scales (Table 1). We also summarized a suite of annually and seasonally variable climate and landscape predictors by catchment, to capture the set of dynamic conditions that potentially influence inter- and intra-annual streamflow patterns.

Baseline Species Distributions

In addition to developing a model that characterizes the controls on streamflow permanence across all sites in our study area, we filtered predictions of stream drying by those catchments supporting bull trout and cutthroat trout to estimate habitat loss for target species under different climate and management scenarios. We used spatial models developed by Isaak et al. (2015a; 2017b) that provide probabilistic estimates of occurrence for bull trout and cutthroat trout under different warming and brook trout (*Salvelinus fontinalis*) invasion scenarios. These species distribution models were optimal for our application of modeling habitat lost to drying, as they include non-permanent stream reaches. We relied on the baseline scenario that represents occurrence under historic climate conditions and minimal invasion by brook trout. We filtered streamflow observations and catchment specific data by streams where probability of baseline occurrence of target species was greater than 50%.

Model Development and Statistical Analysis

We used a random forest classification algorithm to characterize dominant controls on streamflow permanence and predict drying under different climate and management scenarios. Random forest is a supervised classification technique that uses random bootstrap sampling of training data to construct a "forest" of individual classification trees whose aggregate class prediction informs the final class prediction (Breiman, 2001), which was a wet or dry flow class for our application. The non-parametric nature of random forest makes it less susceptible to issues arising from outliers, overfitting, and predictor variable collinearity, making it increasingly popular with ecologists and physical scientists (Cutler et al., 2007; Jaeger et al., 2019; Tyralis et al., 2019). Additionally, it often out-performs linear methods when there are strong interactions among predictor variables (Cutler et al., 2007), as in our data set. We used the "randomForest" package (Liaw & Wiener, 2002) in R (R Core Team, 2024).

Machine learning algorithms, and random forest in particular, perform poorly when they are trained on imbalanced class data (Johnson et al., 2012; Benkendorf et al., 2023). As site selection criteria were highly biased toward perennial streams (Kershner et al., 2004), our data set contained significant class imbalances between wet (94%) and dry (6%) observations. To correct for class imbalance, we used the "caret" package in R

(Kuhn, 2008) to down-sample the training data. Down-sampling randomly selects a subset of the majority class (wet) observations to match the number of minority class (dry) observations. Down-sampling is computationally efficient and has been shown to consistently improve random forest model performance when dealing with imbalanced data (Valavi et al., 2022; Benkendorf et al., 2023).

While down-sampling boosts the performance metrics and predictive abilities of random forest, it uses a reduced set of combinations of the common class to train the model. This excluded 93% of our common class observations whose values could potentially influence variable importance and prediction, particularly for the common class. To incorporate more data into the model's training, we iteratively down-sampled the majority class 1000 times, training the model on different combinations of wet observations in each down-sample. All dry class observations were used in each iteration. This allowed us to characterize the variance associated with model accuracy, sensitivity, and specificity, as well as the variance of each predictor variable's importance.

To optimize our random forest model, we used the "caret" package in R (Kuhn, 2008) to conduct a grid search across 15 sequential, potential values for the parameter controlling the number of predictor variables to randomly sample as candidates at each split in a decision tree. For each parameter value tested, 10-fold cross validation was performed. We used the true skill statistic (TSS) to evaluate model performance across different combinations of parameter values (TSS = sensitivity + specificity - 1). TSS places equal weight on both sensitivity (predicting the rare class) and specificity (predicting the common class) and has been shown to be a more effective performance metric than percent correctly classified, when estimating prevalence of a rare class

(Akosa, 2017; Benkendorf et al., 2023). The number of predictor variables randomly selected for consideration at each node in a tree was set to five and the number of bootstrapped samples and subsequent classification trees built was set to 500, which is the default in "randomForest" (Liaw & Wiener, 2002).

Climate and Landcover Simulations

We then conducted a sensitivity analysis to determine how the availability of wetted habitat area responds to changes in local conditions. We simulated the amount of upstream catchment area lost to drying across a range of climate and management scenarios for all 1941 sites, as well as for bull trout and cutthroat sites specifically. While catchment area is not as direct of a measure of available aquatic habitat as active channel length, the proportional relationship between drainage area and network length is well documented (Horton, 1945; Scheidegger, 1968). Additionally, active channel length has been shown to be highly dynamic, expanding and contracting in response to climate by factors of two or more (Stanley et al., 1997; Godsey & Kirchner, 2014; Prancevic & Kirchner, 2019). This reinforced our choice to use a topographic metric (catchment area) that was both strongly correlated with aquatic habitat quantity and consistent across years and conditions.

We quantified wetted habitat availability under baseline conditions as well as different climate and management scenarios as 1) the percent of total upstream catchment area that supports connected surface flows during summer months and 2) as the amount of catchment area in square kilometers that is lost to drying. We calculated baseline conditions by taking the mean value of all predictor variables whose values changed across the temporal extent of our study. For fixed landscape variables and 30-year normal climate data, values were already consistent across years. In comparing area lost to drying under alternative and baseline conditions, we were able to quantify deviations in streamflow permanence patterns and habitat availability, beyond what has historically occurred.

To establish alternative climate and management scenarios to be used in the sensitivity analysis, we selected and manipulated four climate variables that are important predictors of streamflow in the CRB and upper Missouri River Basin (Payne et al., 2004; Sando & Blasch, 2015; Jaeger et al., 2019; Sando et al., 2022), and two landscape attributes that are directly affected by active land use in the area (Kershner et al., 2004). In the first climate scenario, we scaled May 1st snow water equivalent (hereafter, "SWE") values by 10-200% of site-specific mean baseline conditions, while holding temperature and precipitation constant to mean baseline conditions. SWE was calculated for each site as both a catchment average depth, as well as the volume of snow water accumulated in a catchment by multiplying the catchment's average snow water depth by the contributing drainage area. In the second climate scenario, we scaled May 1st SWE values by 10-200% of site-specific mean historic conditions while also scaling precipitation (as both rain and snow) accumulated in a site in one water year by the same 10-200% of mean baseline conditions. As temperature was held constant to mean baseline conditions, this scenario represented changes to spring SWE as a function of low precipitation. In the third climate scenario, we scaled May 1st SWE values by 10-200% of site-specific baseline conditions and added 2°C and 4°C to mean observed values of average monthly air temperatures summed from January through June. As we held precipitation constant in the third scenario, this scenario represented changes to spring SWE as a function of warming temperatures. While some of these scenarios represented potential climate futures, others are less probable and are included primarily to reveal potential sensitivity of flow permanence class to variations in climate conditions.

Additionally, we manipulated landcover variables that are directly impacted by land use (Kershner et al., 2004), while holding climate conditions constant to their baseline condition. We scaled riparian vegetation cover values by 50-150% of site-specific, mean baseline conditions. For example, if the riparian zone in a specific catchment had a baseline vegetation percent cover of 40% across the temporal extent of our study, that value was scaled to 20% or 60% under different management scenarios. Scaling riparian vegetation cover also impacted our riparian quality metric, which is calculated from ((1- annual vegetation cover) + percent of riparian area in a grazing allotment). This metric is centered around zero and positive values indicate low riparian quality as a function of low vegetation cover and high grazing, and negative values indicate high riparian quality as a function of high vegetation cover and low grazing. We also scaled percent forest cover in the catchment by 50-150% of site-specific mean observed conditions as a proxy for timber harvest and regrowth.

For each iteration of the model trained on different combinations of down-sampled data, we predicted streamflow permanence class and changes to habitat availability for each of our 1941 sites. We then filtered predictions by catchments that overlapped with historic bull trout and cutthroat species occurrence (Isaak et al., 2015a; 2017b), to estimate changes in habitat availability for target species.

Results

Model Performance

Summarized across 1000 iterations of model training and class prediction, the median value of ensemble mean classification accuracy was 0.82, sensitivity was 0.86, and specificity was 0.76 (Figure 2). The TSS was 0.63, indicating the model did much better than random guessing (Benkendorf et al., 2023). Additionally, narrow quantiles within each metric and a balance across metrics indicate that the model performed consistently across all streamflow classes and randomized down-sampled datasets.

Predictor Variable Importance

The importance of individual variables for predicting streamflow permanence was calculated by the percent decrease in classification accuracy resulting from the exclusion of each predictor variable in the model (Liaw & Wiener, 2002). Variability in each predictor variable's importance results from the 1000 iterations of the model trained on different combinations of down-sampled data. Generally, the inclusion of climate variables increases the model's ability to predict streamflow permanence. The volume of snow water remaining in a catchment on May 1st is the most important variable predicting intermittency, followed by snow water depth on May 1st and catchment area, considered independently (Figure 2). The probability of permanent flow increases substantially with increasing snowpack and watershed size (Figure 3a, b, c). Following snowpack and areal extent, precipitation (as both rain and snow) accumulated in a given water year (October through September) ranks as the fourth most important predictor variable (Figure 2). When precipitation reaches about 500mm in a water year, the probability of non-permanent flow declines sharply (Figure 3e). The fifth and sixth most important variables are the annual sum of January through June temperatures, and the 30-year normal temperature calculated for 1980 to 2010 (Figure 2). Warmer winter and spring temperatures significantly increase the probability of stream drying, particularly when cumulative temperatures reach 20°C (Figure 3d). The number of days for which the soil surface in a catchment is not frozen (“FrostFreeDays”) is also a strong predictor of flow and is strongly correlated with winter and spring air temperature (Figure 2). Landscape attributes account for most of the remaining predictor variables important for predicting surface flow (Figure 2). However, riparian vegetation percent cover is the only variable shown whose values were calculated continuously and changed across years. Increasing vegetation cover in the riparian zone has a negative relationship with the probability of no-flow (Figure 3f). While riparian vegetation is important for predicting streamflow, our measure of riparian quality that incorporates interactions between vegetative cover and grazing did not increase the model’s predictive ability. Additionally, percent forest cover measured annually at the catchment scale was not among the top 15 variables important for predicting streamflow. Other variables shown in the variable importance plot that characterize grazing and percent forested from the HUC 8 down to the reach scale were important for predicting streamflow. It is important to note that these variables do not vary across time as they were calculated once at the initiation of the PIBO monitoring program.

Climate and Landcover Simulations

Declines in SWE values initiate strong changes in the amount of habitat area predicted to be available, particularly when loss of spring SWE is driven by reductions in precipitation (Figure 4, 5). In all sites, as well as in only those sites supporting bull trout and cutthroat trout, once SWE and precipitation decline below the historic average conditions (2004 – 2021), the amount of wetted habitat area that remains available declines exponentially (Figures 4a, b, c; 5a, b, c). In scenarios where SWE increases in conjunction with precipitation, and temperature is held constant, the amount of available habitat increases substantially in all sites as well as in sites supporting cutthroat trout. In scenarios where SWE and precipitation are reduced to 10% of historic conditions and temperatures are held to baseline, the percent of habitat remaining declines to just 71% for all sites, 92% for bull trout sites, and 83% for sites supporting cutthroat trout (Figure 4a, b, c). This extreme climate scenario translates to habitat losses of 26,000 square kilometers for all sites, 3,250 square kilometers for bull trout sites, and 7,100 square kilometers for cutthroat sites (Figure 5a, b, c). The warming of air temperatures has a mostly additive effect on habitat loss, with warmer temperatures compounding habitat lost to drying under reduced snowpack scenarios (Figures 4d, e, f; 5d, e, f). However, while there is a substantial decrease in remaining available habitat when temperatures rise by 2°C, habitat loss due to surface flow discontinuity only marginally increases when air temperatures warm to 4°C.

Simulation results indicate that the amount of habitat that remained flowing and available was sensitive to changes in riparian vegetative cover simulated under baseline climate conditions (Figure 6). Reducing riparian vegetative cover had a greater impact on the change in remaining habitat than increasing riparian cover did at the same proportion. A 50% reduction in riparian vegetation diminished the percent of remaining wetted catchment area to 77% for all sites, 95% for bull trout sites, and 90% for cutthroat trout sites. Increasing riparian vegetation by 50% of mean observed values increased the percent of remaining, flowing habitat to 84% for all sites, 97% for bull trout sites, and 95% for cutthroat trout sites. Manipulating percent forest cover at the catchment scale had a negligible effect on streamflow permanence and subsequent changes in remaining habitat area (Figure 6).

Discussion

Streamflow permanence patterns are mediated by interactions between climate and landscape conditions that vary across spatial and temporal extents. Our results indicate that smaller catchments that accumulate and retain less snow incur the greatest risk of non-permanent flow under forecasted warming. Accelerated drying will initiate strong changes in the quantity of habitat remaining for thermally sensitive salmonids. Future research and management of multi-use landscapes needs to consider the implications of increasingly dynamic river networks for fluvial, cold-water species persistence, as well as the ability of watersheds vulnerable to drying to support historic levels of livestock grazing in the riparian zone.

While the climate and landscape attributes characterizing our study area are heterogeneous across space and time, we found that several climate variables consistently ranked as important drivers of surface flow permanence. The volume of snow remaining in a catchment on May 1st is a primary control on surface flow persistence, and reduced SWE scenarios exponentially increase the amount of habitat lost to drying, particularly when coupled with reduced precipitation and warmer temperatures. This is consistent with other research demonstrating the importance of snowpack size and persistence for streamflow in the CRB (Hamlet & Lettenmaier, 1999; Sando & Blasch, 2015; Jaeger et al., 2019). In scenarios where SWE changes proportionally with precipitation, declines in both climate variables below baseline conditions result in exponential losses of year-round flow and remaining habitat. Under dry conditions habitat loss is greatest for all sites, but among sites supporting target salmonid species, flow permanence and habitat availability is most vulnerable in sites supporting cutthroat. In scenarios where May 1st SWE changes occur in conjunction with warmer air temperatures, but water year precipitation is held constant, the most significant changes to available wetted habitat do not occur until SWE declines to 50% of historic conditions, below which climate-induced habitat loss increases sharply. Additionally, we found that air temperatures during the first six months of the year strongly predict streamflow permanence, and catchments with higher air temperatures exhibit more discontinuous flow patterns. Furthermore, we observed the greatest loss of available wetted habitat across all sites in simulations where temperatures increased in conjunction with simulated declines in spring SWE. Among sites supporting target species, this effect was particularly impactful in sites supporting cutthroat. These results are in line with other studies that highlight the sensitivity of streamflow to variations in air temperature (Payne et al., 2004; Jaeger et al., 2014a; 2019b). Interestingly, while a 2°C rise in air temperatures notably decreases remaining habitat, warming to 4°C had a minimal effect on simulated habitat availability. Random forest cannot predict accurate response classes for new input data whose values are outside of the distribution of initial training data (Breiman, 2001). As such, increasing mean site-specific air temperatures by 4°C likely manipulated input data beyond the scope of the model's ability and produced results very similar to 2°C warming scenarios, where simulated values were still described by the upper bounds of the training data. While our model is not mechanistic, physical models have demonstrated that temperature mediates surface flow through several interacting pathways. It regulates the timing of snowmelt, with warmer temperatures shifting melt timing earlier in the year, resulting in lower baseflows and greater risk of summer flow cessation (Stewart et al., 2005; Barnhart et al., 2016). Warmer air temperatures also increase evapotranspiration and loss of soil moisture, reducing water transport through the catchment and subsequent surface flow (Eng et al., 2016, Merritt et al., 2021). Numerous climate models forecast that the CRB will experience increased spring temperatures and a reduced snowpack, as well as increasing variability in these measures (Hamlet & Lettenmaier, 1999; Chase et al., 2011, Rupp et al., 2017). Our results indicate that these anticipated climate scenarios will exponentially reduce the amount of connected, upstream habitat available to threatened and sensitive salmonid species.

Bull trout and cutthroat species rely on a series connected habitat patches to complete their life history (Young, 1995; Schoby & Keeley, 2011; Budy et al., 2019). While these species have evolved diverse life history expressions in response to dynamism in the environments they inhabit (Lytle & Poff, 2004; Muhlfeld & Marotz, 2005; Radinger & Wolter, 2014; Budy et al., 2020), accelerated drying under anticipated climate scenarios will both reduce the size of suitable habitat patches as well as their ability to disperse between them. Hamlet & Lettenmaier (1999) forecasted a 2-3°C increase in temperatures and a subsequent reduction to 60% of historic spring SWE for the CRB by 2045. Our results conservatively estimate that these conditions would reduce the amount of remaining, wetted habitat to 74% across all sites, 94% for bull trout sites, and 87% for cutthroat sites. If loss of spring snowpack occurs as a function of both increasing spring air temperatures *and* reduced precipitation, remaining habitat would likely decline further. Loss of total available habitat as function of decreasing patch size and interrupted connectivity between patches carries significant consequences for the abundance and distribution of these salmonid species across their native range (Young, 1995; Rieman & McIntyre, 1995; Isaak et al., 2022). More recent climate predictions for the CRB indicate that consistent trends of summer warming and precipitation regimes are difficult to predict across large spatio-temporal scales, but that climate patterns will become increasingly variable in the future, characterized by more frequent drought and precipitation extremes (Rupp et al., 2017). As stream networks are sensitive to both antecedent and active climate conditions, increasing interannual variability will likely result in proportional expansion and contraction of the network's extent (Jaeger et al., 2014; Moidu et al., 2021), the scale of which may be described by our results.

While more non-permanent flow significantly decreases the amount of available wetted habitat across all sites, our median model estimates indicate that it has a particularly negative effect on habitat available for cutthroat trout. This suggests that, within the extent of our study area, cutthroat trout occupy drainages that are particularly vulnerable to future drying under climate warming scenarios. Comparing the climate and landscape conditions of cutthroat versus bull trout occupied sites in our study extent reveals that, on average, cutthroat occupy smaller, lower elevation drainages that accumulate and retain less snow, and are subject to warmer spring air temperatures. Given the importance of these variables in predicting non-permanent flow, it is unsurprising that we see the most dramatic declines in available habitat in catchments historically occupied by cutthroat trout species. These findings are consistent with Stewart et al. (2005), who found that mid-elevation drainages are more vulnerable to reductions in summer baseflows, as warming winter and spring temperatures drive earlier snowmelt and cause a greater proportion of precipitation to come as rain. Meanwhile, higher elevation catchments had a buffer against earlier stream drying, as they remained comparatively cooler. These results are consistent with Isaak et al. (2016), who found that elevation is inversely related to climate change velocity, potentially buffering bull trout populations occupying high elevation headwaters from climate-induced threats. However, though median model estimates indicate that habitat lost to drying is more significant for cutthroat trout, the effect of drying on habitat loss for bull trout is still substantial. Additionally, this high elevation buffer against stream temperature warming will be reduced as snowpack declines (Cline et al., 2020). This underscores the importance of snowpack for stream habitat supporting cold water salmonids.

While climate variables were the strongest predictors of flow permanence, landscape variables contributed to predictive ability as well. Catchment size appears to regulate the quantity of snow that accumulates and becomes available for streamflow generation following melt, with larger catchments consistently supporting more surface flow. Catchment size being a strong predictor of surface flow may also result from the ability of larger catchments to store more subsurface water. The capacity for larger catchments to store more groundwater and exhibit dynamic infiltration flow paths has been shown to decouple hydrologic responses from climatic inputs, creating a buffer for streamflow permanence against warmer spring and summer temperatures (Costigan et al., 2015; Brooks et al., 2021; Zipper et al., 2021). However, groundwater recharge has also been shown to be sensitive to climate change (Ng et al., 2010; Goderniaux et al., 2011). Prolonged drought may limit the ability of groundwater storage to prolong surface flow, potentially resulting in more frequent surface flow cessation in large catchments and habitat loss for threatened and sensitive salmonid species.

We also found that the streamflow permanence was sensitive to changes in some landscape attributes that were directly impacted by management actions. Declines in riparian cover adjacent to the streambank corresponded to decreases in the availability of wetted upstream habitat. Among sites supporting target species, this effect was particularly pronounced in cutthroat trout sites, as a site-specific 50% decrease in riparian vegetative cover reduced remaining habitat area to 90%, even when climate variables were held at baseline values. We observed moderate increases in wetted habitat availability when riparian vegetation increased following simulated changes to management, but the effect is less pronounced. It is important to note that there are two sources of variability in the riparian vegetative cover data. This measurement was taken for each site at each sampling event and represents yearly vegetative conditions that changed over time. However, this metric describes vegetative cover broadly, and does not control for the variation inherent among different plant communities that characterize distinct ecoregions. We attempted to address this by scaling site-specific riparian vegetation cover by +/- 50% relative to each site’s unique baseline value. However, it is possible that the heterogeneity in the training data that allowed the model to identify riparian vegetation cover as an important factor for distinguishing streamflow classifications arose from spatial heterogeneity among different regional plant communities rather than from within site variation in cover across time. Future research should include ecoregion or dominant landcover type as an additional variable that may help disentangle spatial correlations.

Our findings have important ramifications for those managing landscapes for resilience. While current land management plans incorporate results from a growing body of research that suggests non-permanent streams are important for stream biota and ecosystem services, grazing regulations around non-permanent streams are still not as robust as in perennial streams, and flow classifications that inform regulations may be increasingly inaccurate. In those low elevation streams that drain small catchments, managers may find that more flow impermanence is correlated with declines in the amount of vegetation cover available for livestock, particularly in streams that were once permanent by now flow seasonally. Sustainable grazing may be hard to achieve if regulations rely on strict and potentially inaccurate streamflow classifications to inform the amount or intensity of allowable activity. Land-use and climate adaptation plans should tend towards a more flexible approach that accounts for flow permanence variability in streams most vulnerable to drying. Greater synchronicity between regulation and realized conditions will lead to more sustainable land-use and ensure that watersheds maintain key processes that make them robust to changing conditions, as streamflow's sensitivity to changes in riparian vegetation may also result from indirect effects of grazing on the movement of water through a catchment.

Livestock grazing and trampling in riparian areas reduces ground cover, which can decrease macropore space in the soil and increase soil temperature, leading to higher rates of evaporation and decreased soil moisture conditions (McGinty et al., 1979; Udom & Nuga, 2014). Soil moisture conditions have a direct impact on streamflow generation (McNamara et al., 2005; Harpold et al., 2016), as saturated soils create hydraulic conductivity and provide a shallow pathway for water to move into a stream, often stabilizing surface flow (Hewlett & Hibbert, 1963; Jensco & McGlynn, 2011; Costigan et al., 2016; Kaplan et al., 2022). While it is unlikely that grazing alone is a dominant control on streamflow, in catchments vulnerable to climate-induced drying and potentially occupied by sensitive species, adaptive grazing management is a pragmatic tool that managers can use to bolster sub-surface hydraulic pathways and mitigate further fragmentation of the stream network. However, more research is needed to assess the mechanistic relationship between livestock grazing and surface flow at scale.

There is little relationship between changes in forest cover at the catchment scale and the loss or gain of wetted habitat. This was surprising given the strong correlation between forest cover and streamflow permanence in other studies classifying flow (González-Ferreras & Barquín, 2017; Jaeger et al., 2019). However, research has also shown that a catchment's water balance and baseflow demonstrate divergent responses to land use practices that affect forest cover at the watershed scale (Hibbert, 1965; Brown et al., 2005; Biederman et al., 2014). For example, surface flow often increases in proportion to the percent of forest cover removed, though the magnitude of this effect varies with climate and topology (Brown et al., 2005; Moore & Wondzell, 2005). Contrarily, Biederman et al. (2014) found that, following deforestation, potential gains in surface flow resulting from decreased evapotranspiration were offset by increases in evaporation, with little net effect on streamflow. Furthermore, Belmar et al. (2016) found that forest maturity had a stabilizing effect on streamflow, bolstering low flows and reducing flood magnitude. The observed limited effect that manipulating forest cover had on streamflow permanence classifications in our study may result from watersheds exhibiting divergent flow responses to variability in forest cover. Additionally, forest cover is correlated with precipitation, and as precipitation is one of the strongest predictor variables included in the model, the relative effect of forest cover may have been masked by the influence of precipitation. As streamflow response to forest cover is strongly influenced by local topology and climate, the scale of our study area likely limited our ability to discern generalizable, regionally consistent trends. Future research leveraging finer scale climate and landscape data may be needed to investigate sub-regional relationships between streamflow and forest cover.

Many of the variables characterizing grazing and percent forested that were important for predicting streamflow did not vary across time. While measures characterizing historic conditions for a snapshot in time may serve as good predictors of flow, they do not accurately represent landscape changes that arise from active climate or management trends and drive variability in streamflow permanence. As such we did not rely heavily on them for simulation modeling or interpretation.

Our results complement the growing body of evidence showing that streamflow permanence patterns are increasingly variable and that a stream's annual flow class is highly sensitive to interannual changes in local conditions. Meanwhile, forest management plans often afford fewer protections to non-permanent streams and the catchments that drain them, on the basis that these streams provide fewer environmental services (USFS, 2003; Kershner et al., 2004). The acceleration of stream drying combined with recent enhancements in mapping capability that enable modeling of flow permanence classes at the reach scale (Jaeger et al., 2019; Sando et al., 2022) could result in more streams with reduced protections on federal land. However, recent research has also shown that habitat permanence is not always synonymous with habitat importance, as non-permanent streams can provide unique resource opportunities that are important for a variety of salmonid life history stages and strategies (Heim et al., 2019; Chapter III, Rousseau, 2024). As more streams demonstrate variability in flow permanence, land management plans should aim conserve the diverse set of habitats that support the fluvial life history of cold-water species of concern, which will increasingly include non-permanent stream reaches.

For watersheds in the CRB whose hydrology is snowmelt driven, our results suggest that anticipated climate conditions will exacerbate drying and fragment critical habitat for threatened and sensitive salmonid species. Processes that reduce area and increase isolation of habitat patches have long been shown to increase the risk of extinction for salmonids in fragmented landscapes (Rieman & McIntyre, 1995; Dunham & Rieman, 1999). The effect of habitat fragmentation due to anthropogenic activity, non-native invasion, and rising in-stream temperatures has been well documented (Reiman et al., 2001; Peterson et al., 2008; Isaak et al., 2016). However, our results demonstrate that pervasive changes in streamflow permanence pose a significant threat to the total availability of habitat, as well as the connectivity between patches that is essential to maintaining diverse life history expressions, gene flow and demographic processes (Neraas & Spruell, 2001; Budy et al., 2020).

Headwater streams are predicted to serve as refuge habitat for cold water salmonid species threatened by warming, as isotherms shift upstream more slowly with increasing elevation (Isaak et al., 2015a; 2016b). However, the ability of thermally sensitive fishes to migrate upstream is dependent upon the local processes governing surface flow continuity (Isaak et al., 2016). Under anticipated climate scenarios, increased stream drying of either the entire stream length, or of stream segments, reduces access to cooler, upstream environments, inducing stress in species with narrow thermal tolerances. Moreover, downstream drying of the network may restrict isolated populations to headwater reaches with low productivity, and will reduce access to warm, low elevation habitats that often support superior forage and growth opportunities (Downs et al., 1997; Schoby & Keeley, 2011; Armstrong et al., 2021). Watershed size is a dominant control structuring riverine environments, habitat complexity (Benda et al., 2004), and the genetic diversity of the populations that occupy them (Neville et al., 2009). Our results suggest that loss of streamflow continuity reduces total habitat size which reduces physical and biological heterogeneity at the landscape scale (Schindler et al., 2015). Homogenization and synchronicity among remaining habitat types and genetically similar populations confers a greater risk of disturbance for both the stream network and its biota.

References

Akosa, J. (2017, April). Predictive accuracy: A misleading performance measure for highly imbalanced data. In *Proceedings of the SAS global forum* (Vol. 12, pp. 1-4). Cary, NC, USA: SAS Institute Inc.

Al-Chokhachy, R., Moran, S., McHugh, P. A., Bernall, S., Fredenberg, W., & DosSantos, J. M. (2015). Consequences of actively managing a small Bull Trout population in a fragmented landscape. *Transactions of the American Fisheries Society*, *144*(3), 515-531. https://doi.org/10.1080/00028487.2015.1007162

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., ... & Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, *11*(4), 354-361. https://doi.org/10.1038/s41558-021-00994-y

Barnhart, T. B., Molotch, N. P., Livneh, B., Harpold, A. A., Knowles, J. F., & Schneider, D. (2016). Snowmelt rate dictates streamflow. *Geophysical Research Letters*, *43*(15), 8006-8016. https://doi.org/10.1002/2016GL069690

Barrett, A. P. (2003). *National operational hydrologic remote sensing center snow data assimilation system (SNODAS) products at NSIDC* (p. 19). Boulder, CO: National Snow and Ice Data Center, Cooperative Institute for Research in Environmental Sciences.

Beaman, W. M. (1928). *Topographic mapping*. US Government Printing Office.

Belmar, O., Barquín, J., Álvarez-Martínez, J. M., Peñas, F. J., & Del Jesus, M. (2016). The role of forest maturity on catchment hydrologic stability. *Hydrology and earth system sciences discussions*, *2016*, 1-17. https://doi.org/10.5194/hess-2016-471

Benkendorf, D. J., Schwartz, S. D., Cutler, D. R., & Hawkins, C. P. (2023). Correcting for the effects of class imbalance improves the performance of machine-learning based species distribution models. *Ecological Modelling*, *483*, 110414. https://doi.org/10.1016/j.ecolmodel.2023.110414

Biederman, J. A., Harpold, A. A., Gochis, D. J., Ewers, B. E., Reed, D. E., Papuga, S. A., & Brooks, P. D. (2014). Increased evaporation following widespread tree mortality limits streamflow response. *Water Resources Research*, *50*(7), 5395-5409. https://doi.org/10.1002/2013WR014994

Breiman, L. (2001). Random forests. *Machine learning*, *45*, 5-32.

Brooks, P. D., Gelderloos, A., Wolf, M. A., Jamison, L. R., Strong, C., Solomon, D. K., ... & Stewart, J. (2021). Groundwater-mediated memory of past climate controls water yield in snowmelt-dominated catchments. *Water Resources Research*, *57*(10), e2021WR030605. https://doi.org/10.1029/2021WR030605

Brown, A. E., Zhang, L., McMahon, T. A., Western, A. W., & Vertessy, R. A. (2005). A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. *Journal of hydrology*, *310*(1-4), 28-61. https://doi.org/10.1016/j.jhydrol.2004.12.010

Budy, P., Rogers, K. B., Kanno, Y., Penaluna, B. E., Hitt, N., Thiede, G. P., ... & DeRito, J. (2019). *Distribution and status of trout and char in North America*.

Budy, P., Thompson, P. D., McKell, M. D., Thiede, G. P., Walsworth, T. E., & Conner, M. M. (2020). A multifaceted reconstruction of the population structure and life history expressions of a remnant metapopulation of Bonneville Cutthroat Trout: implications for maintaining intermittent connectivity. *Transactions of the American Fisheries Society*, *149*(4), 443-461. https://doi.org/10.1002/tafs.10240

Chiu, M. C., Leigh, C., Mazor, R., Cid, N., & Resh, V. (2017). Anthropogenic threats to intermittent rivers and ephemeral streams. *Intermittent rivers and ephemeral streams* (pp. 433-454). Academic Press.

Colvin, S. A., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., ... & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries*, *44*(2), 73-91. https://doi.org/10.1002/fsh.10229

Costigan, K. H., Daniels, M. D., & Dodds, W. K. (2015). Fundamental spatial and temporal disconnections in the hydrology of an intermittent prairie headwater network. *Journal of Hydrology*, *522*, 305-316. https://doi.org/10.1016/j.jhydrol.2014.12.031

Costigan, K. H., Jaeger, K. L., Goss, C. W., Fritz, K. M., & Goebel, P. C. (2016). Understanding controls on flow permanence in intermittent rivers to aid ecological research: Integrating meteorology, geology and land cover. *Ecohydrology*, *9*(7), 1141-1153. https://doi.org/10.1002/eco.1712

Cutler, D. R., Edwards Jr, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*(11), 2783-2792. https://doi.org/10.1890/07-0539.1

Dan Moore, R., & Wondzell, S. M. (2005). Physical hydrology and the effects of forest harvesting in the Pacific Northwest: a review. *JAWRA Journal of the American Water Resources Association*, *41*(4), 763-784. https://doi.org/10.1111/j.1752-1688.2005.tb03770.x

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: a challenge for freshwater ecology. *BioScience*, *64*(3), 229-235. https://doi.org/10.1093/biosci/bit027

Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, *7*(1), 014037. http://doi.org/10.1088/1748-9326/7/1/014037

Downs, C. C., White, R. G., & Shepard, B. B. (1997). Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. *North American Journal of Fisheries Management*, *17*(1), 85-92. https://doi.org/10.1577/1548-8675(1997)017%3C0085:AASMSR%3E2.3.CO;2

Dunham, J. B., & Rieman, B. E. (1999). Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications*, *9*(2), 642-655. https://doi.org/10.1890/1051-0761(1999)009[0642:MSOBTI]2.0.CO;2

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175. https://doi.org/10.2307/3544901

Erman, D. C., & Hawthorne, V. M. (1976). The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Transactions of the American Fisheries Society*, *105*(6), 675-681. https://doi.org/10.1577/1548-8659(1976)105%3C675:TQIOAI%3E2.0.CO;2

Falke, J. A., Fausch, K. D., Magelky, R., Aldred, A., Durnford, D. S., Riley, L. K., & Oad, R. (2011). The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecohydrology*, *4*(5), 682-697. https://doi.org/10.1002/eco.158

Fesenmyer, K. A., Wenger, S. J., Leigh, D. S., & Neville, H. M. (2021). Large portion of USA streams lose protection with new interpretation of Clean Water Act. *Freshwater Science*, *40*(1), 252-258. https://doi.org/10.1086/713084

Fritz, K. M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington Jr, P. J., Leibowitz, S. G., Comeleo, R. L., Ebersole, J. L., & Nadeau, T. L. (2013). Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. *JAWRA Journal of the American Water Resources Association*, *49*(4), 867-882. https://doi.org/10.1111/jawr.12040

Goderniaux, P., Brouyere, S., Blenkinsop, S., Burton, A., Fowler, H. J., Orban, P., & Dassargues, A. (2011). Modeling climate change impacts on groundwater resources using transient stochastic climatic scenarios. *Water Resources Research*, *47*(12). https://doi.org/10.1029/2010WR010082

Godsey, S. E., & Kirchner, J. W. (2014). Dynamic, discontinuous stream networks: Hydrologically driven variations in active drainage density, flowing channels and stream order. *Hydrological Processes*, *28*(23), 5791-5803. https://doi.org/10.1002/hyp.10310

González-Ferreras, A. M., & Barquín, J. (2017). Mapping the temporary and perennial character of whole river networks. *Water Resources Research*, *53*(8), 6709-6724. https://doi.org/10.1002/2017WR020390

Griffith, G. (2010). Level III North American Terrestrial Ecoregions: United States Descriptions. *Prepared for the North American Commission for Environmental Cooperation*, 1-64.

Guptill, S. C. (1990). *An enhanced digital line graph design* (No. 1048). USGPO; Books and Open-File Reports Section, US Geological Survey.

Hafen, K. C., Blasch, K. W., Rea, A., Sando, R., & Gessler, P. E. (2020). The influence of climate variability on the accuracy of NHD perennial and nonperennial stream classifications. *JAWRA Journal of the American Water Resources Association*, *56*(5), 903-916. https://doi.org/10.1111/1752-1688.12871

Hamlet, A. F., & Lettenmaier, D. P. (1999). Effects of climate change on hydrology and water resources in the Columbia River Basin. *JAWRA Journal of the American Water Resources Association*, *35*(6), 1597-1623. https://doi.org/10.1111/j.1752-1688.1999.tb04240.x

Harpold, A. A., Sutcliffe, K., Clayton, J., Goodbody, A., & Vazquez, S. (2017). Does including soil moisture observations improve operational streamflow forecasts in snow-dominated watersheds?. *JAWRA Journal of the American Water Resources Association*, *53*(1), 179-196. https://doi.org/10.1111/1752-1688.12490

Heim, K. C., McMahon, T. E., Calle, L., Wipfli, M. S., & Falke, J. A. (2019). A general model of temporary aquatic habitat use: water phenology as a life history filter. *Fish and Fisheries*, *20*(4), 802-816. https://doi.org/10.1111/faf.12386

Hewlett, J. D., & Hibbert, A. R. (1963). Moisture and energy conditions within a sloping soil mass during drainage. *Journal of geophysical research*, *68*(4), 1081-1087. https://doi.org/10.1029/JZ068i004p01081

Hibbert, A. R. (1965). *Forest treatment effects on water yield* (p. 813). Asheville: Coweeta Hydrologic Laboratory, Southeastern Forest Experiment Station.

Horton, R. E. (1945). Erosional development of streams and their drainage basins; hydrophysical approach to quantitative morphology. *Geological society of America bulletin*, *56*(3), 275-370. https://doi.org/10.1130/0016-7606(1945)56[275:EDOSAT]2.0.CO;2

Isaak, D. J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, *21*(7), 2540-2553. https://doi.org/10.1111/gcb.12879

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374-4379. https://doi.org/10.1073/pnas.1522429113

Isaak, D., M. Young, D. Nagel, D. Horan, M. Groce, and S. Parkes. 2017. Climate Shield bull trout and cutthroat trout population occurrence scenarios for the western U.S. Rocky Mountain Research Station, U.S. Forest Service Data Archive, Fort Collins, CO.

Isaak, D. J., Young, M. K., Horan, D. L., Nagel, D., Schwartz, M. K., & McKelvey, K. S. (2022). Do metapopulations and management matter for relict headwater bull trout populations in a warming climate?. *Ecological Applications*, *32*(5), e2594. https://doi.org/10.1002/eap.2594

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894-13899. https://doi.org/10.1073/pnas.1320890111

Jaeger, K. L., Sando, R., McShane, R. R., Dunham, J. B., Hockman-Wert, D. P., Kaiser, K. E., ... & Blasch, K. W. (2019). Probability of Streamflow Permanence Model

(PROSPER): A spatially continuous model of annual streamflow permanence throughout the Pacific Northwest. *Journal of Hydrology X*, *2*, 100005. https://doi.org/10.1016/j.hydroa.2018.100005

Jencso, K. G., & McGlynn, B. L. (2011). Hierarchical controls on runoff generation: Topographically driven hydrologic connectivity, geology, and vegetation. *Water Resources Research*, *47*(11). https://doi.org/10.1029/2011WR010666

Johnson, R. A., Chawla, N. V., & Hellmann, J. J. (2012, October). Species distribution modeling and prediction: A class imbalance problem. In *2012 Conference on intelligent data understanding* (pp. 9-16). IEEE. https://doi.org/10.1109/CIDU.2012.6382186

Kaplan, N. H., Blume, T., & Weiler, M. (2020). Predicting probabilities of streamflow intermittency across a temperate mesoscale catchment. *Hydrology and Earth System Sciences*, *24*(11), 5453-5472. https://doi.org/10.5194/hess-24-5453-2020

Kaplan, N. H., Blume, T., & Weiler, M. (2022). Event controls on intermittent streamflow in a temperate climate. *Hydrology and Earth System Sciences*, *26*(10), 2671-2696. https://doi.org/10.5194/hess-26-2671-2022

Keleher, C. J., & Rahel, F. J. (1996). Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. *Transactions of the American Fisheries Society*, *125*(1), 1-13. https://doi.org/10.1577/1548-8659(1996)125%3C0001:TLTSDI%3E2.3.CO;2

Kershner, J. L., Archer, E. K., Coles-Ritchie, M., Cowley, E. R., Henderson, R. C., Kratz, K., Quimby, C. M., Turner, D. L., Ulmer, L. C., & Vinson, M. R. (2004). *Guide to effective monitoring of aquatic and riparian resources.* https://doi.org/10.2737/rmrs-gtr-121

Kominoski, J. S., Ruhí, A., Hagler, M. M., Petersen, K., Sabo, J. L., Sinha, T., Sankarasubramanian, A., & Olden, J. D. (2018). Patterns and drivers of fish extirpations in rivers of the American Southwest and Southeast. *Global Change Biology*, *24*(3), 1175-1185. https://doi.org/10.1111/gcb.13940

Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of statistical software*, *28*, 1-26. Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774-1791. https://doi.org/10.1890/1051-0761(2000)010[1774:DOISHR]2.0.CO;2

LANDFIRE: LANDFIRE Percent Canopy Cover layer. (2001- 2022). U.S. Department of Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online on November 1, 2023, at http://landfire.cr.usgs.gov/viewer/

Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, *55*(4), 717-738. https://doi.org/10.1111/j.1365-2427.2009.02322.x

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R news*, *2*(3), 18-22.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in ecology & evolution*, *19*(2), 94-100. https://doi.org/10.1016/j.tree.2003.10.002

Marshall, A. M., Foard, M., Cooper, C. M., Edwards, P., Hirsch, S. L., Russell, M., & Link, T. E. (2020). Climate change literature and information gaps in mountainous headwaters of the Columbia River Basin. *Regional environmental change*, *20*, 1-14. https://doi.org/10.1007/s10113-020-01721-7

McGinty, W. A., Smeins, F. E., & Merrill, L. B. (1979). Influence of soil, vegetation, and grazing management on infiltration rate and sediment production of Edwards Plateau rangeland. *Rangeland Ecology & Management/Journal of Range Management Archives*, *32*(1), 33-37. http://doi.org/10.2307/3897380

McNamara, J. P., Chandler, D., Seyfried, M., & Achet, S. (2005). Soil moisture states, lateral flow, and streamflow generation in a semi-arid, snowmelt-driven catchment. *Hydrological Processes: An International Journal*, *19*(20), 4023-4038. https://doi.org/10.1002/hyp.5869

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391-397. https://doi.org/10.1038/s41586-021-03565-5

Moidu, H., Obedzinski, M., Carlson, S. M., & Grantham, T. E. (2021). Spatial patterns and sensitivity of intermittent stream drying to climate variability. *Water*

Resources Research, *57*(11), e2021WR030314. https://doi.org/10.1029/2021WR030314

Moidu, H., Rodríguez-Lozano, P., Leidy, R. A., Bogan, M. T., Grantham, T. E., & Carlson, S. M. (2023). Ecological consequences of shifting habitat mosaics within and across years in an intermittent stream. *Freshwater Biology*, *68*(7), 1161-1175. https://doi.org/10.1111/fwb.14094

Muhlfeld, C. C., & Marotz, B. (2005). Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management*, *25*(3), 797-810. https://doi.org/10.1577/M04-045.1

Neville, H., Dunham, J., Rosenberger, A., Umek, J., & Nelson, B. (2009). Influences of wildfire, habitat size, and connectivity on trout in headwater streams revealed by patterns of genetic diversity. *Transactions of the American fisheries society*, *138*(6), 1314-1327. https://doi.org/10.1577/T08-162.1

Neraas, L. P., & Spruell, P. (2001). Fragmentation of riverine systems: the genetic effects of dams on bull trout (Salvelinus confluentus) in the Clark Fork River system. *Molecular Ecology*, *10*(5), 1153-1164. https://doi.org/10.1046/j.1365-294X.2001.01269.x

Ng, G. H. C., McLaughlin, D., Entekhabi, D., & Scanlon, B. R. (2010). Probabilistic analysis of the effects of climate change on groundwater recharge. *Water Resources Research*, *46*(7). https://doi.org/10.1029/2009WR007904

Payne, J. T., Wood, A. W., Hamlet, A. F., Palmer, R. N., & Lettenmaier, D. P. (2004). Mitigating the effects of climate change on the water resources of the Columbia River basin. *Climatic change*, *62*, 233-256. https://doi.org/10.1023/B:CLIM.0000013694.18154.d6

Peterson, D. P., Rieman, B. E., Dunham, J. B., Fausch, K. D., & Young, M. K. (2008). Analysis of trade-offs between threats of invasion by nonnative brook trout (Salvelinus fontinalis) and intentional isolation for native westslope cutthroat trout (Oncorhynchus clarkii lewisi). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 557-573. https://doi.org/10.1139/f07-184

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian journal of fisheries and aquatic sciences*, *46*(10), 1805-1818. https://doi.org/10.1139/f89-228

Prancevic, J. P., & Kirchner, J. W. (2019). Topographic controls on the extension and retraction of flowing streams. *Geophysical Research Letters*, *46*(4), 2084-2092. https://doi.org/10.1029/2018GL081799

PRISM Climate Group, (2004). Oregon State University, https://prism.oregonstate.edu, accessed November 2023.

R Core Team (2024). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Radinger, J., & Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish and fisheries*, *15*(3), 456-473. https://doi.org/10.1111/faf.12028

Reynolds, L. V., Shafroth, P. B., & Poff, N. L. (2015). Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change. *Journal of Hydrology*, *523*, 768-780. https://doi.org/10.1016/j.jhydrol.2015.02.025

Rieman, B. E., & McIntyre, J. D. (1995). Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American fisheries Society*, *124*(3), 285-296. https://doi.org/10.1577/1548-8659(1995)124%3C0285:OOBTIN%3E2.3.CO;2

Rieman, B., Peterson, J. T., Clayton, J., Howell, P., Thurow, R., Thompson, W., & Lee, D. (2001). Evaluation of potential effects of federal land management alternatives on trends of salmonids and their habitats in the interior Columbia River basin. *Forest ecology and management*, *153*(1-3), 43-62. https://doi.org/10.1016/S0378-1127(01)00453-4

Rieman, B. E., Isaak, D., Adams, S., Horan, D., Nagel, D., Luce, C., & Myers, D. (2007). Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society*, *136*(6), 1552-1565. https://doi.org/10.1577/T07-028.1

Rogosch, J. S., Tonkin, J. D., Lytle, D. A., Merritt, D. M., Reynolds, L. V., & Olden, J. D. (2019). Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere*, *10*(4), e02681. https://doi.org/10.1002/ecs2.2681

Roper, B. B., Saunders, W. C., & Ojala, J. V. (2019). Did changes in western federal land management policies improve salmonid habitat in streams on public lands within the Interior Columbia River Basin?. *Environmental monitoring and assessment*, *191*(9), 574. https://doi.org/10.1007/s10661-019-7716-5

Rupp, D. E., Abatzoglou, J. T., & Mote, P. W. (2017). Projections of 21st century climate of the Columbia River Basin. *Climate Dynamics*, *49*, 1783-1799. https://doi.org/10.1007/s00382-016-3418-7

Sando, R., & Blasch, K. W. (2015). Predicting alpine headwater stream intermittency: A case study in the northern Rocky Mountains. *Ecohydrology & Hydrobiology*, *15*(2), 68-80. https://doi.org/10.1016/j.ecohyd.2015.04.002

Sando, R., Jaeger, K. L., Farmer, W. H., Barnhart, T. B., McShane, R. R., Welborn, T. L., Kaiser, K. E., Hafen, K. C., Blasch, K., York, B., & Shallcross, A. (2022). Predictions and drivers of sub-reach-scale annual streamflow permanence for the upper Missouri River basin: 1989–2018. *Journal of Hydrology X*, *17*, 100138. https://doi.org/10.1016/j.hydroa.2022.100138

Scheidegger, A. E. (1968). Horton's laws of stream lengths and drainage areas. *Water Resources Research*, *4*(5), 1015-1021. https://doi.org/10.1029/WR004i005p01015

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257-263. https://doi.org/10.1890/140275

Schoby, G. P., & Keeley, E. R. (2011). Home range size and foraging ecology of bull trout and westslope cutthroat trout in the upper Salmon River Basin, Idaho. *Transactions of the American Fisheries Society*, *140*(3), 636-645. https://doi.org/10.1080/00028487.2011.585578

Soil Survey Staff. Gridded National Soil Survey Geographic (gNATSGO) Database for the Conterminous United States. United States Department of Agriculture, Natural Resources Conservation Service. Available online at https://nrcs.app.box.com/v/soils. November 1*, 2023* (FY*2024* official release).

Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, *47*(7), 427-435. https://doi.org/10.2307/1313058

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of climate*, *18*(8), 1136-1155. https://doi.org/10.1175/JCLI3321.1

Thurber, D. M. (2022). Characterizing Karst Mountain Watersheds Through Streamflow Response to Snowmelt. MS Thesis, Utah State University.

Tyralis, H., Papacharalampous, G., & Langousis, A. (2019). A brief review of random forests for water scientists and practitioners and their recent history in water resources. *Water*, *11*(5), 910. https://doi.org/10.3390/w11050910

Udom, B. E., & Nuga, B. O. (2014). Hydraulic conductivity and aggregation of fine-textured soil under intensive cattle grazing. *Journal of Agricultural Science*, *6*(11), 37. http://doi.org/10.5539/jas.v6n11p37

United States Geological Survey, 2007. *Preliminary integrated geologic map databases for the United States*: Western States: California, Nevada, Washington, Oregon, Idaho, and Utah. Version 1.2. Accessed on November 1, 2023, at https://pubs.usgs.gov/of/2005/1305/

United States Geological Survey, 2007. *Preliminary integrated geologic map databases for the United States*: Central States: Montana, Wyoming, Colorado, New Mexico, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas, Iowa, Missouri, Arkansas, and Louisiana. Version 1.2. Accessed on November 1, 2023, at https://pubs.usgs.gov/of/2005/1351/

United States Geological Survey, 2019. *National Hydrography Dataset Plus – High Resolution*, accessed November 1, 2023, at https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

United States Forest Service, Intermountain Region (1995). *Interim strategies for managing anadromous-fish-producing watersheds : pacfish* (Ser. Success stories, no. 3). U.S. Department of Agriculture, Forest Service, Intermountain Region.

United States Forest Service, Intermountain Region. (1995). *Inland native fish strategy, environmental assessment : decision notice and finding of no significant impact* U.S. Department of Agriculture, Forest Service, Intermountain Region.

United States Forest Service, Payette National Forest (2003) *The Payette National Forest Land and Resource Management Plan*. U.S. Department of Agriculture, Forest Service, Intermountain Region, Payette National Forest.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J., & Elith, J. (2022). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*, *92*(1), e01486. https://doi.org/10.1002/ecm.1486

Wappett, Meridian. "Sackett v. Environmental Protection Agency." *Public Land & Resources Law Review* 25 (2024): 1.

Young, M. K. (1995). *Conservation assessment for inland cutthroat trout* (Vol. 256). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Zipper, S. C., Hammond, J. C., Shanafield, M., Zimmer, M., Datry, T., Jones, C. N., ... & Allen, D. C. (2021). Pervasive changes in stream intermittency across the United States. *Environmental Research Letters*, *16*(8), 084033. https://doi.org/10.1088/1748-9326/ac14ec

Tables and Figures

Table II-1: List of variables used in the random forest model predicting streamflow permanence class. Variable statistics are given along with data sources and units of measurement.

Characteristic	Variable	Source	Unit	Mean	Median	25% Quartile	75% Quartile
Landscape							
	Elevation at Catchment Outlet	National Hydrography Dataset Plus – High Resolution (USGS 2019)	Meters	1464	1458	1150	1800
	Slope (levels: C, B, S, R)		Percent	34 (C); 32 (B); 28 (S); 24 (R)	34 (C); 31 (B); 26 (S); 23 (R)	25 (C); 24 (B); 16 (S); 12 (R)	43 (C); 40 (B); 38 (S); 34 (R)
	Catchment Area		Square Kilometers	43	28	13	50
	Streams Density		Kilometers	1.3	1.3	1.0	1.5
	Sinuosity	PacFish/ InFish Biological Opinion Monitoring Program (USDA, USFS, BLM 2023)	Ratio	1.3	1.2	1.1	1.4
	Road Density		Kilometers	1.3	0.90	0.21	2
	Stream Gradient		Percent	2.0	1.7	1.0	2.6
	Bank Stability		Percent	97	100	96	100
	Reach Length		Meters	178	169	157	188
	Percent of Land in Grazing Allotment (levels: H, C, B, S, R)		Percent	49 (H); 57 (C); 58 (B); 60 (S); 61 (R)	51 (H); 90 (C); 90 (B); 100 (S); 100 (R)	0.0 (H); 0.0 (C); 0.0 (B); 0.0 (S); 0.0 (R)	91 (H); 100 (C); 100 (B); 100 (S); 100 (R)
	Riparian Vegetation		Percent	82	82	66	97

Table II-1 (cont.)

	Percent Forest (levels: Annual C; B, S, R)	Landfire (2001, 2014, 2016, 2020, 2022)	Percent	32 (Annual C); 68 (B); 54 (S); 50 (R)	34 (Annual C); 73 (B); 58 (S); 52 (R)	21 (Annual C); 61 (B); 40 (S); 31 (R)	43 (Annual C); 80 (B); 71 (S); 69 (R)
	Soil Frost Free Days (2004-2021)	USDA & NRCS (2023)	Count	219	220	192	245
	Catchment Geology (% Igneous, Metamorphic, Sedimentary)	USGS; Ludington et al. (2007); Stoeser et al. (2007)	Percent	55 (I); 24 (M); 16 (S)	68 (I); 0.0 (M); 0.0 (S)	0.04 (I); 0.0 (M); 0.0 (S)	100 (I); 43 (M); 18 (S)
	Riparian Cover, Grazing Interaction	Calculated Internally	Unitless (± ∞) (1-Riparian Vegetation) + Grazing R	-20	2.5	-78	28
Climate	Total Water Year Precipitation (2004 – 2021)	PRISM Climate Group (2004)	Meters	0.85	0.79	0.61	1.05
	30 Year (1981-2010) Normal Average Annual Precipitation		Meters	0.86	0.82	0.64	1.0
	Total Mean Monthly Temperature January – June (2004 - 2021)		Celsius	13	13.4	3.2	23
	30 Year (1981-2010) Normal Average Annual Temperature		Celsius	4.3	4.4	2.8	5.8
	May 1st Snow Water Equivalent (2004 -2021)	Snow Data Assimilation System (SNODAS) Version 1 (Barrett, 2003)	Meters	0.24	0.1	0.002	0.40
	Snowpack in Catchment (May 1st SWE * Area)	Calculated Internally	Cubic Meters	9691	2580	37	12220

H, C, B, S, R denote variables measured at the **HUC** (Entire HUC 6 that contains the sampled reach), **Catchment** (The entire watershed upstream of the bottom of the sampled reach.), **Buffer** (From the bottom of the reach through the entire watershed (including tributaries) with a 90 m buffer around the NHD+ streamline), **Segment** (From the bottom of the reach to 1000 m past the top of the reach with a 90 m buffer around the NHD+ streamline), and **Reach** (From the bottom of the reach to the top of the reach with a 90 m buffer around the NHD+ streamline) scales.

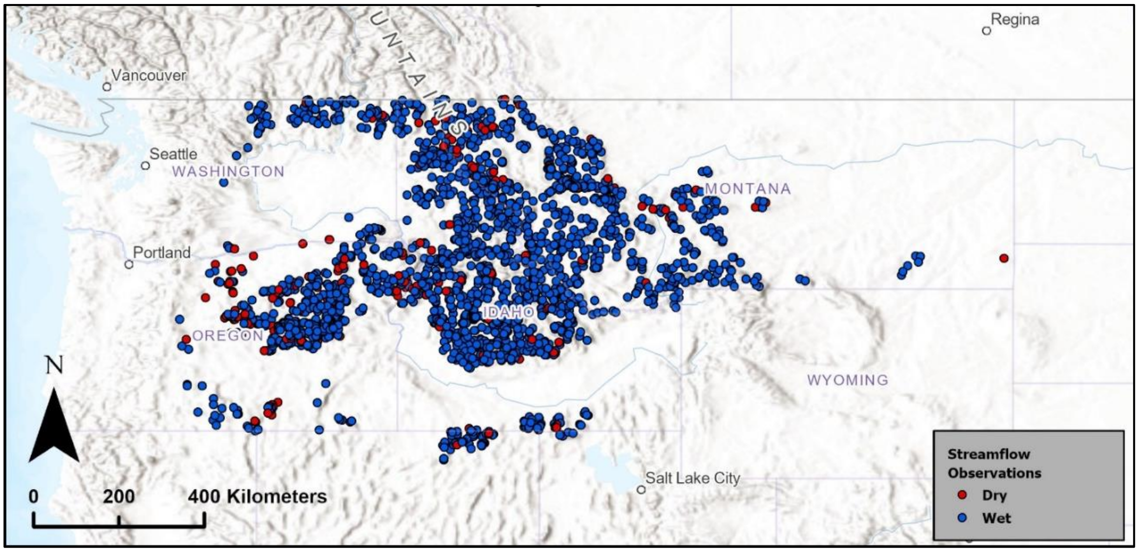

Figure II-1: Map of the study area showing streamflow observations used in the development of a model to predict streamflow permanence.

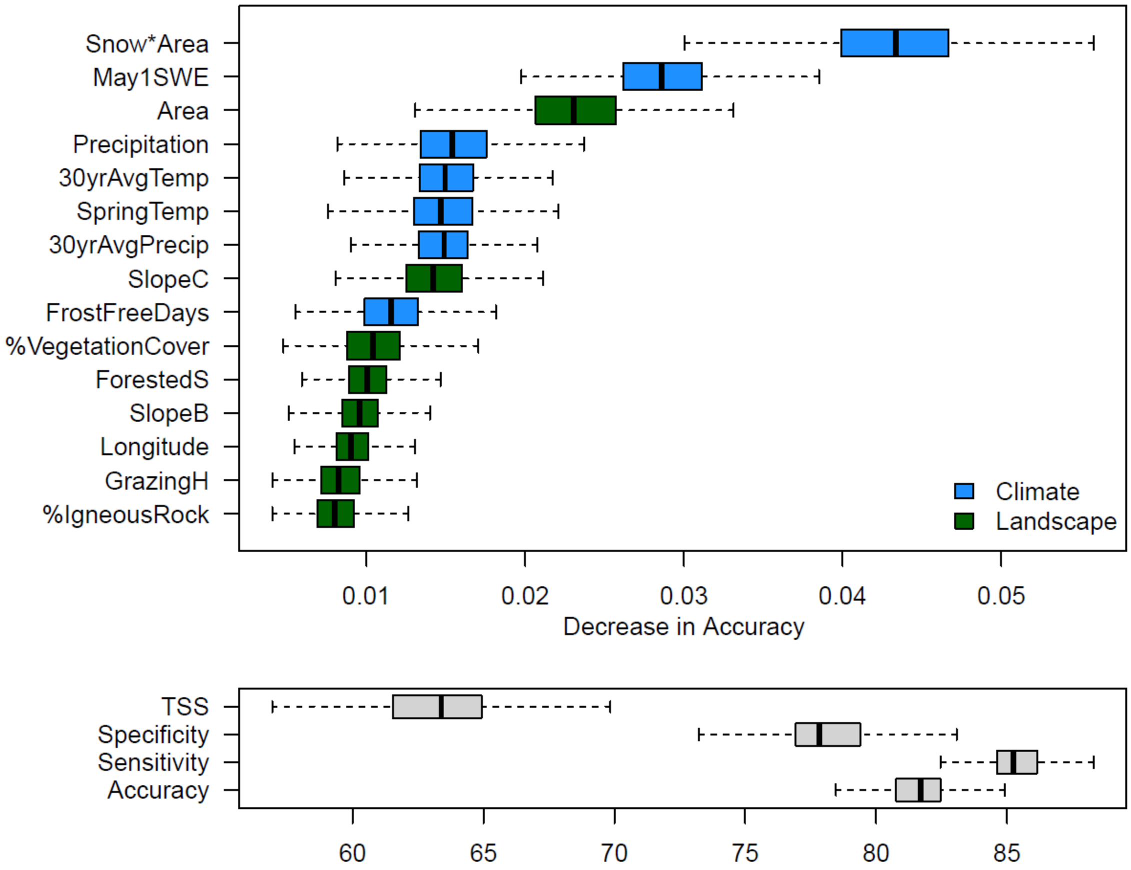

Figure II-2: (Top) Boxplot showing 1.5 times the interquartile range, the interquartile range, and median values of predictor variable importance. Variables are ranked in descending order by mean decrease in model accuracy. (Bottom) Boxplot showing 1.5 times the interquartile range, interquartile range, and median values of model accuracy, sensitivity, specificity, and true skill statistic (TSS).

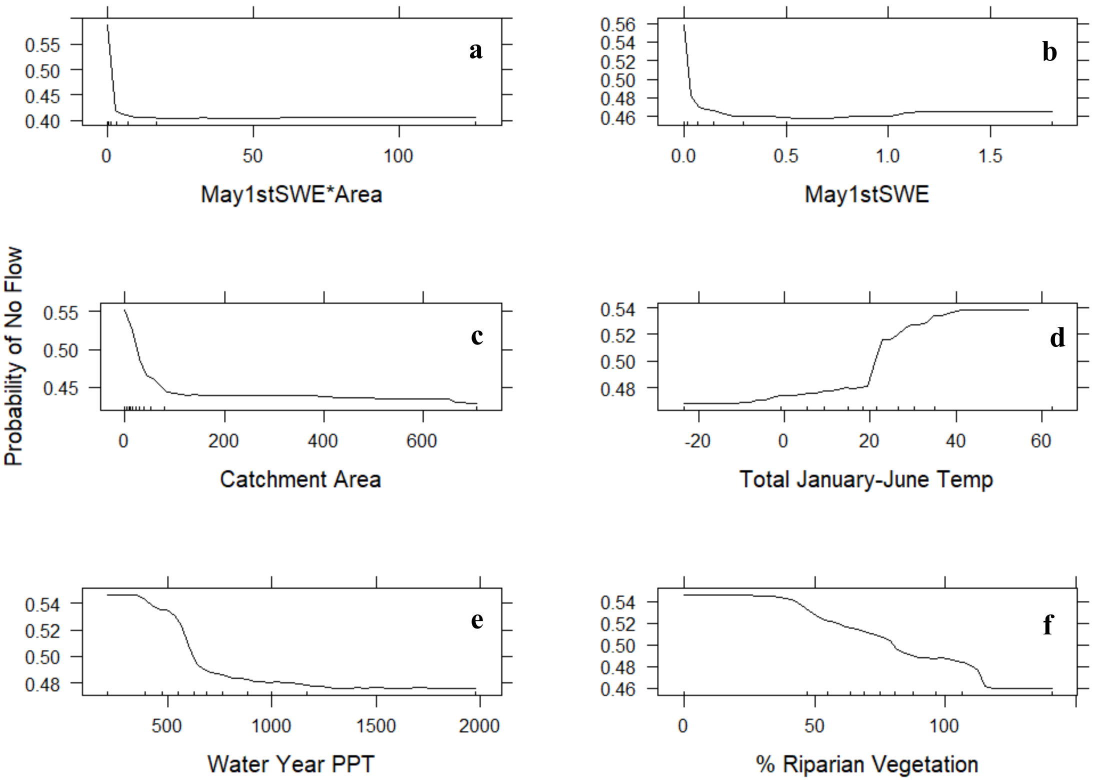

Figure II-3: Partial dependence plots for selected predictor variables showing the relationships between individual variables and predicted probabilities of non-permanent flow observations. Partial dependence is the dependence of the probability of non-permanent flow on one predictor variable after averaging out the effects of other variables in the model (Cutler et al. 2007). The lines extending from the x-axis into plot interiors represent the distribution of the values of the predictor variable in 10% increments.

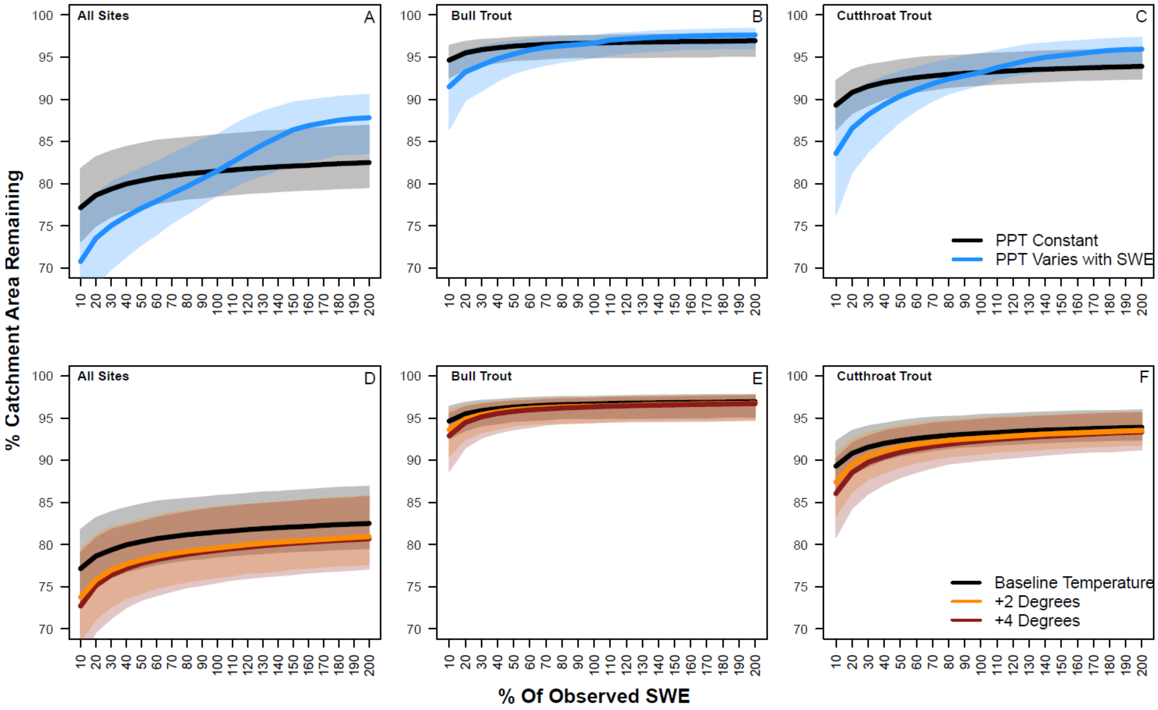

Figure II-4. Simulation results characterizing the effects of different snow water equivalent, precipitation, and temperature scenarios on the percent of catchment area that remains flowing and available across all sites (A, D), bull trout (B, E) and cutthroat trout sites (C, F). In each panel, snow water equivalent varies between 10-200% of historic conditions. In the top panels (A, B, C), precipitation values vary proportionally with snow water equivalent, and temperature is held constant. In the bottom panels (D, E, F), temperatures increase by 2°C and 4°C while snow water equivalent varies, and precipitation is held constant. Median simulation results are given by solid lines whose colors represent precipitation scenarios and warming or cooling scenarios. The 95% quantile for model predictions is given by shaded polygons that are colored according to climate scenario.

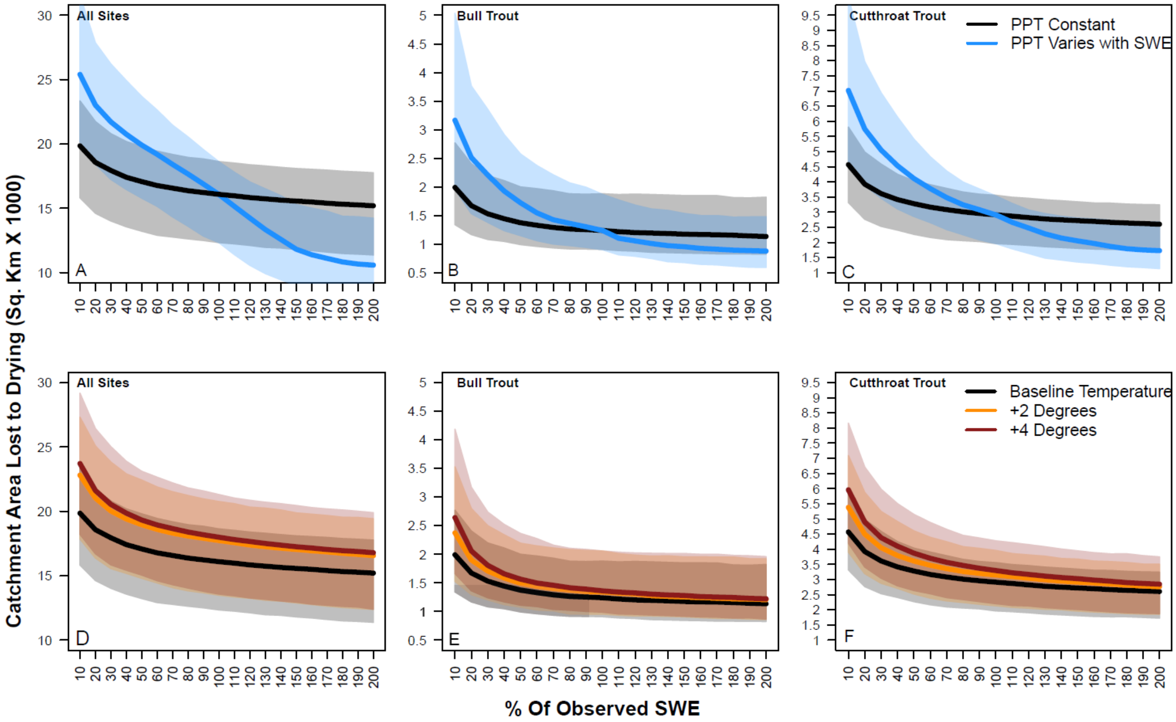

Figure II-5. Simulation results characterizing the effects of different snow water equivalent, precipitation, and temperature scenarios on the catchment area in square kilometers that becomes inaccessible due to drying for all sites (A, D), bull trout (B, E) and cutthroat trout sites (C, F). In each panel, snow water equivalent varies between 10-200% of historic conditions. In the top panels (A, B, C), precipitation values vary proportionally with snow water equivalent, and temperature is held constant. In the bottom panels (D, E, F), temperatures increase by 2°C and 4°C while snow water equivalent varies, and precipitation is held constant. Median simulation results are given by solid lines whose colors represent precipitation scenarios and warming or cooling scenarios. The 95% quantile for model predictions is given by shaded polygons that are colored according to climate scenario.

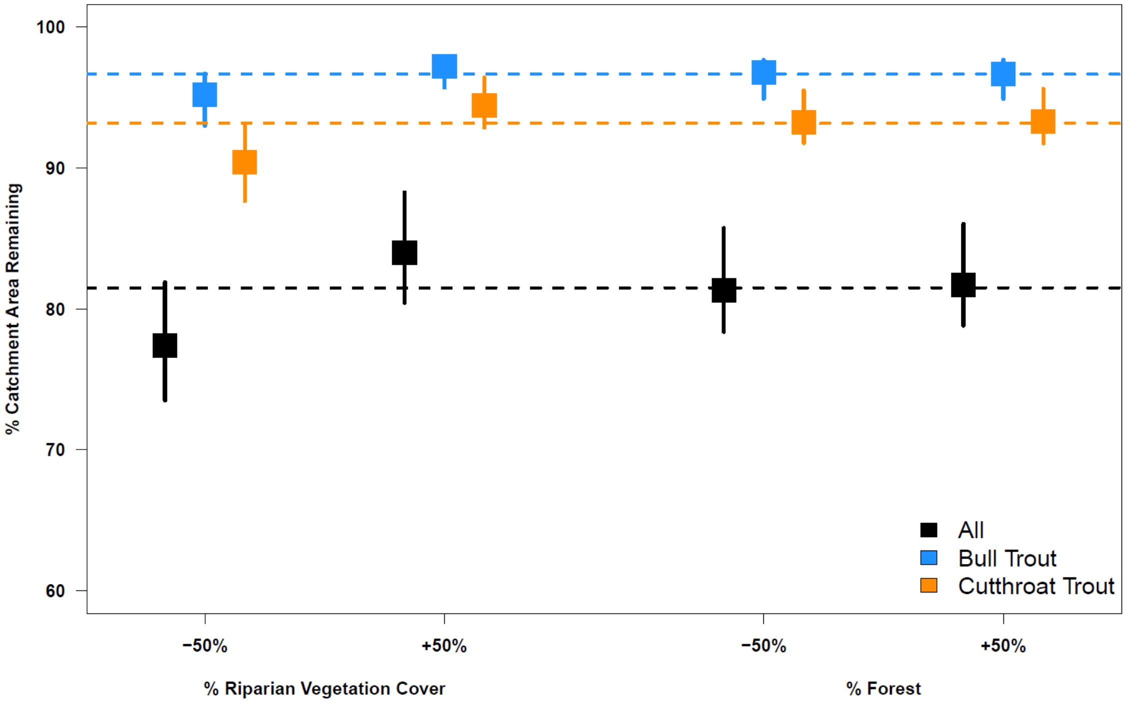

Figure II-6: Simulation results showing the effect of changing landscape conditions on the percentage of catchment area that remains wet and accessible for all sites, cutthroat trout sites, and bull trout sites. Median simulation results are given by solid squares that are colored by species sites. The 95% quantile for model predictions is given by line segments. Dashed horizontal lines indicate the amount of catchment area remaining under mean baseline conditions and are colored by site.

CHAPTER III

RESPONSE DIVERSITY TO ACUTE CLIMATE CONDITIONS AMONG STREAMS WITH VARIABLE FLOW PERMANENCE STABILIZES HABITAT AVAILABILITY FOR SPAWNING SALMONIDS

Abstract

1. Though intermittent streams represent a substantial portion of aquatic habitat available to spring spawning salmonids, there exists significant uncertainty regarding their contribution to early life history expression, particularly under anticipated climate stochasticity.
2. Our research characterizes the dynamic spatio-temporal distribution of viable spawning habitat for native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; hereafter "BCT"), identifies physiographic and climatic controls on the probability that habitats support early life history, and documents the timing and use of these temporary habitats by BCT. We present a novel approach to back-cast temperature and flow regimes in ungauged, non-permanent streams. The resulting temperature and flow profiles allow us to characterize suitable spawning windows by comparing observed degree-day accumulation to estimates of requirements for embryo development from the literature.
3. Results suggest that the spatio-temporal distribution of suitable spawning habitats shifts across years and conditions, with colder perennial streams providing more spawning habitat in a drought year, and warmer non-permanent streams furnishing more suitable habitat in a year with a large snowpack. We found that BCT move to exploit thermally optimal patches as the mosaic of suitable habitats

shift across space and time. Spawning-sized adult BCT occupied temporary streams during their known spawning window, and emergent fry were present in streams whose flow period varied substantially across years. We also found that the interplay between climate and landscape characteristics had divergent effects on flow and temperature, creating heterogeneous patterns of suitability across the network.

4. Our two-year study period occurred under drastically different climate conditions. However, the ability of different tributaries to exhibit diverse responses to the same climatic stimuli buffered total spawning habitat availability against acute climate changes. Our results demonstrate that maintaining connectivity between diverse habitats, even those unsuitable in some years, maximizes spawning opportunities for BCT during climate extremes.

1 Introduction

Species conservation strategies often seek to identify, protect, and restore habitats that are critical to the life history expressions of target species. As mobile species exploit a suite of habitats that support different growth and survival opportunities, the distribution of heterogeneous habitat has long been established as an important factor influencing population dynamics, vital rates, and shaping community assemblages (Dunning et al., 1992; Schlosser, 1995; Stanford et al., 2005). However, contemporary research has established that the matrix of available, suitable habitats is also temporally dynamic, as climate and landscape factors interact to drive plasticity in habitat conditions across different time scales. As such, habitats patches that are often unproductive may be uniquely suitable during a particular season (Armstrong et al., 2021), or in certain years with amenable conditions (Schindler et al., 2010; Brennan et al., 2019; Walsworth et al., 2020). In freshwater systems, the simplification, fragmentation, and destruction of habitat limits the ability of individuals to access the full range of spatio-temporally dynamic habitats. This threatens the life history diversity of many lotic species and has resulted in widespread declines in their abundance and distribution in altered landscapes (Dudgeon et al., 2006; Carlson & Satterthwaite, 2011; Jonsson et al., 2019). Identifying the set of habitats that sustain diverse life history expressions, coupled with an understanding of the drivers of conditions that make alternative habitats profitable, is paramount to sustaining lotic populations.

Much of the research determining which habitats should be prioritized for conservation has disregarded the contribution of temporarily available habitats to ecosystem function and life history diversity (Hermoso et al., 2013; Isaak et al., 2015; Cottet et al., 2023). However, recent research contends that habitat permanence is not always synonymous with habitat importance (Heim et al., 2019; Armstrong et al., 2021). When temporary aquatic habitat availability predictably aligns with life history needs, total habitat availability is expanded (Heim et al., 2019). Populations that exploit alternative resource opportunities, often distinct from those available in perennial habitats, can find improved rates of spawning, growth, refuge, and dispersal (Labbe & Fausch, 2000; Boughton et al., 2009; Colvin et al., 2019; Tsuboi et al., 2022).

In North America, non-permanent streams, which account for intermittent and ephemeral flow classes, account for 60% of stream length (Levick et al., 2008; Datry et al., 2014) and are increasing in abundance across the Intermountain West due to climate change (Stewart et al., 2005; Zipper et al., 2021). In this region, spring snowmelt runoff creates predictable windows of temporary inundation that align with life history strategies of many native stream fishes (Colvin et al., 2019). While our understanding regarding the viability of intermittent stream habitats lags significantly behind our understanding of perennial streams (Datry et al., 2014; Datry et al., 2023), some evidence suggests that intermittent streams may be important to many species, and salmonids in particular, across the western USA. Wigington et al. (2006) found that, in years following drought, abundant foraging opportunities resulted in higher growth rates for coho salmon (*Oncorhynchus kisutch*) using non-permanent reaches than individuals from the same population that foraged in perennial streams. Boughton et al. (2009) found that rainbow trout (*Oncorhynchus mykiss*) preferred to occupy intermittent streams during their seasonal spawn as this habitat contained the optimal substrate size. Erman & Hawthorne (1976) found that rainbow trout preferred intermittent tributaries as spawning habitat as they were inundated earlier and contained fewer predators than perennial tributaries in one drainage in California. While an intermittent stream class was preferred for different reasons in each of these cases, each scenario involves individuals selecting alternative, temporary habitats in pursuit of better conditions and receiving a fitness benefit. Despite some recognition that intermittent streams may support diverse life history expressions for native salmonids, an understanding of the environmental conditions that enable them to support population productivity, stability, and resilience remains critically understudied, particularly as climate uncertainty continues to drive streamflow impermanence (Stewart et al., 2005; Zipper et al., 2021).

Cutthroat trout (*Oncorhynchus clarkii;* hereafter “cutthroat”) encompasses several subspecies that occupy all the major drainages in the western USA (Behnke, 1992).

Cutthroat populations will often exhibit multiple life history strategies (i.e. resident, adfluvial, and fluvial) within the same watershed, and such diversity makes populations more productive and resilient to disturbance (Young, 1995; Budy et al., 2020; Heller et al., 2022). However, cutthroat populations have suffered widespread declines, in large part owing to degradation and fragmentation of complementary habitat patches that support diverse life stages and life history forms (Reiman et al., 2003; Hudy et al., 2007). While it is well understood that fluvial populations require access to tributary sites to fulfill aspects of their life history, we have yet to characterize the full diversity of habitats and life history strategies supporting them (Schrank & Rahel, 2004; Homel et al., 2015). Within the Intermountain West, cutthroat have a spring spawning season (April – July) that aligns with seasonal snowmelt runoff that inundates intermittent and ephemeral streams, providing conditions that may render these temporary habitats useful as spawning habitat. For a stream to provide suitable cutthroat spawning habitat, it must remain inundated long enough to enable spawning site access, redd construction, egg fertilization and embryo development through emergence. Finally, newly emerged fry must be able to migrate to perennial habitat. As the rate of embryonic development is controlled by temperature, warmer stream temperatures allow for faster development and colder temperatures require longer incubation periods (Quinn, 2007). Thus, the interaction of flow duration and stream temperatures will determine the spatio-temporal distribution of suitable spawning habitat.

Duration of continuous surface flow and water temperature are controlled by a suite of dynamic climatic and fixed physiographic characteristics of a watershed (Sando & Blasch, 2015; Cline et al., 2020; Moidu et al., 2021). As such, catchments experiencing spatio-temporal variation in local climates and landscape conditions will experience unique flow magnitudes (Godsey et al., 2014), inundation periods (Stewart et al., 2005; Jaeger et al., 2019), and in-stream temperatures (Cline et al., 2020). While much research has focused on the drivers and ecological consequences of streamflow permanence (Jaeger et al., 2014; Jaeger et al., 2019) and shifting temperature regimes (Isaak et al., 2016; Cline et al., 2020; Armstrong et al., 2021) independently, few studies (Moyle et al., 2013; Ebersole et al., 2020) have incorporated both variables into analyses quantifying environmental effects on the distribution of habitats supporting early life history expressions of salmonids.

The overall goal of this study is to better understand the diversity of temporary habitats supporting the fluvial life history expressions of cutthroat, and how this is mediated by the local climate and physiographic conditions. Focusing on a northern Utah (USA) watershed, our specific objectives were to 1) characterize the spatio-temporal distribution of viable spawning habitat for native Bonneville cutthroat trout (*O. clarkii utah*; hereafter “BCT”), 2) identify physiographic and climatic controls on the probability that habitats can support early life history stages, and 3) document the timing and use of these temporary habitats by BCT across years and conditions. As the abundance of non-permanent streams increases in snowmelt dominated river systems across the Intermountain West, our study provides a blueprint for future research investigating the role of alternative habitats in supporting fluvial populations’ life history expressions.

2 Methods

2.1 Study Area

The Logan River originates in the Bear River Range of southeastern Idaho and northern Utah and flows 64 kilometers downstream before draining into the Bear River and, ultimately, the Great Salt Lake (Thoreson, 1949; Budy et al., 2007). Characteristic of many high mountain rivers, the climate ranges from cold, snowy winters to hot and dry summers (Mohn, 2016). In the spring, the hydrograph is driven by snowmelt (15.7 m^3/s) and retains base flows around 2.8 m^3/s through the summer (Budy et al., 2007). Spring runoff inundates dozens of tributaries throughout the drainage before many become disconnected from the mainstem or go completely dry in the summer or fall (July – September). Potential flow permanence classifications for a stream include: (1) ephemeral, streams that are dry except for several days immediately following precipitation, (2) intermittent, streams that flow and dry seasonally, and (3) perennial, streams that retain year-round surface flow (EPA, 2006). We use the term “non-permanent” to broadly describe both ephemeral and intermittent streams. The Logan River basin is also characterized by a limestone karst geology that directs surface flow into a network of karst aquifers and subterranean channels, amplifying discontinuous flow patterns (Thurber, 2022). Habitat quality is high in the upper drainage owing to minimal anthropogenic disturbance and high levels of connectivity in the mainstem. However, areas surrounding many of the tributaries are subject to annual cattle and sheep grazing, and grated and sediment filled culverts may impede fish passage into tributary habitats from the mainstem river (S. Rousseau, *personal observation*).

The Logan River hosts one of the largest remaining populations of BCT, a subspecies of cutthroat native to the Bonneville Basin whose distribution has been reduced to roughly 35-40% of its historic range (Budy et al., 2020). Spawning in the mainstem Logan River is limited by substrate size, and research has extensively documented BCT's use of perennial tributaries as spawning habitat (Budy et al., 2007a; 2012b; Bennett et al., 2014; Mohn, 2016). However, little is known about how the non-permanent streams that become available following spring runoff contribute to the early life history of this population. Murphy et al. (2020) found that the abundance of the Logan River population cannot be attributed to production in perennial tributaries alone and suggests that non-permanent tributaries may be more important for BCT productivity than was previously assumed. Additionally, a one-time survey by the Utah Division of Wildlife Resources (UDWR) documented extensive use of intermittent tributaries by BCT across a variety of age classes during an exceptionally high-water year in which many of the tributaries that regularly go dry during the summer were flowing well into the fall (Thompson et al., 1999). Little is known about how the availability and subsequent use of non-permanent streams in the Logan River watershed varies across years with different hydrologic and climatic conditions.

We selected 23 ungauged tributaries whose flow permanence patterns varied across years (Figure 1; Table 1). The selected tributaries are distributed along an elevational gradient, beginning from the middle of the Logan River watershed (1688 meters), and extending up to the headwaters (2432 meters). Sites were intentionally selected for elevation criteria, as spawning areas are limited in the mainstem Logan River downstream of the Temple Fork confluence due to poor substrate quality, high stream flow, and low densities of BCT owing to competition with brown trout (*Salmo trutta*; Budy et al., 2007, Mohn, 2016). We included four tributaries below the Temple Fork confluence to evaluate whether suitable substrate and flow conditions exist in tributaries at elevations where the mainstem does not currently support extensive spawning (Figure 1).

We collected temperature, flow period, and substrate data in both 2022 and 2023 to characterize the mosaic of tributary spawning habitats available to BCT under different climate conditions. To be considered viable spawning habitat, a tributary must retain flow long enough for adequate embryo development to occur under the realized stream temperatures. We used a probability of emergence model that first assumes that redd construction and fertilization will occur, and then evaluates the probability that eggs will accumulate enough degree days to hatch before the stream dries, given the measured degree days in a stream and literature estimates of degree day requirements.

2.2 Flow and Temperature Profiles

In each tributary, we deployed either a temperature logger (iButton Logger, Embedded Data Systems, Lawrenceburg, Kentucky, USA) or a water level and temperature logger (HOBO Water Pro U200 data loggers, Onset Computer Corporation, Borne, Massachusetts, USA) to capture the onset and end of flow as well as the temperature at regular intervals (3 to 4 hours, depending on the logger type). As the water level loggers rely on local measurements of atmospheric pressure, we used a network of climate stations (Logan River Observatory & Water Research Laboratory, 2023), and sensors we deployed in dry riparian areas near instream loggers, to calibrate water depth measurements in each stream. In 2022, temperature loggers were deployed immediately following a reduction in spring snowpack such that sites were accessible. To capture the flow period and temperature time series for streams in 2023, we deployed water level and temperature loggers in 16 tributaries in the fall of 2022, deploying the remaining 6 in spring 2023. We removed loggers and downloaded data in October of each year.

To characterize the flow period, temperature profiles, and, ultimately, the spawning suitability of each stream, we had to first determine the start and end dates of flow. For streams equipped with water level loggers, we relied on the device to inform the onset and cessation of continuous flow. For streams outfitted with temperature loggers only, we distinguished the flow period based on the difference in specific heat capacity of water relative to air (Constantz et al., 2001). We used the "Rioja" package (Juggins, 2017) in R (R Core Team, 2024) to implement a chronologically confined, hierarchical cluster analysis on the time series of daily temperature ranges observed in each stream to classify wet and dry periods. The cluster analysis identifies points when the daily temperature range changes suddenly, corresponding to the logger's inundation by surface flow, or to the exposure to air following a period of submersion, as the daily range of water temperatures is reduced relative to that of air (Figure 2). We corroborated these estimates with field observations of surface flow presence or absence.

In 2023, exceptional tributary surface flows washed out water level and temperature loggers in 5 of our 22 sites. Upon realizing the logger's disappearance, we added a replacement. Additionally, in 2022, we were unable to access high elevation sites until significant snowmelt allowed access to our sites, at which point flow had already commenced. This resulted in incomplete time series for temperature data and a missing start date of flow in 8 sites. To account for this, we estimated the date of surface flow onset and then hindcast the daily temperatures on the dates for which we were missing data.

To estimate the date of surface flow onset, we assumed that it was a function of both fixed landscape and dynamic climate factors (Table 2). We summarized annual values by contributing drainage area using delineations from the National Hydrography Dataset Plus – High Resolution (USGS, 2019). As several predictor variables were highly correlated, we used a principal components analysis (hereafter, "PCA") to determine the dominant axes of variation among the climate and landscape variables. As we were only missing data on surface flow onset for tributaries of the intermittent class (as opposed to ephemeral or perennial flow classes), we limited our PCA to the data associated with catchments that supported non-permanent flow in either or both 2022 and 2023. Environmental predictors were log-transformed for normality, centered, and scaled to have a standard deviation of 1 prior to running the PCA. We then used multiple linear regressions to examine the relationship between the principal components that accounted for most of the variation in the environmental data and the start date of flow and compared models by adjusted R-squared, AIC, p-values, and root mean squared error resulting from leave-one-out cross validation (Table 3). The top model included both the additive and interactive effects of the first two principal components (adjusted $R^2 = 0.46$; p-value < 0.05). We then used this model to predict the mean start date of flow for the creeks with missing flow onset dates, as well as the dates at the lower and upper bounds of the 95% confidence interval to determine sensitivity of our results to this start date estimation. Equipped with the complete flow period for all creeks across years, we made year-specific flow permanence classifications for each tributary in each year as: (1)

ephemeral, streams that are dry except for several days immediately following precipitation, (2) intermittent, streams that flow and dry seasonally, (3) perennial, streams that retain year-round surface flow (EPA, 2006).

To back-cast daily temperatures for periods of missing data, we calculated daily creek-specific temperature z-scores from observed daily mean temperature values across a 30-day period when all creeks were represented. A z-score communicates how many standard deviations an observation is away from the sample mean. This produced a distribution of z-scored daily temperatures for each stream, with warmer streams characterized by positive values and colder streams characterized by negative values. We assumed that creek-specific z-scores are normally distributed across creeks. We also assume that theoretical daily average temperatures are distributed normally across creeks, with a true mean ($\hat{\mu}_d$) and standard deviation ($\hat{\sigma}_d$) of temperatures each day. When all streams are observed, the mean and standard deviation can be calculated from the observations, but when only a subset of the streams are observed, estimates of mean and standard deviation of temperatures may be biased by the specific sites being observed. We correct for this bias by estimating the true mean ($\hat{\mu}_d$) and standard deviation ($\hat{\sigma}_d$) from the observed temperatures and creek-specific temperature z-scores:

$$(\hat{\sigma}_d) \ = \frac{\sum_i \sum_{j\neq i} \frac{T_{i,d} - T_{j,d}}{Z_i - Z_j}}{n_d}$$

$$\hat{\mu}_d = \mu_{obs,d} - \hat{\sigma}_d \left(\frac{\sum_i^n Z_i}{n_d} \right)$$

where $T_{i,d}$ is the observed daily mean temperature for creek i on day d, Z_i represents the estimated creek-specific temperature z-score for creek i, n_d is the number of creeks with observed temperatures on day d, $\mu_{obs,d}$ is the mean daily temperature across creeks with observations on day d. We calculate theoretical daily average temperature for each creek on each day of predicted but unobserved flow as:

$$\hat{T}_{i,d} = \hat{\mu}_d + \hat{\sigma}_d(Z_i)$$

where $\hat{T}_{i,d}$ represents the estimated daily average temperature in creek i on day d. This approach maintains the characteristics of warm vs. cold streams as well as seasonal patterns of among-stream thermal variation during periods of missing temperature data.

Using the estimated and observed start and end dates of flow in conjunction with the estimated and observed daily average temperatures, we calculated the thermal degree days accumulated in each creek across the full range of potential spawning dates. First, we determined the first date at which the three-day average stream temperature was greater than or equal to 5 °C, which is the temperature at which BCT begin to demonstrate spawning activity (Thurow & King, 1994; Budy et al., 2012). We then summed mean daily temperatures above 0 °C for each successive day until the creek dried. We estimated the probability that an egg fertilized on each sequential spawn date would accumulate sufficient thermal degree days to warrant emergence before the stream dried for intermittent and ephemeral streams, or before September 15th for perennial streams. September 15th corresponds to the cutoff date when young-of-year (YOY) would be unable to accumulate sufficient growing potential to survive overwinter (Hubert & Gern, 1995) and is in line with other studies characterizing the outmigration timing of emergent BCT from tributaries (Knight et al., 1999; Budy et al., 2012). We calculated the probability of emergence by comparing daily values of cumulative degree days to a normal distribution of the degree days required for cutthroat trout to emerge derived from multiple estimated values in the literature (Merriman, 1935; Zubik, 1983; Roberts, 1988; Kelly, 1993; Magee, 1993; Budy et al., 2012) and reported by BCT hatchery personal, (Kamas Hatchery Utah Division of Wildlife Resources – personal communication; Grace River Hatchery Idaho Department of Fish and Game – personal communication). The required degree day (dd) distribution had a mean of 479.44 dd and a standard deviation of 63.91 dd. For each stream, we then calculated the cumulative emergence potential by summing these daily probabilities across the full period of continuous surface flow. (e.g., a spawn date with a probability of emergence of 0.5 contributes 0.5 days to the creek's emergence potential).

2.3 Climate and Landscape Controls

We examined the climatic and landscape drivers of emergence potential using multiple linear regression. We summarized annual or seasonal values of each variable within the contributing drainage area of each catchment using delineations from the National Hydrography Dataset Plus–High Resolution (Table 2; USGS, 2019). Given the collinearity among many predictor variables, we used PCA to characterize the dominant axes of variation among the climate and landscape parameters. We ran separate PCAs for the two dominant flow permanence classes (intermittent and perennial). For the intermittent streams, we used the first three principal components that had previously been calculated when modeling the start of flow period. We followed a similar process for perennial streams, log-transforming, centering, and scaling the data prior to running the PCA. We selected the first three principal components describing perennial and intermittent stream environmental data for inclusion in regression models. We used multiple linear regressions to examine the relationship between the principal components that accounted for most of the variation in the environmental data and emergence potential for intermittent and perennial streams in 2022 and 2023. We used adjusted *R*-squared, AIC, and *p*-values to identify the model that best described the observed data (Table 4; Table 5).

2.4 Substrate Composition

Given that unsuitable substrate size has been shown to significantly limit recruitment of BCT in this system (Budy et al., 2012), we characterized the proportion of suitable spawning substrate within each tributary immediately upstream of the mainstem river using methods outlined in Wolman (1954). Beginning at a tributaries' confluence with the mainstem of the Logan River, we used a gravelometer to measure the diameter of four pebbles collected laterally across the streambed. We moved upstream five meters and measured another four pebbles, repeating the process until we measured 100 substrate particles. We then calculated a frequency distribution of substrate size which was compared against a substrate suitability index for spawning cutthroat established by Hickman & Raleigh (1982).

2.5 Fish Sampling

We characterized fish use of the tributaries using multiple collection and observation methods. We used environmental DNA (eDNA) to detect presence of BCT in each tributary across the duration of their spring spawn. Environmental DNA is DNA that has been shed by an organism into its environment (Carim et al., 2016) and is particularly effective at detecting rare or low-density species while causing little disturbance to in-stream habitat. We followed the protocol outlined in Carim et al. (2016) and eDNA sampling kits and testing were provided by the U.S. Forest Service National Genomic Center in Missoula, Montana. We sampled each tributary 2 - 3 times between late April and early August during both 2022 and 2023 to increase probability of detection and characterize the variation in the timing of spawning runs within and across years. We determined peak detection rates and timing by comparing the number of DNA copies per liter of water that passed through the DNA collection filter. Ephemeral creeks (except for Creek A) were not sampled in 2022 as surface flow spats result in inaccessible and unsuitable spawning habitat. None of our sites flowed ephemerally in 2023, so they were all sampled. As samples are still being processed, we do not yet have eDNA results for 2023.

We conducted snorkeling and electrofishing surveys in May through August of 2023 to complement eDNA detections and to characterize the size structure of BCT present in the tributaries during their spawn. We used the backpack electrofishing protocol outlined in Meyer et al. (2021), to maximize capture efficiency while minimizing spinal injury to salmonids in small streams. We conducted single pass surveys beginning at each tributary's confluence with the mainstem Logan and ending 100 m upstream. We collected data on total length (millimeters; mm) of all fish captured, and checked gravidity of fish above 150-mm, as that is the minimum size threshold for an adult (age 2) BCT capable of spawning in this population (Budy et al., 2007). We sampled each tributary 1 to 3 times between May and late July 2023. We completed snorkel surveys opportunistically to further document the presence and size structure of BCT in temporary habitats. Snorkel surveys were conducted when water depth was greater than 0.25 meters and turbidity levels permitted, and followed protocol outlined in O'Neal (2007). Snorkel surveys began at the tributary's confluence with the mainstem and continued upstream 100 meters.

We relied on larval drift net surveys to provide evidence that BCT successfully spawn and emerge in intermittent systems. We selected 7 sites (creeks: E, F, H, I, K, J, and P), based on which streams were still inundated at the beginning of the expected emergence window and best represented the various flow permanence classes present in the system. Trap material consisted of 3-mm-mesh hardware cloth that led to a removable holding box constructed out of polyvinyl chloride whose aperture was fitted with a similar 3-mm-mesh hardware cloth as these mesh sizes are safe and effective at holding larval BCT (Knight et al., 1999). We deployed nets near the mouth of each tributary at its confluence with the mainstem to sample out-migrating fry from the predicted beginning of emergence, July 24th, to end of August (Knight et al., 1999; Budy et al., 2012). Nets were deployed in the evening and checked in the morning. Fry were counted, measured (total length to the nearest 1 mm) and returned to the stream.

3 Results

3.1 Distribution of Suitable Habitats

The mosaic of viable spawning habitats shifted spatially in response to changes in local climate conditions. In the dry year (2022), high elevation, colder perennial streams accounted for the majority of suitable spawning habitat while warmer, low elevation streams with variable flow permanence patterns provided more spawning opportunities during the wet year (2023; Figure 3). Streams classified as perennial in 2022 had an unchanged flow period and remained perennial in 2023. The five streams that remained perennial in both years experienced reduced emergence potential in 2023 (Figure 3). The first day at which the mean 3-day average temperature reached 5°C did not occur until much later in the 2023 season in these perennial streams. Additionally, perennial streams were generally colder in 2023, further limiting the accumulation of degree days relative to 2022. In contrast, the flow period increased in 2023 for all streams that were either ephemeral or intermittent in 2022 (Figure 3). The increase in surface flow duration in warmer, mid-elevation intermittent tributaries enabled a greater accumulation of degree days greater cumulative emergence potential in 2023 (Figure 3). Emergence potential in seven out of the 11 streams classified as intermittent in 2022 increased in 2023. The expanded flow window for non-permanent streams in 2023 resulted in more tributaries providing suitable spawning habitat, as 9 out of 20 streams in 2022 and 13 out of 22 streams in 2023 reached at least 90% daily emergence probability (Figure 3). While the number of streams measured in both years that reached 90% daily probability of emergence at some point in their hydrograph increased by 30% in 2023, the total emergence potential that accumulated across all streams measured in both years increased by only 12% across years (732 units in 2022; 820 units in 2023).

3.2 Landscape and Climatic Controls

In intermittent streams, the first three principal components of climatic and physiographic variables explained 79% of the total variation in environmental conditions across years. The first principal component explained 33% of the total variation and primarily distinguished low elevation catchments with a short total stream length (positive values) from large, high elevation catchments with a long stream length, and steep basin and stream slopes (negative values; Figure 4). The second principal component explained 27% of the total variation and distinguished warmer, lower elevation and drier catchments from colder catchments at high elevation that receive more precipitation (negative values). The third principal component explained 19% of the total variation and distinguished catchments with more moisture and high vegetative cover (positive values) from those that were drier and less vegetated (negative values). In intermittent streams, emergence potential was best explained by a model incorporating the additive and interactive effects of PC2 and PC3 (adjusted $R^2 = 0.61$; p-value < 0.05; Table 4). Emergence potential was greatest in catchments and years characterized by warm temperatures, and high moisture and vegetative cover. Emergence potential was limited in colder, high elevation catchments that received a large, persistent snowpack and precipitation in the first six months of the year (Figure 4).

In perennial streams, the first three principal components explained 74% of total variance in environmental conditions across years. The first principal component explained 36% of the total variation and distinguished colder, high elevation catchments with a large snowpack (positive values) from warmer, low elevation catchments characterized by a steep stream slope and high levels of moisture and vegetative cover (negative values; Figure 4). The second principal component explained 24% of the total variation and differentiated between stream catchments with a large drainage area, stream length and basin slope (positive values) and those catchments with low drainage area, stream length and basin slope (negative values). The third principal component explained 14% of the total variation and distinguished catchments containing few springs and a large snowpack (positive values) from catchments with a high number of springs and a small snowpack (negative values). In perennial streams, cumulative probability of emergence was best explained by a model incorporating the additive effect of the first three principal components as well as the interactive effects of PC1 and PC3 (adjusted $R^2 = 0.70$; p-value < 0.05). Emergence potential was greatest in warm drainages characterized by large values for catchment area, spring abundance, basin and stream slope, stream length, moisture, vegetative cover, and low values for elevation and snowpack (Figure 4).

3.3 Substrate Composition

Among the 20 tributaries sampled for substrate composition, we found that 18 contained at least 50% suitable and 25% optimal substrate particles (Figure 5). Creek H had the most suitable substrate composition, with 80% of particles classified as suitable. Only Creeks G and J contained less than 10% suitable substrate particles.

3.4 Fish Distribution and Size Structure

We detected BCT eDNA in 9 out of the 15 streams sampled with eDNA in 2022 (Figure 6). Detection generally occurred within the flow period where thermal conditions in tributaries supported spawning activity and within the known spawning window of this population (April 26th – July 7th; Budy et al., 2012). Peak detection generally occurred in early June, except for Creek B where peak detection occurred in late June when thermal conditions and surface flow cessation limited the probability of emergence if fish attempted to spawn at their peak detection times. BCT eDNA was absent from Creek H and Creek J, despite these creeks supporting significant emergence potential throughout the known spawning period for this population. In contrast, BCT occupied Creek A and

Creek Q despite thermal conditions and flow windows that provide little to no support for spawning activity (Figure 6).

During 2023 physical sampling, most adult sized BCT were captured during periods of high emergence probability and fell within the known spawning window observed for this population (Figure 6). Additionally, in 2023 we captured BCT in Creeks J and P, neither of which hosted any eDNA in 2022. These 2023 detections coincided with increased flow periods and greater emergence potential. Creeks H and L yielded no detections by either eDNA or physical captures across both years, despite in-stream conditions supporting spawning. Most adult BCT were captured in early June 2023 and total length of captured individuals declined throughout the season, largely driven by out-migrating YOY in August. Most juveniles were captured in July and early August.

The drift nets effectively sampled out-migrating YOY and characterized the timing of their downstream migrations. We captured out-migrating YOY in four of the seven creeks sampled (Figure 6). Young-of-year BCT were first detected on July 29th in Creeks E and F and were last detected on August 23rd in Creek E. The highest number of out-migrating YOY of any sampling event occurred in Creek E with 234 fish caught on July 29th. The abundance of YOY caught across all sites declined as the season progressed. The majority of YOY captured were 23-mm total length. Of the 4 creeks in which we caught fry, Creeks E and F were consistently non-permanent and Creek J displayed variable flow permanence across years.

4 Discussion

As climate change and increasing consumptive water use are predicted to increase rates of intermittency in snowmelt driven watersheds characteristic of the northern Rocky

Mountains (Döll & Schmied, 2012, Zipper et al., 2021), it is critical that researchers discern the contribution of this habitat type to the diversity of life history expressions supporting native species. Our findings indicate that the spatio-temporal distribution of spawning habitat varies across years with starkly different climate conditions. However, despite large changes in within-site suitability across years, the total emergence potential at the basin scale does not change dramatically, as individual streams demonstrate diverse responses to changing climatic conditions. Finally, we demonstrate that when intermittent streams become available, native trout can and do take advantage of these habitats for spawning.

The distribution of suitable habitats shifts across years and conditions, with colder perennial streams providing more spawning habitat in a drought year, and warmer, non-permanent headwater streams furnishing more suitable habitat in a year with a larger and more persistent snowpack. Additionally, in characterizing the climatic and physiographic controls on the ability of temporary habitats to support early life history, we found that the interplay between dynamic climate conditions and fixed watershed characteristics have complex effects on flow period and in-stream temperature. There are often trade-offs between these two variables that ultimately dictate the availability of suitable spawning habitat for BCT throughout the basin. While previous research has demonstrated that high elevation catchments that accumulate large and persistent snowpacks can buffer streams from increased summer temperatures (Stewart et al., 2005; Lisi et al., 2013; Cline et al., 2020) and will likely serve as refugia under anticipated climate conditions (Isaak et al., 2015a; 2016b), our results suggest that large snowpacks are not necessarily beneficial for cold water species occupying reaches below their thermal maxima. While increased precipitation and a large snowpack drive the expansion of flow period in some non-permanent streams, those same variables have a negative effect on in-stream temperatures and inhibit growth potential of early-life stages, particularly at high elevations where in-stream temperatures remain low. In perennial streams, increased snowpack and precipitation did not create a longer flow period, and the primary effect was a reduction in stream temperatures, hence the nearly ubiquitous decline in emergence potential amongst perennial streams in 2023. However, decreased spawning opportunity in high elevation streams in high water years was offset by the suite of temporary habitats that emerged at intermediate elevations where increased precipitation interacted with warmer temperatures to extend the flow period but not delay the in-stream temperature cue that initiates spawning. Interestingly, some low elevation non-permanent streams had reduced emergence potential in 2023, when moderate increases in surface flow duration did not offset the associated reduction in in-stream temperature. While the role of temperature (Rieman et al., 2007; Isaak et al., 2016) and, to a lesser extent, surface flow continuance have been well documented as dominant controls shaping the distribution of lotic populations individually (Jaeger et al., 2014), our results suggest that temperature and flow period should be considered in tandem, as their interaction can shape the distribution of viable habitats critical to the early life history of native salmonids.

Our study period was characterized by extreme, dichotomous climate conditions, as peak snow water equivalent values in the Logan River Watershed increased by 132% across the two years of our study (National Water and Climate Center, 2023), driving substantial interannual variability in the spatial arrangement of viable spawning habitat.

However, the total availability of suitable tributary habitats for BCT spawning remained relatively constant across years, as cumulative emergence potential at the watershed scale changed by only 12% across the same period. In concert with other research demonstrating how landscape heterogeneity stabilizes ecosystem function and can buffer population dynamics against climate volatility (Whited et al., 2007; Schindler et al., 2015; Brennan et al., 2019), our results suggest that the ability of different tributaries to exhibit diverse responses to the same climatic stimuli buffers total habitat availability against acute climate changes. If network connectivity is maintained and fluvial individuals can access different habitats, cutthroat should be able to spawn across a wide range of conditions.

Though much research has documented cutthroat's evolved flexibility in life history strategy and habitat use in response to dynamic environments (Budy et al., 2012; Jonsson et al., 2019; Budy et al., 2020), we still have not characterized all the habitat types contributing to cutthroat populations' productivity and persistence, particularly at early life stages (Homel et al., 2015; Murphy et al., 2020). Our research provides evidence that individuals in this fluvial Logan River BCT population move to exploit new spawning habitats as they become available. In 2022, BCT were detected in all streams whose probability of emergence reached 90%, regardless of flow class (Figure 6). In both years, BCT were detected in streams during the known spawning window and during periods of high emergence potential. Additionally, increased emergence potential in Creeks F and P coincided with BCT detection in 2023, when neither stream supported prolonged surface flows nor hosted individuals in 2022. BCT presence in streams at times when those streams didn't support spawning suggests that either BCT use headwater streams to fulfill a variety of life history needs and expressions (Wiggington et al., 2006; Tsuboi et al., 2022), or that BCT are attempting to spawn every year in streams that only periodically provide suitable conditions, potentially due to high rates of site fidelity (Kershner, 1995; Mohn, 2016). In 2023, we documented significant numbers of YOY BCT out-migrating from tributaries that exhibited variable flow patterns. In particular, Creek F illustrates how temporary habitats can be uniquely suitable under the right conditions, as it flowed for less than ten days in 2022 but retained enough surface flow in 2023 to support fry production. Additionally, these results provide some of the first documented evidence of YOY cutthroat emerging and emigrating out of non-permanent streams. The majority of YOY caught were 23-mm, which is the size of BCT YOY immediately after emergence (Knight et al., 1999). This suggests that most of the emigrating YOY captured had just emerged and were immediately migrating to permanent habitat. The ability of BCT to rapidly take advantage of habitats only available in some years illustrates the species' phenological plasticity and is in line with other research demonstrating swift re-occupation of habitat following restoration of connectivity (Colyer et al., 2005; Heller et al., 2022).

We also identified streams that could physically support spawning but were unoccupied, likely because of anthropogenic migration barriers or inadequate spawning substrate. While Creeks G and J possessed flow and thermal conditions amenable to spawning in 2022, we did not detect BCT presence in either stream. Upstream beaver dams may limit the availability of suitable substrate particles, which has been shown to restrict spawning in this system (Budy et al., 2012). However, we did capture YOY in Creek J in 2023 when emergence potential increased, suggesting that suitable substrate patches exist further upstream. Creek H also contained suitable spawning conditions but remained unoccupied in both years. A grated culvert directs this tributary under a highway and is subject to significant sediment accumulation that may prevent passage by spawning fish. The absence of BCT in habitats that could physically support them presents potential opportunities to re-connect streams to the larger river network and increase total habitat availability.

Our findings provide an important foundation for future research to estimate intermittent habitat contributions to productivity and stability at the population level, and how these dynamics may shift under future climate regimes. Future research should also discern whether BCT using habitats with variable interannual availability have adapted to patterns of drying and re-wetting or are opportunistically occupying them. Given that both flow duration and predictability are requirements to local adaptation (Heim et al. 2019), and both are declining with climate change (Milly et al., 2008; Döll & Schmied, 2012; Zipper et al., 2021), anticipated non-stationarity may disrupt potentially evolved or opportunistic strategies to exploit heterogeneity.

Contemporary research regarding the conservation of cold-water, native species is often concerned with identifying and protecting climate refugia to enhance the resilience of thermally sensitive species under climate change (Hermoso et al., 2013; Isaak et al., 2015; Isaak & Young, 2023). While our results highlight the importance of cold, perennial habitats in drought years, analysis at the basin scale reveals that warmer catchments generally confer the greatest growth advantage in streams with an amenable flow period whose water temperatures are not at thermal maxima (Armstrong et al., 2021). Furthermore, as conservation of select habitats often comes at the expense of others (Bottrill et al., 2008), over-valuing the contribution of cold, high elevation perennial streams to pre-emptively mitigate the effect of predicted warming, will likely depreciate warmer, temporary habitats whose protection status is already in flux (Fesenmyer et al., 2021). Our results demonstrate that the loss of warmer, intermittent habitats would contract the distribution of spawning habitats for BCT and that the timing and duration of flow should be considered in tandem with temperature regimes when modeling habitat suitability. Additionally, allocating resources to those productive, lower elevation streams may be a more effective conservation investment as those streams are positioned closer to human activity and suffer more often from migration barriers. Finally, our results underscore the idea that conservation efforts seeking to maximize spawning opportunities should leverage existing ecological mechanisms whereby habitat diversity stabilizes aggregate habitat availability across years and acute conditions.

References

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., ... & Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, *11*(4), 354-361.

Barrett, A. P. (2003). *National operational hydrologic remote sensing center snow data assimilation system (SNODAS) products at NSIDC* (p. 19). Boulder, CO: National Snow and Ice Data Center, Cooperative Institute for Research in Environmental Sciences.

Behnke, R. J. (1992). Native trout of western North America. American Fisheries Society monograph. no. 6.

Bennett, S., Al-Chokhachy, R., Roper, B. B., & Budy, P. (2014). Annual variation of spawning Cutthroat Trout in a small western USA stream: a case study with implications for the conservation of potamodromous trout life history diversity. *North American Journal of Fisheries Management*, *34*(5), 1033-1046.

Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., ... & Possingham, H. P. (2008). Is conservation triage just smart decision making?. *Trends in ecology & evolution*, *23*(12), 649-654.

Boughton, D. A., Fish, H., Pope, J., & Holt, G. (2009). Spatial patterning of habitat for Oncorhynchus mykiss in a system of intermittent and perennial streams. *Ecology of Freshwater Fish*, *18*(1), 92-105.

Brennan, S. R., Schindler, D. E., Cline, T. J., Walsworth, T. E., Buck, G., & Fernandez, D. P. (2019). Shifting habitat mosaics and fish production across river basins. *Science*, *364*(6442), 783-786.

Budy, P., Thiede, G. P., & McHugh, P. (2007). Quantification of the vital rates, abundance, and status of a critical, endemic population of Bonneville cutthroat trout. *North American Journal of Fisheries Management*, *27*(2), 593-604.

Budy, P., Wood, S., & Roper, B. (2012). A study of the spawning ecology and early life history survival of Bonneville cutthroat trout. *North American Journal of Fisheries Management*, *32*(3), 436-449.

Budy, P., Thompson, P. D., McKell, M. D., Thiede, G. P., Walsworth, T. E., & Conner, M. M. (2020). A multifaceted reconstruction of the population structure and life history expressions of a remnant metapopulation of Bonneville Cutthroat Trout: implications for maintaining intermittent connectivity. *Transactions of the American Fisheries Society*, *149*(4), 443-461.

Carim, K. J., McKelvey, K. S., Young, M. K., Wilcox, T. M., & Schwartz, M. K. (2016). *A protocol for collecting environmental DNA samples from streams* (pp. 1-18). United States, Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Carlson, S. M., & Satterthwaite, W. H. (2011). Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(9), 1579-1589.

Cline, T. J., Schindler, D. E., Walsworth, T. E., French, D. W., & Lisi, P. J. (2020). Low snowpack reduces thermal response diversity among streams across a landscape. *Limnology and Oceanography Letters*, *5*(3), 254-263.

Constantz, J., Stonestorm, D., Stewart, A. E., Niswonger, R., & Smith, T. R. (2001). Analysis of streambed temperatures in ephemeral channels to determine streamflow frequency and duration. *Water Resources Research*, *37*(2), 317-328.

Colvin, S. A., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., ... & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries*, *44*(2), 73-91.

Cottet, M., Robert, A., Tronchère-Cottet, H., & Datry, T. (2023). “It's dry, it has fewer charms!”: Do perceptions and values of intermittent rivers interact with their management?. *Environmental Science & Policy*, *139*, 139-148.

Colyer, W. T., Kershner, J. L., & Hilderbrand, R. H. (2005). Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho–Wyoming. *North American Journal of Fisheries Management*, *25*(3), 954-963.

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: a challenge for freshwater ecology. *BioScience*, *64*(3), 229-235.

Datry, T., Boulton, A. J., Fritz, K., Stubbington, R., Cid, N., Crabot, J., & Tockner, K. (2023). Non-perennial segments in river networks. *Nature Reviews Earth & Environment*, *4*(12), 815-830.

Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, *7*(1), 014037.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., ... & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews*, *81*(2), 163-182.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175.

Ebersole, J. L., Quiñones, R. M., Clements, S., & Letcher, B. H. (2020). Managing climate refugia for freshwater fishes under an expanding human footprint. *Frontiers in Ecology and the Environment*, *18*(5), 271-280.

Embedded Data Systems. (2015). Thermochron iButton DS1921Z-F5#. [Apparatus and software]. https://www.embeddeddatasystems.com/DS1921Z-F5--Thermochron-iButton-5%C2%B0C-thru-26%C2%B0C_p_97.html

Erman, D. C., & Hawthorne, V. M. (1976). The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Transactions of the American Fisheries Society*, *105*(6), 675-681.

Fesenmyer, K. A., Wenger, S. J., Leigh, D. S., & Neville, H. M. (2021). Large portion of USA streams lose protection with new interpretation of Clean Water Act. *Freshwater Science*, *40*(1), 252-258.

Godsey, S. E., & Kirchner, J. W. (2014). Dynamic, discontinuous stream networks: Hydrologically driven variations in active drainage density, flowing channels and stream order. *Hydrological Processes*, *28*(23), 5791-5803.

Heim, K. C., McMahon, T. E., Calle, L., Wipfli, M. S., & Falke, J. A. (2019). A general model of temporary aquatic habitat use: water phenology as a life history filter. *Fish and Fisheries*, *20*(4), 802-816.

Heller, M. R., Dillon, J. C., & Quist, M. C. (2022). Occurrence, Abundance, Movement, and Habitat Associations of Bonneville Cutthroat Trout in Tributaries to Bear Lake, Idaho–Utah. *North American Journal of Fisheries Management*, *42*(3), 684-700.

Hermoso, V., Ward, D. P., & Kennard, M. J. (2013). Prioritizing refugia for freshwater biodiversity conservation in highly seasonal ecosystems. *Diversity and Distributions*, *19*(8), 1031-1042.

Hickman, T. J., & Raleigh, R. F. (1982). *Habitat suitability index models: Cutthroat trout* (FWS/OBS 82/10.5). Retrieved from U.S. Fish and Wildlife Service website: https://pubs.usgs.gov/publication/fwsobs82_10_5

Homel, K. M., Gresswell, R. E., & Kershner, J. L. (2015). Life history diversity of Snake River finespotted cutthroat trout: managing for persistence in a rapidly changing environment. *North American Journal of Fisheries Management*, *35*(4), 789-801.

Hubert, W. A., & Gern, W. A. (1995). Influence of embryonic stage on survival of cutthroat trout exposed to temperature reduction. *The Progressive Fish-Culturist*, *57*(4), 326-328.

Hudy, M., Roper, B., & Gillespie, N. (2007, October). Large scale assessments: lessons learned for native trout management. In *Sustaining Wild Trout in a Changing*

World: Proceedings of Wild Trout IX Symposium, edited by RF Carline and C. LoSapio (pp. 223-35).

Isaak, D. J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, *21*(7), 2540-2553.

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., ... & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374-4379.

Isaak, D. J., & Young, M. K. (2023). Cold-water habitats, climate refugia, and their utility for conserving salmonid fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(7), 1187-1206.

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894-13899.

Jaeger, K. L., Sando, R., McShane, R. R., Dunham, J. B., Hockman-Wert, D. P., Kaiser, K. E., ... & Blasch, K. W. (2019). Probability of Streamflow Permanence Model (PROSPER): A spatially continuous model of annual streamflow permanence throughout the Pacific Northwest. *Journal of Hydrology X*, *2*, 100005.

Jonsson, B., Jonsson, N., & Gresswell, R. E. (2019). Life history diversity. Chapter 6. In: Trout and char of the world. American Fisheries Society.

Kelly, B. M. (1993). Ecology of Yellowstone cutthroat trout and an evaluation of potential effects of angler wading in the Yellowstone River. MS Thesis, Montana State University-Bozeman, College of Letters & Science.

Kershner, Jeffrey L. (1995). Bonneville cutthroat trout. Chapter 4. In: Young, Michael K., tech. ed. Conservation assessment for inland cutthroat trout. General Technical Report RM-256. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. p. 28-35

Knight, C. A., Orme, R. W., & Beauchamp, D. A. (1999). Growth, survival, and migration patterns of juvenile adfluvial Bonneville cutthroat trout in tributaries of

Strawberry Reservoir, Utah. *Transactions of the American Fisheries Society*, *128*(4), 553-563.

Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774-1791.

LANDFIRE: LANDFIRE Percent Canopy Cover layer. (2001- 2022). U.S. Department of Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online on November 1, 2023, at http://landfire.cr.usgs.gov/viewer/

Levick, L. R., Goodrich, D. C., Hernandez, M., Fonseca, J., Semmens, D. J., Stromberg, J. C., ... & Kepner, W. G. (2008). *The ecological and hydrological significance of ephemeral and intermittent streams in the arid and semi-arid American Southwest* (p. 116). Washington, DC, USA: US Environmental Protection Agency, Office of Research and Development.

Lisi, P. J., Schindler, D. E., Bentley, K. T., & Pess, G. R. (2013). Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. *Geomorphology*, *185*, 78-86.

Logan River Observatory, Water Research Laboratory. (2023). *Barometric Pressure – Logan River Watershed*. Utah State University [Dataset]. https://lrodata.usu.edu/tsa/?sitecode=LR_FB_C&view=datasets&plot=false#

Magee, J. P. (1993). A basin approach to characterizing spawning and fry rearing habitats for westslope cutthroat trout in a sediment-rich basin, Montana. MS Thesis, Montana State University-Bozeman, College of Letters & Science.

Milly, P. C., Betancourt, J., Falkenmark, M., Hirsch, R. M., Kundzewicz, Z. W., Lettenmaier, D. P., & Stouffer, R. J. (2008). Stationarity is dead: Whither water management?. *Science*, *319*(5863), 573-574.

Merriman, D. (1935). The effect of temperature on the development of the eggs and larvae of the cut-throat trout (Salmo clarkii clarkii Richardson). *Journal of Experimental Biology*, *12*(4), 297-305.

Meyer, K. A., Chiaramonte, L. V., & Reynolds, J. B. (2021). The 100-watt method: A protocol for backpack electrofishing in small streams. *Fisheries*, *46*(3), 125-130.

Mohn, H. (2016). Aligning conservation goals and management objectives for Bonneville cutthroat trout (Oncorhynchus clarki utah) in the Logan River, Utah. MS Thesis, Utah State University.

Moidu, H., Obedzinski, M., Carlson, S. M., & Grantham, T. E. (2021). Spatial patterns and sensitivity of intermittent stream drying to climate variability. *Water Resources Research*, *57*(11), e2021WR030314.

Moyle, P. B., Kiernan, J. D., Crain, P. K., & Quinones, R. M. (2013). Climate change vulnerability of native and alien freshwater fishes of California: a systematic assessment approach. *PLoS One*, *8*(5), e63883.

Murphy, B. P., Walsworth, T. E., Belmont, P., Conner, M. M., & Budy, P. (2020). Dynamic Habitat Disturbance and Ecological Resilience (DyHDER): modeling population responses to habitat condition. *Ecosphere*, *11*(1), e03023.

National Water and Climate Center. (2023). *Snow Water Equivalent in Little Bear – Logan*. U.S. Department of Agriculture, Natural Resources Conservation Service [Dataset]. https://nwcc-apps.sc.egov.usda.gov/awdb/basin-plots/POR/WTEQ/assocHUC8/16010203_Little_Bear-Logan.html

O'Neal, J. S. (2007). Snorkel surveys. *Salmonid field protocols handbook*, 325-339.

Onset Computer Corporation. (2024). HOBO U20L Water Level Logger (U20L-0x) and HOBOware Pro, v2.6. [Apparatus and software]. https://www.onsetcomp.com/products/data-loggers/u20l-0x

Pennock, C. A., Thiede, G. P., & Budy, P. (2023). Density-dependent processes and population dynamics of native sculpin in a mountain river. *Ecology of Freshwater Fish*, *32*(3), 593-605.

PRISM Climate Group, 2004, Oregon State University, https://prism.oregonstate.edu, accessed November 2023

Quinn, T. P. (2007). The behavior and ecology of Pacific salmon and trout (1st ed.). University of British Columbia Press.

Rieman, B., Lee, D., Burns, D., Gresswell, R., Young, M., Stowell, R., ... & Howell, P. (2003). Status of native fishes in the western United States and issues for fire and fuels management. *Forest Ecology and Management*, *178*(1-2), 197-211.

Rieman, B. E., Isaak, D., Adams, S., Horan, D., Nagel, D., Luce, C., & Myers, D. (2007). Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society*, *136*(6), 1552-1565.

Roberts, B. C. (1988). Potential influence of recreational use on Nelson Spring Creek, Montana. PhD Thesis, Montana State University-Bozeman, College of Letters & Science.

Sando, R., & Blasch, K. W. (2015). Predicting alpine headwater stream intermittency: A case study in the northern Rocky Mountains. *Ecohydrology & Hydrobiology*, *15*(2), 68-80.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609-612.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257-263.

Schlosser, I. J. (1995). Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, *303*, 71-81.

Schrank, A. J., & Rahel, F. J. (2004). Movement patterns in inland cutthroat trout (Oncorhynchus clarki utah): management and conservation implications. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(8), 1528-1537.

Stanford, J. A., Lorang, M. S., & Hauer, F. R. (2005). The shifting habitat mosaic of river ecosystems. *SIL Proceedings, 1922-2010*, *29*(1), 123–136.

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of climate*, *18*(8), 1136-1155.

Thompson, P., Tolentino, S., Sorenson, K., Nielson, B. (1999). Bonneville cutthroat trout (Oncorhynchus clarkii Utah) survey and monitoring activities in the Logan River (sections 05-07) Drainage, 1999 (Report No. 00-3). Utah Division of Wildlife Resources.

Thoreson, N. A. (1949). An evaluation of trout stocking in the Logan River drainage. MS Thesis, Utah State University.

Thurber, D. M. (2022). Characterizing Karst Mountain Watersheds Through Streamflow Response to Snowmelt. MS Thesis, Utah State University.

Thurow, R. F., & King, J. G. (1994). Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. *Transactions of the American fisheries Society*, *123*(1), 37-50.

Tsuboi, J. I., Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D., ... & Kanno, Y. (2022). Small giants: Tributaries rescue spatially structured populations from extirpation in a highly fragmented stream. *Journal of Applied Ecology*, *59*(8), 1997-2009.

United States Environmental Protection Agency, 2006. *Field Operations Manual for Assessing the Hydrologic Permanence and Ecological Condition of Headwater Streams*. Accessed February 19, 2022, at https://www.epa.gov/cwa-404/field-operations-manual-assessing-hydrologic-permanence-and-ecological-condition-headwater

United States Geological Survey, 2019. *National Hydrography Dataset Plus – High Resolution*, accessed November 1, 2023, at https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

Vermote, E., Justice, C., Claverie, M., & Franch, B. (2016). Preliminary analysis of the performance of the Landsat 8/OLI land surface reflectance product. Remote Sensing of Environment, 185, 46-56. Landsat Spectral Indices products courtesy of the U.S. Geological Survey Earth Resources Observation and Science Center.

Walsworth, T. E., Baldock, J. R., Zimmerman, C. E., & Schindler, D. E. (2020). Interaction between watershed features and climate forcing affects habitat profitability for juvenile salmon. *Ecosphere*, *11*(10), e03266.

Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S., & Stanford, J. A. (2007). Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. *Ecology*, *88*(4), 940-953.

Wigington Jr, P. J., Ebersole, J. L., Colvin, M. E., Leibowitz, S. G., Miller, B., Hansen, B., ... & Compton, J. E. (2006). Coho salmon dependence on intermittent streams. *Frontiers in Ecology and the Environment*, *4*(10), 513-518.

Wolman, M. G. (1954). A method of sampling coarse river-bed material. *EOS, Transactions American Geophysical Union*, *35*(6), 951-956.

Young, M. K. (1995). *Conservation assessment for inland cutthroat trout* (Vol. 256). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Zipper, S. C., Hammond, J. C., Shanafield, M., Zimmer, M., Datry, T., Jones, C. N., ... & Allen, D. C. (2021). Pervasive changes in stream intermittency across the United States. *Environmental Research Letters*, *16*(8), 084033.

Zubik, R. J. (1983). The fishery of Hyalite Reservoir, Montana, with an evaluation of Cutthroat Trout reproduction in its tributaries. MS Thesis, Montana State University-Bozeman, College of Letters & Science.

Tables and Figures

Table III-1. List of actual creek names, labels, and the years for which we have emergence probability and physical detection data. Labels are alphabetical and ordered by increasing elevation at a tributary's confluence with the mainstem Logan River.

Alphabetized Label	Full Name	Elevation at Confluence with Logan River (m)	Years with Data
A	Woodcamp Creek	1629	2022; 2023
B	Cottonwood Creek	1688	2022; 2023
C	Chicken Creek	1702	2022; 2023
D	Blind Hollow	1758	2023
E	Bear Hollow	1818	2022; 2022
F	Twin Creek	1833	2022; 2023
G	West Hodges Creek	1871	2022; 2023
H	Theurer Hollow	1875	2022; 2023
I	Little Bear Creek	1889	2022; 2023
J	Tony Grove	1908	2022; 2023
K	Bunchgrass Creek	1918	2022; 2023
L	Little White Pine	1956	2022; 2023
M	White Pine	1956	2023
N	Steam Mill	2099	2022; 2023
O	Hell's Kitchen	2103	2022; 2023
P	Peterson Hollow	2163	2022; 2023
Q	Steep Hollow	2227	2022; 2023
R	Crescent Lake	2261	2022; 2023
S	Boss Canyon	2320	2022; 2023
T	Hodge Nibley	2355	2022; 2023
U	White Canyon	2363	2022; 2023
V	Corral Hollow	2410	2022
W	North White Canyon	2432	2023

Table III-2. List of variables in models predicting the first day of surface flow and identifying drivers of emergence potential.

Characteristic		Abbreviation	Source
Landscape			
	Minimum Elevation	Min_Elev	National Hydrography Dataset Plus – High Resolution (USGS 2019)
	Maximum Elevation	Max_Elev	
	Catchment Area	Area	
	Stream Length	LengthS	
	Stream Slope	SlopeS	
	Number of Springs in Catchment	# Springs	
	Basin Slope	SlopeB	LANDFIRE (2022)
	Percent Forest (2021 – 2022)	PctFst	
	Normalized Difference Vegetation Index – July (2022, 2023)	NDVI	Landsat 8 (USGS; Vermote et al. 2016)
	Normalized Difference Moisture Index – July (2022, 2023)	NDMI	
Climate			
	Total Precipitation January – June (2022, 2023)	Ppt	PRISM Climate Group (2004)
	Mean Monthly Average Temperature January – June (2022, 2023)	Temp	
	Snow Water Equivalent - May 1st (2022, 2023)	SWE	Snow Data Assimilation System (SNODAS) Version 1 (Barrett 2003)

Table III-3. Performance results from four different multiple regression models analyzing the relationship between principal components describing variation in environmental data and the first day of surface flow. Model performance metrics include adjusted *R*-squared, AIC, RMSE derived from Leave-One-Out cross-validation, and *p*-values.

Model	*R*-Squared Adjusted	Akaike Information Criterion (AIC)	Root Mean Squared Error (RMSE)	*p*-Value
$\hat{\gamma} = \beta_0 + \beta_1(PC1) + \beta_2(PC2)$	0.39	126.7	16.1	0.02*
$\hat{\gamma} = \beta_0 + \beta_1(PC1) + \beta_2(PC2) + \beta_3(PC3)$	0.34	128.6	16.6	0.06
$\hat{\gamma} = \beta_0 + \beta_1((PC2)^2)$	0.39	126.8	16.0	0.02*
$\hat{\gamma} = \beta_0 + \beta_1(PC1) + \beta_2(PC2) + \beta_3(PC1 * PC2)$	0.46	125.5	14.9	0.001**

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Table III-4. Performance results from five different multiple regression models describing the relationship between the emergence potential of intermittent streams and the principal components that describe variation in the environmental data of those streams. Model performance metrics include adjusted *R*-squared, AIC, and *p*-values.

Model	*R*-Squared Adjusted	Akaike Information Criterion (AIC)	*p* Value
$\hat{\gamma} = \beta_0 + \beta_1(PC1) + \beta_2(PC2)$	0.05	235.9	0.22
$\hat{\gamma} = \beta_0 + \beta_1(PC2) + \beta_2(PC3)$	0.51	220.6	0.0003***
$\hat{\gamma} = \beta_0 + \beta_1(PC1) + \beta_2(PC2) + \beta_3(PC3)$	0.49	222.4	0.001***
$\hat{\gamma} = \beta_0 + \beta_1(PC2 * PC3)$	0.07	234.5	0.11
$\hat{\gamma} = \beta_0 + \beta_1(PC2) + \beta_2(PC3) + \beta_3(PC2 * PC3)$	0.61	216.2	0.00009***

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

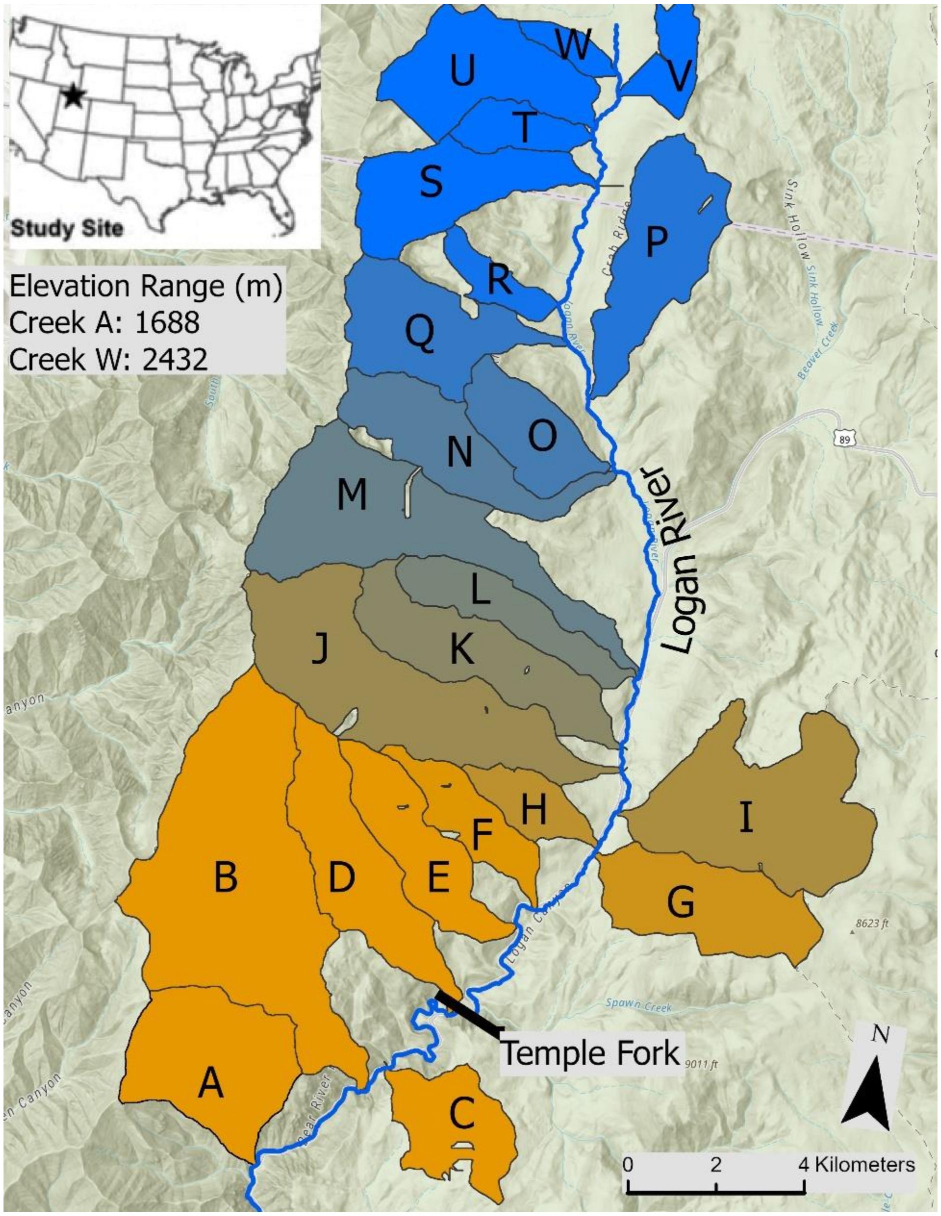

Figure III-1. Location of tributary watersheds within the Logan River Basin in northern Utah. Drainages are colored and ranked alphabetically in in order of increasing elevation at their confluence with the mainstem Logan. The Logan River watershed's location within the continental USA is given by a black star in the top left map inlay.

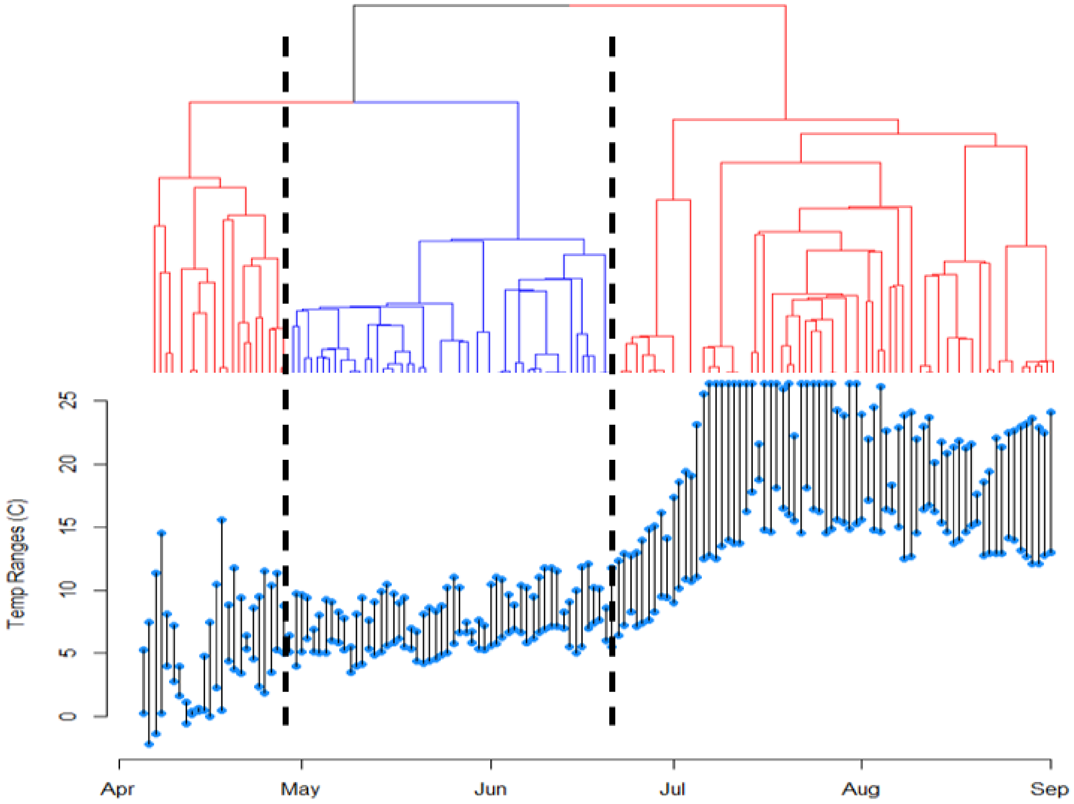

Figure III-2. Example of chronological clustering analysis (top) to characterize period of surface flows based on daily temperature range (bottom) detected at a site each year. Red clusters correspond to dry periods with elevated daily temperature variation, while blue cluster represents period of surface flow with lower daily temperature variation. Data presented are from Creek B in 2022.

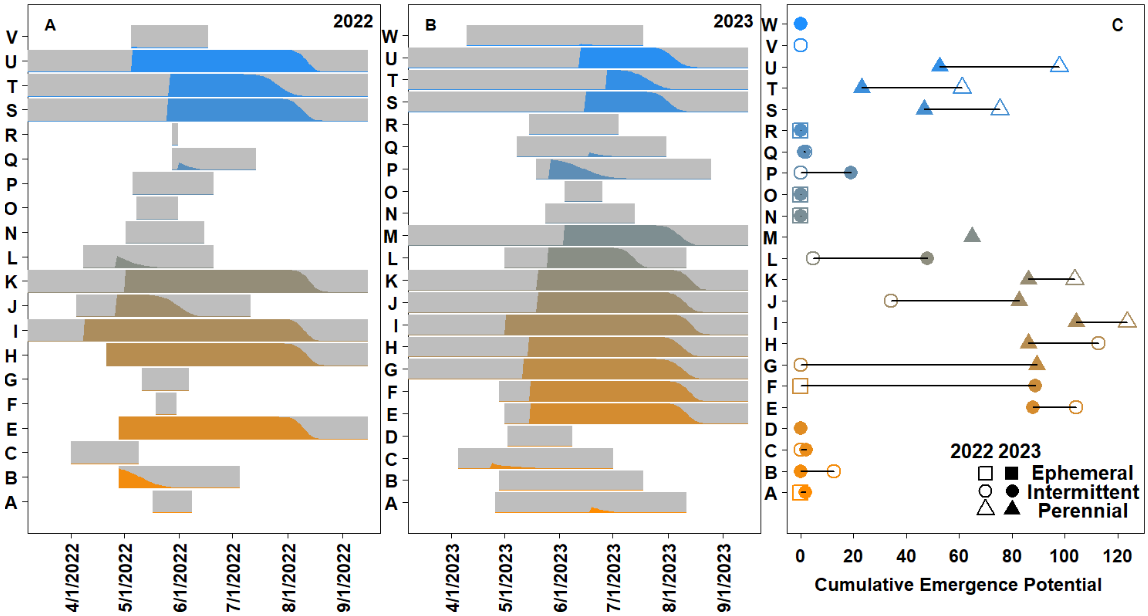

Figure III-3. Pannels A and B: stream specific time series of flow period (horizontal grey bar) and daily emergence potential (colored polygon) between March 15th and September 15th for 2022 (A) and 2023 (B). Emergence potential polygons are scaled between 0-100% and colored in order of increasing elevation. Creeks are increasingly ordered by rank elevation along the y-axis. Pannel C: Stream specific transitions between flow class and values of cumulative emergence potential (x-axis) across 2022 (empty symbol) and 2023 (filled symbol). Creeks are increasingly ordered by rank elevation along the y-axis.

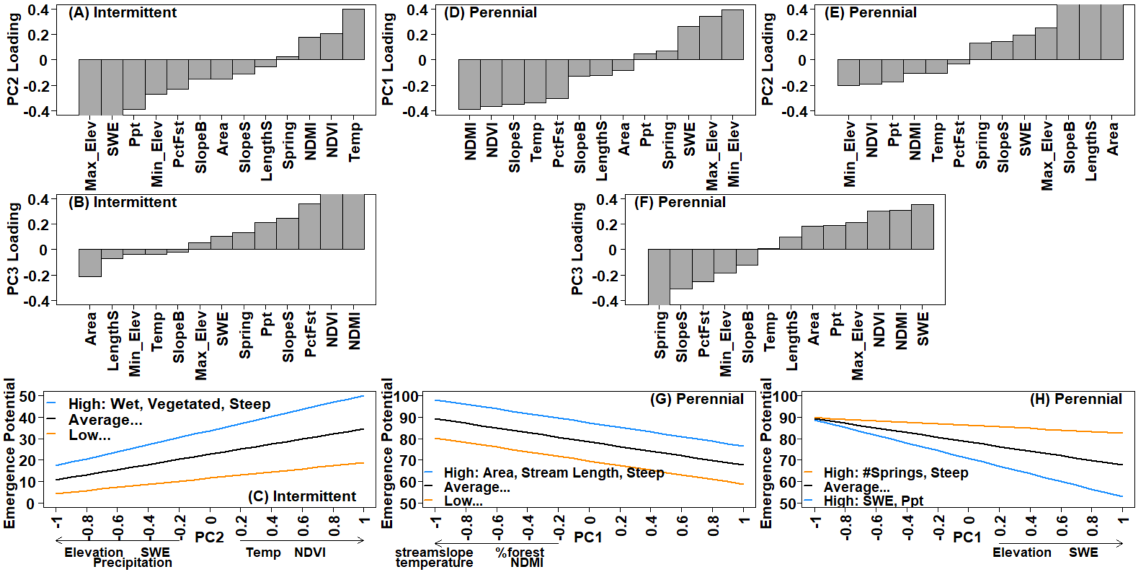

Figure III-4. Landscape and climate variable loadings onto the second (A) and third (B) principal components for intermittent streams and the first (D), second (E), and third (F) principal components for perennial streams. The order of variables presented is not constant but is presented in increasing order for each principal component. Regression model predictions for emergence potential in intermittent streams (C) and perennial streams (G, H) as a result of the additive and interactive effects of principal components characterizing climate and landscape variables.

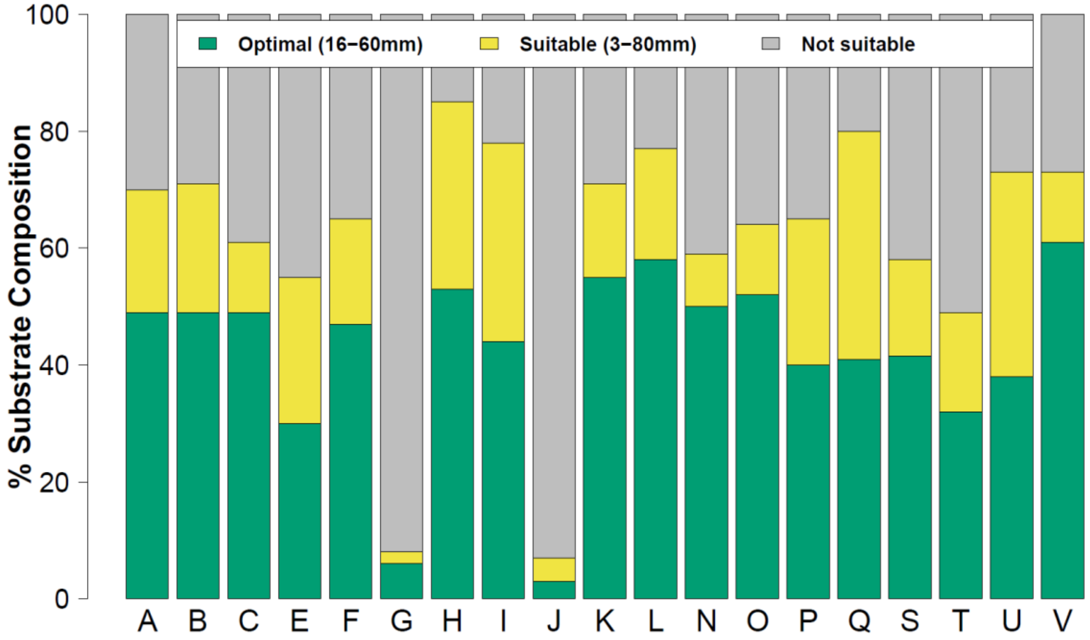

Figure III-5. Percent composition of optimal, suitable, and unsuitable substrate available to spawning BCT in 20 out of our 23 sites. Creeks are ordered along the x-axis from left to right by increasing elevation.

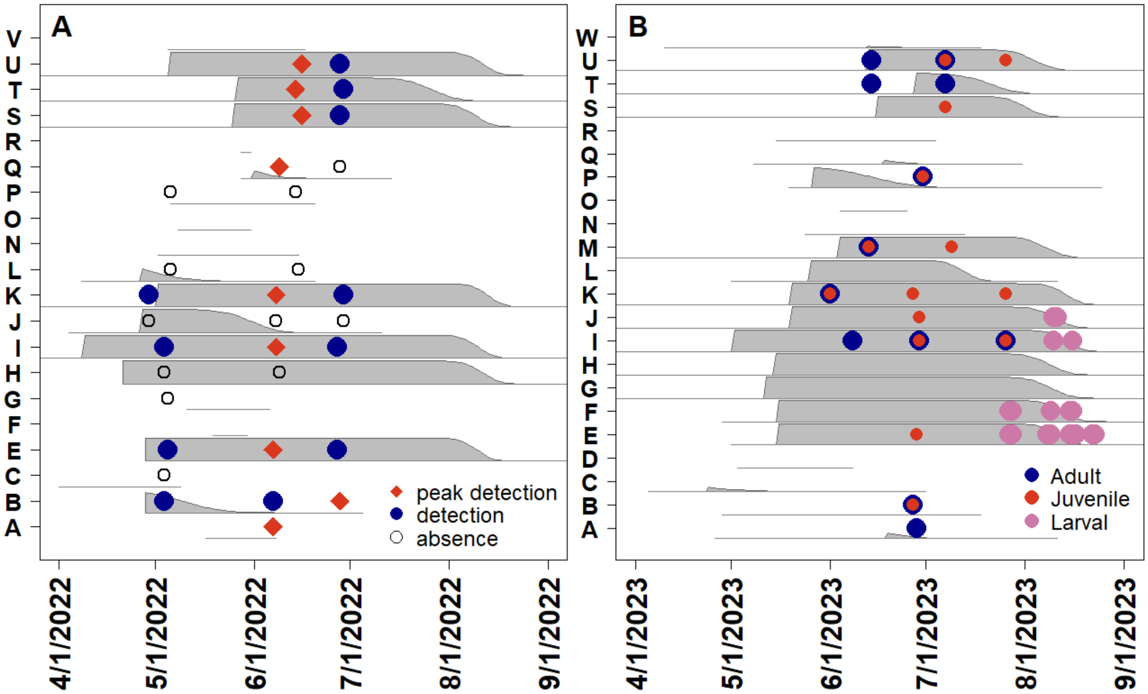

Figure III-6. Panel A: eDNA detection in each stream across the duration of sampling events (x-axis) in 2022. Peak detection is given by a red diamond while all other presence detections are given by a blue circle. Absence is denoted by an empty circle. Panel B: stage classes of BCT captured in different sampling events in 2023 are given by colored circles. Overlap between adult and juvenile classes are denoted by a smaller red circle superimposed on a larger blue circle. Creeks are increasingly ordered by rank elevation along the y-axis. Grey polygons represent time series of daily emergence probabilities across the flow period.

CHAPTER IV

CONCLUSIONS

Non-permanent waterways account for more than half of the stream network in North America and are becoming more common with climate warming. In snow fed drainages characteristic of the northern Rocky Mountains, spring melt and runoff create predictable windows of surface flow for streams that have historically been non-permanent. While non-permanent flow is a natural phenomenon for many drainages in this region, warmer winter and spring temperatures create earlier melt and runoff timing and cause a greater fraction of winter and spring precipitation to fall as rain rather than snow (Stewart et al., 2005). Resultingly, peak streamflow occurs earlier, subjecting non-permanent streams to earlier and longer periods of drying. Additionally, historically permanent streams are subject to higher variability in minimum flows which increases their risk of impermanence. While precipitation and temperature have been shown to be primary determinants of streamflow persistence (Sando et al., 2015; Jaeger et al., 2019; Brooks et al., 2021), watersheds do not display homogenous responses to climate conditions, as a stream network's particular resilience or vulnerability to drying is also mediated by a suite of regionally specific physiographic conditions (Reynolds et al., 2015; Belmar et al., 2016; Kaplan et al., 2020; Thurber, 2022). While recent hydrologic research has used physical and statistical modeling techniques to map the spatio-temporal distribution of non-permanent streams and characterize the climatic and landscape controls on flow permanence (Döll & Schmied, 2012; Kaplan et al., 2020; Moidu et al., 2021) fisheries research often overlooks the importance of streamflow permanence as a force regulating the abundance and distribution of stream fishes as well as the habitats that support their persistence (Heim et al., 2019). As the consequences of climate change become increasingly evident in the physical and biological processes that define riverscapes in the CRB, there exists a significant need to better evaluate the drivers and function of non-permanent and discontinuous streamflow patterns in the context of their ecological ramifications for native, cold-water species of concern.

In this thesis, I evaluated the drivers and importance of streamflow permanence patterns for regulating salmonid habitat availability and supporting early life history function. I identified the climatic and landscape controls on streamflow permanence for watersheds across the northern Rocky Mountains and characterized the potential and realized ability of non-permanent streams to support the spawning and early life history of cutthroat trout.

In Chapter II, I applied a random forest classification algorithm to a multi-decadal dataset to 1) identify the dominant climatic and landscape drivers of streamflow permanence for watersheds on federal land in the Columbia River and upper Missouri River basins and 2) conduct a sensitivity analysis of simulated climate and management scenarios to predict loss of summer habitat for native salmonid species of concern. I found that climate conditions were strongest predictors of flow permanence class, though landscape attributes like catchment area largely regulate the amount of precipitation that accumulates and becomes available for streamflow generation. Climate scenarios characterized by diminished spring snow water equivalent, precipitation, and warmer air temperatures were strongly correlated with non-permanent streamflow. Wetted summer habitat availability was highly sensitive to changes in these variables, and climate-induced drying was most probable in smaller, more arid catchments historically occupied by cutthroat trout species. These findings indicate that anticipated climate warming will initiate strong changes in the availability of flowing summer habitat for stream fishes, and cutthroat trout, in particular. As cold-water salmonids rely on a series of quality, connected habitat patches to fulfill their life history (Young, 1995; Schoby & Keeley, 2011; Budy et al., 2019), species management plans and future research evaluating threats to cold-water species persistence need to consider how changing flow permanence patterns may impact continuity, patch size, and access to habitats with slower climate velocities that are expected to serve as refugia under climate change (Isaak et al., 2016).

My Chapter II results also suggest that streamflow permanence classes and habitat availability are sensitive to changes in landcover variables that are directly affected by land use practices. Catchments with reduced vegetative cover in the riparian zone had a higher probability of discontinuous summer surface flow. As the model is non-mechanistic, causal relationships between land-management practices that impact riparian cover and surface flow patterns cannot be established. However, other research has demonstrated that grazing activity can result in high soil evaporation rates (McGinty et al., 1979; Udom & Nuga, 2014) which limits water's ability to move through a catchment and into a stream (Jensco & McGlynn, 2011). While it is unlikely that grazing alone is a dominant control on streamflow, in catchments vulnerable to climate-induced drying and potentially occupied by sensitive species, adaptive grazing management is a pragmatic tool that managers can use to bolster sub-surface hydraulic pathways and mitigate further fragmentation of the stream network. Alternatively, vegetation's ability to predict streamflow permanence class may reflect that wetter catchments can simply support both more vegetation and more surface flow. Regardless of mechanism, as flow non-permanence becomes more common, managers may find that drainages have a reduced capacity to support grazing activity, particularly in streams that once flowed permanently but have since transitioned to more intermittent states. My results improve our understanding of the direct and indirect relationships between land-use practices, the landscape attributes they affect, and streamflow permanence patterns that shape the mosaic of viable habitat available to native salmonid populations. As such, they can help guide land management and climate adaptation plans in an increasingly uncertain hydrologic future.

Given that streamflow permanence patterns can shape the biotic assemblages that inhabit them (Datry et al., 2014), and non-permanent flow patterns are increasing, it critical to understand the ways in which non-permanent streams provide useful, temporary habitat for species of conservation concern. In Chapter III of my thesis, I characterized the potential and realized ability of streams with variable flow permanence patterns to support spawning for a native salmonid species in one high-mountain drainage in northern Utah. I conducted a two-year field study to 1) characterize the spatio-temporal distribution of viable spawning habitat for native Bonneville cutthroat trout (*O. clarkii utah*; hereafter, “BCT”), 2) identify physiographic and climatic controls on the probability that habitats support early life history, and 3) document the timing and use of these temporary habitats by BCT across years and conditions. Findings indicated that the spatio-temporal distribution of spawning habitat varied across years with starkly different climate conditions. In a warm drought year, colder, permanent streams accounted for much of available spawning habitat, as most non-permanent streams didn’t sustain surface flows long enough to support spawning. The following year was characterized by a large and persistent snowpack, and those warm, non-permanent streams became more suitable for spawning. Meanwhile, many permanent streams remained too cold for much of the spawning season. However, despite large changes in within site suitability across years, spawning opportunities at the basin scale did not change dramatically, as suitability gains in non-permanent streams offset losses in permanent ones. Finally, I demonstrated that when non-permanent streams become available, native trout can and do take advantage of these habitats for spawning.

Synthesizing the results of both thesis research chapters, I demonstrate that non-permanent streamflow will likely continue to become increasingly prevalent under climate warming and accelerated drying will initiate serious changes to summer habitat quantity and accessibility. Processes that reduce total habitat and increase fragmentation among patches increase the risk of extinction for cold-water fluvial salmonids (Rieman & McIntyre, 1995; Dunham & Rieman, 1999). As such, it is important for conservation plans to address changing streamflow patterns. Additionally, forest management plans have reduced protections for the riparian zone in watersheds draining non-permanent streams (Kershner et al., 2004). As non-permanent stream prevalence grows (Zipper et al., 2021) and flow permanence mapping abilities are enhanced (Sando et al., 2022), more streams may be afforded fewer protections. As such, it is imperative to establish whether non-permanent streams support the diverse life history expressions of species of concern to better inform conservation practices. My Chapter III findings are in line with a growing body of research that recognizes that habitat permanence is not always synonymous with habitat importance (Heim et al., 2019). I demonstrated that non-permanent streams provide substantial spawning habitat in years with amenable conditions. Additionally, they greatly contribute to the habitat diversity that enables ecosystem portfolio effects (Schindler et al., 2015) to buffer basin-wide suitability against climate volatility. My results suggest that the temporary nature of non-permanent streams should not exclude them from protections afforded to permanent streams, as they provide complementary, alternative habitat that supports the diverse life history expressions of valuable species.

References

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., ... & Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, *11*(4), 354-361.

Boughton, D. A., Fish, H., Pope, J., & Holt, G. (2009). Spatial patterning of habitat for Oncorhynchus mykiss in a system of intermittent and perennial streams. *Ecology of Freshwater Fish*, *18*(1), 92-105.

Brennan, S. R., Schindler, D. E., Cline, T. J., Walsworth, T. E., Buck, G., & Fernandez, D. P. (2019). Shifting habitat mosaics and fish production across river basins. *Science*, *364*(6442), 783-786.

Brooks, P. D., Gelderloos, A., Wolf, M. A., Jamison, L. R., Strong, C., Solomon, D. K., ... & Stewart, J. (2021). Groundwater-mediated memory of past climate controls water yield in snowmelt-dominated catchments. *Water Resources Research*, *57*(10), e2021WR030605.

Budy, P., Rogers, K. B., Kanno, Y., Penaluna, B. E., Hitt, N., Thiede, G. P., ... & DeRito, J. (2019). Distribution and status of trout and char in North America.

Colvin, S. A., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., ... & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries*, *44*(2), 73-91.

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: a challenge for freshwater ecology. *BioScience*, *64*(3), 229-235.

Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, *7*(1), 014037.

Dunham, J. B., & Rieman, B. E. (1999). Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications*, *9*(2), 642-655.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175.

Erman, D. C., & Hawthorne, V. M. (1976). The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Transactions of the American Fisheries Society*, *105*(6), 675-681.

Fritz, K. M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington Jr, P. J., Leibowitz, S. G., ... & Nadeau, T. L. (2013). Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. *JAWRA Journal of the American Water Resources Association*, *49*(4), 867-882.

Hafen, K. C., Blasch, K. W., Rea, A., Sando, R., & Gessler, P. E. (2020). The influence of climate variability on the accuracy of NHD perennial and nonperennial stream classifications. *JAWRA Journal of the American Water Resources Association*, *56*(5), 903-916.

Heim, K. C., McMahon, T. E., Calle, L., Wipfli, M. S., & Falke, J. A. (2019). A general model of temporary aquatic habitat use: water phenology as a life history filter. *Fish and Fisheries*, *20*(4), 802-816.

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., ... & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374-4379.

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894-13899.

Jaeger, K. L., Sando, R., McShane, R. R., Dunham, J. B., Hockman-Wert, D. P., Kaiser, K. E., ... & Blasch, K. W. (2019). Probability of Streamflow Permanence Model

(PROSPER): A spatially continuous model of annual streamflow permanence throughout the Pacific Northwest. *Journal of Hydrology X*, *2*, 100005.

Jencso, K. G., & McGlynn, B. L. (2011). Hierarchical controls on runoff generation: Topographically driven hydrologic connectivity, geology, and vegetation. *Water Resources Research*, *47*(11).

Kaplan, N. H., Blume, T., & Weiler, M. (2022). Event controls on intermittent streamflow in a temperate climate. *Hydrology and Earth System Sciences*, *26*(10), 2671-2696.

Kershner, J. L., Archer, E. K., Coles-Ritchie, M., Cowley, E. R., Henderson, R. C., Kratz, K., … Vinson, M. R. (2004). *Guide to effective monitoring of aquatic and riparian resources*. doi:10.2737/rmrs-gtr-121

Kominoski, J. S., Ruhí, A., Hagler, M. M., Petersen, K., Sabo, J. L., Sinha, T., ... & Olden, J. D. (2018). Patterns and drivers of fish extirpations in rivers of the American Southwest and Southeast. *Global Change Biology*, *24*(3), 1175-1185.

Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774-1791.

Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, *55*(4), 717-738.

McGinty, W. A., Smeins, F. E., & Merrill, L. B. (1979). Influence of soil, vegetation, and grazing management on infiltration rate and sediment production of Edwards Plateau rangeland. *Rangeland Ecology & Management/Journal of Range Management Archives*, *32*(1), 33-37.

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., ... & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391-397.

Moidu, H., Obedzinski, M., Carlson, S. M., & Grantham, T. E. (2021). Spatial patterns and sensitivity of intermittent stream drying to climate variability. *Water Resources Research*, *57*(11), e2021WR030314.

Peterson, D. P., Rieman, B. E., Dunham, J. B., Fausch, K. D., & Young, M. K. (2008). Analysis of trade-offs between threats of invasion by nonnative brook trout (Salvelinus fontinalis) and intentional isolation for native westslope cutthroat trout (Oncorhynchus clarkii lewisi). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 557-573.

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian journal of fisheries and aquatic sciences*, *46*(10), 1805-1818.

Reynolds, L. V., Shafroth, P. B., & Poff, N. L. (2015). Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change. *Journal of Hydrology*, *523*, 768-780.

Rieman, B. E., & McIntyre, J. D. (1995). Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American fisheries Society*, *124*(3), 285-296.

Rieman, B., Peterson, J. T., Clayton, J., Howell, P., Thurow, R., Thompson, W., & Lee, D. (2001). Evaluation of potential effects of federal land management alternatives on trends of salmonids and their habitats in the interior Columbia River basin. *Forest ecology and management*, *153*(1-3), 43-62.

Rogosch, J. S., Tonkin, J. D., Lytle, D. A., Merritt, D. M., Reynolds, L. V., & Olden, J. D. (2019). Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere*, *10*(4), e02681.

Sando, R., & Blasch, K. W. (2015). Predicting alpine headwater stream intermittency: A case study in the northern Rocky Mountains. *Ecohydrology & Hydrobiology*, *15*(2), 68-80.

Sando, R., Jaeger, K. L., Farmer, W. H., Barnhart, T. B., McShane, R. R., Welborn, T. L., ... & Shallcross, A. (2022). Predictions and drivers of sub-reach-scale annual streamflow permanence for the upper Missouri River basin: 1989–2018. *Journal of Hydrology X*, *17*, 100138.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609-612.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257-263.

Schoby, G. P., & Keeley, E. R. (2011). Home range size and foraging ecology of bull trout and westslope cutthroat trout in the upper Salmon River Basin, Idaho. *Transactions of the American Fisheries Society*, *140*(3), 636-645.

Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, *47*(7), 427-435.

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of climate*, *18*(8), 1136-1155.

Tsuboi, J. I., Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D., ... & Kanno, Y. (2022). Small giants: Tributaries rescue spatially structured populations from extirpation in a highly fragmented stream. *Journal of Applied Ecology*, *59*(8), 1997-2009.

Thurber, D. M. (2022). Characterizing Karst Mountain Watersheds Through Streamflow Response to Snowmelt. MS Thesis, Utah State University.

Udom, B. E., & Nuga, B. O. (2014). Hydraulic conductivity and aggregation of fine-textured soil under intensive cattle grazing. *Journal of Agricultural Science*, *6*(11), 37.

Walsworth, T. E., Baldock, J. R., Zimmerman, C. E., & Schindler, D. E. (2020). Interaction between watershed features and climate forcing affects habitat profitability for juvenile salmon. *Ecosphere*, *11*(10), e03266.

Wigington Jr, P. J., Ebersole, J. L., Colvin, M. E., Leibowitz, S. G., Miller, B., Hansen, B., ... & Compton, J. E. (2006). Coho salmon dependence on intermittent streams. *Frontiers in Ecology and the Environment*, *4*(10), 513-518.

Young, M. K. (1995). *Conservation assessment for inland cutthroat trout* (Vol. 256). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Zipper, S. C., Hammond, J. C., Shanafield, M., Zimmer, M., Datry, T., Jones, C. N., ... & Allen, D. C. (2021). Pervasive changes in stream intermittency across the United States. *Environmental Research Letters*, *16*(8), 084033.