WHEN BEAVERS GET BURNED, DO FISH GET FRIED? THE ROLE OF BEAVERS TO MEDIATE WILDFIRE EFFECTS ON ARCTIC GRAYLING IN BOREAL ALASKA

By

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

in

Fisheries

University of Alaska Fairbanks

December 2023

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Abstract

Wildfire is a dominant natural disturbance process throughout boreal North America and fires are increasing in size, frequency, and severity. However, little is known about how wildfire affects boreal fish populations and aquatic habitat despite the substantial impacts of fire on ecosystem processes, and even less is known about how fire effects are mediated by species interactions. For example, North American Beavers (*Castor canadensis*) are affected by and can influence wildfire dynamics, and their engineering has complex effects on aquatic habitats. North American Beavers therefore have the potential to mediate wildfire effects on aquatic ecosystems and fish populations. Here I investigated relationships between wildfire and the distribution of beavers and a common fish species across a fire-dominated riverscape in Interior Alaska. First, I used satellite imagery to locate and enumerate beaver ponds throughout five large watersheds (total area: 20,711 km^2) and modeled the relationship of beaver pond density (ponds per km^2) as a function of wildfire history, stream geomorphology, hydrology, and vegetation composition. I then used a simulation to conceptualize the impacts of wildfire and beaver dams on Arctic Grayling (*Thymallus arcticus*) habitat availability under variable hydrologic conditions. Next, I sampled 62 streams for Arctic Grayling environmental DNA (eDNA) and sampled 10 of those streams for Arctic Grayling abundance. I used a generalized linear model (GLM) and N-mixture model to understand the relationship between eDNA concentration and Arctic Grayling abundance and distribution throughout the study area. I found that wildfire metrics explained most variation in beaver pond density (pseudo $R^2 = 0.75$) across the landscape and were positively associated with beaver pond density, although geomorphological and hydrological parameters were also important. My simulations indicated that beaver dams can create substantial barriers to fish dispersal during low water conditions (up to 20% reduced habitat

availability in some river basins) and can severely reduce (up to 65%) habitat availability in some tributary streams. I found that eDNA concentration was moderately correlated with Arctic Grayling abundance (GLM: pseudo $R^2 = 0.45$) and unexplained variation was likely due to the spatial mismatch between fish sampling and scale of eDNA representation. However, I estimated eDNA residence time of about 6.7 hours in one stream, and eDNA appeared to accumulate longitudinally throughout the tributary, indicating that an eDNA sample near the downstream end was likely a good relative representation of Arctic Grayling abundance in a tributary. Results from the N-mixture model indicated that stream geomorphology and hydrology were the most important predictors for Arctic Grayling abundance (eDNA concentration), wildfires had a negative effect, and beaver dam density had a mixed effect on Arctic Grayling abundance. Overall, this study illustrated that beaver densities can increase after wildfires in Interior Alaska stream networks, which could result in negative impacts on Arctic Grayling habitat availability if beavers impair fish passage; however, these effects are dependent on the environmental context and suggest beaver-fish interactions may be best managed on a case-by-case basis.

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Acknowledgments

First, I would like to thank my advisor Dr. Jeff Falke for all his support throughout this project. He provided excellent research advice, especially when considering different analyses and trying to bring together the “big picture” I am also thankful for the advice and support from my committee members, Dr. Ken Tape, Dr. Andy Seitz, and Dr. Santosh Panda. Their support and guidance were invaluable. Further, I would like to thank the entire Falke lab for support and helpful advice throughout my degree. I would especially like to thank Elizabeth Hinkle, who assisted with my fieldwork often and was very helpful in brainstorming about my research questions, study design, and results. I would also like to thank the other volunteers who assisted in the field, including Taylor Cubbage, Deanna Strohm, Dr. Jeff Muehlbauer, and Lauren Yancy. Thank you to all of the technicians who helped throughout my research: Rachel Allen, Evan Brashear, Joey Ilada, Jackie Tauberman, Monica Gosseling, and Ethan Stone. A big thank you to Josh Paul, who played an important role in facilitating ArcGIS analyses and managing our data. Thank you to Dr. Andres Lopez for advice on eDNA collection and analysis. Thank you to Christina Sutton, who was always on top of things and made getting help easy. I appreciated the support from Dr. Jeff Muehlbauer and his entire lab during the end of my degree. Thank you to the numerous other people who contributed along the way. This work was funded by the U.S. Department of Defense Strategic Environmental Development and Research Program, the Alaska Climate Adaptation and Science Center (U.S. Geological Survey), and the Alaska Established Program to Stimulate Competitive Research (National Science Foundation) Fire and Ice project. Thank you to Jonah Bacon, who was a great peer, and an even better friend. A big thank you to my family for preparing me for this journey. Most importantly, thank you to my fiancé, Lauren Yancy, for her unwavering support through long days of fieldwork and coding.

General Introduction

Wildfire is a major driver of natural ecological change in boreal forests and influences numerous aspects of upslope and riparian vegetation by opening the canopy, providing opportunities for regeneration, and creating a mosaic of successional communities (Rowe and Scotter 1973; Kasischke and Stocks 2012). For example, terrestrial plant communities can be completely reorganized following high-severity fires, shifting from black spruce-dominated to deciduous landscapes (Johnstone et al. 2010). Wildfire also has direct and indirect effects on aquatic systems through the input of nutrients, wood, and heat, altering erosion/sedimentation dynamics, and changing hydrologic regimes (Gresswell 1999; Bixby et al. 2015). Indeed, wildfire is recognized as an important natural disturbance agent in the formation and maintenance of complex and productive aquatic habitats because of its propensity to connect terrestrial and aquatic systems (Reeves et al. 1995). Instream physical processes are closely linked to the surrounding landscape, therefore wildfire effects on aquatic systems vary with watershed geomorphology, topology, and size, as well as the type and condition of upslope forests (Minshall 2003; Tetzlaff et al. 2007). Such fine- and broad-scale habitat variations may affect fauna across life stages, with implications for resource availability, growth, survival, and population structure (Rosenberger et al. 2015; Jager et al. 2021). Further, wildfire frequency, size, and severity are increasing in boreal forests (Flannigan et al. 2005; Girardin and Mudelsee 2008; Balshi et al. 2009), with potential to impact fish and wildlife communities. These landscape-level changes may create important biological responses, so understanding baseline biological responses to wildfire is essential for understanding the future condition of fish and wildlife in boreal ecosystems (Reist et al. 2006; Jager et al. 2021).

North American beavers (*Castor canadensis;* hereafter referred to as "beavers") are "ecosystem engineers" that modify small streams via damming and consequently alter the physical and biological conditions of lotic systems (Collen and Gibson 2000; Johnston 2017; Orr et al. 2019). Severe wildfires have been shown to have adverse effects on beaver populations, including local extirpation by altering beaver habitat and forage conditions (Fellers et al. 2004; Hood et al. 2007; Fellers and Osbourn 2009; Figure 1). Conversely, wildfires act as a disturbance mechanism, resetting vegetation to early successional communities (e.g., willows *Salix* spp. and alder *Alnus* spp.; Zasada et al. 1987; Johnstone et al. 2010; Gerwing et al. 2013), which are primary food sources for beavers; thus, fire has the potential to stimulate beaver population growth (Johnston 2017; Touihri et al. 2018). Additionally, beaver activity has been shown to buffer aquatic and riparian habitats from the effects of wildfire by maintaining vegetation during fires and facilitating regrowth after burns (Fairfax and Whittle 2020; Markle et al. 2022). This limited research suggests a complex negative feedback (stabilizing) relationship between wildfires and beavers which is influenced by wildfire characteristics like burn frequency and severity.

Due to their potential to mediate wildfire effects on streams, and their considerable impacts on lotic physical and biological process, beavers are an important mechanism that shapes aquatic habitats and have the potential to build or reduce species resilience in fire-affected aquatic ecosystems (Collen and Gibson 2000; Kemp et al. 2012; Fairfax and Whittle 2020; Jordan and Fairfax 2022; Markle et al. 2022). However, wildfire-beaver relationships lack documentation, especially in boreal ecosystems where beavers and wildfires are widespread. The few studies that have considered wildfire-beaver relationships were concentrated in the Western U.S. and Canada, in biomes with different landscapes, weather, climate, and vegetation communities compared to boreal ecoregions (Fellers et al. 2004; Hood et al. 2007; Fellers and Osbourn 2009; Fairfax and Whittle 2020). Additionally, beaver reintroductions are being conducted widely across the U.S. and in Europe, where beavers were nearly extirpated for historical fur trades (Boyce 1981; Gibson and Olden 2014). Many of these areas have both natural and heavily suppressed/managed wildfire regimes that overlap beaver ranges (Hurteau et al. 2014; Thompson et al. 2018; Fairfax and Whittle 2020; Young et al. 2020), so understanding relationships between beavers and wildfire could have implications for wildlife and fire management. Finally, understanding the role of beavers to promote ecological resilience in riverscapes with changing wildfire conditions could provide important insights about protection of infrastructure (Hood et al. 2018), maintenance of ecosystem services (Thompson et al. 2021), and resilience for aquatic organisms (Pollock et al. 2014; Williams et al. 2015; Weber et al. 2017). By studying these processes in a relatively pristine area (compared to the contiguous U.S.), my thesis research minimizes confounding factors such as beaver trapping, commercial fish harvest, intensive wildfire suppression, and human development.

The effects of beaver dams and ponds on fishes have been widely studied across North America and worldwide (Hägglund and Sjöberg 1999; Collen and Gibson 2000; Kemp et al. 2012; Bylak et al. 2014; Malison and Halley 2020). Beaver activities have highly variable effects on fishes but are generally thought to increase productivity (e.g., individual fish growth and/or diversity) but reduce habitat connectivity and potentially overall fish abundance (Collen and Gibson 2000; Kemp et al. 2012; Johnson-Bice et al. 2018). Individual- and population-level fish responses to beaver modification depend on stream hydrologic and geomorphic conditions, beaver dam size, permeability, and persistence, and fish species, life-stage, swimming/jumping abilities, sensitivity/selectivity to habitat, and a variety of other factors (Collen and Gibson 2000;

Schlosser and Kallemeyn 2000; Kemp et al. 2012; Cutting et al. 2018). Therefore, the effects of beaver dams should not be assumed analogous among biomes or across fish species as local conditions and fish life histories are important determinants of how dams impact fishes. Accordingly, research is needed to investigate regionally specific patterns of beaver-fish relationships for each fish species of interest and importance.

To date, research about beaver dam and fish interactions in boreal regions has centered around juvenile anadromous salmonids (Kemp et al. 2012; Malison et al. 2014, 2015, 2016; Malison and Halley 2020). However, resident fishes such as Arctic Grayling (*Thymallus arcticus*) may be more vulnerable to beavers and/or wildfire because they spend their complete life cycle (e.g., spawning, rearing, feeding) in beaver- and fire-affected ecosystems. Only two studies have considered beaver and Arctic Grayling interactions in a substantive way: an Alaska Department of Fish and Game Report (Fairbanks, AK, U.S.) which showed that beaver dams prevented fish dispersal to important spawning habitat (Wuttig 2002); and a radiotelemetry study in Montana (U.S.) which found little overall effect of beaver dams on Arctic Grayling dispersal, but showed that flow conditions are a key determinant of fish migratory success (Cutting et al. 2018). Due to the conflicting conclusions of these and other studies, further investigation is required to assess how beavers affect resident fish distribution and dispersal in a boreal ecosystem.

I explored the cumulative effects of beavers and wildfires on fish habitat and the distribution and abundance of Arctic Grayling. The objectives of this thesis were to 1) understand how geomorphological, hydrological, wildfire, and vegetation parameters influence beaver activity in a boreal ecosystem, 2) estimate the impact of beaver dams on fish dispersal across a gradient of beaver densities and flow scenarios, and 3) empirically evaluate the effect of beavers, wildfires, and environmental covariates on the distribution and abundance of Arctic Grayling in Interior Alaska using eDNA. The results from these studies will be useful for informing beaver and fish management at a broad scale in landscapes that experience disturbances such as wildfires. Further, this study will act as a broad review of beaver, fish, and fire interactions in boreal ecosystems for comparison to other regions, and to act as a guide for future research.

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Chapter 1: When beavers get burned, do fish get fried? The role of beavers in mediating wildfire effects on Arctic Grayling in boreal Alaska[1]

ABSTRACT

Wildfire is a dominant natural disturbance process throughout boreal North America and fires are increasing in size, frequency, and severity. However, little is known about how wildfire affects boreal fish populations and aquatic habitat despite the substantial impacts of fire on ecosystem processes, and even less is known about how fire effects are mediated by species interactions. For example, North American beavers (*Castor canadensis*) are affected by and can influence wildfire dynamics, and they have complex effects on aquatic habitats. Therefore, beavers have the potential to mediate wildfire effects on aquatic ecosystems and fish populations. Here we investigated relationships between wildfire (incidence, severity) and the abundance and distribution of beaver ponds across a fire-prone riverscape in Interior Alaska. We used satellite imagery to locate and enumerate beaver ponds across five large watersheds (total area = 20,711 km^2) and modeled the relationship of beaver pond density (ponds per km^2) as a function of wildfire history, stream geomorphology, hydrology, and vegetation composition. We then used a simulation to conceptualize the impacts of wildfire and beaver dams on fish habitat availability under variable hydrologic conditions. Wildfire severity explained the majority of variation in beaver pond density (pseudo $R^2 = 0.75$); pond density was positively correlated with severe burns and negatively with moderate severity burns. Geomorphological and hydrological covariates such as stream sinuosity, floodplain width, elevation, stream power, and mean annual

[1]Samuel, W.T., J.A. Falke, K.D. Tape, A.C. Seitz, S.K. Panda. When beavers get burned, do fish get fried? The role of beavers in mediating wildfire effects on Arctic Grayling in boreal Alaska. Formatted for *Transactions of the American Fisheries Society*.

discharge were also important predictors of beaver pond density (pseudo $R^2 = 0.31$). Vegetation parameters were only important in basins without wildfire history and explained relatively little variation in beaver density (pseudo $R^2 = 0.19$), potentially due to the spatial and temporal resolution of the source data. Simulations indicated that beaver dams may create substantial barriers to fish dispersal during low water conditions (up to 20% reduced habitat availability in some river basins) and can severely reduce tributary habitat availability (up to a 65% reduction in some tributaries). Overall, this study shows the substantial impact of wildfires as a disturbance process in boreal aquatic ecosystems and its trickle-down interactive effects on aquatic organisms such as beavers and fish.

INTRODUCTION

Wildfires are increasing in size, frequency, and severity throughout North America, especially in the boreal biome (Flannigan et al. 2005; Girardin and Mudelsee 2008; Balshi et al. 2009), and North American Beavers (hereon referred to as "beavers") are emerging as a key mediator of wildfire impacts to aquatic ecosystems (Fairfax and Whittle 2020; Jordan and Fairfax 2022; Markle et al. 2022). Beavers are ecosystem engineers that modify aquatic habitats by damming streams, flooding riparian areas, and reshaping river channels into wetland complexes, which has implications on surrounding ecological processes (Naiman et al. 1988; Collen and Gibson 2000; Levine and Meyer 2019; Majerova et al. 2020; Brazier et al. 2021). In fact, beavers have been shown to buffer streams from wildfire impacts by increasing the wetness of valley bottoms and facilitating vegetation recovery after fires (Fairfax and Whittle 2020; Markle et al. 2022). Wildfires can affect beaver populations in multiple ways; high severity fires have been shown to reduce and locally extirpate beaver populations in the Western U.S. and Canada (Fellers et al. 2004; Hood and Bayley 2008; Fellers and Osbourn 2009). Alternatively, moderate or patchy wildfires may stimulate early successional plant growth (e.g., Willow *Salix* spp.) which is ideal beaver forage and could bolster beaver populations (Zasada et al. 1987; Gerwing et al. 2013; Johnston 2017). Accordingly, research is needed to understand how beavers will respond to changing wildfire regimes in the boreal region and consider impacts on aquatic ecosystems.

Remote sensing has been used to survey beaver populations by using their dams and lodges as a proxy for population status (Tape et al. 2018, 2022; Taylor 2020; Fairfax et al. 2023; Zhang et al. 2023). Because beavers significantly modify streams, satellite imagery is generally an effective way to detect beaver presence/abundance (Taylor 2020). Additionally, remotely sensed data can be paired with other geospatial data to create informative models of beaver occupancy and abundance (Johnston and Windels 2015; Broschart et al. 2016; Macfarlane et al. 2017; Dittbrenner et al. 2018). By aligning geospatial data such as beaver surveys, remotely sensed wildfire data, and other landscape-level covariates, broadly applicable models can be used to inform holistic questions about ecological patterns and future trends. Further, these types of models have implications for understanding beaver effects on fishes and other aquatic organisms (Pollock et al. 2004; Malison et al. 2016). By considering the distribution of organisms (beavers and fishes) in the context of landscape disturbances, managers can respond appropriately to current needs and future changes.

Beaver effects on fishes have been studied widely, but research in Alaska and the boreal biome is sparse (but see Wuttig 2000, 2002; Lang et al. 2006; Malison et al. 2014, 2015, 2016; Randy Brown, U.S. Fish and Wildlife Service, *unpublished data*). Benefits and negative effects of beavers on fishes appear to vary by region, species, life stage, flow, and other habitat factors like stream gradient (Collen and Gibson 2000; Kemp et al. 2012; Johnson-Bice et al. 2018).

Many benefits related to beavers, such as increased fish growth and diversity, are associated with studies seeking to understand beavers' potential as a restoration agent, often in high gradient streams that have experienced some level of degradation from human development (Pollock et al. 2012, 2014, 2022; Wheaton et al. 2013; Bouwes et al. 2016; Weber et al. 2017). In the context of habitat restoration in impaired streams, it appears that beavers have potential to be an affordable, low maintenance restoration tool that can benefit fish and wildlife communities (Bouwes et al. 2016; Jordan and Fairfax 2022). However, negative impacts of beavers such as habitat fragmentation, which reduces fish dispersal and abundance, are important to consider, especially in relatively intact ecosystems where beavers are abundant. In undisturbed landscapes, the benefits of beavers may not be as pronounced because there are already sufficient high-quality habitats available to stream fishes, therefore research priorities tend to focus on habitat fragmentation and potential limitations to fish production (Parker and Ronning 2007; Taylor et al. 2010; Malison et al. 2016; Feddern et al. 2023). As beaver and fish interactions are changing across multiple regions, it is important to study the broad patterns and implications of these relationships throughout North America.

The overall goal of this study was to understand the landscape-level relationship between a dominant disturbance process, wildfire, and an ecosystem engineer, beaver, and how they cumulatively affect fish habitat availability (Figure 1.1). Specifically, we set out to 1) assess how wildfire and environmental covariates affect beaver pond density in Interior Alaska, and 2) estimate the amount of fish habitat restricted by beaver dams across tributaries under variable flow conditions. We expected that stream and landscape characteristics (e.g., stream power, elevation, etc.) would affect beaver pond density, wildfire would have an important negative effect on the distribution of beaver ponds, and vegetation characteristics would be positively related to beaver pond density. Additionally, we expected that beavers would reduce fish habitat availability, especially during low flows.

METHODS

Study Area—This study was conducted in five river systems in Interior Alaska: The Chatanika (drainage area = 4,460 km^2), Chena (5,350 km^2), Salcha (5,740 km^2), and Goodpaster rivers (4,120 km^2), and Shaw Creek (1041 km^2; Figure 1.2). Within this approximately 21,000 km^2 extent, about one quarter burned from 1984 to 2022. Widespread fires occurred in 1990, 2004, 2009, 2011, 2015, 2019, and 2022 (Figure 1.2), although 2004 was the most dominant fire year -the largest fire year on record in Alaska with over 27,200 km^2 burned statewide (Wendler et al. 2011). This landscape is covered in a patchy distribution of deciduous and coniferous forests (Paper Birch *Betula papyrifera*, Aspen *Populus* spp., Alder *Alnus* spp., Willow *Salix* spp., Cottonwood *Populus deltoides*, Black Spruce *Picea mariana*, White Spruce *Picea glauca*, and Tamarack *Larix laricina*), and forest composition is heavily driven by wildfire history and discontinuous permafrost (Nawrocki et al. 2021; Macander et al. 2022). Streams in the study area are mostly fed via a combination of snowmelt, rain, and groundwater, and vary from swampy wetlands to clear, fast-flowing streams. Tributaries have discharge ranging between 0.006 and 35 m^3/s, and the mainstem rivers have discharge ranging between 30 and 300 m^3/s, depending on the season and location, and peak flows typically occur in May/June (due to snowmelt) and August (rainy season; USGS 2023).

Much of the study area is difficult to access by humans. Beavers were historically trapped in Alaska at varying rates beginning in the 1600s (Obbard et al. 1987); however, detailed trapping records do not exist aside from a few recent years (1989–1995; Alaska Department of Fish and Game). Since then, trapper survey questionnaires have been used to estimate population trends, and beaver populations in the study area are considered stable (Bogle 2021). For the purposes of this study, we assumed that beaver populations in our study area have recovered from historical trapping, were near or at carrying capacity, and that variability in density/distributions was due to non-human influences.

Arctic Grayling (hereafter "grayling") is a widespread boreal fish species that occurs from western Russia to Hudson Bay, Canada (Northcote 1995). Grayling have important ecological, recreational, and subsistence roles to Alaska peoples (Alaska Department of Fish and Game (ADFG) 2021). They are widespread across most of Alaska and utilized by Indigenous and rural individuals as a portion of subsistence harvests (ADFG 2021). As a sport fish, they are valued by tourists and locals by being easy to catch and abundant, and support sportfishing guide operations. In addition, grayling are ubiquitous throughout the region, making them a useful sentinel species to evaluate the conditions of aquatic systems (Northcote 1995). In Interior Alaska, the species overwinters in the lower reaches of large rivers, migrate to (often groundwater-fed) spawning habitats in the spring, and move to summer feeding areas located throughout boreal river networks (Armstrong 1986). During the ice-free season, adults and sub-adults typically occupy the middle to upstream reaches of tributaries for feeding (Hughes and Reynolds 1994). A broad suite of literature on grayling in Alaska forms the assumptions upon which this study is based: primarily that grayling are abundant and ubiquitous generalists that prefer summer rearing habitats located upstream in watersheds (e.g., tributary streams; Hughes and Dill 1990; Deegan and Peterson 1992; Hughes 1992, 1998, 2000; Hughes and Reynolds 1994; Deegan et al. 1999; Buzby and Deegan 2000, 2004; Larocque et al. 2014; Heim et al. 2016a, 2016b, 2018; McFarland et al. 2018; Bozeman and Grossman 2019; Falke et al. 2019).

Data Collection— We assessed the spatial distribution of beaver ponds across the study area using satellite imagery. The study area was divided into sub-basins (tributary streams) based on 12th level hydrological units (HUC 12; mean sub-basin area = 102 km^2) from the National Hydrography Dataset (USGS 2020). Sub-basins contained first through fifth order streams and were assumed to be of maximum size that beavers are capable of damming. Each sub-basin was surveyed for beaver ponds by manually locating and georeferencing ponds using a high resolution (0.5 by 0.5 m) satellite imagery composite created in 2017 (AKDNR 2017). Once located, ponds were manually traced by creating polygon vectors in ArcGIS ver. 10.4 (ESRI, Redlands, California), and pond extent (i.e., beaver-affected wetted area; calculated as the area of the pond in m^2) was calculated. Ponds were classified by type (main-channel, side-channel, or off-channel), condition (active (holding water) or inactive (no longer holding water)), and by confidence of the surveyor that the pond was created by beavers (high confidence, low confidence, or not a beaver pond).

Geospatial data used for analysis were collected from a variety of sources and at different spatial scales. We used output from the program NetMap (Benda et al. 2007; TerrainWorks, Mt. Shasta, CA) to estimate stream and watershed attributes for the study area. NetMap uses Digital Elevation Models (DEMs; 5 by 5 m spatial resolution) to derive a synthetic stream network (referred to here as "streamlines") and delineate the unique land surface area that drains into a reach (hereon "reach contributing areas" (RCAs)). Attributes used in this study (e.g., mean annual flow, stream order, stream power, etc.) were estimated for streamlines and RCAs in NetMap using models described in Benda et al. (2007) and Clarke et al. (2008), typically based off drainage area, mean annual precipitation, and DEMs. We then summarized the remaining geospatial data by valley bottom polygons (VBs), where a single VB was contained within each

RCA but the area pf the polygon is restricted to the valley bottom, removing potentially confounding data from the hillslopes. Wildfire data were collected from Monitoring Trends in Burn Severity (MTBS 2022), including annual wildfire perimeters and burn severity data (30 by 30 m). Remotely sensed vegetation data were sourced from Macander et al. (2022) which classified landcover into plant functional types (e.g., coniferous tree, deciduous shrub), had a 30 by 30 m spatial resolution, and a temporal resolution of every five years. We used data from 2015 because these data were closest in time to our beaver surveys. See Table 1.1 for a complete list of covariates and associated datasets.

Data Analysis: Beaver relationships with wildfire— We used a regression approach to investigate relationships between beaver ponds and environmental characteristics. We summarized beaver pond data within polygons that represented the valley bottoms (VB) surrounding each confluence-to-confluence stream reach (Appendix A; Benda et al. 2007; Clarke et al. 2008); beaver pond density (number of ponds per km^2) was also summarized for each VB. We only included ponds that were confidently determined to be created by beavers (high confidence ("HC") ponds) by the surveyors. We also filtered out ponds that were on side channels, were inactive, potentially subject to mining, and other confounding factors. This resulted in N=195 valley bottom polygons with varying levels of beaver pond density, which were used as the response variable in our model. We did not include any valley bottom polygons that were surveyed but did not contain beaver ponds (n = 5264) due to challenges associated with modeling absences in a regression model. See Table 1.1 for the complete list of covariates.

We used an information theoretic approach and model averaging (Anderson and Burnham 2002) to identify the most parsimonious set of covariates to predict beaver density (ponds per km^2) across our study area, given the data. We assessed multicollinearity among covariates using Variance Inflation Factor (VIF); all predictors had VIF values < 10 so we retained the original set (Table 1.1). Next, we developed a global generalized linear model (GLM) which included all predictors (Table 1.1 and 1.2) and candidate models that included subsets of covariates (e.g., wildfire, vegetation, geomorphology covariates; Table 1.2). We considered permafrost as a potential covariate that might have affected beaver distribution, although the only geospatial permafrost data that were available had a 1-km^2 spatial resolution, which was determined to be too coarse to include in these models. To elucidate potentially variable relationships in burned and unburned basins, we trained each alternative model using three different datasets: 1) the full set of valley bottoms with beaver ponds (n = 195), 2) valley bottoms that had wildfire history (n = 92), and 3) valley bottoms that had no wildfire history (n = 103). We evaluated these alternative models using Akaike information criterion corrected for a small sample size (AICc) and pseudo R^2 (mean of McFadden, Cox and Snell, Nagelkerke, and Efron R^2; Table 1.2). Then the function *modavg* in the package AICcmodavg in Program R (ver. 4.1.2, Indianapolis, IN, United States) was used to determine the model-averaged estimate of each covariate for each dataset, which describes their relative effect on beaver density (Table 1.3). We considered model-averaged parameters to be important when their 90% unconditional confidence intervals did not overlap zero.

Data Analysis: Beaver effects on fish dispersal— We utilized a simulation to estimate how beavers may affect Arctic Grayling dispersal across the landscape. We snapped the subset of points representing the HC beaver pond locations from remote sensing surveys (described above) to the closest second order or larger streamline. Fish habitat (km) was summarized at the scale of a 12th level Hydrologic Unit (HUC 12), which acted as a good representation of “tributary streams” that Arctic Grayling inhabit during the summer season (Hughes 1992, 1998, 2000; Hughes and Reynolds 1994).

First, we calculated the Potential Fish Habitat (PFH) for each sub-basin using a simple distribution model (Appendix B). The distribution model is based on mean annual flow (m^3/s), stream gradient (%), and historical observations of fish occurrence throughout the Yukon River basin in Alaska within which our study area was nested. Next, to determine the effect of beavers on fish dispersal, we calculated the Available Fish Habitat (AFH) for each sub-basin in light of the observed beaver distribution. To do so, streamlines were classified as mainstem or tributary streams: river mainstems were identified as streamlines that flowed through a HUC (i.e., did not originate within the HUC) and tributaries were classified as streams that originated within the HUC and terminated into a mainstem. Next, origin points (where fish initially began dispersing upstream) were determined, defined as the confluences of tributaries with mainstems (Figure 1.3). A standard population of fish (e.g., 100 fish or 100%) was assigned to each origin, and we assumed they would move upstream to occupy the total PFH within the sub-basin unless a barrier to passage existed (e.g., a beaver dam). When a confluence was encountered, the fish population was split proportionally according to mean annual discharge on each side of the tributary.

When the population encountered a dam, a pre-determined proportion of fish ascended based on individual fish’s Probability of Passage (POP). We chose POP rates based on field observations in the study area (Appendix C), passage rates described in Cutting et al. (2018), and observations from Wuttig (2000, 2002), and we informed our choices with similar studies on other species (Taylor et al. 2010; Lokteff et al. 2013; Niles et al. 2013; O’Keefe 2021; Wolf et al. 2022). Our observations (Appendix C) and other local research (Wuttig 2000, 2002) suggest a substantially lower POP than described in Cutting et al. (2018; mean POP = 88%), and potentially a bimodal relationship (e.g., some dams are passed by a majority of fish, some dams only are passed by a few or no fish). To balance these observations with the limited available empirical data, we selected a probability of passage rate of 50% to represent a mean POP rate across the study area, and the habitat that is accessible with that given POP was termed "available fish habitat 50%" (AFH_{50}). While recognizing that individual dams may have significantly higher or lower POP, we considered a 50% POP to be most representative of beaver/fish dynamics across this broad study area and appropriately generalized for the purposes of this study. As the fish population ascends each dam, a proportion of the population is left behind (e.g., 50%), eventually reaching an asymptote near zero. We chose 5% as a minimum population size threshold, below which the stream was no longer considered available for fish for use as habitat. The final product resulting from these analyses was a linear distance (km) of suitable habitat accessible by fish within each tributary (e.g., AFH_{50}; Figure 1.3).

Flows are an important contributing factor to fish dispersal in beaver-affected streams (Brown 2001; Mitchell and Cunjak 2007; Cutting et al. 2018) so we repeated the dispersal simulation for "high flow" and "low flow" scenarios in which we varied the POP to represent changes in flows (80% and 20%, respectively; "AFH_{80}", "AFH_{20}") based off our field observations, changes in POP observed in Cutting et al. (2018; *unpublished data*), and flow relationships observed in other studies (Taylor et al. 2010; Lokteff et al. 2013; O'Keefe 2021; Wolf et al. 2022). See full description and demo files of this process at https://github.com/Joshdpaul/FishPassage.

RESULTS

Beaver relationships with wildfire— We located 890 potential beaver ponds throughout the study area (Figure 1.4) and constructed our models using a subset of 435 ponds which we were highly confident (HC) were created by beavers. Beaver pond density (number HC of ponds per km^2) was summarized across 195 valley bottom polygons (mean beaver density = 7.6 ponds/km^2 ± 10.8 SD). There were 92 burned valley bottoms (mean area = 0.49 km^2 ± 0.37 SD), that averaged 27 ± 20 SD years since the last burn, and had mean beaver density of 8.5 ponds per km^2 ± 10.6 SD. Unburned valley bottoms (n=103) were larger (0.76 km^2 ± 1.05 SD; T-test: T = -2.44, DF = 119.92, $p = 0.06$) and had mean beaver density of 6.8 ponds per km^2 ± 11.0 SD. Pond density between burned and unburned valley bottoms was not significantly different (T-test: T = 1.10, DF = 192.30, $p = 0.27$). Pond area averaged 2803 m^2 (± 4803 SD), and ponds were smaller in burned basins (2014 m^2 ± 2374 SD) relative to unburned basins (3599 m^2 ± 6328 SD; T-test: T = -2.28, DF = 120.53, $p = 0.03$). Overall vegetation composition was relatively consistent across valley bottoms; burned valley bottoms had 67.8% ± 8.1 SD woody cover, 7.0% ± 5.2 SD broadleaf tree, 16.0% ± 8.0 SD percent conifer tree, 28.4% ± 8.4 SD deciduous shrub, and 6.7% ± 3.1 SD evergreen shrub; in unburned valley bottoms there was 65.5% ± 12.4 SD woody cover, 6.6% ± 6.7 SD broadleaf tree, 21.8% ± 7.0 SD conifer tree, 23.5% ± 8.3 SD deciduous shrub, and 6.0% ± 3.2 SD evergreen shrub. Coniferous trees occurred at lower proportions (T-test: T = -5.39, DF = 189.07, $p < 0.01$) and deciduous shrubs at a higher proportion (T-test: T = 4.11, DF = 191.98, $p < 0.01$) in burned basins, likely due to wildfire history and resulting successional processes.

Across all basins, wildfire, geomorphological, and hydrological parameters were the best predictors of beaver density. The Geo/Hydro/Fire model performed best (pseudo $R^2 = 0.88$, AICc

= 312.6, w_i = 0.81), followed by Geo/Fire model (pseudo R^2 = 0.86, AICc = 315.5, w_i = 0.19). In burned valley bottoms, the top selected models remained the same: the Geo/Hydro/Fire model performed best (pseudo R^2 = 0.83, AICc = 312.6, w_i = 0.81), followed by Geo/Fire model (pseudo R^2 = 0.86, AICc = 315.5, w_i = 0.19). However, in unburned valley bottoms, models explained less variability in beaver density; the Geo/Veg model was the top selected model (pseudo R^2 = 0.33, AICc = 771.2, w_i = 0.87), followed by Geo/Hydro/Veg (pseudo R^2 = 0.34, AICc = 776.4, w_i = 0.06) and Veg (pseudo R^2 = 0.20, AICc = 776.9, w_i = 0.05).

Model averaging highlighted key predictors of beaver density: across all valley bottoms beaver pond density was negatively associated with floodplain width, drainage area, and mean annual discharge. Beaver pond density was positively related to stream width, stream power, and stream sinuosity. Pond density was positively associated with percent severe burn, but negatively with percent moderate burn. Burned valley bottoms had the same set of significant predictors. In unburned valley bottoms, beaver density was negatively associated with drainage area, elevation, and vegetation parameters (Table 1.3, Figure 1.5).

Beaver effects on fish dispersal— Beaver density in each HUC varied between 0.2 to 137.3 ponds/km², with a mean density of 23.6 ± 26.5 SD ponds/km². Across the study area, there was a total of 4,525,597 km of potential fish habitat, and it was reduced by 1.1% at an 80% POP, 6.2% at a 50% POP, and 11.5% at a 20% POP (Table 1.4). However, in one river basin, the AFH_{20} was 19.6% less than the PFH, a loss of 177,548 km of stream habitat (Table 1.4). At a local level, beaver impacts were occasionally more severe (e.g., Figure 1.3), and some tributaries lost up to 64.5% (34,539 km) of habitat at a 20% POP.

DISCUSSION

We assessed the effects of wildfire and environmental characteristics on beaver density and distribution in Interior Alaska and simulated the effect of beavers on fish dispersal across a range of beaver dam density and stream flow conditions. We found clear linkages between beaver density, wildfire, and geomorphological and hydrological conditions, and found that beavers have the potential to substantially reduce tributary habitat availability for grayling, especially during low water conditions. Due to their role as ecosystem engineers, beaver abundance and related habitat modification is an important factor influencing fisheries resilience, and beaver activity should be closely monitored alongside disturbances and fish distributions.

Beaver relationships with wildfire— Wildfire was a key predictor of beaver density in Interior Alaska. Surprisingly, the time since the last burn (years) was not an important predictor of beaver density in any model combination. We believe this is due to relatively low variability of wildfire timing across the study area, when 44.6% of fires occurred in 2004, and 57.6% occurred since 2003, therefore the burn scars and their effects were relatively homogenous across the study area. There may also be interactions between burn severity and time since the last burn for which our models did not account. For example, a recent moderate burn might have similar successional status to an older severe burn. We would expect, given broader variability in time since the last burn, that it would be an important predictor for beaver density. The percentage of valley bottom that was burned also did not have a significant effect on the models. However, when parsed by burn severity, percent burn severity (severe and moderate) were important predictors across all models that included wildfire parameters. Percent severe burn had a negative relationship with beaver density, whereas percent moderate burn had a positive relationship with beaver density, and percent mild burn had a neutral and nonsignificant effect, which generally aligns with previous research (Fellers et al. 2004; Fellers and Osbourn 2009). Severe wildfires can burn through duff layers and significantly delay revegetation after the fire, reduce channel stability, and increase peak streamflow (Bisson et al. 2003; Shakesby and Doerr 2006; Dunham et al. 2007; Bixby et al. 2015), which has lasting effects on beaver populations (Fellers et al. 2004; Hood and Bayley 2008; Fellers and Osbourn 2009). However, moderate wildfires tend to stimulate post-burn revegetation with deciduous vegetation, including ideal beaver forage (Zasada et al. 1987; Johnstone et al. 2004; Cuevas-González et al. 2009; Chu et al. 2016; Gustafsson et al. 2020), which appears to stimulate rapid recolonization in this study area. It is also possible that wildfire reduced permafrost extent, causing increased groundwater connections which could favor beaver inhabitation, but our parameters did not capture this effect. Our hypothesized effects of wildfires on beaver habitat suitability generally align with the patterns in beaver density and burn severity in this study: high severity fires only burned an average of 3.75% (± 5.34 SD, maximum of 34.67%) of valley bottoms, and moderate fires burned 15.84% (± 13.82 SD) on average (max 50.61%). As a result, future increases in wildfire frequency and severity could affect future beaver distributions. Additionally, this suggests that, not only an increase in wildfire frequency, but changes in burn severity composition could affect future beaver distributions.

Geomorphological and hydrological parameters had less of an effect on beaver density than expected. However, drainage area, stream sinuosity, stream width, floodplain width, mean annual flow, and stream power were important predictors (Table 1.3). Drainage area and mean annual discharge had a negative relationship with beaver density. These relationships were generally expected because beavers tend to build dams in higher density in small streams because dams can persist longer in areas with lower flows and because small streams encourage dam building to provide refugia from predators, which is already available in larger rivers. Stream power was positively associated with beaver density, but only slightly, and this relationship may not be biologically significant. Stream width was positively associated with beaver density, whereas stream sinuosity and floodplain width were negatively associated with beaver density. This suggests a complex relationship between basin geomorphology and habitat selection by beavers, which may also be mediated by extrinsic factors such as wildfire history and vegetation. Previous studies have shown these parameters to be important predictors of beaver distribution (Dittbrenner et al. 2018). Stream gradient was surprisingly not a significant predictor of beaver density in our models, but was found to be important in other studies for predicting beaver distribution and their subsequent effects on fishes (Collen and Gibson 2000; Kemp et al. 2012; Macfarlane et al. 2017; Dittbrenner et al. 2018; Johnson-Bice et al. 2018). The stream gradients in this study were lower than those in the Western U.S., and overall homogenous across the study area (mean 1.6% ± 1.6 SD), which may explain why it was not an important predictor of beaver density in this study and why the negative effects on fish were more pronounced than in studies from high gradient streams (e.g., Bouwes et al. 2016; Pollock et al. 2022). Overall, we were surprised by the minor role that stream and basin geomorphology played in predicting beaver distribution which could be a result of 1) coarse scale: our models were developed off of 5-m DEMs, which is a moderate scale, but these attributes were then averaged by confluence-to-confluence stream reaches (valley bottom polygons), which could reduce their overall precision, and 2) a general homogeneity of habitats across the landscape, where the greatest variability in any given watershed is wildfire history.

Vegetation was a surprisingly poor predictor of beaver density. In fact, vegetation characteristics were only included in the AICc selected models when wildfire data were not available (e.g., unburned basins). Moreover, all vegetation parameters had a negative relationship with beaver pond density. It is possible that these relationships are due to survey bias (lower beaver pond detection in areas with higher vegetation density). Alternatively, there was some temporal mismatch between the source vegetation data and the rest of the data used in the study Specifically, the input dataset used for vegetation was derived from satellite imagery in 2015 (the closest time period available to our survey), whereas all other data in our study were developed off of imagery from 2017, which could cause some additional variation. Although, the overall vegetation composition was unlikely to have changed substantially during that time period; only a single wildfire occurred from 2015 to 2017 in the study area and it burned an insignificant area (< 1%) of a single valley bottom. We believe the primary reason that the vegetation model did not predict beaver pond density well is that it was developed from Landsat imagery (30-m^2 spatial resolution), which may not be detailed enough to represent fine-scale variation in vegetation to which beavers likely respond. Additionally, it is possible that landscape-scale vegetation homogeneity, or overall abundance of beaver forage, resulted in vegetation not being a limiting resource for beavers.

We were conservative with respect to beaver pond data included in our models; only 47% of the total detected ponds ("high confidence" ponds) identified during our surveys were considered in the models. Regardless, the general distribution and density of all ponds was consistent with the subset we used for modeling. Although we believe our results are accurate and useful, there are limitations to the remote sensing approach we used. First, we assumed that beaver pond density and the abundance of beavers was correlated, and that our covariates had more or less an identical effect on pond density and beaver abundance. Beavers can thrive in larger river systems and in areas with banks conducive to lodge construction without building dams, and therefore the meta-population dynamics and overall abundance is likely less affected by wildfire than shown in the study. However, this does not discount the important associations discovered between wildfire and beaver *damming*, and the clear implications for fish dispersal and habitat availability. Second, we assumed that historical and current beaver trapping was uniform across the study area due to lack of beaver harvest data. Finally, we assumed that dam detectability was consistent across the study area but acknowledge may be affected by vegetation cover and satellite image quality.

Beaver effects on fish dispersal— Beaver dams have the potential to substantially fragment tributary habitat and limit fish dispersal. We believe that we could have *underestimated* effects of beaver habitat fragmentation on grayling because 1) we were highly selective in the type and number of beaver ponds we included in the simulation (only 47% of all ponds surveyed), and 2) we did not account for proportional decreases in habitat use (e.g., after four dams at a 50% POP, only 6% of the population utilized that habitat, but we still counted it as "100% available for fish"). Additionally, it is important to note that dam density is not the sole predictor of fish habitat availability, but the position of beaver dams in the tributary (e.g., in the headwaters vs. near the terminus) had an important effect on fish dispersal and thus the absolute amount of available stream habitat (Figure 1.3, Figure 1.6). At a tributary scale, beaver-caused habitat fragmentation could disrupt important fish life history events like spawning, rearing, and migration to seasonal feeding habitats, which may attract attention from the public, user groups, and managers. In cases like this, beaver or dam removal may be necessary to preserve fish habitat and support public interest (Wuttig 2000, 2002; Taylor et al. 2010; von Finster 2019). Future research could consider the overlap between fishes and beaver habitat to understand these effects, and beaver removal, if justified, might focus on positions low in tributaries that impede the greatest amount of fish habitat. Although we did not account for them, additional site-level impacts from beaver habitat modification may affect fishes, such as increased sedimentation, deoxygenation, flow reduction, changes in forage availability/composition, and fish behavior (e.g., territoriality; Kemp et al. 2012; Johnson-Bice et al. 2018).

Although beaver effects on fish distributions at the tributary level could be extreme, these effects are moderated across an otherwise intact and connected landscape with a patchwork of beaver densities. Across the landscape in this study and various flow scenarios, beavers reduced grayling habitat availability from -1.1 (high water) to -11.5% (low water). We expect that mobile fishes like grayling could respond to beaver damming by occupying other tributaries, although in this case they were restricted to tributaries within their respective river basin (Figure 1.2), which could result in a significant overall reduction in fish habitat (Table 1.4). Although not the focus of this study, less mobile fishes (e.g., Slimy Sculpin *Cottus cognatus,* Burbot *Lota lota,* and whitefishes *Coregonidae* spp.) could also be substantially affected by beaver damming owing to their lower leaping abilities which could limit regular seasonal migrations. Other research suggests that fish communities and beaver dam impacts differ in lentic vs lotic habitats, although the relationships are still clearly mediated by flow (Brown and Fleener unpublished data). On occasion, even mobile fishes like grayling can become trapped in and around beaver ponds due to beaver damming and dewatering, which may lead to mass mortality unless pulses of high water provide a route for escape (W. Samuel *personal observation*). Although these events are a natural part of the ecosystem, managers may be interested in minimizing them in targeted areas (e.g., near development, important spawning habitat) by reducing beaver populations to support important species of cultural, commercial, or sport fishing interest (Avery 2002; Wuttig 2002;

Taylor et al. 2010; Niles et al. 2013; Malison et al. 2016; Johnson-Bice et al. 2018; von Finster 2019; Wolf et al. 2022).

The direction of effects of beavers on fishes and stream ecosystems are mixed in the literature (Kemp et al. 2012). Beavers have been shown to reverse stream incisement, increase groundwater connectivity and water storage, and moderate water temperatures, creating habitat heterogeneity and diverse thermal refugia, and increased fish growth and diversity (Collen and Gibson 2000; Schlosser and Kallemeyn 2000; Kemp et al. 2012; Malison et al. 2014, 2015; Pollock et al. 2014; Weber et al. 2014, 2017; Bouwes et al. 2016; Touihri et al. 2018; Brazier et al. 2021). Many of these effects, while still notable, may be more pronounced because the respective study ecosystem baselines were initially compromised (e.g., incised streams, developed/degraded watersheds). This presents a dichotomy in which beaver reintroductions or beaver removal may be appropriate depending on the circumstance and habitat conditions in each region. This study, in its nature as a remote sensing survey, could not investigate these positive effects, which are measured at an individual and site scale. Other studies in Alaska found increased Pacific salmon (*Oncorhynchus* spp.) smolt growth rates/size in beaver ponds, but they were less numerous overall, and the increased size did not reduce mortality enough to offset the negative effects of beavers (Malison et al. 2014, 2015, 2016). Emerging research in Canada shows similar concerns of beaver-caused habitat fragmentation, and subsequent limiting of fish dispersal (von Finster 2019). Further research is needed to assess the potential trade-offs of beaver-caused habitat modifications at various spatial scales and careful consideration should be made about how to contextualize beaver management for each region.

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FIGURES

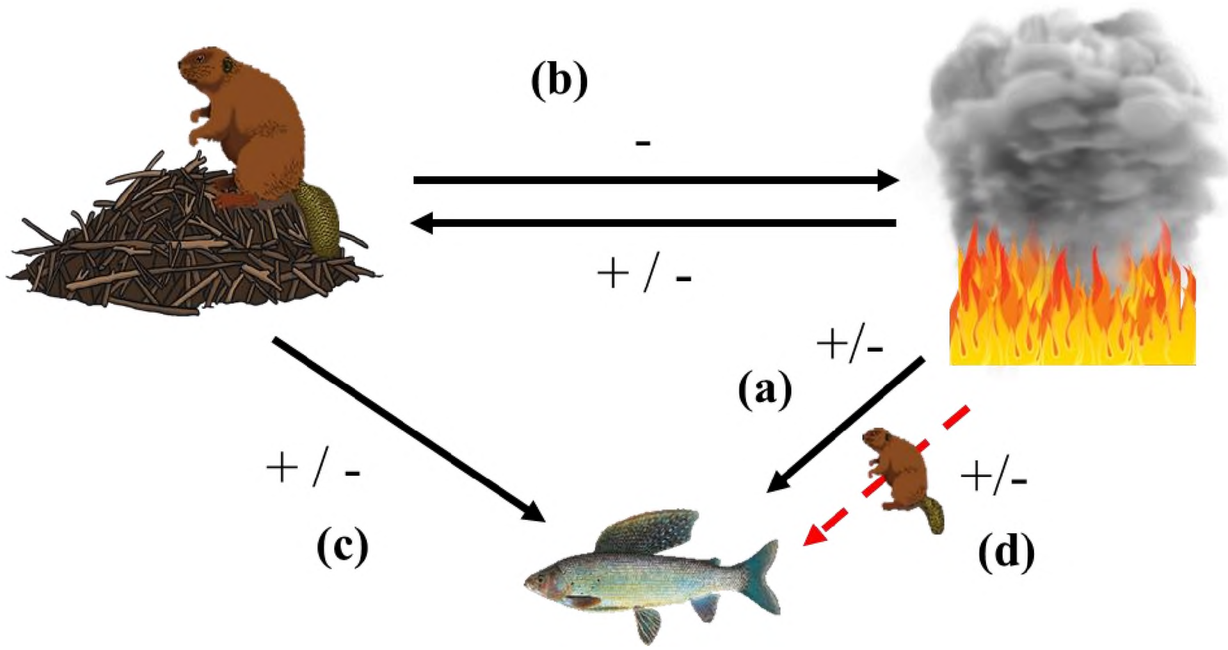

Figure 1.1. A conceptual model illustrating hypothesized interactions among wildfire, North American Beavers, and Arctic Grayling in a boreal ecosystem. Solid arrows denote direct relationships/effects and red dashed arrows denote indirect effects. A “+” indicates a hypothesized positive influence, “-” indicates a hypothesized negative influence. (A) Wildfires have numerous effects on fish and aquatic habitat. (B) Beavers and wildfire may have a negative feedback (stabilizing) effect. (C) Beavers may maintain productive aquatic habitat and support Arctic Grayling or could fragment its habitat and prevent fish dispersal. (D) Through their effects on fishes (C) and their interactions with wildfire (B), beavers have the potential to magnify or reduce the effects of wildfire on fishes.

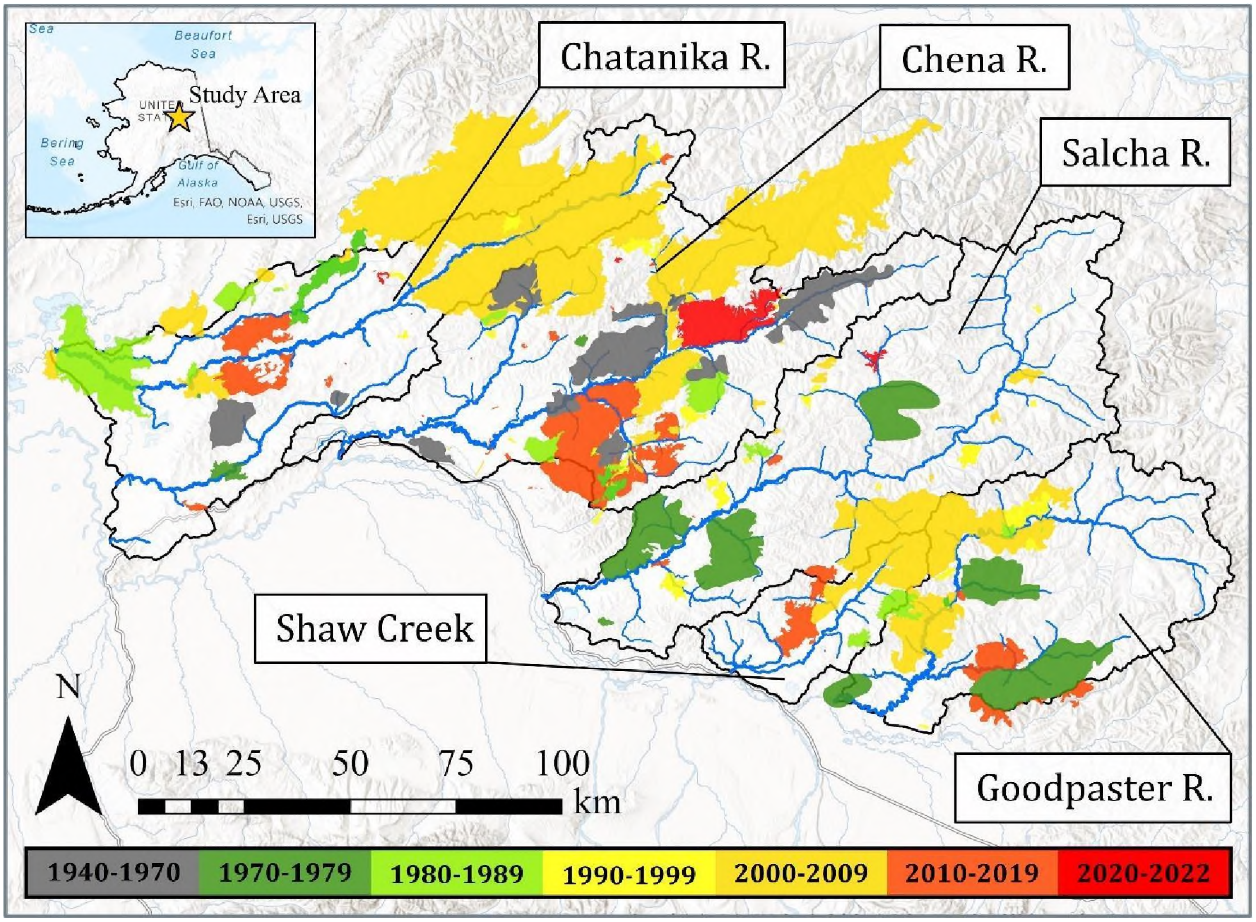

Figure 1.2. Location of the study area in Alaska, U.S.A. (inset), rivers basins, and wildfire history. Colored polygons represent historical fire perimeters (MTBS 2022). Blue lines represent major rivers and tributaries, and black lines represent the drainages for major rivers.

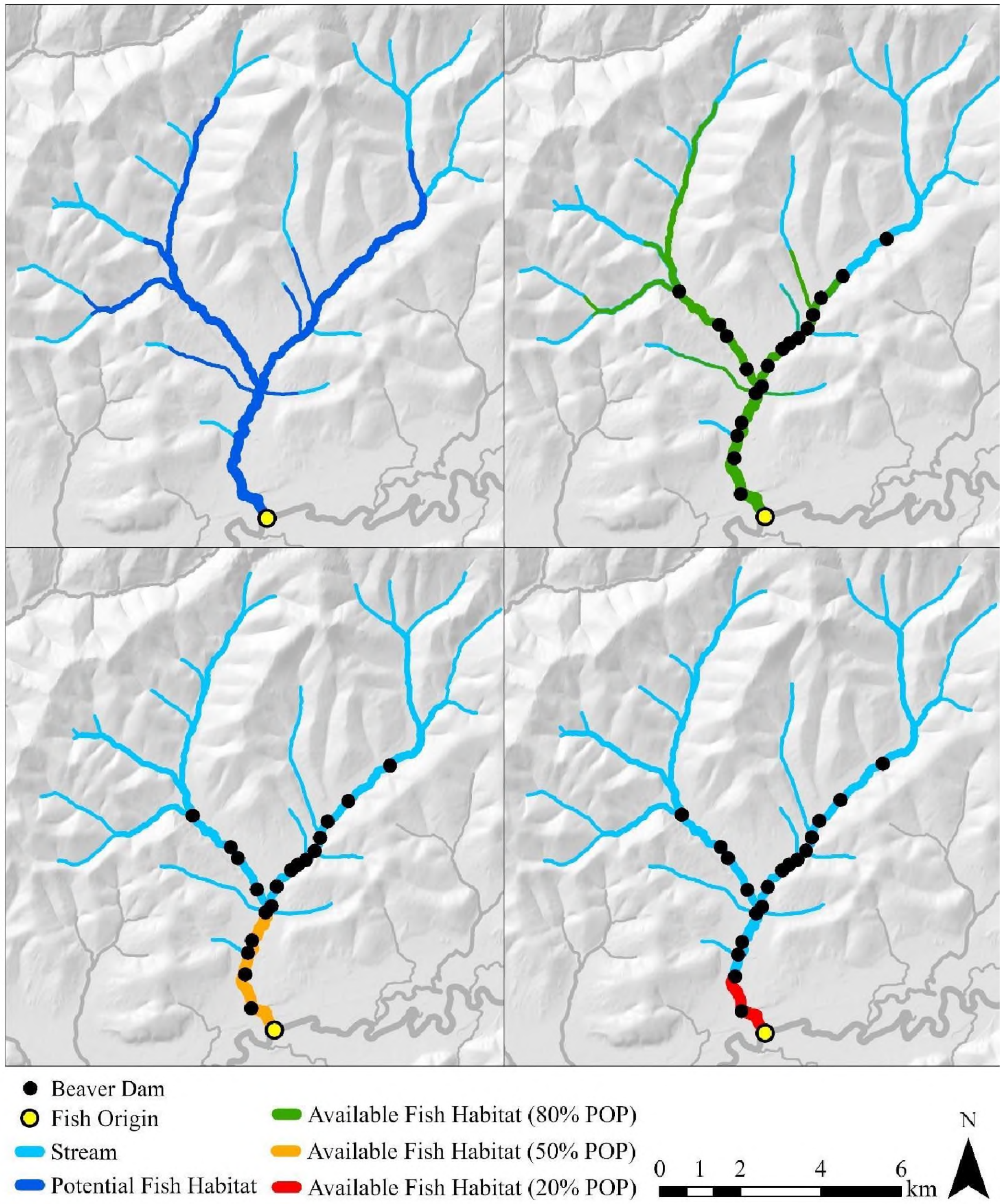

Figure 1.3. Example of how North American Beaver dams could reduce fish habitat under various flow conditions. Black circles are beaver dams. Red, orange, and green lines correspond to the assigned probability of passage (POP) in a low (20% POP), normal (50% POP), and high-water (80% POP) scenario. In a beaver-affected tributary, the available fish habitat in high water conditions is substantially greater than that of a normal or low water year, and under all flows, beaver dams reduce habitat availability to some extent.

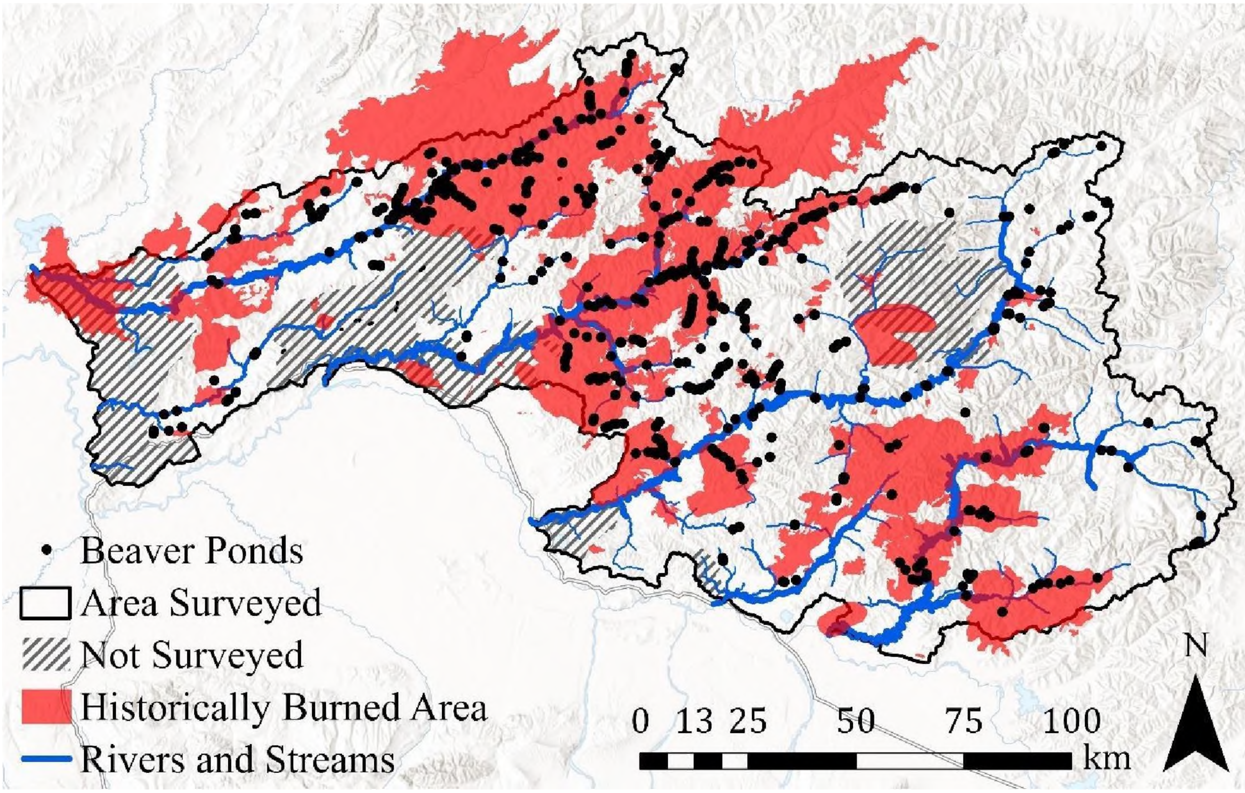

Figure 1.4. Observed North American Beaver pond distribution in Interior Alaska. Black points represent potential beaver ponds (n=890) located using satellite imagery surveys.

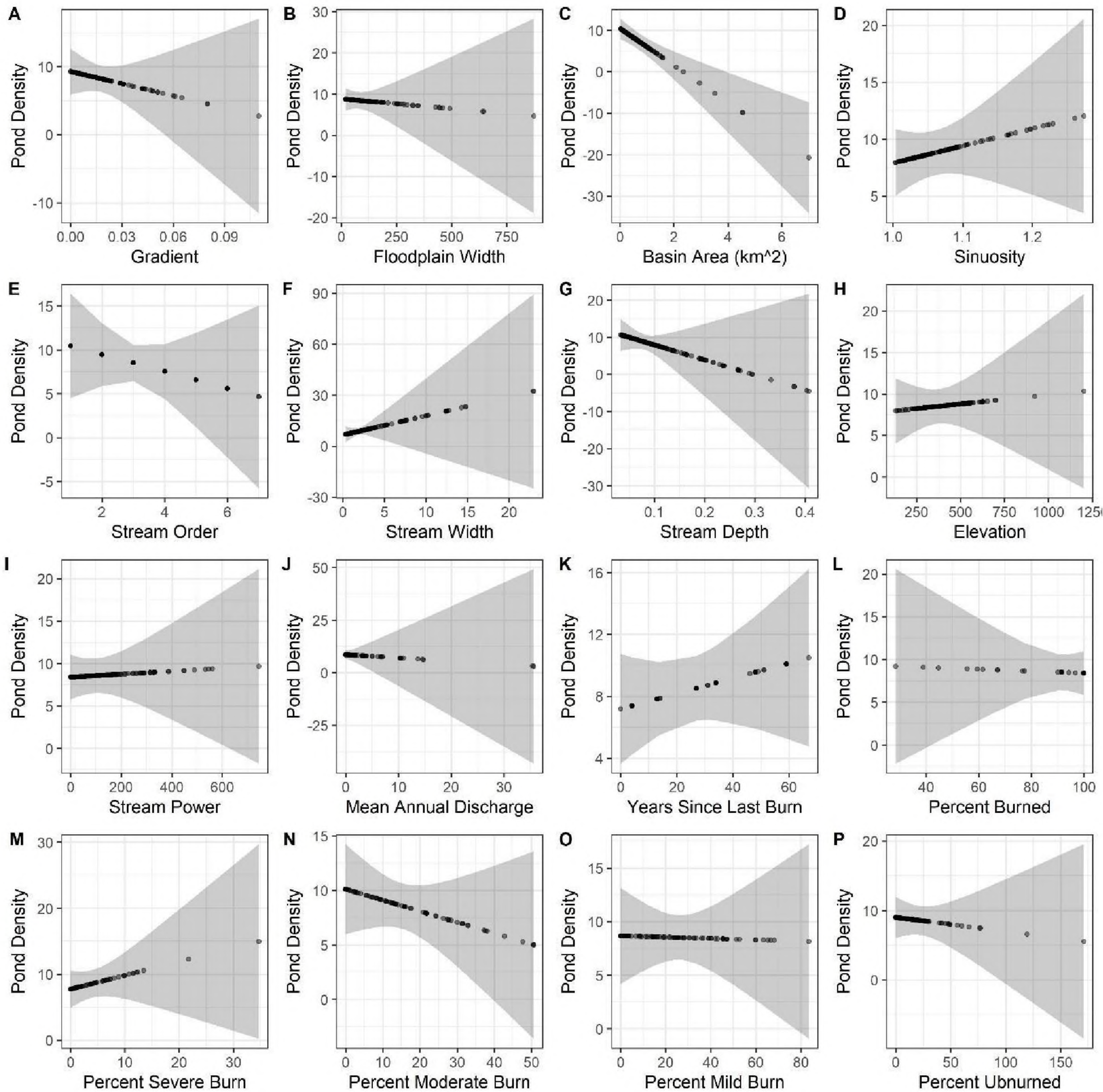

Figure 1.5. Model-predicted relationships between North American Beaver pond density and environmental covariates in Interior Alaska. Points represent the relationship of environmental data with beavers summarized at the valley bottom scale and predicted by predicted by the top performing model using AICc (Geo/Hydro/Fire; Table 1.2), and grey polygons are ± 1 standard error.

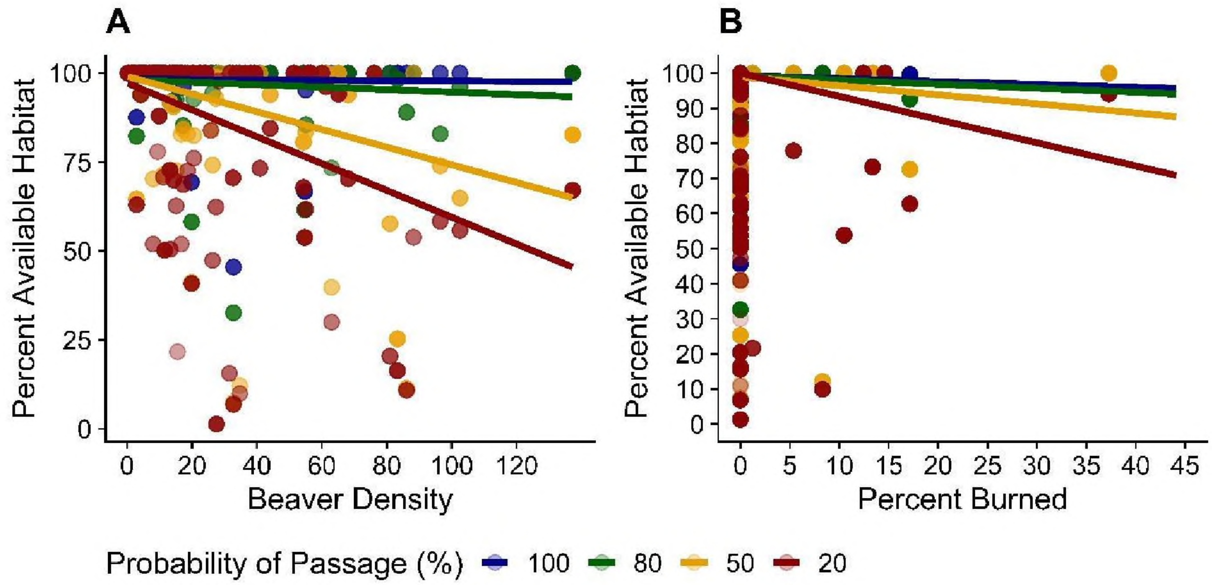

Figure 1.6. Relationship between the percentage of available fish habitat and **(A)** beaver density and **(B)** percent burned by wildfire in Interior Alaska. Probability of fish passage (POP) rates (a proxy for flow) are presented by flow levels: Blue = 100% probability of passage (no beaver dams), green = a high flow scenario (80% POP), orange = normal flow scenario (50% POP), and red = low flow scenario (20% POP).

TABLES

Category	Parameter	Abbreviation (Table 2)	Hypothesized Relationship with Beavers	Supporting Literature	Covarjate Dataset
Geomorphology	Stream Gradient (mean)	GRA	+/-	a, b, d	i
	Floodplain Width	FP_WID	+	a	i
	Drainage Area	AREA	+	a	i
	Sinuosity	SIN	+	c	i
	Stream Order	STRM_ORD	-	NA	i
	Stream Width	WIDTH	+	a	i
	Stream Depth	DEPTH	-	a	i
	Elevation	ELV	+/-	NA	i
Hydrology	Stream Power	STRM_PWR	+/-	a, b, d	i
	Mean Annual Discharge	MAQ	+/-	NA	i
Wildfire	Time Since Last Burn (years)	TSLB	+	g	j
	Percent Burned (RCA, VB)	PER_BURN	-	e, f	j
	Percent Severe Burn	PSB	-	e, f	j
	Percent Moderate Burn	PMoB	+	e, f	j
	Percent Mild Burn	PMiB	+	e, f	j
	Percent No Burn	PNB	+	e, f	j
Vegetation	Percent Woody Cover	PWC	+	a, b, d	k
	Percent Conifer Tree	CON_TREE	-	d, h	k
	Percent Broadleaf	BROAD_TREE	+	b, d, h	k
	Percent Deciduous Shrub	DECID_SHRUI	+	a, b, d, h	k
	Percent Evergreen shrub	EVER_SHRUB	-	d, h	k
	Percent Forb	FORB	-	d, h	k
	Percent Graminoid	GRAM	-	d, h	k
	Percent Lichen	LICHEN	-	d, h	k

Supporting literature: [a]Dittbrenner et al. 2018, [b]MacFarlane et al. 2007, [c]Rosell and Campbell-Palmer 2022, [d]Stoll and Wesbrook 2020, [e]Feller and Osbourn 2009, [f]Fellers et al. 2004, [g]Hood et al. 2007, [h]Jonestone and

Dataset: [i]Benda et al. 2007, [j]MTBS 2022, [k]McCander et al. 2022

Table 1.1.— List of the parameters used for modeling beaver pond density throughout Interior Alaska, hypothesized relationship with beavers, supporting literature, and data sources. The categories "geomorphology" and "hydrology" are occasionally referred to as "NetMap" parameters when used in tandem, due to their common data source.

Model Name	Model	Mean Pseudo R^2	AICc	AICc weight
Global	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + STRM_PWR + MAQ + PER_BURN + TSLB + PSB + PMoB + PMiB + PNB + PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.91	338.0	0.00
NetMap	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + STRM_PWR + MAQ	0.31	1379.6	0.00
Fire	PER_BURN + TSLB + PSB + PMoB + PMiB + PNB	0.75	324.1	0.00
Veg	PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.19	1445.4	0.00
Dredge	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + STRM_PWR	0.32	1373.0	0.00
NetMap (Geo Hydro), Fire	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + STRM_PWR + MAQ + PER_BURN + TSLB + PSB + PMoB + PMiB + PNB	**0.88**	**312.6**	**0.81**
NetMap (Geo Hydro), Veg	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + STRM_PWR + MAQ + PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.39	1357.6	0.00
Veg, Fire	PER_BURN + TSLB + PSB + PMoB + PMiB + PNB + PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.83	326.6	0.00
Geo, Fire	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + PER_BURN + TSLB + PSB + PMoB + PMiB + PNB	**0.86**	**315.5**	**0.19**
Hydro, Fire	STRM_PWR + MAQ + PER_BURN + TSLB + PSB + PMoB + PMiB + PNB	0.76	326.9	0.00
Geo, Veg	GRA + FP_WID + AREA + SIN + STRM_ORD + WIDTH + DEPTH + ELV + PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.39	1355.6	0.00
Hydro, Veg	STRM_PWR + MAQ + PWC + CON_TREE + BROAD_TREE + DECID_SHRUB + EVER_SHRUB + FORB + GRAM + LICHEN	0.20	1447.9	0.00

Table 1.2.— Various model combinations used for inputs for model averaging to determine what parameters are the most important for predicting beaver pond density in Interior Alaska. Parameter abbreviations in Table 1. Mean Pseudo R2 is the mean of McFadden, Cox and Snell, Nagelkerke, and Efron R2. AICc is the Akaike information criterion corrected for a small sample size, and AICc weight is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed. Psuedo R^2, AICc, and AICc weight was calculated for models trained on the full dataset, models trained with only drainages that had wildfire history ("burned only"), and models trained with catchments that did not have wildfire history ("unburned only"). Bold values indicate that the AICc weight is ≥ 0.05, and the model was included in model averaging (Table 1.3). Bold values represent the models that had a AICc weight > 0.5.

Mean Pseudo R^2 (burned only)	AICc (burned only)	AICc weight (burned only)	Mean Pseudo R^2 (unburned only)	AICc (unburned only)	AICc weight (unburned only)
0.87	338.0	0.00	--	--	--
0.56	576.1	0.00	0.16	786.9	0.00
0.69	324.1	0.00	--	--	--
0.38	344.8	0.00	**0.20**	**776.9**	**0.05**
0.54	576.7	0.00	0.14	784.2	0.00
0.83	**312.6**	**0.81**	--	--	--
0.65	567.5	0.00	**0.34**	**776.4**	**0.06**
0.78	329.6	0.00	--	--	--
0.81	**315.5**	**0.19**	--	--	--
0.71	326.9	0.00	--	--	--
0.62	574.7	0.00	**0.33**	**771.2**	**0.87**
0.38	661.2	0.00	0.21	780.4	0.01

Table 1.2. cont.

Parameter	Model Averaged Estimate	Unconditional Standard Error	90% Unconditional Confidence Interval	Model Averaged Estimate (Burned only)	Unconditional Standard Error (Burned only)	90% Unconditional Confidence Interval (Burned only)
Geomorphology						
Stream gradient (mean)	-58.95	99.28	-222.25, 104.35	-58.95	99.28	-222.25, 104.35
Floodplain width	**-0.02**	**0.02**	**-0.05, 0.00**	**-0.02**	**0.02**	**-0.05, 0.00**
Drainage area	**-8.09**	**2.29**	**-11.87, -4.32**	**-8.09**	**2.29**	**-11.87, -4.32**
Sinuosity	**-49.07**	**21.91**	**-85.11, -13.03**	**-49.07**	**21.91**	**-85.11, -13.03**
Stream order	0.11	1.06	-1.64, 1.85	-0.11	1.06	-1.64, 1.85
Stream width	**5.59**	**3.36**	**0.06, 11.11**	**5.59**	**3.36**	**0.06, 11.11**
Stream depth	-101.18	68.36	-213.62, 11.26	-101.18	68.36	-213.62, 11.26
Elevation	0.00	0.01	-0.02, 0.01	0.01	0.01	-0.02, 0.01
Hydrology						
Stream power	**0.01**	**0.01**	**0.00, 0.03**	**0.01**	**0.01**	**0.00, 0.03**
Mean annual discharge	**-4.71**	**2.26**	**-8.43, -0.98**	**-4.71**	**2.26**	**-8.43, -0.99**
Wildfire						
Percent burned	-0.03	0.03	-0.09, 0.02	-0.03	0.03	-0.09, 0.01
Time since last burn	0.33	0.23	-0.05, 0.70	0.33	0.23	-0.04, 0.7
Percent severe burn	**0.38**	**0.11**	**0.20, 0.57**	**0.38**	**0.11**	**0.02, 0.57**
Percent moderate burn	**-0.18**	**0.06**	**-0.27, -0.08**	**-0.18**	**0.06**	**-0.27, -0.08**
Percent mild burn	0.04	0.05	-0.04, 0.12	0.04	0.05	-0.04, 0.12
Percent no burn	-0.02	0.02	-0.05, 0.02	-0.02	0.02	-0.05, 0.02
Vegetation						
Percent woody cover	--	--	--	--	--	--
Percent conifer	--	--	--	--	--	--
Percent broadleaf tree	--	--	--	--	--	--
Percent deciduous shrub	--	--	--	--	--	--
Percent evergreen shrub	--	--	--	--	--	--
Percent forb	--	--	--	--	--	--
Percent gramminoid	--	--	--	--	--	--
Percent lichen	--	--	--	--	--	--

Table 1.3.— Model averaged estimates for each parameter which affects beaver pond density in Interior Alaska. Model averaged estimates were generated only using the top ranked models using AICc (e.g., AICc weight ≥ 0.05) for each dataset. "--" indicates the parameters were not suggested in any of the top ranked models using AICc.

Model Averaged Estimate (Unurned only)	**Unconditional Standard Error (Unurned only)**	**90% Unconditional Confidence Interval (Unurned only)**
11.80	90.59	-160.81, 137.21
0.00	0.02	-0.03, 0.02
-3.38	**1.24**	**-5.41, -1.34**
32.84	22.59	-4.27, 69.95
-0.20	1.59	-2.81, 2.41
0.43	0.95	-1.13, 2.00
-42.69	33.47	-97.74, 12.36
-0.02	**0.01**	**-0.04, -0.01**
0	0.01	-0.02, 0.02
-0.55	0.71	-1.72, 0.61
--	--	--
--	--	--
--	--	--
--	--	--
--	--	--
--	--	--
-0.08	0.17	-0.36, 0.19
-0.87	**0.29**	**-1.35, -0.39**
-0.65	**0.26**	**-1.12, -0.18**
-0.92	**0.33**	**-1.47, -0.37**
0.64	0.75	-0.59, 1.87
-1.98	**1.11**	**-3.8, -0.16**
-1.73	**0.46**	**-2.48, -0.97**
-3.68	**1.25**	**-5.74, -1.63**

Table 1.3 cont.

River Basin	Potential Fish Habitat (km)	Available Fish Habitat (80% POP; km)	Percent of Habitat Reduced (80% POP)	Available Fish Habitat (50% POP; km)	Percent of Habitat Reduced (50% POP)	Available Fish Habitat (20% POP; km)	Percent of Habitat Reduced (20% POP)
Chatanika River	932,906	927,253	-0.6%	812,877	-12.9%	749,705	-19.6%
Chena River	1,368,448	1,323,765	-3.3%	1,239,530	-9.4%	1,181,095	-13.7%
Salcha River	1,139,103	1,138,513	-0.1%	1,120,476	-1.6%	1,040,521	-8.7%
Goodpaster River	607,049	607,047	0.0%	600,717	-1.0%	591,138	-2.6%
Shaw Creek	478,091	477,338	-0.2%	471,405	-1.4%	443,316	-7.3%
Total	**4,525,597**	**4,473,916**	**-1.1%**	**4,245,005**	**-6.2%**	**4,005,775**	**-11.5%**

Table 1.4.— Summaries of the linear length of potential fish habitat (km) for each river basin, and the available fish habitat (km) under different flow scenarios/probabilities of passage in five river basins in Interior Alaska. Difference in available habitat also shown as a percent for each flow scenario.

Chapter 2: Assessing beaver effects on fish distribution in a fire-dominated ecosystem using eDNA[2]

ABSTRACT

Arctic Grayling (*Thymallus arcticus*) experience a mosaic of disturbances, including wildfires, floods, erosion, and beaver modifications to their habitat. Wildfires and beavers interact with each other and have the potential to mediate fish habitat suitability and availability. We used a combination of traditional *in situ* fish sampling (angling and electrofishing) and environmental DNA (eDNA) to assess the effects of beavers, wildfire, and habitat characteristics on Arctic Grayling (*Thymallus arcticus*) abundance and distribution in Interior Alaska during summer 2022. We sampled 10 tributaries multiple times each (total of n = 26) for Arctic Grayling abundance and eDNA concentration and collected environmental parameters during each sampling event. We then sampled an additional 52 tributaries (once each) for eDNA to estimate relative Arctic Grayling abundance across the landscape. eDNA samples collected longitudinally within a tributary suggested that a sample near the bottom of the tributary was representative of fish abundance throughout the network. Overall, there was a moderate correlation (Generalized Linear Model: pseudo $R^2 = 0.45$) between eDNA concentration and catch per unit effort when environmental parameters such as water temperature (°C), stream velocity (m/s), turbidity, and day of year, and number of liters filtered were included. We then fit an N-mixture model across 62 sites using predictors that affect eDNA detection and abundance (concentration). Stream geomorphology, hydrology, wildfire, and beaver parameters were all important predictors of Arctic Grayling eDNA concentration. Generally, larger streams had

[2]Samuel, W.T., J.A. Falke, K.D. Tape, A.C. Seitz, S.K. Panda. Assessing beaver effects on fish distribution in a fire-dominated ecosystem using eDNA. Formatted for *Transactions of the American Fisheries Society*.

higher eDNA concentration (fish abundance), and stream gradient and mean annual discharge were positively associated with eDNA concentration, likely due to a combination of fish habitat suitability and increased eDNA transport. Wildfires had mixed effects on eDNA concentration but were overall negative. In the raw data, beaver dam density had a negative logarithmic relationship with eDNA concentration, however, in the N-mixture model it was positive. This suggests that, although beaver dams can restrict fish dispersal/abundance, the effects are dependent on habitat factors like stream gradient and mean annual discharge and historical burn status.

INTRODUCTION

Arctic Grayling (hereafter "grayling") are a widespread boreal fish species that occur from western Russia to Hudson Bay, Canada (Northcote 1995). Grayling have important ecological, recreational, and subsistence roles to Alaskan people (Alaska Department of Fish and Game (ADFG) 2021). They are widespread across most of Alaska and utilized by Indigenous and rural individuals as a portion of subsistence harvests (ADFG 2021). As a sport fish, grayling are valued by tourists and locals by being easy to catch and abundant, and support sportfishing guide operations statewide. In addition, they are ubiquitous throughout the region, making them a useful sentinel species to evaluate the conditions of aquatic systems (Northcote 1995). In Interior Alaska, the species overwinters in the lower reaches of large rivers, migrates to (often groundwater-fed) spawning habitats in the spring, and moves to summer feeding areas located throughout boreal river networks (Armstrong 1986). During the ice-free season, adults and sub-adults migrate to occupy the middle to upstream reaches of tributaries for feeding (Hughes and Reynolds 1994). Studies have found benefits in growth when Arctic Grayling are able to access headwater streams, suggesting that local habitat conditions and stream connectivity are important for individual and population productivity (Hughes and Dill 1990; Hughes 1992, 1998, 2000; Hughes and Reynolds 1994). However, the effects of wildfire and beaver activity, common disturbances in Interior Alaska, on grayling distribution and abundance are poorly understood.

Arctic Grayling in the boreal region experience a mosaic of cyclical disturbance (Resh et al. 1988; Reeves et al. 1995) including wildfires which are among the most substantial disturbances due to their strong effects on community succession and stream productivity (Rowe and Scotter 1973; Shakesby and Doerr 2006; Johnstone et al. 2010; Kasischke and Stocks 2012). Additionally, wildfires have been increasing in size, severity, and frequency in recent decades in the boreal forest ecosystem in North America, raising concerns about effects on community ecology (Flannigan et al. 2005; Girardin and Mudelsee 2008; Balshi et al. 2009). Generally, wildfires reset terrestrial plant communities, create erosion and reduce channel stability, and warm land surface and stream temperatures (Helvey 1980; Gresswell 1999; Dunham et al. 2007; Bixby et al. 2015; Schoen et al., *in prep*). Wildfires can stimulate biological productivity by releasing key nutrients (carbon, nitrogen, phosphorus) into streams, which has been linked to increased macroinvertebrate abundance and diversity (Minshall 2003; Malison and Baxter 2010a, 2010b; Jackson et al. 2012, Hinkle et al. *in prep*). Across North America, wildfire has been shown to affect fishes by increasing water temperatures which can either enhance growth or stress fishes, increase abundance and diversity of invertebrate drift and large wood habitat, reduce stream connectivity, change inputs of chemicals including heavy metals, increase turbidity which can affect drift feeding efficiency, and more (Bisson et al. 2003; Dunham et al. 2003, 2007; Neville et al. 2009; Luce et al. 2012; Neuswanger et al. 2014; Falke et al. 2015; Jager et al. 2021). The response and related resilience of fishes to wildfire depends on the fish's mobility, life history strategies (e.g., a "stayer" or a "mover"), and the connectivity of the stream network (Falke et al. 2015; Jager et al. 2021). It is unclear how wildfire affects freshwater fishes in the boreal region, although emerging research shows that grayling are strong colonizers of burned areas, and that burned streams are associated with higher fish biomass and diversity (Hinkle et al. *in prep*).

Wildfires also have indirect effects on stream habitats and fishes via interactions with semi-aquatic ecosystem engineers like the North American Beaver (*Castor canadensis*), hereafter referred to as "beavers" (Chapter 1). Wildfires have been shown to affect beaver populations in the Western U.S. and Canada, and severe wildfires can have adverse effects on beaver populations (Fellers et al. 2004; Hood et al. 2007; Fellers and Osbourn 2009). In Interior Alaska, wildfires are positively associated with beaver density, likely due to the increase in deciduous vegetation associated with wildfires, which is ideal beaver forage, and other geomorphological changes to streams such as diminished permafrost extent (Chapter 1). However, beavers can fragment streams and restrict fish dispersal, especially during low water conditions, which could homogenize river networks and reduce population resilience (Chapter 1; Wuttig 2000, 2002; Malison et al. 2016). Alternatively, beavers have been shown to buffer streams from wildfire effects in dryland ecosystems by preserving riparian vegetation (Fairfax and Whittle 2020), which could benefit stream fishes. Additionally, beaver-affected habitat can offer potential benefits such as increased individual growth and species diversity (Collen and Gibson 2000; Kemp et al. 2012; Malison et al. 2014, 2015). These effects vary across sites and biomes, and it is challenging to assess the cumulative impacts of beavers and wildfires at scale.

In situ fish sampling across large regions can be challenging, especially in remote areas with limited access. Environmental DNA (eDNA) is rapidly emerging as a tool for aquatic ecology, primarily for assessing species distribution and community composition. Recently, eDNA has been used to estimate fish abundance and biomass (Yates et al. 2019; Rourke et al. 2022), and studies show promising results for this application (Di et al. 2020; Yates et al. 2020, 2021, 2022; Coyne 2021). However, correlations between fish abundance/biomass and eDNA concentration can vary greatly (R^2 ranging from 0.08 to 0.96; Takahara et al. 2012; Doi et al. 2015; Lacoursière-Roussel et al. 2016; Baldigo et al. 2017; Klobucar et al. 2017; Yates et al. 2019, 2020; Coyne 2021; Fukaya et al. 2021; Sepulveda et al. 2021; Spear et al. 2021; Rourke et al. 2022), and may be dependent on habitat type (e.g., lotic vs lentic systems). In streams, eDNA removal (degradation *and* deposition of eDNA) is a key factor in the relationship between eDNA concentration and fish abundance. eDNA removal is affected by variety of factors, including water temperature, turbidity, eDNA particle size, pH, ultraviolet radiation, stream velocity, microbial activity, habitat structure, and other unknown factors (Eichmiller et al. 2016; Lacoursière-Roussel et al. 2016; Tsuji et al. 2017; Harrison et al. 2019; Jo et al. 2019; Saito and Doi 2021; Sepulveda et al. 2021; Lamb et al. 2022; Rourke et al. 2022; Brandão-Dias et al. 2023). eDNA removal also affects the distance in a stream that eDNA can be transported, which varies from 100 m to 100 km depending on species abundance and environmental factors (Jane et al. 2015; Sansom and Sassoubre 2017; Shogren et al. 2017; Tillotson et al. 2018; Wood et al. 2021; Cantera et al. 2022; Jo and Yamanaka 2022). It is important to test the relationships between eDNA and fish abundance across a gradient of local conditions to assess the feasibility of eDNA as a tool for research and management.

The overall goal of this study was to understand how wildfire, beaver activity, and stream characteristics interact to affect grayling distribution and relative abundance in Interior Alaska tributary streams. Our specific objectives were to 1) test the efficacy of eDNA as a method to compare the relative abundance of Arctic Grayling in Interior Alaska tributary streams, and 2) understand how stream geomorphology, hydrology, wildfire, and beavers affect the distribution and relative abundance of Arctic Grayling. We expected that eDNA concentration would be a useful predictor of Arctic Grayling abundance (catch per unit effort). Further, we expected stream attributes like mean annual flow to have a positive effect on grayling abundance, stream gradient to have a dome shaped relationship, wildfire to have a positive effect, and beaver dams to negatively affect Arctic Grayling abundance due to their effects on habitat suitability and accessibility (Chapter 1).

METHODS

Study Area—This study was conducted in five river systems in Interior Alaska: the Chatanika (drainage area = 4,460 km^2), Chena (5,350 km^2), Salcha (5,740 km^2), and Goodpaster rivers (4,120 km^2), and Shaw Creek (1041 km^2; Figure 2.1). Within this approximately 21,000 km^2 extent, about one quarter burned from 1984 to 2022 (Figure 2.1). Widespread fires occurred in 1990, 2004, 2009, 2011, 2015, 2019, and 2022; 2004 was the largest fire year on record in Alaska with over 27,200 km^2 burned statewide (Wendler et al. 2011). This landscape is covered in a patchy distribution of deciduous and coniferous forests, primarily Paper Birch (*Betula papyrifera*) and spruce (*Picea* spp.), respectively. Forest composition and successional trajectories are heavily affected by wildfire history and discontinuous permafrost (Nawrocki et al. 2021; Macander et al. 2022), where regrowth after wildfires tends to be deciduous trees (Chapter 1), and areas with permafrost are associated with coniferous trees. Streams in the study area are mostly fed via a combination of snowmelt, rain, and groundwater, and vary from slow-flowing wetlands to clear, fast-flowing streams. The tributaries considered in this study (1st–5th order) have catchment areas between 0.34 and 98.4 km^2 and discharges ranging between 0.006 and 35 m^3/s, while the mainstem rivers have discharges ranging between 30 and 300 m^3/s depending on the season and location. Peak flows typically occur in late May and early June (due to snowmelt) and August (rainy season). Some fish and eDNA sampling for this study occurred within Caribou Poker Creek (CPC) Long Term Ecological Research site (Figure 2.1), which is a 107-km^2 catchment that had significant wildfires in 1999 and 2004 and contains beaver and grayling populations. Caribou Poker Creek was identified as an ideal study site that is representative of many streams in Interior Alaska but was relatively accessible which was necessary to address the objectives in this study.

Much of the study area is difficult to access by people. Beavers were historically trapped in Alaska at varying rates beginning in the 1600s (Obbard et al. 1987); however, detailed trapping records do not exist aside from a few recent years (1989–1995; Alaska Department of Fish and Game). Since then, trapper survey questionnaires have been used to estimate population trends and beaver populations in the study area are considered stable (Bogle 2021). For the purposes of this study, we assumed that beaver populations in our study area have recovered from historical trapping, were near or at carrying capacity, and that variability in density/distributions was due to non-human influences. Further, we assumed that the overall density of beavers/beaver dams in tributary watersheds remained similar to the data collected using satellite imagery from 2017 (Chapter 1).

Data Collection— We collected two sets of eDNA samples during summer 2022 to develop a model to predict grayling abundance from eDNA and assess grayling distribution and abundance in tributary streams with varying levels of beaver and wildfire disturbance. First we sampled eDNA at 10 sites from 1 to 3 times each (Figure 2.1) and sampled grayling abundance immediately thereafter. Four of the 10 sites were located longitudinally in Caribou-Poker Creek where we assessed accumulation of eDNA throughout the stream network. Next, we sampled 52 additional streams during single visits to assess the broader patterns of Arctic Grayling distribution and abundance (Figure 2.1).

Data Collection: Fish Sampling— Grayling were sampled in stream reaches that varied from 250 to 1000 m in length. Each reach was sampled using a combination of two-pass angling and electrofishing. Effort was recorded, including the number of minutes each person spent angling and the number of minutes electrofished, and each reach was measured for bank-full width (the area below woody vegetation) every 10 m along the thalweg to calculate the area sampled (m^2). Captured fish were anesthetized with Aqui-S 20E (AQUI-S New Zealand LTD, Lower Hutt, New Zealand), and measured for fork length (FL; mm) and weight (nearest gram).

Data Collection: eDNA Sampling— With a few exceptions (noted below) eDNA sampling followed the standard protocol outlined in Carim et al. (2016). We used a 47 mm fiberglass filter with a 1.5-µm pore size for all samples. Samples were collected in triplicate, and when there were non-uniform patterns of sediment on the filters (indicating a hole, etc.), additional samples were collected. At all sites we attempted to filter 5 L of water through each filter. When filters were occasionally clogged with sediment, additional filters were collected with a goal of filtering a total of 15 L of water per site and sampling event. The volume of water filtered was recorded to the nearest 0.1 L in every instance. In addition, a negative control was collected using 1 L of distilled water at each sampling site/event to monitor for filter contamination. In all cases, disturbance upstream of the eDNA sampling site was avoided to minimize interfering with eDNA samples by displacing sediment and potentially releasing sequestered eDNA. Filters were then folded into quarters (longways) and then in half and stored in a 15-ml centrifuge tube with silica desiccant beads, out of daylight. All samples were frozen at -80°C the day they were collected, except for samples from the Salcha River which were stored in a cooler with ice for three days or less before being frozen due to remote travel logistics. All sampling gear that was reused (filter holders, forceps) were bleached in 30% household bleach for > 20 minutes and then rinsed and dried prior to being reloaded and used to prevent cross-contamination.

Data Collection: Intensive eDNA Sampling— We sampled eDNA to develop a regression model to predict fish abundance from eDNA concentration. eDNA and fish sampling occurred during 1 to 3 fish sampling events at 10 sites (Figure 2.1; N = 28 sampling events); however, one site became dewatered for the latter two sampling events, resulting in 26 usable eDNA/fish abundance samples. eDNA samples were collected in triplicate at the downstream end of each reach prior to fish sampling. During eDNA sampling, a Eureka Manta Probe 30+ (Austin, TX) was used to collect point water quality samples (pH, turbidity, temperature, specific conductance, oxygen saturation), and a Swoffer Flow Meter 2100 was used to measure water velocity. Fish sampling (see above) occurred immediately following eDNA collection.

Data Collection: Broad eDNA Sampling— We sampled 52 additional 1st through 5th order tributaries once each for eDNA to gather a broad understanding of grayling abundance and distribution throughout the study area (Figure 2.1). These streams were selected with a convenience sampling design which was mostly limited by access, and the dataset represents roughly one quarter of tributary streams in the study area. Generally, streams were sampled 100 to 500 m upstream of their confluence with the next major river to avoid mixing of eDNA from the mainstem river; however, occasionally access near a confluence was limited and samples were collected farther upstream.

eDNA Processing—eDNA samples were processed and analyzed by Jonah Ventures (Boulder, Colorado), as follows: DNA was extracted from each whole filter using Qiagen

Qneasy Blood and Tissue Extraction Kit (250; Qiagen Inc, Hilden, Germany) following the manufacturer's protocol. Genomic DNA was eluted to 200 µl and frozen at -20°C. An amplicon from the COI gene was amplified via qPCR from genomic DNA samples using Arctic Grayling forward and reverse primers, and probe (forward primer: 5'CCTTTCCCCGAATAAATAACATGAG'3, reverse primer: 5'ATACTGTCCACCCTGTCCCG'3; Carim et al. 2015). A standard curve was generated for each run to correspond to the targeted region of the Arctic Grayling COI gene. Each qPCR reaction was run in triplicate and contained 8.0 uL of QuantaBio PerfeCTa qPCR ToughMix Low ROX (Catalog Number 97065-966), 500 nM of each primer, 300 nM of probe, 4.0 uL of gDNA, and 4.8 uL of Nuclease-Free H_2O for a total reaction volume of 20 uL. qPCR amplification was carried out on the QuantStudio 5 qPCR instrument with the following thermal profile conditions: 1 cycle of initial denaturation for 5 minutes at 95°C; followed by 50 cycles of 15 seconds at 95°C and 1 minute at 60°C.

Data Collection: Geospatial Data— We summarized geospatial data to understand how environmental parameters (e.g., stream characteristics, beaver, wildfire) affected eDNA concentration; these data were sourced from Chapter 1. In brief, stream geomorphology and hydrology attributes were estimated using the program NetMap (Benda et al. 2007; Clarke et al. 2008), a synthetic stream network based on 5 m by 5 m digital elevation models that calculate reach-scale stream attributes (e.g., gradient, mean annual discharge). Wildfire data were sourced from Monitoring Trends in Burn Severity (MTBS 2022). Beaver dam density data were collected during a survey (Chapter 1) based on using a 0.5 by 0.5 m satellite imagery composite from 2017 (AKDNR 2017). All data were summarized at the valley bottom scale (Clarke et al. 2008; Falke and Paul *in prep*) due to the biological relevance of the valley bottoms for beavers and fish and limited effect of upslope disturbances on stream ecology (Chapter 1, Falke and Paul. *in prep*), and then values were averaged throughout each tributary (upstream of the respective eDNA sample).

Data Analysis— We calculated effort based on total time angled and time electrofished to nearest minute and catch-per-unit-effort was standardized by the area sampled (CPUE&A). Relative abundance was estimated by calculating CPUE&A, as the number of fish captured (n) divided by the number of anglers (a) times the angling time (t) times the area of the reach (m^2; $n/(a*t*A)$). CPUE&A for electrofishing was calculated as $n/(t*A)$. Multi-Gear Mean Standardization was then used to combine CPUE&A for angling and electrofishing (Gibson-Reinemer et al. 2017).

The qPCR values (copies of DNA) for each filter were standardized by liters of water filtered (i.e., the number of eDNA copies divided by L filtered, hereafter eDNA concentration). Water velocity and chemistry data were evaluated as covariates due to their potential to affect eDNA concentration and detection (especially flow, temperature, and turbidity; Tillotson et al. 2018; Sepulveda et al. 2021). We fit a generalized linear regression model (GLM) to evaluate the relationship between fish abundance and eDNA concentration and environmental covariates. To fit the model, multicollinearity among covariates was assessed using Variance Inflation Factor (VIF), and all covariates had VIF values < 10 so they were retained for further analysis. Then, the GLM was used to predict eDNA copies/L as a function of fish abundance, flow (velocity, m/s), water temperature, stream turbidity, day of year, and L filtered. Correlation between CPUE&A and eDNA concentration was evaluated using pseudo R^2, calculated as the mean of McFadden, Cox and Snell, Nagelkerke, and Efron R^2.

We used N-mixture models in a two-stage approach to first understand environmental effects on eDNA (detection) and then understand how environmental variables affected fish abundance (eDNA concentration) at tributary sites using the function *pcount* in the package *unmarked* in Program R (ver. 4.1.2, Indianapolis, IN, United States; Clawson et al. 2022; Kellner et al. 2023). These models included covariates that were expected to affect eDNA detectability (e.g., turbidity, water temperature, stream velocity, day of year, and liters filtered; using a binomial distribution), and site-level covariates modeled with a Poisson distribution (e.g., mean annual flow, wildfire history) which we hypothesized would affect grayling abundance. First, we assessed *in situ* parameters that could affect eDNA detection (Table 2.1). Models that included all subsets of detection covariates, a global model with all covariates, and a null model with no covariates were compared using Akaike's information criterion (AIC; Table 2.1). The model with the lowest AIC and the highest Akaike weight (w_i) was considered the best model. Next, we fit models that included the best detection covariates and subsets of covariates hypothesized to affect fish abundance/eDNA concentration. These models included parameters for each area of interest (geomorphology, hydrology, wildfire, beaver; Table 2.2). The top model was determined as described above.

RESULTS

We collected eDNA at a total of 62 sites during the summer of 2022. eDNA concentration, averaged across triplicate samples for each site, had a mean of 1491 (± 1903 SD), and ranged from 0 to 8771 copies/L (Figure 2.2). Grayling eDNA was detected at 95% of tributary sites. There was high overall agreement among replicate samples; only 3 of 62 sites had replicate samples that suggested differences in fish presence/absence (i.e., capture histories other than [1 1 1] or [0 0 0]). Nine sites had detectable eDNA contamination in the negative control samples (ranging from 7 to 813 copies/L), but most (6/9) of those sites had relatively low contamination (≤ 80 copies/L; Figure 2.2 B). We removed 7 out of 9 sites/sampling events for use in the N-mixture model, and the remaining sites had low contamination (7 and 14 copies/L) so were retained for analysis. Overall, contamination occurred mostly (7 out of 9 times) on the days when both fish and eDNA sampling occurred, likely due to cross contamination during gear handling and transport.

eDNA as a predictor of fish abundance— We found a moderate correlation between eDNA concentration and fish CPUE&A (GLM: pseudo $R^2 = 0.45$; Figure 2.3). Within the model, log(eDNA concentration) had a null relationship with log(CPUE&A) ($\beta = 0.00 \pm 0.00$ SE, $p = 0.971$), stream velocity was positive ($\beta = 0.58 \pm 972$ SE, $p = 0.558$), water temperature was negative ($\beta = -1.35 \pm 0.527$ SE, $p = 0.021$), turbidity was negative ($\beta = -0.158 \pm 0.292$ SE, $p = 0.7701$), day of year was slightly positive ($\beta = -0.015 \pm 0.051$ SE, $p = 0.770$), and liters filtered was positive ($\beta = 0.793 \pm 0.223$ SE, $p = 0.726$).

eDNA transport in tributaries— We sampled eDNA longitudinally in Caribou Poker Creek at four sites multiple times coincident with fish sampling. We then plotted eDNA concentration and fish CPUE&A (averaged across all sampling events), where the size of the points represented the relative concentration or CPUE&A (Figure 2.4). eDNA concentration ranged from 604 to 3528 copies/L, with a mean of 1836 ± 1266 SD. eDNA appeared to accumulate throughout the tributary, resulting in the most downstream sample being roughly representative of the cumulative eDNA from all samples collected upstream. In fact, the largest eDNA concentration observed was at the lowest site (Figure 2.4 A), and this amount is roughly equivalent to the sum of eDNA collected in the other samples (3528 and 3896 copies/L respectively). We calculated the distance that eDNA would theoretically need to travel from the uppermost fish surveys to be observed at the lowest site (8251 m) and averaged the stream velocity measurements we collected during eDNA sampling (0.34 m/s), which would suggest an average eDNA/water residence time of roughly 6.7 hours (*8251 m / 0.34 m/s = 24,267.64 s / 60 s/min = 404 min / 60 min/hr = 6.74 hours*).

Contrary to the distribution of eDNA, Arctic Grayling in Caribou Poker Creek were uniformly distributed. The maximum CPUE&A was 5.43 and occurred at an upstream site in Caribou Creek (Figure 2.4) below a beaver pond that prevented fish from moving upstream resulting in fish being concentrated and artificially easy to catch (Figure 2.4 B). Interestingly, this concentration of fish appeared to be represented in the eDNA data, as the Caribou Creek eDNA concentration was larger than the Poker Creek concentration (1087 vs 604 copies/L, respectively; Figure 2.4 A). The minimum CPUE&A was 0.44, with a mean of 1.57 ± 1.59 SD.

N-mixture model—We conducted model selection using AIC selection for *in situ* covariates collected that might affect eDNA detection, including stream temperature (°C), turbidity (NTUs), velocity (m/s), day of year the sampling occurred, and the mean number of liters filtered, and our results clearly indicated that the model containing all predictors was preferred (AIC = 17984.5, ΔAIC = 0.0, w_i = 1.00; Table 2.1). In this model (*Occu*, Table 2.2), temperature had a negative effect on eDNA detection (β = -0.096, SE = 0.013, 95% CI = -0.118, -0.074), turbidity had a negative effect (β = -0.104, SE = 0.006, 95% CI = -0.113, -0.094), flow had a positive effect (β = 0.318, SE = 0.079, 95% CI = 0.189, 0.449), day of year had a negative effect (β = -0.008, SE = 0.032 95% CI = -0.012, -0.004), and liters filtered had a negative effect (β = -0.623, SE = 0.032, 95% CI = -0.676, -0.571; Figure 2.5).

We fit six alternative N-mixture models to assess potential drivers of eDNA concentration (and inferred fish abundance). The *Global* model was the highest ranked model by AICc (AICc = 15602.7, ΔAICc = 0.0, w_i = 1.00; Table 2.2). The *Geo* model followed (AICc = 16093.1, ΔAICc = 490.5, w_i = 0.00), then the *Hydro*, *Wildfire*, *Occu*, and *Beaver* models (Table 2.2). Therefore, we used the *Global* model for further inference. All but one parameter (stream velocity "FLOW"; Table 2.3) had a significant positive or negative relationship effect on eDNA concentration. Overall, stream gradient had the most significant effect -a positive relationship with eDNA concentration (Table 2.3). eDNA concentration increased with drainage area and stream order. Sinuosity had a negative relationship with eDNA concentration. Stream power had a slight negative effect, but eDNA increased with and mean annual discharge. Wildfire metrics had mixed effects on eDNA concentration; time since last burn was slightly positive, percent burned was slightly negative, and burned (binary) was positively associated with eDNA concentration. Beaver density had a positive association with eDNA concentration in the Global model, however, the raw data suggest a negative relationship which takes a logarithmic shape (e.g., fish abundance decreases exponentially as beaver density increases; Figure 2.6).

DISCUSSION

Beavers, wildfires, and watershed characteristics had strong influences on Arctic Grayling distribution and abundance in Interior Alaska boreal stream networks. We found only a moderate correlation between eDNA concentration and grayling numerical fish abundance; we concluded that this relationship was not strong enough to precisely predict fish biomass across multiple streams but could be used to estimate relative or categorical abundance. The modest correlation between eDNA concentration and abundance was likely due, in part, to the spatial scale of fish and eDNA sampling being spatially mismatched, where the fish sampling reaches appeared to represent fish abundance in a much smaller area than the eDNA represented. We found that a repeated count-based model framework, the N-mixture model, was better suited for modeling eDNA concentration data and allowed us to evaluate the effect of imperfect detection in addition to abundance. Below we discuss the utility of eDNA as a tool to assess boreal fish abundance across broad regions, and the ecology of grayling across a beaver and wildfire dominated landscape.

eDNA concentrations were positively associated with grayling abundance across ten sites and multiple sampling events, yet the correlation was moderate (Pseudo $R^2 = 0.45$) and similar or slightly lower than other studies with similar study designs (Baldigo et al. 2017; Doi et al. 2017; Levi et al. 2018; Tillotson et al. 2018; Yates et al. 2019; Sepulveda et al. 2021). The moderate correlation was likely due to a mismatch between the spatial scale at which fish sampling occurred and the scale reflected in eDNA concentrations. For example, our fish sampling reaches ranged from 250 to 1000 m yet we demonstrated that eDNA samples in a stream may represent a much greater length. Therefore, depending on the occupied length of a tributary, eDNA concentration is *relatively* representative of grayling abundance, despite the fact that it was only moderately correlated with local CPUE&A. This suggests that traditional fish sampling was insufficient to represent fish abundance throughout the tributary, since the eDNA signal represents a much greater upstream distance than the fish sampling reaches. In warm streams, eDNA can persist in a freshwater environment for 24–72 hours depending on water conditions (Eichmiller et al. 2016; Kasai et al. 2020; Lamb et al. 2022), although it is subject to removal (degradation, settling, etc.). Streams in our high latitude study area are colder, have less microbial activity, and less UV radiation on average than streams where most eDNA research has been conducted, potentially resulting in above average eDNA persistence (WHO 2016; Saito and Doi 2021; Lamb et al. 2022; Rourke et al. 2022; NOAA 2023).

Our results suggest that eDNA measured at tributary confluences with a main stem river may be a good relative representation of overall fish abundance in that tributary. For example, our rough calculations (6.7 hours to transport eDNA through an 8.3 km section of stream) if extrapolated at the same stream velocity (1.3 km/hr), suggest eDNA could be transported 29.4 (24 hrs) to 88.1 (72 hrs) km before fully degrading. Although extreme, this illustrates that our sampling was likely representative of fish abundance in smaller tributaries, at least relative to each other. However, further research is needed, particularly in cold-water systems, to assess factors that affect eDNA persistence and removal across spatial scales and environmental conditions.

Alternative methods for analysis, such as the N-mixture model discussed here, are valuable to compensate for the infeasibility of intensive fish sampling throughout entire tributaries (Goldstein and de Valpine 2022; Rourke et al. 2022). Additionally, N-mixture models, by nature, handle absences and right skewed data well since they are designed to accept count survey data, whereas linear regression techniques require a normal distribution to meet model assumptions (Goldstein and de Valpine 2022). Using this framework, we found that site-level covariates (stream temperature, turbidity, velocity, day of year, and liters filtered) had a significant effect on eDNA detection (or persistence/degradation, they are indistinguishable in this context). The patterns we revealed were logical: water temperature had a negative relationship with detection probability, likely due to its effects on eDNA degradation (Eichmiller et al. 2016; Tsuji et al. 2017; Jo et al. 2019; Kasai et al. 2020; Saito and Doi 2021; Lamb et al. 2022; Brandão-Dias et al. 2023), turbidity had a negative effect on detection probability because it clogs filters (Harrison et al. 2019; Takasaki et al. 2021), stream velocity had a positive relationship with eDNA detection because faster flowing streams have the ability to transport eDNA farther (eDNA remains suspended longer; Shogren et al. 2017; Harrison et al. 2019), and probability of detection decreased with liters filtered, due to filter saturation or sediment inhibition during eDNA extraction (Kumar et al. 2020; Takasaki et al. 2021). Surprisingly, the day of year had a negative relationship with eDNA detection probability, potentially because fish continued to migrate (possibly out of tributaries to consume Pacific salmon (*Oncorhynchus* spp.) subsidies) during the summer season (Scheurell et al. 2007; Bentley et al. 2012; Falke et al. 2019). This further supports the idea that stream connectivity is an important factor in grayling feeding strategies (Heim et al. 2016a, 2018).

As measured by eDNA concentrations, the distribution and abundance of Arctic Grayling in tributaries was correlated with numerous factors that included stream geomorphology, wildfire history, and beaver density; models with single categories (e.g., beaver, geomorphology) were not supported, given the data. Stream gradient was positively associated with eDNA concentration and had the strongest effect out of all the predictors, likely due to a combination of eDNA transport capacity and habitat suitability for grayling (Chapter 1; Larocque et al. 2014; Bozeman and Grossman 2019; Ellenor et al. 2021). Stream sinuosity had the opposite relationship, likely a result of reduced eDNA transport and habitat suitability through low gradient, sinuous reaches with relatively slow water velocities may not be conducive to drift feeding. Overall, it appears that larger streams had a higher abundance of grayling (eDNA), both stream order and mean annual discharge were positively associated with eDNA concentration, likely due to the increased habitat availability in larger streams. This broad result was generally compatible with our more intensive longitudinal sampling in Caribou and Poker Creeks, where a point sample within the stream network roughly represented the cumulative fish abundance upstream, and therefore larger streams would tend to have higher overall eDNA concentrations.

Grayling eDNA was higher in burned basins, yet also positively associated with time-since-last-burn (i.e., grayling abundance was higher the longer a basin had time to recover from a wildfire). Additionally, eDNA concentration was negatively associated with the percentage of valley bottom burned, suggesting that overall, wildfires have a negative relationship with Arctic Grayling. However, some research suggests that productivity increases after wildfires, which has the potential to benefit fishes (Hinkle et al. *in prep*), although biological responses may be different if fires occur in valley bottoms rather than hillslopes (Falke and Paul *in prep*). In the short term, wildfires can extirpate beaver populations, which may provide increased habitat accessibility for migratory fishes (Chapter 1) while concurrently increasing stream productivity via nutrient inputs. However, in the long term, wildfires stimulate beaver colonization and subsequently damming, which can reduce fish habitat availability (Chapter 1).

Beaver dam density was positively associated with eDNA concentration in the global model, potentially due to interactions with wildfire and stream characteristics. It is likely that beaver effects on Arctic Grayling vary across stream gradients and flow regimes -local context is key for understanding the effects of beavers on fishes. However, when used as the sole predictor (e.g., "*Beaver*" model; Table 2.2), beaver dam density had a negative relationship with eDNA concentration. Additionally, the raw data suggest a negative logarithmic relationship between beaver dam density and eDNA concentration (Figure 2.7), in which eDNA concentration drops off steeply as beaver dam density increases. Therefore, we believe that beaver dam density does have a negative effect on overall fish abundance due to limitation of dispersal. However, this relationship is context dependent, and beavers may not limit fish dispersal in certain stream types (e.g., high gradient, flashy flows). This conclusion generally aligns with the results of Chapter 1, which suggested that beavers do fragment grayling habitat, but that this effect is reduced under high flows. Further, this supports our hypothesis that wildfires mediate beaver effects on grayling in Interior Alaska.

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FIGURES

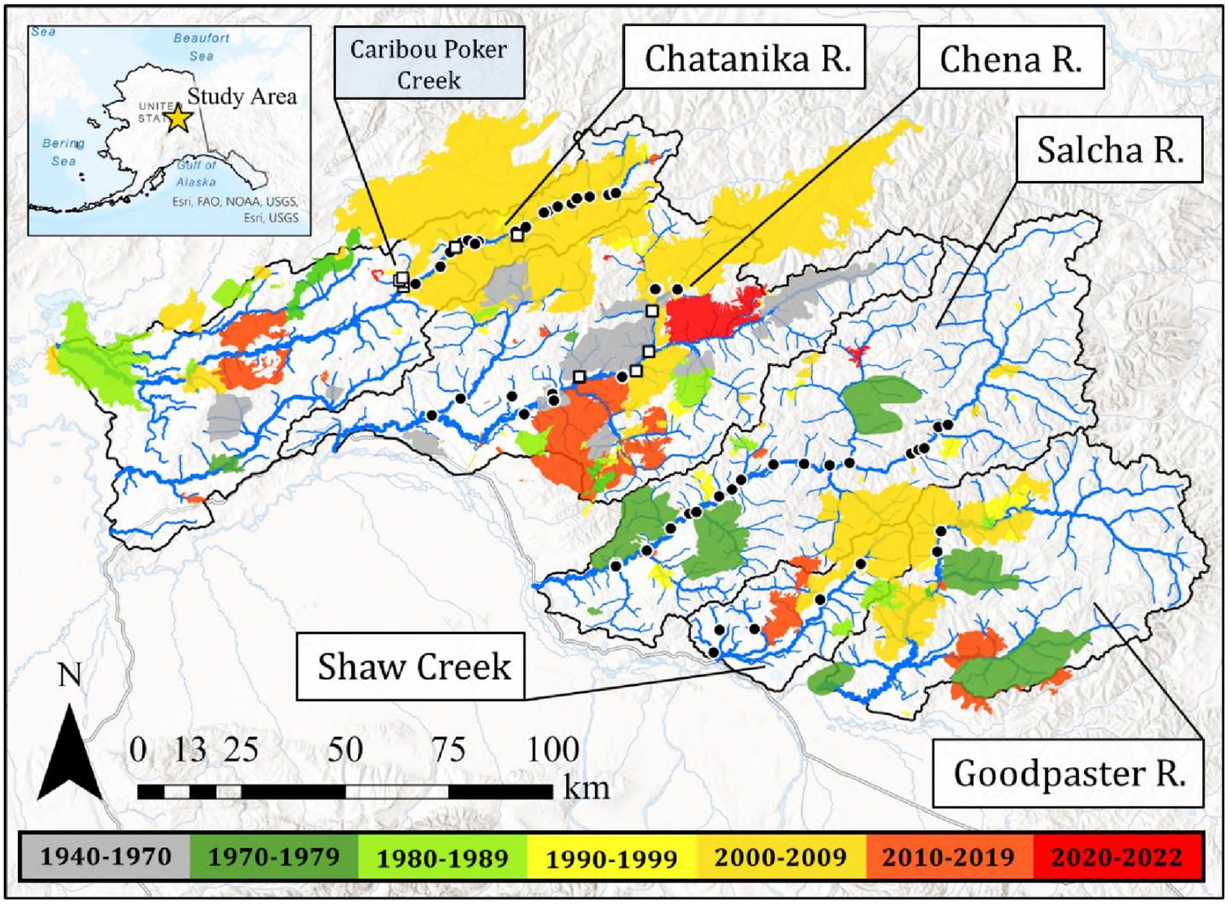

Figure 2.1. Location of the study area in Alaska, USA (inset), rivers basins, and fire history. Colored polygons represent historical fire perimeters (MTBS 2022). Blue lines represent major rivers and tributaries, and black lines outline drainages. eDNA sites are represented as black points (eDNA only samples) and white squares (eDNA samples that coincided with fish sampling).

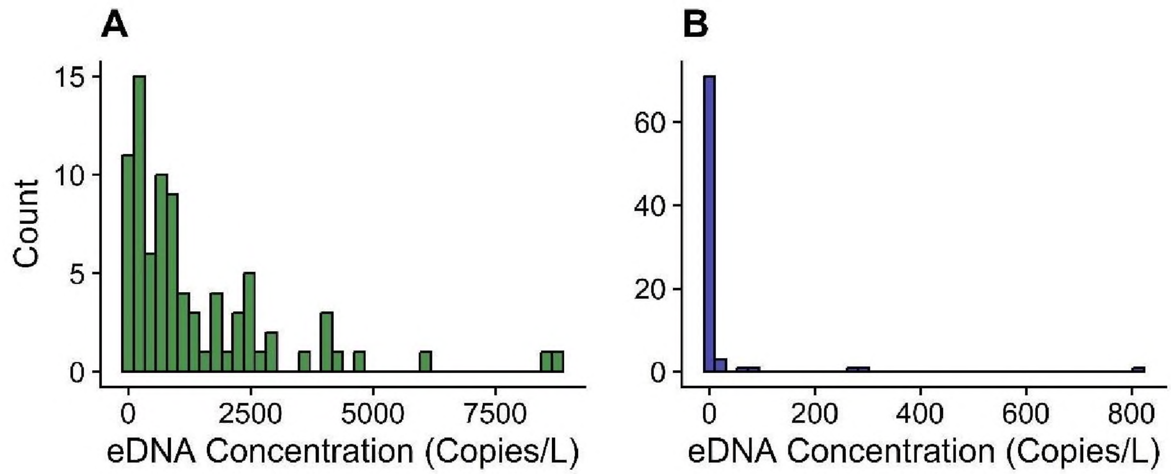

Figure 2.2. **(A)** Histogram of eDNA concentration for Arctic Grayling at 62 sites in Interior Alaska, averaged across triplicate samples for each site. **(B)** eDNA concentration in negative control samples.

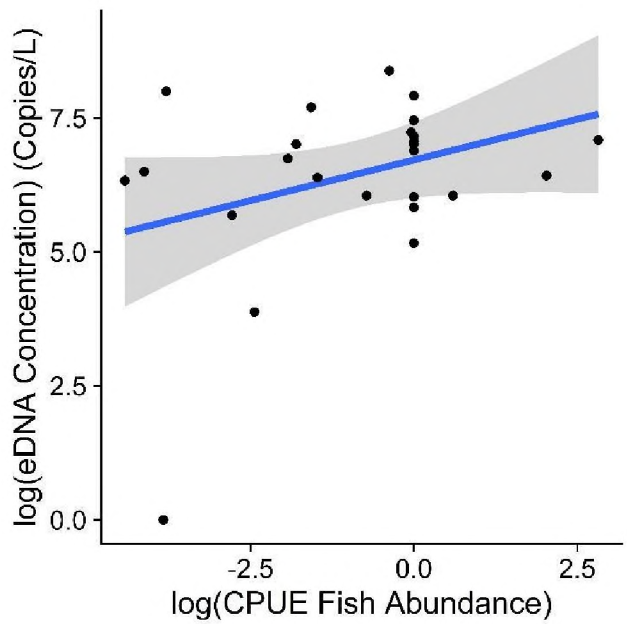

Figure 2.3. Log-transformed Arctic Grayling eDNA concentration (mean of triplicate samples) as a function of the log of catch per unit effort standardize by stream area (CPUE&A) for 26 sampling events in Interior Alaska. Points represent individual fish/eDNA sampling events, the blue line represents a linear regression best fit line, and the gray shaded area represents the standard error surrounding the regression line.

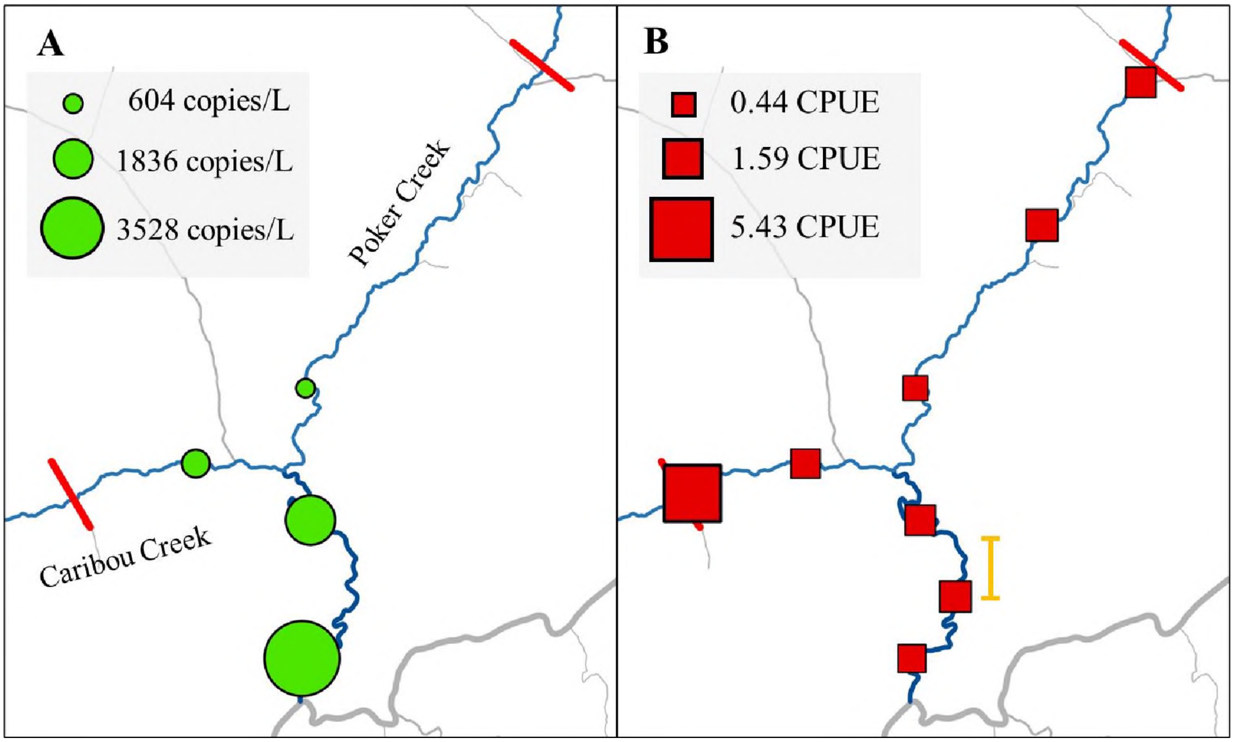

Figure 2.4. eDNA concentration **(A)** and Arctic Grayling abundance **(B)** from locations in Caribou-Poker Creek, Alaska (Figure 1.1). Green circles are eDNA concentration, where the size represents the relative concentration of eDNA (copies/L). Red squares represent the multi-gear mean standardized estimate of fish abundance for each fish sampling reach. Legends show the minimum, mean, and maximum values for eDNA and catch per unit effort standardized by are. Points (circle or square) are averaged across multiple sampling events during the summer season. The gold bar (**B**) represents an example of a 500 m fish sampling reach. Red lines represent the furthest upstream area where Arctic Grayling were captured.

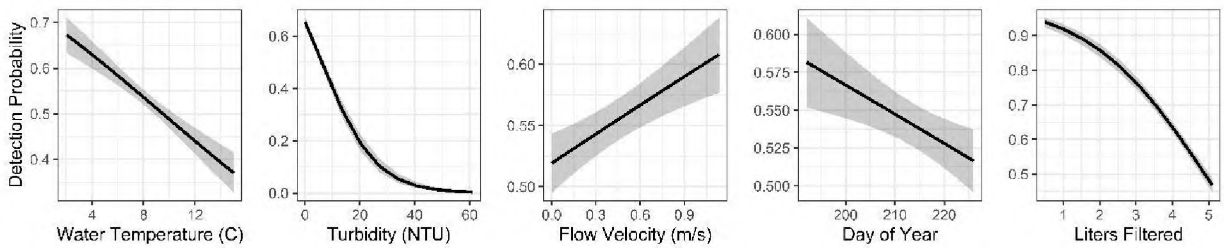

Figure 2.5. N-mixture-modeled relationship between Arctic Grayling eDNA detection probability and *in situ* covariates in Interior Alaska modeled using an N-mixture model (Table 1).

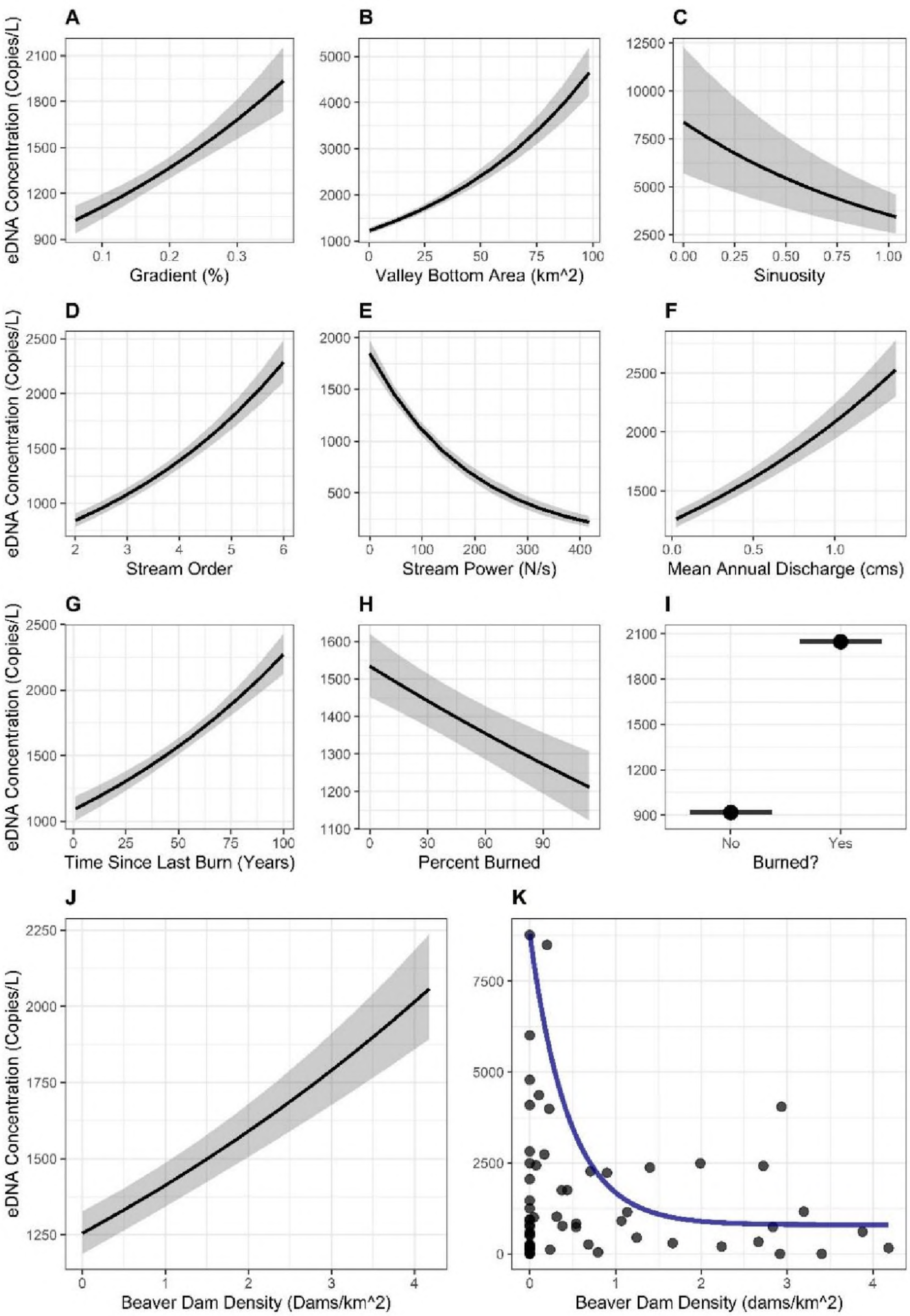

Figure 2.6. **(A–J)** Model predicted relationships between environmental covariates and Arctic Grayling eDNA concentrations from the top ranked N-mixture model in Interior Alaska (Table 2). **(K)** Raw data (eDNA concentration) as a function of North American Beaver dam density. The logarithmic blue line is plotted for illustration purposes.

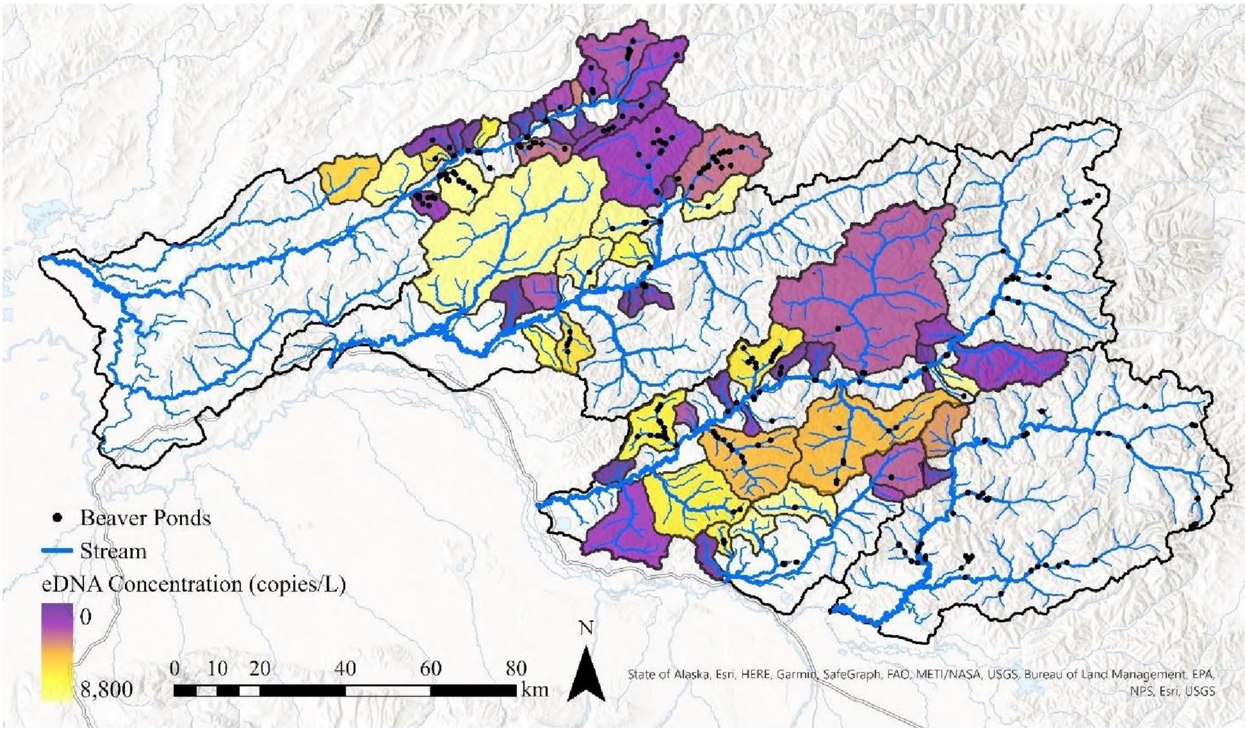

Figure 2.7. Tributary streams (n = 62) sampled in Interior Alaska during Summer 2022, colored by Arctic Grayling eDNA concentration. Black points are beaver ponds identified by remote sensing (Chapter 1).

TABLES

Detection Predictors	Log-Lik	AIC	ΔAIC	W_i
TEMP + TURB + FLOW + DOY + L_FILTERED	-8985.2	17984.5	0.0	1.00
TEMP + TURB + FLOW + L_FILTERED	-9011.5	18035.0	50.5	0.00
TEMP + TURB + L_FILTERED	-9018.7	18047.5	63.0	0.00
TURB + DOY + L_FILTERED	-9028.2	18066.4	81.9	0.00
TURB + FLOW + L_FILTERED	-9028.6	18067.1	82.7	0.00
TURB + L_FILTERED	-9029.9	18067.8	83.3	0.00
TURB + FLOW + DOY + L_FILTERED	-9027.9	18067.8	83.3	0.00
TEMP + FLOW + DOY + L_FILTERED	-9136.8	18285.7	301.2	0.00
TEMP + DOY + L_FILTERED	-9158.3	18326.6	342.1	0.00
TEMP + FLOW + L_FILTERED	-9194.7	18399.4	414.9	0.00
TEMP + FLOW + DOY	-9209.2	18428.4	443.9	0.00
TEMP + L_FILTERED	-9211.1	18430.2	445.7	0.00
TEMP + DOY	-9212.3	18432.5	448.0	0.00
DOY + L_FILTERED	-9227.4	18462.9	478.4	0.00
FLOW + DOY + L_FILTERED	-9227.5	18464.9	480.4	0.00
TURB + FLOW + DOY	-9232.5	18475.1	490.6	0.00
FLOW + L_FILTERED	-9236.3	18480.7	496.2	0.00
L_FILTERED	-9240.1	18486.1	501.6	0.00
TEMP + TURB + FLOW + DOY	-9242.9	18497.7	513.2	0.00
TEMP + TURB + DOY	-9244.6	18499.1	514.6	0.00
TURB + DOY	-9254.1	18516.2	531.7	0.00
TEMP + TURB + FLOW	-9253.7	18517.5	533.0	0.00
FLOW + DOY	-9262.4	18532.8	548.3	0.00
DOY	-9263.6	18533.2	548.7	0.00
TEMP + TURB	-9262.7	18533.5	549.0	0.00
TEMP	-9289.2	18584.5	600.0	0.00
TEMP + FLOW	-9289.1	18586.1	601.6	0.00
TURB	-9291.6	18589.3	604.8	0.00
TURB + FLOW	-9291.4	18590.9	606.4	0.00
FLOW	-9299.1	18604.2	619.7	0.00
TEMP + TURB + DOY + L_FILTERED	-10250.4	20512.8	2528.3	0.00

Table 2.1.— Model selection on an N-mixture model to determine which site level predictors affect Arctic Grayling eDNA detection in tributaries across Interior Alaska. Log-Lik is the Log Likelihood, AIC is Akaike information criterion, ΔAIC is the difference between the top ranked (global) model, and w_i is the AIC weight in the respective model. TEMP is water temperature (°C), TURB is stream turbidity (NTUs), FLOW is the stream velocity (m/s), DOY is day of year when the sample was collected, and L_FILTERED is the average number of liters filtered for the replicates.

Model	Model Predictors (~ *occupancy predictors ~ abundance predictors)*	Log Link	AICc	ΔAICc	W_i
Global	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ GRAD + AREA + SIN + STRM_ORD + STRM_PWR + MAQ + TSLB + PER_BURN + BURNED + DAM_DENS	-7777.4	15602.7	0.0	1.00
Geo	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ GRAD + AREA + SIN + STRM_ORD	-8032.9	16093.1	490.5	0.00
Hydro	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ STRM_PWR + MAQ	-8592.0	17205.5	1602.8	0.00
Wildfire	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ TSLB + PER_BURN + BURNED	-8959.8	17943.8	2341.2	0.00
Occu	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ 1	-8981.1	17980.9	2378.3	0.00
Beaver	~ TURB + TEMP + FLOW + DOY + L_FILTERED ~ DAM_DENS	-8985.3	17986.6	2383.9	0.00

Table 2.2.— Alternative model combinations evaluating the importance of different environmental parameters (e.g., wildfire, beavers) for predicting Arctic Grayling eDNA concentration across 62 streams in Interior Alaska. Log link, Akaike information criterion corrected for a small sample size (AICc), change in AICc (ΔAICc), and AICc weight (w_i) shown for each model.

Category	Parameter	Abbreviation (Table 2)	Parameter Estimate	Standard Error	95% Confidence Interval
Detectability	Temperature	TEMP	-0.202	0.012	-0.221, -0.182
	Turbidity	TURB	0.032	0.009	0.017, 0.046
	Flow	FLOW	0.082	0.081	-0.051, 0.215
	Day of Year	DOY	-0.061	0.002	-0.064, -0.057
	Liters Filtered	L_FILTERED	-0.118	0.032	-0.171, -0.065
Geomorphology	Stream Gradient (max)	GRAD	2.058	0.277	1.602, 2.513
	Drainage Area	AREA	0.014	0.001	0.013, 0.015
	Sinuosity	SIN	-0.858	0.064	-0.964, -0.753
	Stream Order	STRM_ORD	0.250	0.015	0.225, 0.275
Hydrology	Stream Power	STRM_PWR	-0.005	0.000	-0.006, -0.005
	Mean Annual Discharge	MAQ	0.516	0.038	0.524, 0.651
Wildfire	Time Since Last Burn	TSLB	0.007	0.001	0.006, 0.009
	Percent Burned	PER_BURN	-0.002	0.000	-0.003, -0.002
	Burned? (binary)	BURNED	0.803	0.064	0.698, 0.908
Beaver	Dam Density	DAM_DENS	0.118	0.011	0.100, 0.136

Table 2.3.— List of the parameters that influence Arctic Grayling eDNA concentration across 62 streams in Interior Alaska. Parameters and related estimates, standard error, and 95% confidence intervals were derived from the Global model (Table 2.2).

General Conclusions

I used remote sensing and modeling techniques to demonstrate that wildfire was a key predictor of North American Beaver (hereafter referred to as "beavers") pond density in Interior Alaska, and that geomorphological and hydrological parameters were important to understand the distribution of beaver ponds on the landscape. Next, I used a simulation to show that beaver dams, especially in high density, have the potential to substantially limit fish dispersal during normal and low flow conditions. I then tested this relationship by evaluating the distribution and relative abundance of Arctic Grayling, and found that stream attributes (gradient, mean annual flow), wildfires, and beavers, were all important in explaining patterns in Arctic Grayling abundance. Key results included:

- Beaver ponds in the Chena, Chatanika, Salcha, and Goodpaster rivers and Shaw Creek were surveyed using satellite imagery from 2017. I located 890 potential beaver ponds and selected 435 ponds for analysis which I was confident were created by beavers. Beaver ponds have the highest density in the Chena and Chatanika river, especially in areas where wildfires occurred in the past 33 years (Figure 1.4). Ponds had a smaller wetted area in burned valley bottoms than unburned valley bottoms (T-test: T = -2.28, DF = 120.53, $p = 0.03$). Deciduous vegetation was more common than coniferous vegetation in burned areas (T-test: T = 4.11, DF = 191.98, $p < 0.01$; T-test: T = -5.39, DF = 189.07, $p < 0.01$, respectively)
- A Generalized Linear Model that contained wildfire, hydrology, and geomorphology parameters was identified as the most parsimonious to predict beaver density and had a pseudo-R^2 of 0.88 (AICc = 312.6, $w_i = 0.81$). Wildfire parameters alone explained 75% of variation in beaver density (pseudo $R^2 = 0.75$, AICc = 324.1, $w_i = 0.00$). Based on

model averaging, key predictors were percent severe burn, percent moderate burn, drainage area, stream sinuosity, stream width and mean annual discharge.

- Patterns in beaver pond density were relatively consistent across all catchments and burned-only catchments. However, in unburned catchments beaver pond density was less predictable, and vegetation characteristics were more important for predicting density.
- A simulation suggested that beaver dams can fragment fish habitat and affect dispersal, particularly under low flow conditions. Beaver dams were estimated to reduce fish habitat availability by up to ~65% in some tributaries, and up to ~20% (183,201 km) in a river basin during low water conditions. Across the whole study area, beaver dams appear to reduce fish habitat availability between ~1 to ~12% (51,681 to 519,822 km) during high and low water conditions, respectively (Table 1.4).
- eDNA concentration (log transformed) and fish abundance (catch per unit effort standardized by area, log transformed) were moderately correlated (pseudo $R^2 = 0.45$) in a model that included *in situ* environmental parameters. Some unexplained variance was likely due to the fish sampling reaches being too small to sufficiently match the spatial extent represented by eDNA.
- Based on CPUE, fish abundance in Caribou Poker Creek was relatively uniform throughout the stream network during summer 2022, although eDNA appeared to accumulate longitudinally within the tributary, suggesting that a sample near the downstream end is likely representative of fish abundance throughout the tributary. I estimated a mean eDNA residence of 6.7 hours from the highest point that fish were observed, indicating that eDNA can likely travel a substantial distance even in large tributaries before degrading (24–72 hours).

- Using an N-mixture model, I modeled eDNA concentration as a proxy of fish abundance across 62 streams. eDNA concentration varied across streams with different beaver, wildfire, and watershed characteristics, key predictors were stream gradient, drainage area, and stream order, and mean annual discharge with larger streams tending to have higher eDNA concentration (Figure 2.6). Wildfire parameters were negatively associated with eDNA concentration. In the *Global* model, beaver density had a positive relationship with eDNA concentration, but raw data suggested a negative logarithmic relationship.

Overall, I found that beavers are a key component for determining the condition of aquatic habitat in boreal Alaska, including mediating wildfire effects and influencing the suitability/availability of fish habitat. My results suggest that both beavers and wildfires have the potential to affect fishes negatively through changes in habitat conditions. However, Arctic Grayling are relatively abundant and widespread throughout Interior Alaska, suggesting that they are resilient to these changes, and other research suggests that wildfires have positive benefits to fishes (e.g., individual level effects) not captured in this study (Hinkle et al *in prep*). An important factor that contributes to grayling's resilience is their mobility; grayling are able to select for certain habitats throughout a season depending on the environmental conditions and individual needs (Hughes 2000; Bentley et al. 2012; Heim et al. 2018). This indicates that habitat connectivity is essential to maintain grayling resilience to wildfire and other disturbances (Falke et al. 2015; Heim et al. 2016; Jager et al. 2021), and beavers have the potential to limit the ability of grayling to access high quality habitats located upstream in tributaries (Wuttig 2002; Taylor et al. 2010; Lokteff et al. 2013; von Finster 2019; Wolf et al. 2022).

My results suggest a positive relationship between wildfires and beaver dam density, which could have long term implications for fish if wildfire continues to increase. Although there is potential for a negative feedback relationship between beavers and wildfires (Fairfax and Whittle 2020; Markle et al. 2022), the consequences for fish are largely unknown. Episodic fires may be necessary to occasionally reduce beaver populations and restore stream connectivity (Fellers et al. 2004; Hood et al. 2007; Fellers and Osbourn 2009), although in the long term this may be counterproductive for fish by stimulating further beaver-caused habitat fragmentation. Consideration should be given to the concept of the "portfolio effect" (Schindler et al. 2010, 2015), in which habitat diversity, including habitats which are currently unproductive, is important through time due to changes in environmental and climatic regimes and related changes in habitat suitability. In this context, the patterns described (e.g., habitat fragmentation in certain areas) in this study may be acceptable because of the potential for climatic shifts to make new habitats available in the future. For example, if flows increase in the future (Bennett et al. 2023), some small streams previously dominated by beavers may experience higher rates of fish passage over time, and the habitats that were previously high-quality fish habitat become inhospitable due to the change in flow regime (e.g., fish distributions would shift to the most suitable habitats). However, if there is potential for positive feedback between beavers and wildfires, the portfolio effect concept may not be compatible with the patterns observed in this system. Further, my results suggest that Interior Alaska is relatively homogenous in stream conditions (gradient, flow, Chapter 1 and 2), therefore the "portfolio" of habitats that are available may not provide significant benefits to fish under different environmental conditions; however, continued habitat fragmentation has substantial downsides. Future research should consider the temporal aspects of these beaver, wildfire, and fish dynamics, and evaluate the potential for habitat diversity -or homogeneity- to build or reduce resilience of freshwater fishes.

Species with specialized habitat niches, or species that are sensitive to change, may be more affected by wildfire, beavers, and habitat suitability relative to habitat generalists like Arctic Grayling. One example is anadromous fishes which generally return to a natal stream and depend on stream connectivity to disperse to spawning/rearing habitats to complete their life cycle (Taylor et al. 2010; Bouwes et al. 2016; von Finster 2019). For instance, if a wildfire occurred in a key tributary, and stimulated increase in beaver abundance (dam density) over time (5–20 years), fish habitat availability could slowly be reduced (Chapter 1). Beavers, due to their own suitability requirements, would select for certain stream characteristics, potentially overlapping with suitable fish habitats, creating homogeneity and reduced suitability in the overall tributary (Malison et al. 2016). Although not necessarily an urgent threat to fish abundance, beavers could reduce fish populations' overall resilience to change, such as environmental change or urban development. Beaver and fish management should be considered in tandem, and across spatiotemporal scales to conduct precise management actions which maintain population resilience.

Modern beaver management can vary from reintroductions to lethal and nonlethal removal of beavers and beaver dams (Avery 2002; Wuttig 2002; Wheaton et al. 2013; Pollock et al. 2014; Johnson-Bice et al. 2018; von Finster 2019; Ruid 2023). Beaver reintroductions in the Western U.S. have garnered significant public and scientific momentum and may be the best management strategy for those areas. However, I contend that targeted beaver removal remains a valid management strategy to support fish habitat connectivity, as demonstrated in the Midwest and boreal regions (Wuttig 2002; Johnson-Bice et al. 2018; von Finster 2019; Ruid 2023). Beaver trapping and dam removal by professionals and/or recreational trappers may be necessary to preserve key fish habitats, especially in areas of high beaver abundance. Because beavers can inhabit diverse habitats, including large rivers, removal on a local level (e.g., a single tributary) is unlikely to affect their overall population. However, it is possible that targeted beaver removal could provide access to high quality fish habitats that were previously unavailable due to a variety of factors (e.g., beaver dams, climate, etc.). Recent fisheries declines in the boreal region have raised interest in the potential for beaver removal to spur fishery recoveries and support subsistence user groups (Feddern et al. 2023), and examples of reasonable beaver removal for fish habitat management can act as a template for further efforts, if appropriate (Wuttig 2002; von Finster 2019; Ruid 2023). Further research is needed to investigate the potential feasibility and consequences of this type of management strategy in boreal streams.

Beaver effects on fish and the surrounding ecosystems are highly variable, and specific to the conditions of any given region or site (e.g., fish species, jumping ability, and life stage, stream flow regime, dam persistence and permeability, etc.). Emerging research shows strong regional effects of beaver impacts on fishes (Collen and Gibson 2000; Kemp et al. 2012; Johnson-Bice et al. 2018). For example, studies in the Midwestern U.S generally find negative effects on fishes, while positive effects are most often cited in the Western U.S. (where most beaver/fish research has been conducted). Key factors affecting fishes include stream gradient and related flow regimes (low in the Midwest, high in the West) which affect dam persistence and permeability, fine sediment loads (limited in the West but limiting to fishes in the Midwest), and overall beaver abundance which is much higher in the Midwest. Our results indicate that beaver and fish relationships in Interior Alaska and the boreal biome overall are more closely aligned with those seen in the Midwest, but experience less sedimentation issues. Although there are key landscape-level differences across these regions, especially wildfires and other disturbance regimes, common concerns of beaver-caused habitat fragmentation should be investigated further.

Beaver and salmonid ranges are expanding north into the Alaska Arctic (Craig and Haldorson 1986; Nielsen et al. 2013; Tape et al. 2018, 2022), and are associated with a variety of risks and opportunities. While I considered beaver effects on fisheries resilience in their current range, the information from this study should be considered when assessing potential limitations beavers could impose, or the potential to facilitate fish colonization in the Arctic. Although current beaver expansion rates into the Arctic appear to be relatively rapid, colonization of Pacific salmon (*Oncorhynchus* spp.) appears to be limited by cold freshwater thermal conditions (Craig and Haldorson 1986; Nielsen et al. 2013; Tape et al. 2022). Streams in the Arctic are low gradient and fed by combinations of snowmelt and groundwater, with less influence from rain, which has resulted in persistent beaver dams (Tape et al. 2022). Persistent beaver dams (e.g., dams that last > 3–5 years) can create limitations to fish dispersal and diversity (Snodgrass and Meffe 1998; Wuttig 2002; Taylor et al. 2010; Lokteff et al. 2013; O'Keefe 2021; Wolf et al. 2022). However, the potential for beavers to create warm water refugia via riparian removal may allow for colonization of new species which could compete with the present-day fish community (Craig and Haldorson 1986; Nielsen et al. 2013). This creates potential risks to freshwater ecological communities, including important subsistence fishes (Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007; Bilous and Dunmall 2020). Additionally, beavers in the Arctic can initiate permafrost thaw (Jones et al. 2020, 2021), which poses a series of other risks to aquatic communities including the release of concentrated chemicals and minerals (e.g., "rusting rivers") and changes to microbial communities (Barker et al. 2022; Clark et al. 2023; Shannon et al. 2023). As beaver management practices are developed in boreal regions, strong considerations should be made about how to manage expansion of keystone species like beaver and anadromous fishes into the north.

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Appendices

APPENDIX A

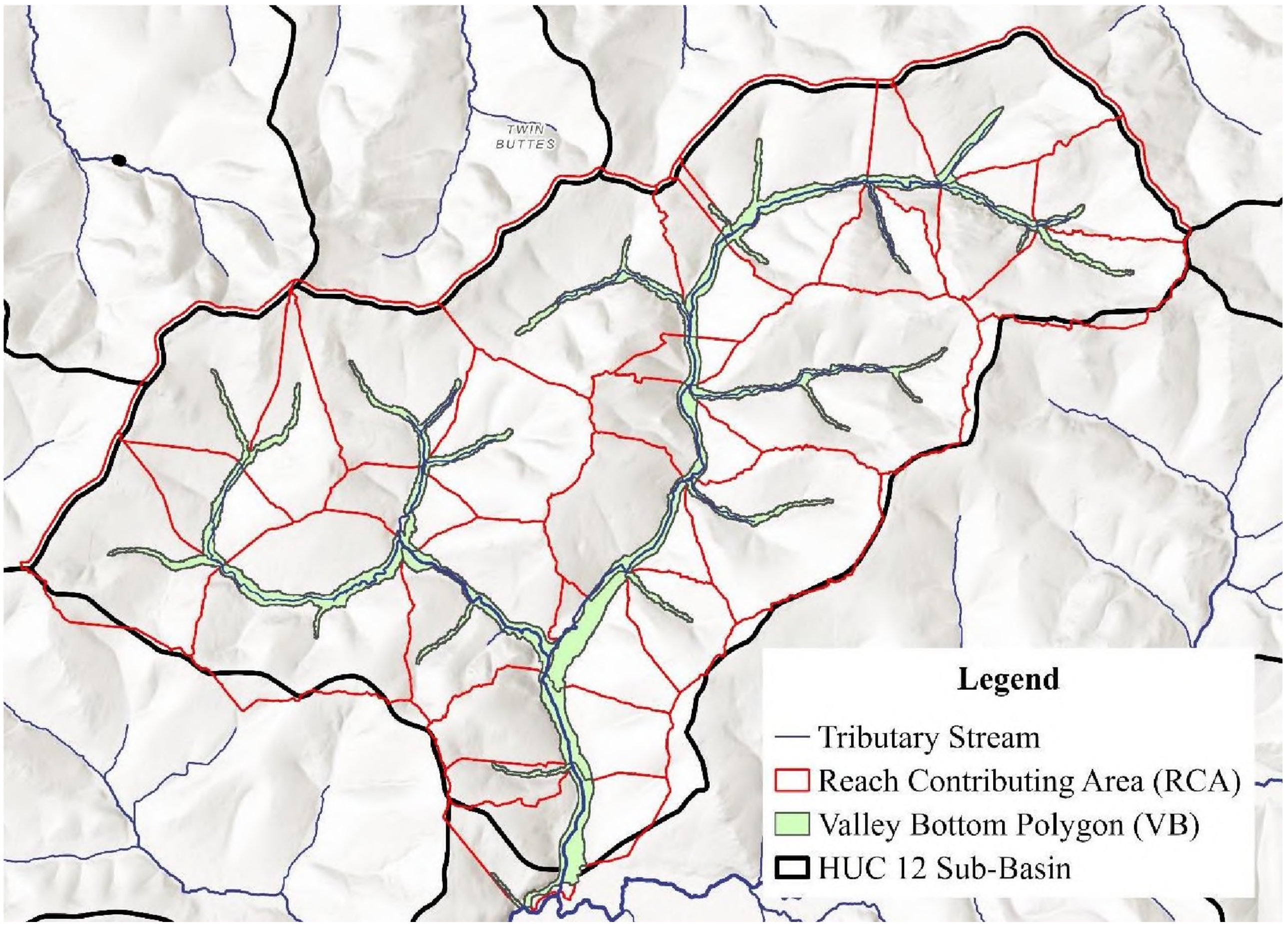

Figure A1. Examples of reach contributing areas (RCAs), valley bottom polygons (VBs), and the NetMap streamlines in a tributary stream in Interior Alaska, within a single Hydrologic Unit Code (HUC) 12 sub-basin.

APPENDIX B

We estimated the distribution of Arctic Grayling within our study area based on observations from the Alaska Department of Fish and Game Alaska Freshwater Fish Inventory Database (AFFID), and a digital watershed model. The AFFID is a cumulative catalog of fish observations across the State of Alaska. AFFID data is collected via ADF&G personnel and other researchers conducting sampling in Alaska. Sampling includes a wide variety of collection methods, but Arctic Grayling in this dataset were collected using angling, electrofishing, minnow trapping, visual surveys, and various netting techniques (hoop nets, seine nets, etc.).

We predicted the distribution of Arctic Grayling (hereafter grayling) based on stream reach-scale geomorphologic and hydrologic attributes that represented stream size and habitat accessibility derived using the program NetMap (Benda et al. 2007). Attributes were applied to 50–100 m digital stream reaches and included: mean annual stream flow (MAF; m^3/s), gradient (GRAD; %), stream width (m), and stream depth (m). Descriptions of how attributes were calculated are available in Falke and Paul (*in prєp*). Because stream width and depth were highly correlated with MAF (r = 0.86 and 0.89, respectively) and likely characterize the range of stream size and geometry in the study area, we limited our model to MAF and GRAD.

Grayling observations from the AFFID were restricted to those within the Yukon and Kuskokwim river basins in Alaska (N=899). Point observations were snapped to the nearest NetMap streamline, and a list of stream reaches where the species was present were identified. Based on "occupied" reaches, we first developed histograms to investigate the range of MAF and GRAD values that characterized streams where grayling were present (Figure B1). Next, we identified values at the 5^{th} and 95^{th} quantiles for MAF and GRAD. We considered all habitats with MAF > 5^{th} percentile, and GRAD < 5^{th} percentile (Table A1) as potential grayling habitat because grayling are limited in streams that are too small, and those with high gradients. Once threshold values were identified, we considered all reaches with MAF > 0.06 m^3/s and GRAD < 4% as the distribution of grayling in the study area.

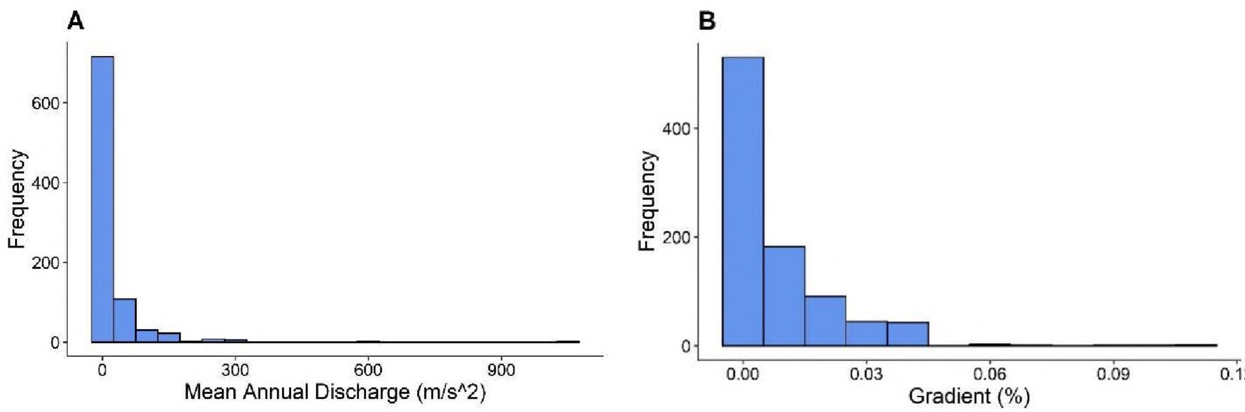

Figure B1. Histograms of Arctic Grayling occurrence with respect to mean annual flow **(A)** and stream gradient **(B)** in the Yukon River drainage, Interior Alaska.

Table B1.— Summary statistics for mean annual flow and gradient from the Yukon River drainage in Interior Alaska.

Parameter	**Min**	**5th percentile**	**Mean**	**Median**	**95th percentile**	**Max**
Mean annual stream flow (m^3/s)	0.02	0.06	27.10	5.00	28.99	105.84
Gradient	0%	4%	9%	7%	12%	11%

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APPENDIX C

During the summer of 2022 we sampled Arctic Grayling for abundance at six sites, and at each site we sampled below (control) and above (treatment) beaver dams (12 reaches total). Sites were selected using these criteria; sites were 1) accessible by foot, 2) an intact beaver dam was be present, and 3) the stream was appropriately sized to sample (i.e., wade-able and dam-able -4th order or smaller). See Chapter 2 for details about sample sites (e.g., "intensive" sites). Grayling were sampled using a dual pass technique including angling and electrofishing (whenever possible). Catch (number of individuals) and effort (minutes angled and minutes electrofished) were recorded, and each reach was measured for bank-full width every 10 m along the thalweg to calculate the area sampled (m^2). Captured fish were anesthetized with Aqui-S 20E (AQUI-S New Zealand LTD, Lower Hutt, New Zealand), and measured for fork length (FL; mm) and weight (g).

Effort (minutes angled and time electrofished to nearest minute) was used to calculate catch-per-unit-effort standardized by stream area (CPUE&A), and we used multi-gear mean standardization (MGMS) to calculate an unbiased estimate of fish abundance across gear types (Gibson-Reinemer et al. 2017). First, we calculated CPUE&A for angling, as the number of fish captured (n) divided by the number of anglers (a) times the angling time (t) times the area of the reach (m^2; $n/(a*t*A)$). Then CPUE&A for electrofishing was calculated as $n/(t*A)$. Finally, MGMS was used to combine CPUE&A for angling and electrofishing by standardizing each CPUE&A estimate by the mean of its respective CPUE&A (Gibson-Reinemer et al. 2017).

Fish abundance was lower in the beaver ponds than the control reaches for all but one site and sampling event (Figure B1; Colorado Creek, sampling event 1). Fish abundance tended to increase throughout the season, although this was not always the case. Three out of six sites

(Angel, Belle, and Rock Creek) had ≤ 1 fish pass the dam during the entire summer. The remaining sites appeared to have relatively unrestricted fish passage across the beaver dams, mostly due to partial dam failures or constant hydrologic linkages, although these were reduced throughout the summer as beavers built the dams up. Overall, these data suggest a bimodal relationship between Arctic Grayling passage over beaver dams, and a rough average of ~50% probability of passage, which was selected as the baseline in this study.

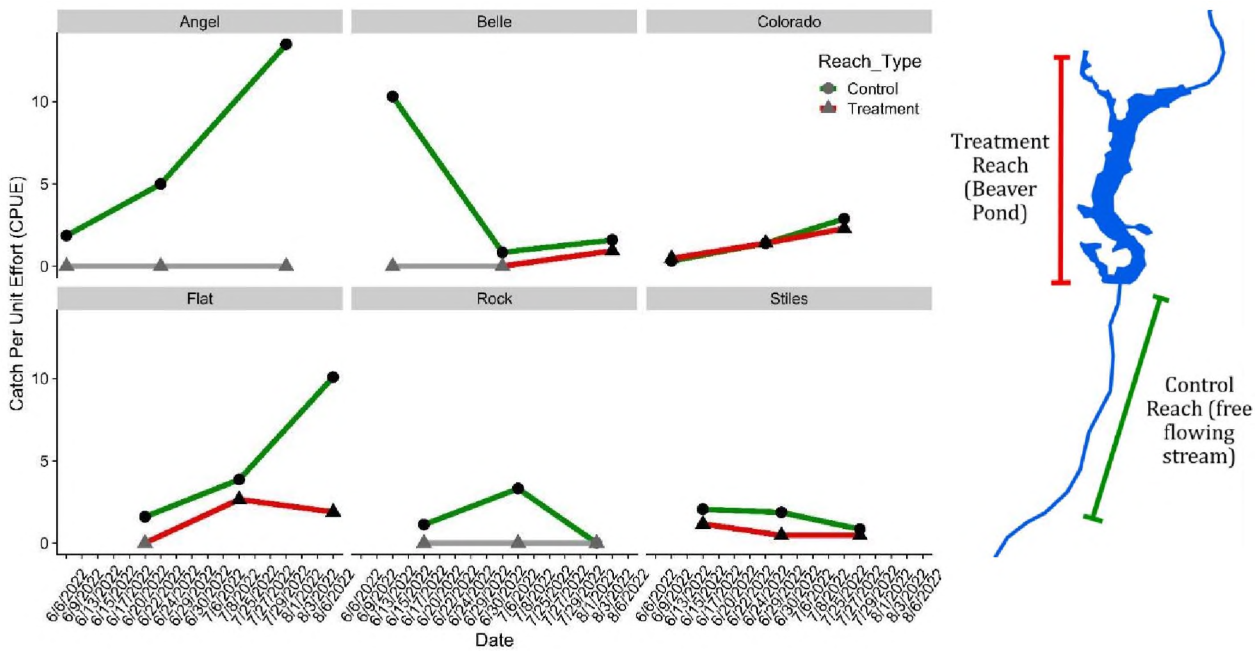

Figure C1. Estimated fish abundance across six sites and three sampling events during summer 2022. Green lines and circles represent fish abundance in control reaches (below dams), red lines and triangles represent fish abundance in treatment reaches (above dams). Greyed out shapes/colors mean that no fish were observed.

APPENDIX D

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 22, 2022

To:	Jeffrey Falke, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[1877773-4] When beavers get burned, do fish get fried? The role of beavers to mediate the effects of wildfire on freshwater fish habitat in Boreal Alaska

The IACUC reviewed and approved the New Project referenced above by Designated Member Review.

Received:	July 14, 2022
Approval Date:	July 22, 2022
Initial Approval Date:	July 22, 2022
Expiration Date:	July 22, 2023

This action is included on the August 11, 2022 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

(The following information is also available in a printable format in the IRBNet Forms and Templates)

HOW DO I REPORT CONCERNS ABOUT ANIMALS IN A UAF RESEARCH FACILITY?

- All "live" animal concerns related to care and use should be reported to the IACUC
- Email: uaf-iacuc@alaska.edu Phone: 474-7800
- Report form: www.uaf.edu/iacuc/report-concerns/
- IACUC Committee Members: www.uaf.edu/iacuc/iacuc-info/
- Additional information: www.uaf.edu/orl/responsible-conduct/research-misconduct/ and www.uaf.edu/orl/responsible-conduct/conflict-of-interest/

WHAT SHOULD I DO IF AN ACCIDENT OR INCIDENT OCCURS IN AN UAF ANIMAL FACILITY?

- **For all immediate human emergencies call 911** or UAF Dispatch at 474-7721 for less immediate emergencies.
- If you have **suffered an animal bite or other injury**, complete an "Accident/Incident Investigation form" (personal injury) form available at https://uaf.edu/safety/occupational-safety/accident-reporting.php.
- If an accident such as a **chemical spill** occurs, contact the Environmental Health, Safety, and Risk Management (EHS&RM) Supervisor at 474-5617 or the Hazmat Coordinator at 474-7889.

WHO DO I CONTACT IF I FIND A DEAD, INJURED, OR DISTRESSED ANIMAL IN A UAF RESEARCH FACILITY?

- During regular business hours, immediately contact facility staff and/or Veterinary Services Staff at 474-7020.
- After hours or on weekends, immediately contact facility staff and/or Veterinary Services Staff using the contact numbers posted on the "Emergency Contact Information" in the facility or call UAF Dispatch at 474-7721.
- Contact the IACUC at 474-7800 or uaf-iacuc@alaska.edu if an "Emergency Contact Information" sign is NOT posted in the facility.
- Contact the IACUC if you are not satisfied with the response from Vet Services.

HOW DO I REPORT ANY CONCERNS REGARDING WORK HAZARDS OR ANY GENERAL UNSAFE CONDITIONS?

- Complete an "Unsafe Condition Reporting Program" form, available at the EHS&RM website: www.uaf.edu/safety/unsafe-condition/

WHERE CAN I OBTAIN GENERAL OCCUPATIONAL SAFETY INFORMATION?

- https://www.uaf.edu/iacuc/uaf-policies-procedures/occupational-health-safety/