UNDERSTANDING HOW NORTHERN NORTH AMERICAN FRESHWATER FISHES ARE RESPONDING TO RAPID ENVIRONMENTAL CHANGE

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Abstract

Many northern fishes are experiencing unprecedented environmental changes across their ranges. However, limited empirical evidence exists for understanding how these changes may combine and potentially interact to influence fish diversity, individual species loss and gains, and overall productivity at broad spatial scales relevant for informing evidence-based conservation and management efforts.

This dissertation investigated how northern fishes are being impacted by cumulative and potentially interacting environmental changes across broad spatial scales including climate change, water quality, and land use. I examined two main research questions including 1) what are the key environmental variables currently influencing northern freshwater fishes? And 2) how is climate interacting with other variables to produce non-additive effects (i.e., antagonistic or synergistic interactions). To do this, I used fish community data from small streams across relatively intact regions of Alaska, small boreal streams in a more developed region of Alberta, Canada, and subarctic lakes in a rapidly changing permafrost region in the lower Mackenzie River basin.

Warming temperatures were linked to increased community diversity and abundance in small streams. However, this trend was not observed for fish communities in small subarctic lakes, where water quality degradation appeared to have a stronger role in regulating fish community health than direct warming. In all three chapters, there was evidence for localized gains and losses of individual fish species presence or relative abundance in association with mounting environmental changes that included warming, changes in precipitation, and land use. Some species may be temporarily benefiting from warmer conditions across their northern ranges, for example, Pacific salmon species including Coho *Oncorhynchus kisutch*, Chinook *Oncorhynchus tshawytscha*, and Sockeye *Oncorhynchus nerka* appeared to be experiencing a net distribution gain possibly due to warmer and longer growing seasons. In contrast, species declines associated with environmental changes were more likely to occur for Arctic specialists, species intolerant to environmental degradation, and large-bodied benthic species. Interactions between climate warming and land use were synergistic (i.e., the combined effect of both stressors was greater than the sum of their individual effects), highlighting the potential for amplified species declines under future warming and land use scenarios. Together, these results provide new information

that can be used to inform improved northern conservation planning amid rapid environmental changes.

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Figure 3. Partial plots for square-root transformed species richness with drainage area, frost-free period and watershed linear density. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

Figure 4. Partial plots for log-transformed catch per unit effort with drainage area and maximum July temperature. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

Figure 5. Partial plots for logit-transformed lithophils (%) with log-transformed drainage area and slope (top), with maximum July temperature by change in summer precipitation (ΔSMPP) (mm) (middle), and with square-root transformed linear disturbance by maximum July temperature (°C) (bottom). Cross sectional plots are shown at the 10th, 50th, and 90th percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence interval.

Figure 6. Partial plots for the Assemblage Tolerance Index (ATI) with log-transformed slope (top), with change in summer precipitation by log-transformed drainage area (m^2) (middle), and with logit-transformed land use by maximum July temperature (°C) (bottom). The ATI is a scale from one to ten, with a high value indicating a more tolerant community, and a low value indicating a more sensitive community. Cross sectional plots are shown at the 10^{th}, 50^{th}, and 90^{th} percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

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Figure 1. Study area in the lower Mackenzie River basin, Northwest Territories, Canada. Sites used for the regional water quality analysis of 203 lakes are coloured by study source, with

General Introduction

There is now overwhelming scientific evidence that environmental stressors may combine and interact in unexpected ways to threaten biodiversity, strongly suggesting that considering impacts in isolation is no longer sufficient for protecting ecosystems (Crain et al. 2008; Jackson et al. 2016). One key challenge that remains is understanding how potentially numerous co-occurring stressors will vary in natural systems with differing ecological processes and biological communities. For example, freshwater fishes are often under pressure from simultaneous multiple stressors including harvesting, habitat loss, pollution, and climate change, but their response may vary depending on local geo-climatic or biological factors with the potential to either amplify or dampen the overall effect (Reid et al. 2019). As the global biodiversity crisis deepens, strengthening our scientific understanding of cumulative and potentially interacting environmental effects in complex real-world systems will be an essential step forward for devising impactful conservation solutions.

One region that would greatly benefit from additional understanding of cumulative environmental effects is the North American north. Northern biodiversity faces a unique combination of growing threats as warmer and more variable precipitation regimes are leading to transformational landscape and ecosystem changes, particularly in regions historically associated with continuous permafrost or glacial inputs (Prowse et al. 2015; Wrona et al. 2016). In addition, mounting local human development pressures (e.g., new roads, oil and gas, mining, forestry) may combine and interact with co-occurring climate change pressures, leading to unanticipated impacts on northern biodiversity (Heino et al. 2009; Reist et al. 2016). Collectively, these changes are already influencing the distributions and abundances of northern fish species, and future changes are predicted to have substantial impacts on northern commercial, recreational, and subsistence fisheries (Meredith et al. 2019). These impacts will not be trivial, as current estimates for northern fisheries range high from 4.4 million CAD for the subsistence valuation of Arctic charr *Salvelinus alpinus* in Nunavut, to one billion US for northern salmon commercial and sport fisheries (Christiansen et al. 2013; Schoen et al. 2017). Further, the food security, culture, and overall well-being of hundreds of thousands of northern Indigenous citizens are deeply tied to their traditional knowledge, which is being increasingly undermined by rapid environmental change (Meredith et al. 2019).

Northern North American regions are enduring some of the greatest climate change rates on the planet, with some areas warming more than three times the global rate (Bush and Lemmen 2019). As a result, northern coldwater species are being pressed towards their northernmost range limits, and are experiencing increasingly novel habitat conditions and species interactions (Reist et al. 2006b; Dunmall et al. 2013; Heino et al. 2020). Temperature is both directly and indirectly related to fish populations at multiple ecosystem levels, making it difficult to disentangle climate-driven pathways. For example, climate change may alter hydrological patterns, ice cover, water quality, biogeochemical cycling, and food availability, all of which can influence fish population dynamics (Tonn et al. 2015). The cold-adaptive life histories of northern fish may also put them at greater risk to direct warming effects, as temperature is known to closely govern many important physiological processes including growth, reproduction, and survival (Magnuson et al. 1979). Warming impacts on individual fish species are predicted to vary depending on the combination of species' thermal tolerances, local conditions, and adaptive potential (Heino et al. 2009; Crozier and Hutchings 2014; Comte and Olden 2017). However, predictions may be further complicated as individual species are often influenced by multiple and potentially counteracting environmental effects acting over varying life stages and habitats. For example, Alaskan Pacific salmon may benefit from warmer water temperatures during the adult marine phase and the juvenile freshwater rearing phase, but warming during the upstream spawning migration can prevent fish from successfully reaching their spawning grounds (Ohlberger et al. 2016; Cunningham et al. 2018; Jones et al. 2020). At the community-level, ecological theory suggests that warming may produce increases in northern biodiversity and productivity due to longer growing seasons, more abundant food resources, and a shorter winter period (Shuter and Post 1990; Reist et al. 2006b; Shuter et al. 2012). However, it is currently unknown if this extends to northern fish communities where unprecedented levels of climate change may outpace the adaptive capacity of individual species, or the potential for thermal niche tracking and species reassembly (i.e., where warmer water fishes replace colder water fishes).

Anthropogenic effects are a growing concern in sensitive northern regions that have remained relatively undisturbed from direct human influence to-date (CAFF 2013; Meredith et al. 2019). In particular, new development projects have the ability to open up previously intact landscapes to a myriad of potentially negative, cascading effects including road development, novel

recreational fishing access, and additional development projects (Chetkiewicz et al. 2017). Permafrost landscapes provide additional challenges to developers, and best practices for minimal effects on ecosystems are often actively managed as more information is gathered (Dillon Consulting Limited 2007; Raynolds et al. 2014). Gravel roads are commonly employed in the far north, however excessive road dust has been linked to changes in local ecology, including water chemistry, with potentially negative effects on aquatic food web health (Walker and Everett 1987; Zhu et al. 2019). In addition to direct aquatic habitat loss, land use changes are known to alter local hydrology, remove stabilizing riparian vegetation, increase sedimentation and nutrients, reduce food and woody debris inputs, and increase water temperatures (Mantyka-Pringle et al. 2014; Cott et al. 2015). Because northern systems tend to be naturally nutrient-poor, moderate increases in nutrients or sedimentation may be beneficial in the short-term. However, nutrient increases due to anthropogenic inputs have demonstrated that northern systems are not immune to potential eutrophication-driven declines in aquatic diversity (Schindler and Smol 2009; Hayden et al. 2019).

Based on our relatively limited empirical knowledge of northern fishes, it is difficult to predict if environmental stressor interactions will occur, or in which direction. Here, multiple stressor research on southern fishes may be used as a starting point for identifying potential *a priori* predictions for northern fish. For example, meta-analyses of freshwater stressor studies have revealed that antagonisms, (i.e., when the combined effect of two stressors is less than the sum of their individual effects), may be more common in freshwater systems compared to either marine or terrestrial areas, possibly due to a naturally wide range of environmental variability (Jackson et al. 2016). Further, warming in freshwater systems was most commonly affiliated with reversal interactions (i.e., a type of antagonistic interaction with opposing effect directions), suggesting that temperature may have a mediating effect on co-occurring stressors (Jackson et al. 2016). When considering ecosystem level, the tendency for the community level response to be more antagonistic than the population or individual levels seemed to hold true for the majority of studies (e.g., Crain et al. 2008; Jackson et al. 2016). In these cases, it was suggested that more stress-tolerant species were able to take advantage of local diversity loss, so that the net effect was not as strong at the community level (i.e. buffered impacts via compensatory species dynamics).

Northern fish demonstrate a range of common traits allowing them to thrive in their often harsh and dynamic ecosystems that can be viewed as their initial 'toolkit' for dealing with rapid environmental change. Certain adaptive characteristics common to many northern fishes (e.g., diet flexibility, enhanced migratory or exploratory behaviours, and delayed or infrequent maturation), combined with the known prevalence of antagonistic interactions in freshwater systems suggests that northern biological communities may have some built-in capacity for withstanding environmental change (Vinebrooke et al. 2004; Jackson et al. 2016). In contrast, other defining characteristics such as low species diversities, slow growth, cold tolerance, complex migrations, and lowered agonistic behaviour may put northern fish communities at higher risk to novel stressors acting on different adaptive pathways (Power 2002; Power et al. 2008; Tonn et al. 2015).

In recent years, there has been a major push towards understanding biodiversity trends within the context of rapid northern environmental change. There have been several International initiatives detailing the potential and observed effects of climate change and other anthropogenic activities on northern freshwater biodiversity, and these efforts have been instrumental in underscoring the sheer magnitude and scope of this critical conservation issue (Arctic Climate Impact Assessment 2005; CAFF 2013; Prowse et al. 2015; Wrona et al. 2016; Lento et al. 2019; Heino et al. 2020). Some important first steps have been to coordinate an International Arctic freshwater monitoring plan (Culp et al. 2012), to collate existing freshwater biodiversity data across the circumpolar north (Lento et al. 2019), and to examine broad-scale freshwater biodiversity trends and key environmental drivers such as glacial history, climate, and hydraulic connectivity (e.g., Laske et al. 2016, 2019; Lento et al. 2020).

Despite these increasing efforts, bridging the gap between science and conservation remains a monumental challenge for decision-makers across the circumpolar north (Heino et al. 2020). The current escalation of northern environmental changes threatens to outpace our ability to document, predict, and mitigate impacts on northern biodiversity across vast and ecologically complex northern landscapes. Furthermore, many northern regions remain historically understudied, challenging our ability to recognize trends amid a backdrop of changing baselines (Lento et al. 2019). Although there has been much written on the potential effects to northern freshwater fish diversity with ongoing environmental changes, very few studies have provided

empirical evidence of co-occurring environmental changes, and fewer have examined cumulative impacts across broad spatial scales relevant for informing evidence-based conservation and management efforts (but see: Ohlberger et al. 2016; Hayden et al. 2017, 2019; Cunningham et al. 2018; Connors et al. 2020; Jones et al. 2020). Big-picture assessments of biodiversity change using broad spatial datasets are particularly needed as they provide critical insight into climate change processes over space, which is an important proxy for time due to the lack of long-term monitoring in northern regions (Pearson and Dawson 2003; Brucet et al. 2013; Heino et al. 2020). Further, geographically broad studies often inherently include wider ecological variability revealing important context-dependence that could mediate impacts on local biodiversity (i.e., local climate and landscape factors, regional species pools, and the unique combination of regional threats; Reist et al. 2006; Heino et al. 2009). Finally, if northern biodiversity stewardship is not conducted with the big picture in mind, northern species may be increasingly vulnerable to numerous small impacts that have no measurable effect alone, but in combination may be significant i.e. “Death by 1000 cuts” (Seitz et al. 2011).

Here, I present three research chapters that examine how northern fishes are being impacted by cumulative and potentially interacting environmental changes across broad spatial scales including climate change, water quality, and land use. To do this, I acquired large, previously unanalyzed datasets that collectively span more than 25 major drainage basins and over 650,000 km^2 across northern North America. In addition, my PhD fieldwork collected new data from 50 lakes in the Mackenzie River Delta, one of the most quickly changing regions in northern Canada. In the first chapter, I looked at how multiple environmental variables including current and long-term climate change, landscape factors, anthropogenic land use, and fire disturbance, were contributing to stream fish diversity trends across the state of Alaska. With this broadscale dataset, I aimed to examine three research questions: 1) which key environmental variables are influencing Alaskan stream fishes? 2) Is climate interacting with other environmental variables to produce non-additive effects (i.e. antagonistic or synergistic interactions (Piggott et al., 2015))? And 3) is the overall effect of climate change positive or negative? As Alaska contains an extremely diverse range of ecoregions and a wide climate gradient, this study provided an important setting for elucidating broad patterns of change, as well as for identifying key mediating factors at smaller scales. In the second chapter, the interactive effects of climate change and anthropogenic land use conversion on stream fishes were more closely examined in a

northern region experiencing relatively heightened land use pressures. For this study, I asked (1) how are cumulative land use pressures influencing boreal stream fish community structure? And (2) is climate producing a buffering (antagonistic) or amplified (synergistic) effect on concurrent stressors across a broad, real-world landscape? As many northern regions remain relatively undisturbed from direct human impacts, this study provided an important first look at how climate change and development pressures may combine and interact to influence northern fish diversity. Lastly, in the third chapter I aimed to answer the research question: what are the current drivers of fish community health in lower Mackenzie River basin lakes? A supplementary analysis further explored the question: is there any evidence for the effects of climate change or road use on water quality in regional lakes? Results from this chapter contributed new information about emerging stressors to fish diversity across the taiga-tundra transition in a rapidly changing ice-rich permafrost region. Further, my study findings provided valuable insight into the potential for fish habitat degradation due to the indirect effects of climate warming and new road development across sensitive permafrost terrain.

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Chapter 1: Impacts of co-occurring environmental changes on Alaskan stream fishes

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AM, CMP, and SS conceived the research ideas; AM acquired funding and data, analysed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Freshwater Biology.

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Summary

1. Freshwater fishes are now facing unprecedented environmental changes across their northern ranges, especially due to rapid warming occurring at higher latitudes. However, empirical research that examines co-occurring environmental effects on northern fish communities remains limited.
2. We used fish community data from 1587 Alaskan stream sites to examine the potential combined and interacting effects of climate change, current weather, habitat, land use, and fire on two community-level metrics (species richness, relative abundance), and on the distributions of three Alaskan fish species.
3. Our models were 71-76% accurate in predicting the distribution of Alaskan stream fishes using a combination of climate and habitat variables. In contrast to other freshwater ecosystems that are most threatened by land use pressures, we did not detect any evidence for the potential stress of anthropogenic land use or fire on stream fishes.
4. Warming temperatures increased overall community richness and abundance but produced differing responses at the species level. Juvenile salmon presence was positively associated with several climate variables including warmer spring and fall temperatures and wetter summers. In comparison, warmer seasonal temperatures contributed to declines for northern-adapted species such as Arctic grayling and Dolly Varden.
5. This study highlights the overarching role of current and changing climate in regulating northern stream fish biodiversity. Although many fish species may benefit from climate change across their northern ranges, localized declines are likely to occur and may prove detrimental for communities with limited fishing portfolios. Climate change adaptation and mitigation strategies customized for rapidly changing northern ecosystems will play an essential role in preserving ecologically unique northern species.

Introduction

Freshwater ecosystems are now facing an unprecedented biodiversity crisis worldwide, with potentially alarming implications for water, food and economic security (Reid et al. 2019). Even the most remote corners of the planet, such as northern North America, are becoming increasingly impacted by heightened climatic changes, exploitation, resource extraction, and invading southern competitors (CAFF 2013). Despite these mounting changes, our understanding of co-occurring environmental effects remains limited worldwide (Jackson et al. 2016), and even more so in ecologically unique northern ecosystems that have received relatively less attention (Reist et al. 2006b).

Climate change is quickly emerging as the leading threat to northern freshwater biodiversity, surpassing land use as the number one stressor observed at lower latitudes (Heino et al. 2009; Reid et al. 2019). In northern ecosystems, the greatest rates of climate warming starkly intersect with the most cold-adapted species, and freshwater landscapes are being rapidly altered following widespread permafrost degradation and glacial recession (Wrona et al. 2013; Schoen et al. 2017). In particular, the rapidly changing winter period is producing some of the greatest impacts on northern species, with potential benefits including improved overwintering survival, leading to increases in biodiversity and productivity (Reynolds 1997; Reist et al. 2006b; Heino et al. 2009). Additionally, earlier spring break-up and warmer summer temperatures have been linked to increased growth opportunities for Alaskan juvenile salmon, promoting size-dependent overwintering survival and ultimately productivity (Schindler et al. 2005; Ohlberger et al. 2016; Cunningham et al. 2018; Cline et al. 2019). While many climate change impacts have the potential to produce positive effects on northern fishes in the short-term, continued warming may produce negative effects once species' warming tolerances are surpassed (Heino et al. 2009; Crozier and Hutchings 2014; Comte and Olden 2017). Further, changes to summer streamflow may negatively impact stream fishes if feeding or migration activities are compromised, and species are unable to adapt (Neuswanger et al. 2015; Heim et al. 2015; Cunningham et al. 2018).

The possibility of 'ecological surprises', where an unexpected outcome is revealed based on a key interacting variable, can yield detrimental outcomes for environmental managers if left undiscovered (Ormerod et al. 2010; Jackson et al. 2016; Reid et al. 2019). In northern systems, the potential for environmental interactions is largely unexplored territory, suggesting that there

may be many ecological surprises to uncover in the future (Wrona et al. 2013). In particular, interactions may occur between the current climatic conditions and the rates of change being experienced, possibly revealing complex trade-offs between preferred ecological niches and the ability of fishes to adapt (Crozier and Hutchings 2014; Sloat et al. 2017). Further, interactions between climate and terrain may arise due to the complexity of the northern landscape, owing to a wide range of ecoregions that span from coastal to alpine, and with varying magnitudes of permafrost integrity and glaciation (Nowacki et al. 2001; Reist et al. 2006b).

The objective of this study was to identify how Alaskan stream fishes are responding to multiple environmental variables (climate change, current weather, habitat, land use, and fire). Habitat variables such as mean watershed elevation and drainage area were included as they are naturally important determinants of fish presence and abundance and are also strongly linked to water temperature in Alaskan streams (Mauger et al. 2017). We aimed to examine three research questions: 1) which key environmental variables are influencing Alaskan stream fishes? 2) Is climate interacting with other environmental variables to produce non-additive effects (i.e. antagonistic or synergistic interactions (Piggott et al., 2015))? And 3) is the overall effect of climate change positive or negative? Based on these questions, we derived hypotheses for two community-level metrics (species richness, catch-per-unit-effort) and for three Alaskan fish species including Arctic grayling, Dolly Varden, and juvenile salmon species (Table 1). Generally, we predicted that:

i) Warmer and wetter winters would benefit most species due to the potential for increased overwintering habitat (e.g., Craig, 1989; Prowse et al., 2006; Prucha et al., 2011); increased summer warming would negatively affect species once individual species thermal optima were surpassed (Reist et al. 2006b); changes in precipitation during the ice-free season would produce varying responses depending on species, life stage, and regional climate (Table 1);

ii) Interactions between environmental variables would vary depending on local conditions (Table 2). For example, we expected that incubating eggs may be increasingly sensitive to scouring flows in warmer and wetter regions (Sloat et al. 2017), and that high elevation streams would provide climate refuges amid rising ambient air temperatures (Lisi et al. 2015; Mauger et al. 2017).

iii) At the species-level, the positive effects of warmer winters and spawning seasons (spring and fall) paired with longer growing seasons would outweigh any negative effects due to thermal stress (Reist et al. 2006a, 2006b; Leppi et al. 2014); at the community-level, warming in both seasons would yield predominantly positive effects resulting in increased richness and community abundances (Heino et al. 2009; Christiansen et al. 2013).

Methods

Study area

The state of Alaska has an area of 1,700,000 km^2, and a wide range of climatic conditions with mean annual temperatures ranging from 5°C in the south to –11°C in the north (Figure 1). Further, Alaska's 32 distinct ecoregions signify the wide diversity of terrain and climate types found across the state, including coastal temperate rainforests, the highest mountain ranges in North America, and barren, polar deserts (Nowacki et al. 2001). Over the past sixty years, Alaska has warmed more than twice the global rate (+1.7°C), with most warming and changes in precipitation occurring during the winter season (Bieniek et al. 2014; Schoen et al. 2017).

Study species

Our study focused on three Alaskan stream fish species or closely related genera including Arctic grayling *Thymallus arcticus*, Dolly Varden *Salvelinus malma*, and Pacific salmon species that exhibit a freshwater rearing phase such as Coho *Oncorhynchus kisutch*, Chinook *Oncorhynchus tshawytscha*, and Sockeye *Oncorhynchus nerka*. Potential climate variables that may influence each species were identified *a priori* based on a review of the existing literature (Table 1) and are described briefly below.

Arctic grayling is a widely distributed, spring-spawning salmonid that displays extensive seasonal migrations between spawning, feeding, and overwintering habitats (Stewart et al. 2007). We predicted that Arctic grayling would benefit from warmer winter and spring weather, and from wetter conditions during their critical migratory period to overwintering habitats in late summer and fall (Craig 1989; Wedekind and Kung 2010; Betts and Kane 2015; Heim et al. 2015, 2016). Based on previous studies, we also predicted that summer climate variables would

produce differing impacts on grayling depending on life stage and habitat conditions (Deegan et al. 1999; Jones et al. 2003; Stewart et al. 2007; Heim et al. 2015).

Dolly Varden is a cold-adapted char that heavily relies on groundwater-fed habitats for providing cold water refuges in summer and overwintering habitats in winter (Stewart et al. 2010). Alaska supports two recognized sub-species of Dolly Varden which are divided into northern and southern forms by the Alaska Range (COSEWIC 2010). Further, Dolly Varden exhibit both anadromous and non-anadromous life history types, with anadromous fish migrating to the marine environment for summer feeding and returning to freshwater for spawning and overwintering. We predicted that Dolly Varden would benefit from warmer and wetter winters, provided that important groundwater inputs were not disrupted to key spawning and overwintering areas (Craig 1989; Prowse et al. 2006a; Reist et al. 2006b; Stewart et al. 2010; Prucha et al. 2011; Brown et al. 2014). In contrast, we expected that summer warming would produce mixed effects on Dolly Varden presence, with the potential for declines due to thermal stress, increased interactions with warmer water species, and impacts to streamflow and water chemistry following permafrost degradation (Bryant et al. 2004; Stewart et al. 2010; Durand et al. 2011).

Alaska supports all five Pacific salmon species, however, only Coho, Chinook, and Sockeye salmon spend one or more years in freshwater before migrating to the ocean (Bryant 2009). Considerable research has been conducted investigating climate change effects on Alaskan salmon species at the local and regional scales, providing a strong foundation for developing our predictions that may be observed at the state-scale. Based on these studies, we expected that juvenile salmon presence would increase with warmer winter and fall temperatures, due to increased survival of incubating eggs (Leppi et al. 2014; Neuswanger et al. 2015; Dunmall et al. 2016). Warmer spring and summer conditions also have the potential to facilitate salmon establishment due to a longer and more productive growing season, lowering the risk of size-dependent mortality (Schindler et al. 2005; Ohlberger et al. 2016; Cunningham et al. 2018). Despite these many potential benefits, several studies have also highlighted the potential negative implications of a warmer and wetter climate for Alaskan salmon due to thermal stress, lowered foraging abilities, scouring of incubating eggs, and phenology mis-matches (Bryant

2009; Leppi et al. 2014; Shanley and Albert 2014; Neuswanger et al. 2015; Wobus et al. 2015; Mauger et al. 2017; Cunningham et al. 2018; Adelfio et al. 2019).

Data sources and processing

Stream fish catch data were obtained from the Alaska Freshwater Fish Inventory online database, created and maintained by the Alaska Department of Fish and Game (AFFI 1973). For this study, catch data from 1587 stream sampling sites were kept for inclusion after individual vetting for sufficient sampling information, efficiency, and comparable habitat types. To aid in comparability, only one-pass backpack electrofishing data from wadeable streams were used. All sampling occurred during the ice-free months (May-Oct) from 1988 to 2016, however, most sampling targeted the maximum stream fish residency period of August (mean date of sampling = August 15, standard deviation = 13 days). In instances where sites were sampled repeatedly or where sites were within the same stream reach, a single sampling event was selected for inclusion based on numerous criteria including the higher sampling efficiency score, more comparable date of capture (i.e. July/August was preferred over June), greater completeness of water temperature data, and/or higher total number of fish caught.

Water temperature data (°C) were collected during the fish sampling event. Although repeated sampling would have been preferable to ensure adequate representation of thermal conditions, the use of *in situ* data was important for capturing potential local processes influencing thermal habitat (e.g., presence of groundwater inputs, glacial melt, and upstream lakes) that would have been missed using air temperature proxies alone (Mauger et al. 2017; Schoen et al. 2017).

Watershed delineation was completed for each sampling site using a 2-arc-second digital elevation model grid from the USGS National Elevation Dataset. The lower watershed extent was chosen based on the nearest downstream reach break, using the USGS NHD reach codes. Drainage basin area (m^2) and mean watershed elevation (m) were calculated for each delineated watershed.

Land use data collection followed an altered version of the National Fish Habitat Partnership 2015 Human Disturbance Data for Alaska methodology (Crawford et al., 2016). Road data were obtained from the US Census Tiger Road dataset dating back to 2000 (www.census.gov/geo).

Pipeline, railway, and mine location data were available from the Alaska State Geospatial Data Clearinghouse (http://www.asgdc.state.ak.us/). Airport locations were identified using the USGS National Transportation dataset (2017; https://catalog.data/gov/dataset). Discharge and contaminated site locations were obtained from the US Environmental Protection Agency's National Pollutant Discharge Elimination System (NPDES) and the Alaska Department of Environmental Conservation's Contaminated Site Program database, respectively. In addition to acquiring land use data, we obtained fire disturbance data from the Northwest Boreal Landscape Conservation Cooperative (https://nwblcc.org/).

We calculated linear density by summing all roads, railways and pipelines that intersected a watershed, divided by the total watershed area. Similarly, point density was the total number of airports, mines, discharges, and contaminated sites per unit of drainage area. For mine analyses, sites identified as either mines or prospect locations were included. Only fires that occurred within a ten-year window prior to sampling were selected for analyses. To ensure that all other land use and development data were reflective of the sampling time period, metadata and historic imagery on Google Earth were examined where possible to verify appropriateness for inclusion in analyses. All GIS data processing was completed in ArcMap Desktop 10.5.

Climate data were obtained from the ClimateNA program (version 5.5) which has an approximately 4 km resolution and was available for the period 1901-2016 (Wang et al. 2016). Seasonal variables were chosen to reflect the long winter period in Alaska, with winter being from November to March, spring from April to May, summer from June to August, and fall from September to October. Climate variables were split into two groups, the first being 'current weather' and the second being 'climate change'. All current weather means were based on the thirty years prior to the fish collection date. Climate change variables were calculated as the mean difference between the recent thirty-year period and the previous thirty-year period.

Data analyses

We used two community-level metrics (species richness, CPUE = total catch per 100s of electrofishing effort) and three species-level metrics (individual species presence/absence for three species). Individual species models were created for the most abundant and widespread species or closely related genera: Arctic grayling, Dolly Varden, and juvenile salmon species

(Coho (71% of total captured), Chinook (25% of total captured), and Sockeye (4% of total captured)).

Predictor variables were divided into four main categories: current weather, climate change, habitat, and land use and fire (Table 3). Select variables were transformed where required to improve the graphical interpretation of highly skewed data distributions, and to improve the normality of the final model residuals (Bolker et al. 2009). Specifically, these transformations included log-transformation of drainage area and total CPUE, and square-root transformation of species richness.

To select final models, we followed data analysis steps recommended for investigating co-occurring and interactive predictor variables as outlined in Feld, Segurado, and Gutiérrez-Cánovas (2016; Figure A1). First, boosted tree analyses were conducted as an initial screening of metric-specific predictor variables identified in Table 1. Following the removal of variables with no predictive power (Figure A1), final boosted tree models allowed us to identify important predictors, assess the relative contribution of each predictor, and to determine potential interacting variables (Elith and Leathwick 2017). Next, using variables and potential interactions identified with boosted trees, we ran linear and logistic regression mixed models to determine standardized effect sizes and classify interaction types. To account for potential nonlinear relationships, quadratic functions were included in the initial mixed model for select variables. For mixed model selection we used an information-theoretic approach following Johnson and Omland (2004) and Grueber et al. (2011), and by employing the *dredge* function from the Multi-Model Inference package (*MuMin*) (Barton 2018). We selected the best model based on the lowest AICc value. In the event that a final model contained an interaction or quadratic term, we also retained the lower order term. Year of sampling and HUC8-level watershed were included as random intercepts to reduce spatial and temporal autocorrelation. To reduce potential effects of spatial outliers, we only retained watersheds that had more than three sites, resulting in a dataset of n=1571 for mixed models. Predictor variables were standardized using the function *standardize* in the *arm* package which converts all variables to a comparable, unitless scale (Gelman et al. 2018). Final model performance was also examined with a Pseudo-R^2 statistic for mixed models using the function *r.squaredGLMM* from the *MuMIn* package (Nakagawa et al. 2017). The reported conditional and marginal variances explained are the variances with and

without the random effects, respectively. We tested for potential multicollinearity among predictor variables by calculating variance inflation factors (VIFs) on the final standardized models. All final models had variance inflation factors less than 4, indicating acceptable levels of collinearity (James et al. 2013).

To compute classification success of the final presence/absence models, we split data into independent training (70%) and testing (30%) datasets. The threshold for classifying predicted probability of capture was determined using a receiver operating characteristic curve, which aims to maximize model sensitivity (proportion of true positives) and specificity (proportion of true negatives) (Fielding and Bell 1997). For logistic regressions, mixed effects were removed during the classification step as the number of levels were not equal in testing and training datasets.

To classify the direction of each potential environmental effect, we inspected partial plot trends within one standard deviation of the mean value. For example, species richness demonstrated a unimodal relationship with water temperature, however, the majority of the data (within one standard deviation of the mean for water temperature, see Table 3) demonstrated a positive relationship. Therefore, this relationship was conservatively classified as positive. Last, we used terminology adapted from Piggott et al. (2015) to classify interaction types as either synergistic or antagonistic.

Results

Which key environmental variables are influencing Alaskan stream fishes?

Alaskan stream fish metrics (species richness, total CPUE, and presence/absence for Arctic grayling, Dolly Varden, and juvenile Pacific salmon species) were best explained by current weather (56%) and climate change variables (24%), followed by habitat variables such as elevation and drainage area (20%) (Table A1). Land use and fire variables did not provide any predictive ability in the boosted tree models and were subsequently removed.

Warmer summer water temperatures were positively related to species richness and total community CPUE, whereas Dolly Varden were negatively related, and the two remaining species had mixed results that were dependent on interactions with other climate variables (Tables 4-5, Table A2, Figures 2-3). Regions with currently warmer fall, winter, and spring seasons supported more species and higher total community abundances, with the exception of

Arctic grayling which were more prevalent in colder regions. In contrast, when considering long-term winter temperature changes, both Dolly Varden and juvenile salmon presence were lower in regions experiencing higher rates of winter warming. Notably, several temperature variables that were included in our original predictions (Table 1) were screened out during model selection, including summer air temperature variables for all five metrics, spring temperature and change in spring temperature for Arctic grayling, and winter temperature for juvenile salmon.

Seasonal precipitation variables yielded mixed results for total community abundance and for all three fish species examined (Tables 4-5, Figures 2-3). Dolly Varden presence was positively related to wetter winters, except in regions where current baseline values were already high (Figure 4). Juvenile salmon presence was greater in regions with currently wetter summers, whereas declines were observed in regions experiencing more fall precipitation. Arctic grayling presence was also associated with changes in fall precipitation, although the relationship was unimodal with peak values occurring at approximately +10mm. Overall community catch was highest in regions that have been trending toward drier summers, and lowest in regions experiencing wetter summer climate. There was no support for retaining several hypothesized precipitation variables in our final models (Table 1), including summer precipitation variables and current fall precipitation for Arctic grayling, and change in winter and change in summer precipitation for juvenile salmon.

Is climate interacting with other environmental variables to produce non-additive effects (i.e. antagonistic or synergistic interactions)?

Five potential interactions were observed, including two current weather interactions, one current weather × climate change interaction, and two current weather × habitat interactions (Figure 4, Figure A2). Three interactions were identified as antagonistic and two as synergistic (Table A3).

Warmer winters appeared to enhance the potential positive effects of increased drainage basin size on species richness (Figure 4a). In contrast, the positive effect of warmer winters on species richness was removed and possibly even reversed at higher elevations (Table A3, Figure A2).

Current weather interactions revealed differing species responses depending on local climatic conditions. For Arctic grayling, the negative effects of warmer water temperatures were enhanced in colder regions and reduced in warmer regions (Figure 4b). An antagonistic

interaction was observed between winter precipitation and change in winter precipitation for Dolly Varden, where the positive effects of increasing winter precipitation were lessened in regions that were already experiencing wetter winters (Figure 4c). Additionally, water temperature interacted with summer precipitation for juvenile salmon, with increasing precipitation dampening the negative effects of warmer water temperatures (Figure 4d).

Is the overall effect of climate change positive or negative?

Species richness, total CPUE, and juvenile salmon demonstrated predominantly positive responses to climate-related variables, whereas Arctic grayling and Dolly Varden demonstrated more mixed and negative associations (Figures 2-3). Species richness and total CPUE increased in regions with warmer winter air temperatures, warmer summer water temperatures, and at lower elevations (Figure 2). For juvenile salmon, strong positive effect sizes relating to warmer current spring and fall temperatures and wetter summers outweighed potential negative effects relating to higher water temperatures, wetter fall conditions, and higher winter warming rates (Figure 3).

The overall effect of climate change on the two northern-adapted species we examined was less straightforward given more equal proportions of positive and negative effects, and more 'mixed' effects due to nonlinear and interactive relationships (Figure 3). For example, Dolly Varden were positively related to warmer and wetter winters but appeared equally, if not more vulnerable to summer warming as they were strongly associated with colder, high elevation sites and lower water temperatures. Further, the potential benefit of warmer winters was complex as Dolly Varden also decreased in regions experiencing high levels of winter warming (Figure A3). Overall, Arctic grayling demonstrated the highest number of negative and mixed effects relating to climate change variables, including a strong decline observed in regions with warmer winters (Figure 3). However, grayling were also positively related to wetter fall conditions, and warmer summers in regions with milder winters (Figure 4b), potentially offsetting some of the negative effects associated with rapidly warming Alaskan winters (Table 3).

Discussion

Our study provides novel empirical evidence for combined and interacting environmental effects on Alaskan stream fishes. Species distributions were best predicted using a combination of current climate, climate change, and habitat variables, suggesting that climate may play an

elevated role in determining northern stream fish assemblages. We identified several potential climatic trade-offs that stream fishes may be facing amid their rapidly changing environments, highlighting the need to consider a wide range of cumulative and potentially interacting positive, negative, and context-specific effects that may yield unexpected results for fisheries managers. Overall, our results suggest that stream fish richness and abundance may be benefitting from ongoing climate change including warmer and wetter winters. Individual species had more complex responses to climate variables, with Pacific salmon distributions potentially increasing and the distributions of northern-adapted species such as Arctic grayling potentially decreasing in response to a changing climate.

Environmental effects on Alaskan stream fishes

Community-level responses

Our results suggest that stream fish richness and abundance may benefit from increasingly warmer and wetter winters forecasted for many Alaskan ecoregions, particularly as the winter season is experiencing the highest rates of environmental change (Bieniek et al., 2014). Our findings agree with ecological theory derived from latitudinal gradient studies, which describe the key role of climate in regulating ecosystem diversity and abundance (e.g., Abell et al., 2008; Brucet et al., 2013; Rypel & David, 2017). As many small, northern streams are often uninhabitable during the long and harsh winter, warmer winters have the potential to significantly reduce this bottleneck by increasing suitable overwintering habitat, shortening the resource-poor period, and by facilitating a longer ice-free growing season (Shuter and Post 1990; Reynolds 1997; Reist et al. 2006b). Further, more winter precipitation has the potential to increase overwintering habitat if streamflows are enhanced, or if an increased snowpack provides additional insulation and under-ice stability (Prowse et al., 2006; Reist et al., 2006b; Prucha et al., 2011).

Summer warming had positive effects at the community-level despite mixed results for individual species. The positive relationship between summer warming and Alaskan stream fish diversity may be somewhat unexpected based on the cold thermal requirements of these northern species, however, summer water temperatures in this dataset typically remained below or near the upper thermal preferences for many Alaskan stream fishes including Arctic lamprey *Lethenteron camtschaticum*, burbot *Lota lota*, longnose sucker *Catostomus catostomus*, northern

pike *Esox lucius*, rainbow trout *Oncorhynchus mykiss*, stickleback (Gasterosteidae) species, sculpin (Cottidae) species, and southern Arctic grayling populations (5.8 – 12.2°C; Hasnain, Minns, & Shuter, 2010). Further, although mainly positive effects were observed in this dataset, significant quadratic terms suggest that additional warming may begin to reduce both richness and CPUE if cold-adapted fishes are not adequately replaced by warmer water species.

Although climate variables produced predominantly positive effects at the community level, we observed a few exceptions including declines in warmer, high elevation regions and in areas receiving more summer precipitation. While the mechanism for declining species richness in high elevation regions with warmer winters is unclear, it is possible that these habitats may be more vulnerable to increased winter scouring flows, negatively impacting the survival of incubating eggs (Sloat et al. 2017).

The relationship between increased summer precipitation and declining community abundance was unexpected, particularly as summer drought has been identified as a potential stressor with ongoing climate change in southcentral Alaska (Schoen et al. 2017). In addition, juvenile salmon presence was found to be higher in regions with more summer precipitation in this dataset, suggesting that other species with lower summer flow requirements may be driving this overall community level trend. However, changes in stream flow have the potential to be either positive or negative depending on the baseline condition and the life history requirements of the species present (Bradford and Heinonen 2008). For example, studies of Alaskan Arctic grayling have revealed that increasing streamflow benefitted adult growth while concurrently reducing juvenile growth (Deegan et al. 1999). As many juvenile fish were present in this dataset, the community level decline with increasing summer precipitation may be due to a small, negative effect on juvenile feeding efficiency (Jones et al. 2003; Neuswanger et al. 2015; Cunningham et al. 2018), with potential implications for size-dependent overwintering survival and ultimately abundance (Shuter and Post 1990).

Species responses

Similar to what was observed for our community-level models, winter climate variables were often the strongest predictors in our species distribution models. As predicted, we found that Dolly Varden were positively related to winter temperature and precipitation, likely due to increased overwintering opportunities. In contrast, Arctic grayling were unexpectedly more

prevalent in colder regions, despite inherently shorter growing seasons and more limited overwintering habitat (Craig 1989). Although more research would be required to substantiate and examine the correlation with colder winters, Arctic grayling populations are well adapted for survival in harsh, northern conditions as exemplified by their under-ice spawning events, complex seasonal migrations, and extensive holarctic distribution (Stewart et al. 2007). In contrast, Arctic grayling have been threatened or extirpated throughout much of their southern range owing to several stressors including interactions with warmer water species (Van Kirk and Benjamin 2001).

Juvenile salmon presence was most strongly related to warmer spring and fall temperatures and wetter summer conditions in our models. The positive link between spring climate and species fitness has been established by several Alaskan salmon studies, with an earlier and warmer spring providing enhanced juvenile growth opportunities during the freshwater rearing phase (e.g., Schindler et al., 2005; Ohlberger et al., 2016; Cunningham et al., 2018). In addition, cool fall temperatures have been identified as a key barrier for northward establishment, as successful salmon spawning and early embryo survival are greatly reduced at lower temperatures (Leppi et al. 2014; Neuswanger et al. 2015; Dunmall et al. 2016). Although our model identified summer precipitation as being positive at the state-scale, the impacts of summer streamflow on juvenile salmon are likely to vary depending on regional conditions and life stage. For example, salmon survival and productivity declines were linked to high discharge during the freshwater rearing period in interior Alaska streams (Neuswanger et al. 2015; Cunningham et al. 2018), whereas low flows contributed to pre-spawning mortality in Alaska's Bristol Bay region (Tillotson and Quinn 2017).

Examining current weather and climate change variables simultaneously provided us with additional insight into how species may be adapting to rapid environmental changes. For example, despite positive relationships with current winter temperature, high winter warming rates were correlated with declines for both Dolly Varden and juvenile salmon. However, as areas experiencing higher rates of winter warming were often different from those with warmer current winter temperatures (pearson correlation coefficient $r = 0.2$), the significant inclusion of both predictors in our final models suggests that warmer winters are generally beneficial if changes to winter habitat occur at a manageable rate for adaptation (Heino et al. 2009; Wrona et

al. 2013). Many salmonid fishes display strong winter site fidelity, and any sudden changes to the quality or quantity of this habitat, or to adjacent migratory routes, may impact winter survival (Quinn, 2004; Stewart et al., 2010). Warming winters may indirectly affect important groundwater processes in overwintering refuges, or increase scouring and infilling of redds in natal spawning grounds (Stewart et al. 2010; Wobus et al. 2015; Dunmall et al. 2016; Sloat et al. 2017). Further, direct effects on developmental rates for incubating salmonids may lead to detrimental phenology mismatches, causing fish to hatch too early and face starvation (Quinn 2004).

Change in fall precipitation was an additional climate change variable that was identified as important for both Arctic grayling and juvenile salmon distributions. The decline in juvenile salmon presence may be attributed to scouring of incubating eggs during larger or more frequent fall floods, lowering egg-fry survival (Holtby and Healey 1986; Leppi et al. 2014; Neuswanger et al. 2015). In addition, changes in streamflow have been linked to both earlier and later spawning timing, although implications for overall salmon productivity remain unclear (Kovach et al. 2015). In agreement with our predictions, Arctic grayling appeared to benefit from modest increases in fall precipitation likely due to improved connectivity during this critical migration period (Betts and Kane 2015; Heim et al. 2015). However, the relationship was unexpectedly unimodal, with declines occurring in regions experiencing the highest increases in fall precipitation. Although the mechanism for this decline is unclear, we note that large increases in streamflow have the potential to reduce the foraging ability of juvenile grayling which have been shown to feed in small streams well into the fall season (Deegan et al. 1999; Heim et al. 2016).

We observed potential summer thermal stress for all three species examined in this study. However, it is important to note that the water temperatures used in our models were generally measured during the late summer period, and therefore do not reflect maximum water temperatures likely occurring mid-summer. Further, life stages with increased sensitivity to warming such as salmon embryos may be experiencing either higher or lower temperatures depending on local spawning timing (US EPA 2003). Therefore, results in the following discussion should not necessarily be interpreted as absolute thresholds for determining fish presence, but rather as relative trends if the limiting thermal period did not occur during the sampling event.

Overall, our findings suggested that Dolly Varden may be the most vulnerable Alaskan stream fish to summer thermal stress despite their strong reliance on high-elevation and groundwater fed sites as potential climate refuges (Stewart et al. 2010). While the review of temperature requirements in Stewart et al. (2010) revealed that Dolly Varden typically reside in water temperatures less than 11°C, our results demonstrate clear declines over the entire range of temperatures examined. In contrast, juvenile salmon were relatively more tolerant of warmer water temperatures, with presence peaking between ~8-15°C depending on the summer precipitation regime. The interaction between water temperature and summer precipitation provides possible evidence for the buffering effect of streamflow on direct and indirect warming effects, such as degraded water quality (Reist et al. 2006b; Schoen et al. 2017).

Our results indicated that northern Arctic grayling populations may be relatively more vulnerable to warming summer temperatures, with grayling presence peaking around 8°C in colder regions. In contrast, grayling populations residing in warmer regions demonstrated a predominately positive relationship over the range of experienced temperatures. The interaction with local winter temperature suggests that Arctic grayling may have evolved differing thermal optima, possibly reflecting regional bioenergetics trade-offs (Eliason et al. 2011). While no previous sublethal temperature thresholds have been reported for Arctic grayling, critical thermal limits typically vary from 23 – 29°C and have been shown to depend on acclimation temperature (Stewart et al. 2007).

Land use and fire

Land use and fire disturbance variables were not important determinants of Alaskan stream fish distributions in our dataset. Although the linear density gradient examined was low (mean = 70 m/km^2, SD = 320 m/km^2, max = 4200 m/km^2), other studies have identified negative impacts on sensitive salmonid species at comparably low levels (e.g., Bradford & Irvine, 2000; Ripley, Scrimgeour, & Boyce, 2005). Other land disturbance types were even less frequent in our study area, with point density and fire occurring in 11% and 8% of site catchments, respectively. It is likely that the low frequency and magnitude of these disturbance variables prevented any detection of trends across Alaska, and future work should aim to incorporate wider disturbance gradients.

Study limitations

Given the broad spatial scale and correlative nature of this study, there are several potential limitations that may be considered before applying our results elsewhere. First, while our hypotheses are meant to reduce the potential for spurious results, relationships observed in this study would require experimental testing to confirm a causal link. Second, as Alaska supports a wide range of diverse ecoregions, we recognize that our state-scale results may not be applicable at smaller scales. Instead, our results are meant to identify some of the more common underlaying environmental mechanisms that may warrant further investigation at the local scale. Finally, this study uses data gathered from a wide variety of sources via the ADFG's AFFI database, and as for any broad real-world studies we recognize that there will be some unavoidable bias in data collection. Our individual vetting of sampling events and use of only backpack electrofishing data in small streams aimed to mitigate some of this inherent variability.

Management implications

Our finding that climate change impacts best explained stream fish communities across Alaska highlights the pressing need for incorporating climate adaptation strategies into current fisheries management and habitat restoration plans. Increased mitigation and protection will be particularly important for stocks of management concern, which includes several Alaskan Chinook salmon populations and the Western Arctic population of Dolly Varden (COSEWIC 2010; Munro 2018). We have provided new information regarding potential species-specific thermal habitat requirements during their late summer stream residency and the identification of climatically vulnerable habitats (e.g., lowland streams, warm areas prone to summer drought, regions experiencing higher fall flows or winter warming), all of which could be integrated into current conservation and management efforts. For example, thermally sensitive watersheds could be identified and protected from additional land use development, watersheds experiencing an elevated flooding risk during the salmon incubation period could have more stringent riparian zone protections applied, and fishing quotas could be reduced in dangerously warm years, as has been successfully implemented for Fraser River sockeye salmon populations (Whitney et al. 2016). Another consideration specific to northern regions will be to account for the impending loss of permafrost, which has the ability to degrade streamside habitat and alter streamflow and connectivity, further impacting the climatic resilience of northern stream biota (Wrona et al. 2013; Kokelj et al. 2013).

We identified several important climate change implications for northern biodiversity, including the heightened risk to northern-adapted species such as Dolly Varden and Arctic grayling. To help preserve these climatically vulnerable species, important groundwater-fed areas that provide buffering to warmer summer temperatures will need to be cataloged, monitored, and protected (Dunmall et al. 2016), and activities resulting in flow alterations should be limited in critical migration corridors. Lastly, as interspecific interactions were a potential driver of Arctic grayling declines elsewhere, future research should focus on how this species may fare following climate-mediated invasions (Stewart et al. 2007).

As climate change progresses, northern environmental managers will be facing an increasingly dynamic ecosystem that may vary depending on local species assemblages and regionally specific ecological processes (Reist et al. 2006b; Heino et al. 2009). Our study provides an important initial step for identifying the modes of environmental change that may be broadly structuring Alaskan stream fish communities and reveals the possible benefits of a warming Arctic for many species when viewed at the state-scale. However, potential threats identified in our individual species models suggest that localized declines may still occur, potentially affecting thousands of Alaskans and numerous upstream Canadian communities with limited fishing portfolios (Schoen et al. 2017). As Alaska's economy and quality of life are deeply dependent on the health of their world-renowned fisheries, the continued study of combined and potentially interacting environmental effects will be imperative for developing forward-thinking and timely conservation solutions.

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Tables and Figures

Table 1. Predicted climate effects on Alaskan stream fishes. For climate change variables, the observed climatic trends for this dataset are indicated as either positive (+) or mixed (+/-). Refer to Table 3 for climate summary statistics.

Metric	Variable	Predicted effect	Potential mechanism
Species richness and Total CPUE	current winter temperature	Positive	Shorter winter starvation period, increased critical overwintering habitat availability and survival, northward range expansions (Wrona et al. 2005; Reist et al. 2006b; Shuter et al. 2012)
	current winter precipitation change in winter precipitation* (+)	Mixed	In snow-dominated systems, increased stable overwintering refugia and winter survival (Reist et al. 2006c); increased winter streamflows providing additional critical overwintering habitat and increasing survival (Prowse et al. 2006a; Prucha et al. 2011); reduced winter survival in transient systems that experience more rain-on-snow events (Shanley and Albert 2014; Wobus et al. 2015)
	current summer temperature	Positive	Increased growth and overwintering survival facilitated by a longer and more productive growing season (Shuter and Post 1990; Chapin et al. 2014)
	current summer precipitation change in summer precipitation* (+/-)	Mixed	Changes in summer precipitation may impact habitat quantity, quality, and/or connectivity during this critical feeding and migration period (Deegan et al. 1999; Jones et al. 2003; Bryant 2009)
Arctic grayling	current winter temperature	Positive	Colder regions provide less overwintering habitat, limiting northern Arctic grayling populations (Craig 1989; Reynolds 1997; Heim et al. 2016)
	current spring temperature	Positive	Longer growing season, increasing fish growth and overwintering survival (Heim et al. 2015)
	change in spring temperature* (+)	Mixed	Earlier spawning timing may extend the growing season, increasing juvenile growth and survival (Shuter and Post 1990); earlier spawning may decrease survival if incubation occurs at lower than optimal temperatures (Wedekind and Kung 2010)
	current summer temperature	Mixed	Increased growth and survival of juvenile Arctic grayling in warmer streams (Deegan et al. 1999; Jones et al. 2003); increased nutrient availability from warming may

			promote Arctic grayling growth (Prowse et al. 2006a; Stewart et al. 2007); increased evaporation from streams may heighten the risk of stranding during the late summer – fall migration period (Betts and Kane 2015; Heim et al. 2015)
	current summer precipitation change in summer precipitation* (+/-)	Mixed	Lower summer discharge was associated with increased growth of juvenile Arctic grayling, whereas higher summer discharge was associated with increased growth for adults (Deegan et al. 1999; Jones et al. 2003); changes in summer hydrology patterns may impact Arctic grayling migrations in late summer to overwintering areas (Betts and Kane 2015; Heim et al. 2015)
	current fall precipitation change in fall precipitation* (+)	Positive	Lowered risk of stranding during migrations to overwintering areas during fall (Betts and Kane 2015; Heim et al. 2015)
Dolly Varden	current winter temperature	Positive	Colder regions provide less overwintering habitat, limiting northern Dolly Varden populations (Craig 1989; Reist et al. 2006b; Brown et al. 2014)
	change in winter temperature* (+)	Mixed	Alterations to groundwater-fed overwintering refugia, impacting critical Dolly Varden overwintering habitat availability and survival (Stewart et al. 2010)
	current winter precipitation change in winter precipitation* (+)	Positive	Increased winter streamflows due to warmer, wetter winter climate may increase stream overwintering habitat availability and survival (Prowse et al. 2006a; Prucha et al. 2011; Wobus et al. 2015)
	current summer temperature	Negative	Dolly Varden tend to reside in high elevation and cold water sites <11°C, and may be vulnerable to competition and predation from warmer water species (Bryant et al. 2004; Stewart et al. 2010)
	change in summer temperature* (+)	Mixed	Melting permafrost with implications for changes in groundwater flow and water chemistry (Durand et al. 2011)
Juvenile salmon	current winter temperature	Positive	Warmer winter water temperatures, increasing survival of incubating salmon eggs (Leppi et al. 2014)
	change in winter temperature* (+) change in winter precipitation* (+)	Mixed	Accelerated development rates for incubating salmonids, potentially extending the growing season or causing spring emergence mis-matches (Quinn 2004; Wobus et al. 2015; Adelfio et al. 2019); increased mid-winter thaw events (Wobus et

			al. 2015); increasing potential for scouring of incubating salmon eggs (Mantua et al. 2010; Leppi et al. 2014; Shanley and Albert 2014)
	current spring temperature current summer temperature	Mixed	Longer, warmer, and more productive growing season, increasing salmon growth and survival (Schindler et al. 2005; Ohlberger et al. 2016; Cunningham et al. 2018; Cline et al. 2019); potential for negative effects if temperatures surpass optimal thresholds for rearing, spawning, or incubation (Bryant 2009; Mauger et al. 2017) or result in lowered age structure diversity (Cline et al. 2019)
	current summer precipitation change in summer precipitation* (+/-)	Mixed	Higher summer discharge was negatively related with juvenile salmon survival, possibly due to lowered foraging success (Neuswanger et al. 2015; Cunningham et al. 2018); lower summer flows were associated with increased pre-spawning mortality (Tillotson and Quinn 2017); reduced summer flows may negatively impact the quantity and quality of juvenile salmon rearing habitat, decreasing growth and possibly increasing mortality (Bryant 2009)
	current fall temperature	Positive	Increased critical early incubation survival (Leppi et al. 2014; Neuswanger et al. 2015), promoting salmon establishment at northern extent of the current range (Dunmall et al. 2016)
	change in fall precipitation* (+)	Mixed	Altered spawning timing (Kovach et al. 2015); increased fall streamflows, scouring incubating eggs (Mantua et al. 2010; Leppi et al. 2014; Shanley and Albert 2014; Neuswanger et al. 2015); increased risk of landslides, infilling or scouring spawning beds (Bryant 2009)

Current weather variables are defined as the most recent thirty-year average; *Climate change variables are defined as the difference between the current thirty-year mean and the previous thirty-year mean; CPUE = Catch Per Unit Effort

Table 2. Examples of potential predicted environmental interactions on Alaskan stream fishes

Interacting variables	Antagonistic
Δ winter temp × Δ winter precip	Negative effects from increased winter scouring flows on incubating eggs may be dampened by warmer incubating temperatures that increase evapotranspiration and improve egg survival (Leppi et al. 2014)
Current annual temp × Water temp	Fish species may have adapted to maximize their fitness under local thermal conditions, resulting in higher thermal optima in warmer regions (Reist et al. 2006b; Eliason et al. 2011)
Current summer temp × Stream type	Negative effects of summer warming are dampened at higher elevations and/or in smaller, snow-dominated drainages that tend to maintain lower stream temperatures (Lisi et al. 2015; Mauger et al. 2017)
Current annual temp × Land Use	Low levels of land use disturbance may provide thermal or nutrient subsidies, possibly benefiting fish in naturally colder and more nutrient-poor regions (Heino et al. 2009)
	Synergistic
Δ summer temp × Δ summer precip	Negative effects of summer warming may be exacerbated in areas receiving less precipitation due to higher risk for low-flow stranding and degraded water quality (Reist et al. 2006b; Schoen et al. 2017)
Δ winter temp & precip × Current winter temp	Transitional snow-rain watersheds experiencing warmer and wetter winters may have enhanced flooding vulnerability over time, lowering spawning habitat for incubating salmonids (Sloat et al. 2017)
Δ temp &/or Δ precip × Stream turbidity	Warmer catchment temperatures and/or higher runoff may enhance stream sedimentation over time, amplifying negative effects in systems vulnerable to erosion (Bryant 2009; Wrona et al. 2013)
Δ fall-winter temp &/or Δ precip × Stream type	Confined, higher elevation streams may be more susceptible to scouring flows in regions experiencing warmer and wetter climate over time during the fall-winter incubation period (Heino et al. 2009; Sloat et al. 2017)
Δ winter precip × Stream type	Increased winter precipitation over time may be more detrimental in large, low elevation drainages that experience greater winter flows, possibly lowering the survival of incubating eggs (Leppi et al. 2014)
Δ summer temp &/or precip × Land Use	Fish residing in fragmented watersheds following catchment land use development may be further exacerbated by climate-induced stressors (Mantyka-Pringle et al. 2013)

Temp = annual or seasonal air temperature unless specified as water temperature, Precip = precipitation, Δ = change

Table 3. Summary statistics of predictor variables used to model community and species metrics for Alaskan stream fishes

Variable Type	Variable	Units	Mean	SD	n
Current Weather	winter temperature	°C	-11.9	5.6	1587
	spring temperature	°C	1.6	3.4	1587
	summer temperature	°C	11.9	1.6	1587
	fall temperature	°C	1.9	3.1	1587
	winter precipitation	mm	253	184	1587
	spring precipitation	mm	77	55	1587
	summer precipitation	mm	255	103	1587
	fall precipitation	mm	188	118	1587
	water temperature	°C	9.0	3.2	1501
Climate Change	Δ winter temperature	°C	1.7	0.4	1587
	Δ spring temperature	°C	1.3	0.4	1587
	Δ summer temperature	°C	0.7	0.2	1587
	Δ fall temperature	°C	0.2	0.4	1587
	Δ winter precipitation	mm	16	22	1587
	Δ spring precipitation	mm	4	8	1587
	Δ summer precipitation	mm	3	13	1587
	Δ fall precipitation	mm	15	14	1587
Habitat	watershed mean elevation	m	486	368	1587
	drainage area	m^2	63866533	190163020	1587
Land use and fire	linear density	m^2 / m^2	69.4	321.2	1587
	point density	# / m^2	0.01	0.08	1587
	fire area	m^2	1496171	18920089	1587

SD = standard deviation, Δ = change

Table 4. Overall linear and generalized linear mixed model performance for community metrics (species richness, total catch per unit effort) and species metrics (presence absence) for three species groups

Regression Models	Performance Metrics	Species Richness	Total CPUE	Arctic grayling	Dolly Varden	Juvenile salmon species
Mixed Models †	R^2	38 (24)	34 (16)	59 (38)	65 (48)	58 (41)
Generalized Models	Classification Success (%)	-	-	76	75	71
	Sensitivity (%)	-	-	76	71	69
	Specificity (%)	-	-	79	79	75

CPUE = Catch Per Unit Effort
†Pseudo-R^2 values for mixed models, showing the conditional variance explained, followed by the marginal variance explained in brackets

Table 5. Summary of significant relationships between environmental variables and Alaskan stream fishes

Variable Type	Environmental variable	Direction	Biological indicators
Temperature	current winter temperature	Positive	Species richness, Total CPUE, Dolly Varden
		Negative	Arctic grayling
	current spring temperature	Positive	Juvenile salmon
	current fall temperature	Positive	Juvenile salmon
	increase in winter temperature	Negative	Juvenile salmon
		Unimodal	Dolly Varden
	current summer water temperature	Positive	Species richness, Total CPUE, Arctic grayling†, Juvenile salmon†
		Negative	Dolly Varden
		Unimodal	Arctic grayling†, Juvenile salmon†
Precipitation	current winter precipitation	Positive	Dolly Varden†
		Negative	Dolly Varden†
	increase in winter precipitation	Positive	Total CPUE, Dolly Varden
	current summer precipitation	Positive	Juvenile salmon
	increase in summer precipitation	Negative	Total CPUE
	decrease in summer precipitation	Positive	Total CPUE
	increase in fall precipitation	Negative	Juvenile salmon
		Unimodal	Arctic grayling
Land Use and Fire	linear density	n/a	none
	point density	n/a	none
	fire	n/a	none

† Relationships that vary depending on an interactive term. CPUE = Catch Per Unit Effort

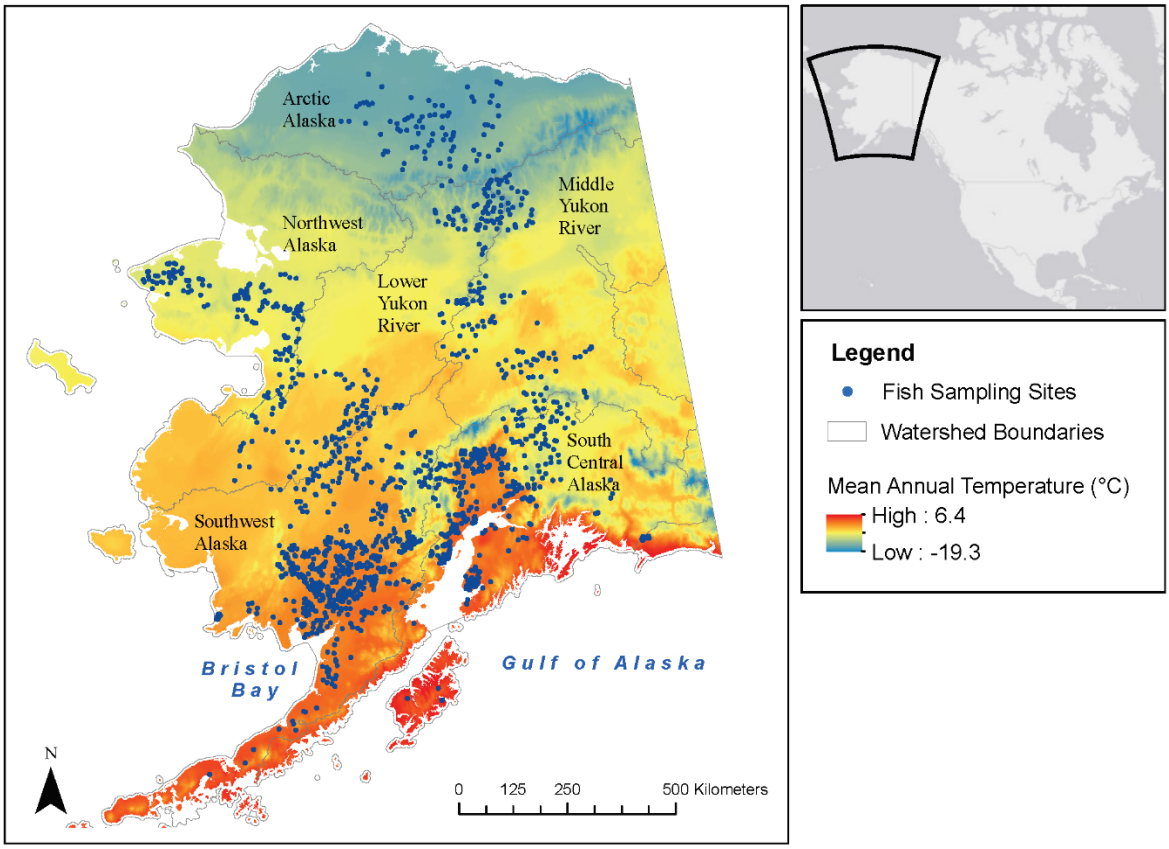


Figure 1. Map of the study area, showing the distribution of fish sampling sites over six major hydrological units (HUC4).

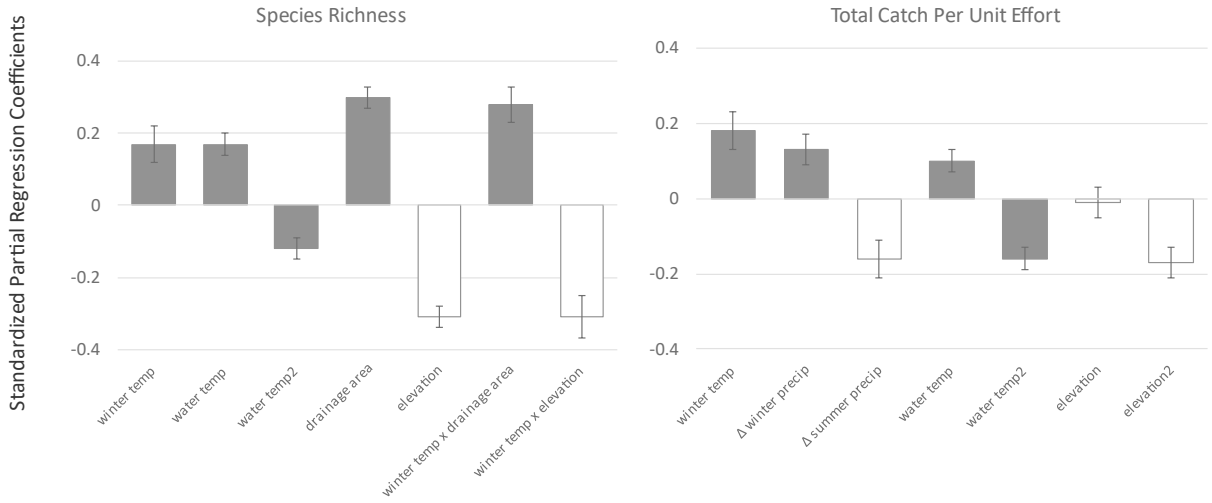
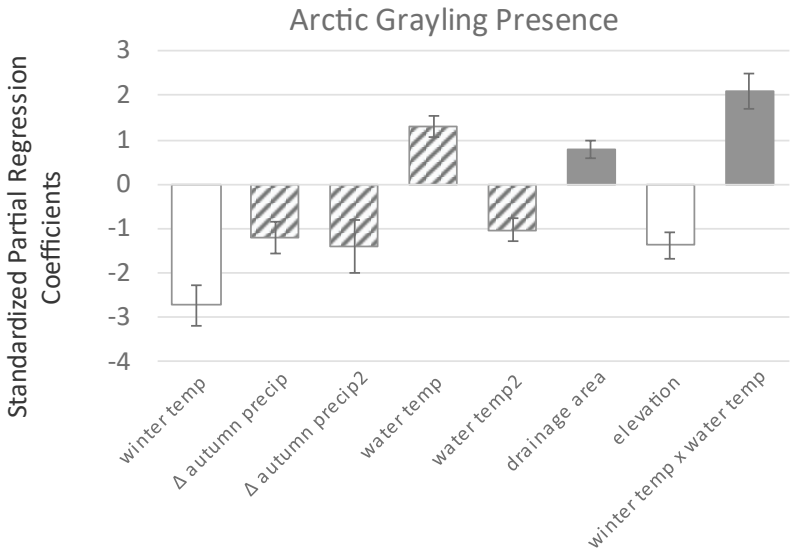
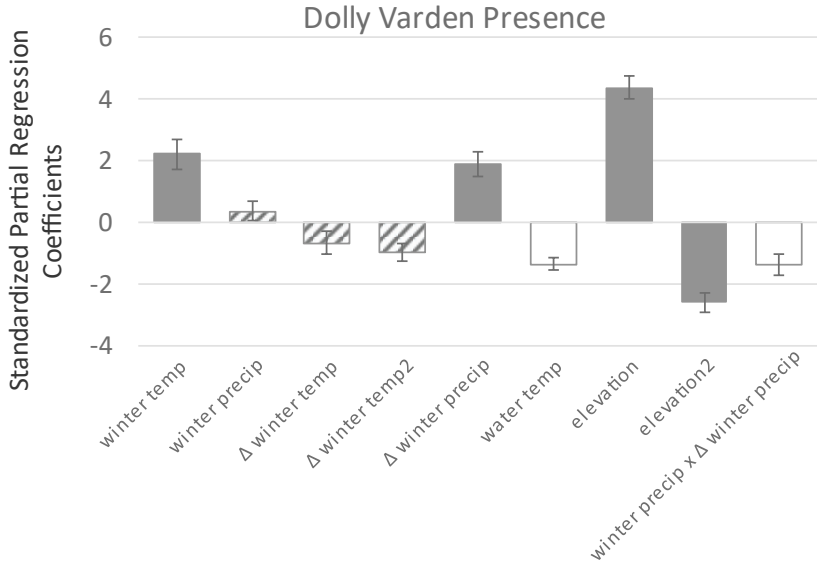


Figure 2. Standardized partial regression coefficients for the top community-level mixed models. Colour coding indicates if the relationship with each predictor term is overall positive (solid gray), or negative (white). A suffix of "2" indicates a quadratic term and Δ = change. Bars indicate ±1 standard error.


Arctic Grayling Presence
Standardized Partial Regression Coefficients
3
2
1
0
-1
-2
-3
-4
winter temp
Δ autumn precip
Δ autumn precip2
water temp
water temp2
drainage area
elevation
winter temp x water temp


Dolly Varden Presence
Standardized Partial Regression Coefficients
6
4
2
0
-2
-4
winter temp
winter precip
Δ winter temp
Δ winter temp2
Δ winter precip
water temp
elevation
elevation2
winter precip x Δ winter precip

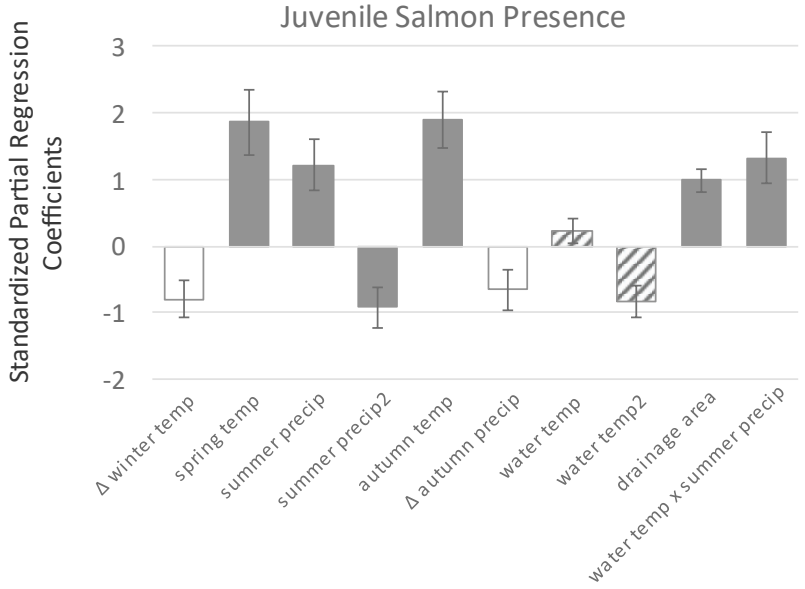

Juvenile Salmon Presence
Standardized Partial Regression Coefficients
3
2
1
0
-1
-2
Δ winter temp
spring temp
summer precip
summer precip2
autumn temp
Δ autumn precip
water temp
water temp2
drainage area
water temp x summer precip

Figure 3. Standardized partial regression coefficients for the top species distribution mixed models. Colour coding indicates if the relationship with each predictor term is overall positive (solid gray), mixed (striped), or negative (white). A suffix of "2" indicates a quadratic term and Δ = change. Bars indicate ±1 standard error.

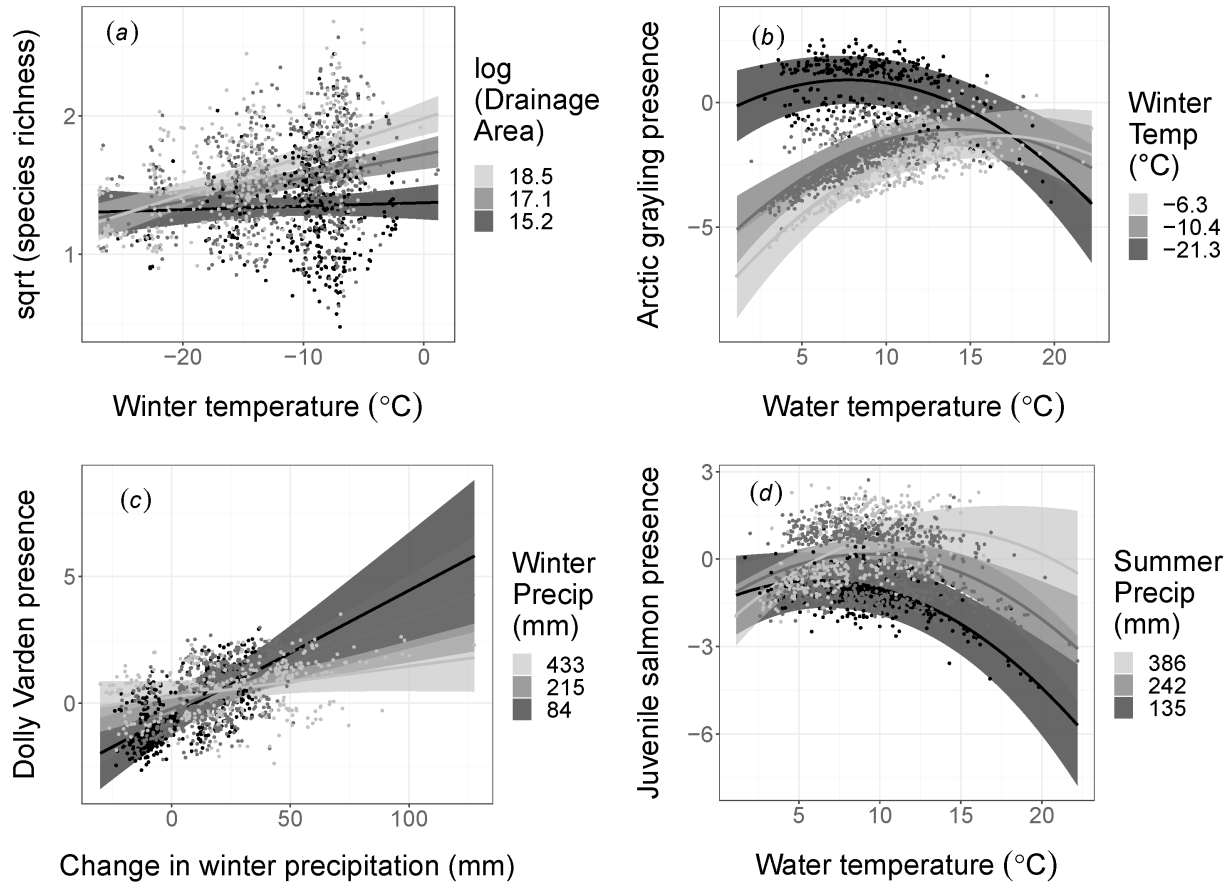


Figure 4. Generalized linear mixed model partial plots demonstrating the interactions between a) current winter air temperature and log-transformed drainage area for square-root transformed species richness, b) water temperature and current winter air temperature for Arctic grayling presence, c) change in winter precipitation and current winter precipitation for Dolly Varden presence, and d) water temperature and current summer precipitation for juvenile salmon species presence. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shading indicates 95% confidence intervals and y-axes of species models are plotted on the linear predictor (logit) scale.

Chapter 2: The interactive effects of climate change and land use on boreal stream fish communities

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Author's Contributions:

AM, CMP, and SS conceived the research ideas; AM acquired funding and data, analysed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Science of the Total Environment.

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Summary

Ongoing and projected climate change is likely to greatly alter co-occurring stressor mechanisms, yet these potential interactions remain poorly understood in natural freshwater systems worldwide. As the global biodiversity crisis deepens, successful conservation efforts will hinge on developing mechanistic multiple stressor frameworks that have been ground-truthed in natural systems containing complex species dynamics and ecological processes. Our study examined the combined and interacting effects of potential climate and land use stressors on boreal stream fishes using data from over 300 catchments across a broad 250,000 km^2 region. To characterize boreal fish community health, we examined four indicators including species richness, total catch per unit effort, the proportion of lithophilic spawners (fish sensitive to sedimentation), and the assemblage tolerance index which provides a measurement of the overall community tolerance to disturbance. Land use stressors included total anthropogenic land use area and linear disturbance at multiple watershed scales as well as two site-specific habitat degradation indicators (dissolved oxygen and the proportion of fine substrate). Overall community richness and catch per unit effort were not negatively related to land use changes indicating potential compensatory dynamics (e.g. where intolerant species are replaced with more tolerant species as habitat quality degrades). In contrast, we observed declines for sensitive species, including highly valued salmonids, that varied depending on interactions between local climate, land use, and stream type. Sensitive species declines were concentrated in regions experiencing increased land use and warming, whereas increases were observed in cooler regions consistent with a subsidy-stress response. In addition, lithophilic spawners declined in watersheds experiencing warmer and wetter conditions owing to potential indirect effects on spawning habitat quality. Results from our study provide novel insight into complex climate and land use interactions occurring across a broad, real-world landscape, and highlight the potential for amplified species declines under future warming and land use scenarios.

Introduction

The global human footprint continues to expand at an alarming rate, with a disproportionate amount of pressure being placed on vital freshwater resources (WWF 2018). While land use change remains the leading threat to freshwater biodiversity worldwide, climate change is rapidly emerging as a significant secondary stressor with the ability to alter land use mechanisms in potentially unexpected ways (Piggott et al. 2015b; Reid et al. 2019). Certain stressor combinations may produce ecological 'surprises', or dampened (antagonistic) responses, potentially nullifying or even worsening management actions based on single-stressor predictions (Côté et al. 2016). As evidence for the global biodiversity crisis continues to mount, ecosystem managers remain vastly ill-equipped for managing the numerous potential stressor interactions that may arise in ecologically complex real-world systems (Nõges et al. 2016; WWF 2018).

The successful conservation of aquatic resources hinges on the immense task of elucidating multiple stressor relationships amid novel and potentially regional-specific direct and indirect climate change processes. Many freshwater species experience ecological advantages within their specific environmental niche, potentially making them vulnerable to any unprecedented changes in temperature, stream flow, substrate, or water quality (Magnuson et al. 1979). For instance, increased summer temperatures will likely favour the establishment of species with warmer thermal preferences, reducing the abundances of many highly valued species that are dependent on cooler waters for their survival (Heino et al. 2009). Further, climate-altered stream flows may limit fish movements or degrade water quality, shifting community assemblages towards more stationary and tolerant fishes (Schindler et al. 1996; Lake 2003). Climate processes are also likely to vary depending on local conditions, for example, lowered stream flows may be more detrimental in smaller streams with a higher risk for low-flow stranding (Lake 2003). Further, regions experiencing warmer summer temperatures in combination with more precipitation may experience impacts due to enhanced nutrient and sediment run-off (Goudie 2006; Goode et al. 2012).

While there has been ample research examining potential climate change effects on fish, understanding how these effects may combine and potentially interact with co-occurring stressors remains a critical and understudied question for freshwater ecosystems (Mantyka-

Pringle et al. 2014; Nõges et al. 2016). The growing body of ecological literature investigating freshwater multiple stressors indicates a high prevalence of antagonistic interactions, as well as potential reversal effects associated with warming (Jackson et al. 2016). For example, the stimulatory effect of higher temperatures may increase animal metabolism or plant assimilation, potentially dampening the negative effects of other stressors such as nutrification (e.g., Thompson et al. 2008). Cooler, less productive regions may also be more positively impacted by low disturbance subsidies (e.g. increased sunlight or nutrients), with benefits decreasing in warmer regions (Allan 2004; Piggott et al. 2012). Despite the prevailing evidence, there is still the possibility of negative (synergistic) interactions following increasing land use and climate change in freshwater systems, particularly when involving changes in precipitation (Mantyka-Pringle et al. 2013). As lotic systems are highly vulnerable to fragmentation, imposing additional thermal, high-flow, or low-flow barriers could exacerbate local land use effects if fish are stranded in increasingly stressful environments (Radinger et al. 2017). Further, enhanced sediment and nutrient run-off in wet, disturbed watersheds could accelerate water quality degradation or bury important gravel beds for lithophilic spawners (Schindler 2001; Bryant 2009). However, the mechanistic understanding of climate interactions has been largely derived from small-scale experimental studies to-date, and there is an urgent need to validate potential mechanisms in natural systems containing complex ecological processes (Jackson et al. 2016; Bruder et al. 2017).

Identifying key threats to freshwater biodiversity and how they may vary depending on climate conditions is greatly needed for the successful conservation and management of northern fishes within their rapidly changing environments. Therefore, the objectives of this study were to determine: (1) how cumulative land use pressures are influencing boreal stream fish community structure, and (2) if climate is producing a buffering (antagonistic) or amplified (synergistic) effect on concurrently acting stressors across a broad, real-world landscape. We predicted that (1) sensitive species would decline in response to rising land use impacts, whereas overall community metrics would be more robust (at low-mid disturbance levels) owing to species compensatory dynamics (Vinebrooke et al. 2004), and (2) that warming would dampen the effects of co-occurring stressors on boreal fishes owing to its stimulatory effect (Jackson et al. 2016), whereas amplified (synergistic) species declines would be observed when stressors interacted with changes in summer precipitation (Mantyka-Pringle et al. 2013, 2019). Few others

have provided field-based empirical data of cumulative land use on fishes over broad spatial scales (e.g., Esselman et al. 2011; Schinegger et al. 2012; Daniel et al. 2015; Cooper et al. 2017), and fewer have investigated climate – land use interactions beyond a local study scale (e.g., Radinger et al. 2016; Gutowsky et al. 2019), providing us with a unique opportunity to test findings from a recent freshwater meta-analysis using regional-scale *in situ* data (Jackson et al. 2016).

Materials and Methods

Study area

The boreal ecozone of Alberta, Canada, contains several major rivers that combine to form the headwaters of the second largest drainage in North America, the Mackenzie River system (Figure 1). Substantial anthropogenic land use has occurred within this region, including major hydroelectric development, forestry, agriculture, as well as extensive oil sands mining concentrated in the lower Athabasca watershed (Schindler and Lee 2010; Lima and Wrona 2019). Notably, oil extraction in Canada's western boreal is poised to quickly escalate and may eventually impact a region greater than 25 times the current areal footprint (Kreutzweiser et al. 2013). Over the 1950-2010 period, the region has also experienced substantial warming (1 - 4 °C change) and a range of regional-specific annual precipitation trends (Clark and Kienzle 2019; Zhang et al. 2019). Future climate projections indicate that this region will endure considerable additional warming (1.9 - 6.5 °C) and an overall increase in precipitation (6 – 15%) by the year 2100 (Zhang et al. 2019).

Data sources and processing

Fish catch data were obtained from the Alberta Government's Fish and Wildlife Management Information System (FWMIS) (Figure 1; AEP 2018a). The fish dataset was subset to focus on small streams and rivers (drainage area <1000 km^2; Esselman et al. 2011) sampled with backpack electrofishing, during the 2010-2016 period. We only included survey data that aimed to sample the entire fish community, which was achieved by removing any targeted species sampling (as indicated by a column in the FWMIS database). All sites were sampled during the open water season (May – October). Where available, site-specific habitat quality data (dissolved

oxygen in mg/L, water temperature, conductivity, and percentage of fine substrates) were also obtained from FWMIS.

Watersheds were delineated using spatial data from the Alberta ArcHydro Phase 2 dataset (AEP 2018b). We used pre-defined local catchments (the immediate catchment where the fish survey was located), and delineated network catchments (the entire upstream area) using ArcHydro tools version 2.0 (Redlands, CA, USA). In addition, we used Unit 8 from the Hydrologic Unit Code Watersheds of Alberta spatial dataset to represent an even larger, watershed-level spatial scale (AEP 2017). We further refined the fish dataset based on available data in each local catchment. First, we selected local catchments with a minimum of 15 individual fish sampled, and then summarized this data at the catchment level (n = 301 local catchments, mean = three surveys per catchment) to minimize sampling bias and high spatial autocorrelation from repeated sampling (Figure 2). As a result, each catchment had an average of four species (standard deviation = 3, minimum = 1, maximum = 15) and 132 individual fish captured (standard deviation = 542, minimum = 15, maximum = 8169), with lake chub *Couesius plumbeus*, brook stickleback *Culaea inconstans*, white sucker *Catostomus commersoni*, and longnose sucker *Catostomus catostomus* being the most dominant species present (Table B1). Further, each catchment received an average electrofishing effort of 926 seconds per survey ± one standard deviation of 641 seconds. Mean elevation for each watershed was calculated using data from the Canadian Digital Elevation Model (Natural Resources Canada 2017). Local catchment slope (%) was derived using elevation data.

Land use data were obtained from the Boreal Ecosystem Anthropogenic Disturbance dataset (2008-2010), which was originally created to assess anthropogenic effects on boreal caribou (Pasher et al. 2013). The dataset is unique in that it quantifies all disturbed areas for a range of development activities in a standardized way (e.g., agriculture, cutblocks, hydroelectric dams, settlements, and oil and gas), and it includes many features that are commonly missed in other geospatial datasets, such as forestry roads and seismic lines. Total linear density (m/km^2) and anthropogenic land use (%) were calculated for five different spatial scales: local riparian, local catchment, network riparian, network catchment and HUC8 watershed level (Figure 2). Multiple spatial scales were considered as the spatial extent of disturbance pathways are known to vary depending on disturbance type and the life histories of response biota (Allan 2004; Esselman et

al. 2011). On average, local, network and HUC8 catchments represented a median area of 10 km^2, 58 km^2, and 1710 km^2, respectively. The riparian area was defined as land within 30m on either side of the drainage line. All GIS data processing was conducted in ArcMap Desktop 10.6.

Climate data were obtained from the ClimateNA program (version 5.5) (Wang et al. 2016). Climate data were extracted at each sampling site, and then averaged by catchment. Current weather means were based on the thirty years prior to the fish collection date and included maximum July air temperature (°C), summer precipitation (June – August) (mm), and frost free period (days). Change in summer precipitation (mm) and summer temperature (°C) were calculated as the difference between the current thirty year mean and the previous thirty-year mean.

Data analysis

Fish metrics representing biological integrity in Albertan watersheds were calculated (Table 1), including species richness, fish catch per 100s of electrofishing effort (CPUE = catch per unit effort), percent lithophils, and the assemblage tolerance index (ATI) (e.g., Bramblett et al. 2005; Whittier et al. 2007; Stevens et al. 2010). The ATI provides an index of the overall community tolerance, with a high score indicating relatively more tolerant individuals and a low score indicating relatively more intolerant individuals. Species richness was rarefied using the *rarefy* function from the *vegan* package to 15 individuals. Pearson's correlation coefficients between response variables ranged from -0.54 to 0.34, with ATI and lithophils having the strongest correlation (r = -0.54). To improve normality, we log-transformed CPUE, summer precipitation, drainage area, elevation, and slope, square-root transformed species richness and linear disturbance, and logit-transformed percent lithophils and land use. As many disturbance variables had high disturbance outliers, we corrected outliers to the 99^{th} percentile value for each variable (e.g., Esselman et al. 2011).

Prior to analyses, we checked for potential multicollinearity between predictor variables resulting in the omission of two variables, summer precipitation and change in summer temperature, as they were highly correlated with maximum July air temperature (Table B2). July temperature was positively correlated with change in summer temperature (r = 0.77) and negatively correlated with summer precipitation (r = -0.9). Further, regions that were warming the fastest (i.e., change in summer temperature) tended to have lower current summer

precipitation (r = -0.82) and were experiencing more summer drying (i.e., change in summer precipitation; (r = -0.6). We retained July temperature due to its demonstrated influence on species fitness, including implications for overall freshwater productivity (Schindler 1997; Sharma et al. 2007; Ficke et al. 2007). However, because summer precipitation was also moderately correlated with change in summer precipitation (r = 0.48), and both precipitation variables were expected to produce similar effects on important streamflow processes (Ashmore and Church 2001), we additionally explored competing models to determine which variable would provide the greatest statistical fit (Table B3; see more detailed methods information below for linear mixed models). Summer precipitation did not alter model interpretation or improve model performance for any metric and was therefore omitted from further analyses. All other predictor variables demonstrated low potential for multicollinearity issues and were retained for further analyses (Pearson correlation coefficients < 0.7 and variance inflation factors < 2; Dormann et al. 2013) .

Linear mixed models were used to analyze relationships between fish community metrics and predictor variables. For each metric, an initial model was run using all explanatory variables: total linear density, total land use percent, catchment slope, drainage area, maximum July temperature, frost free period, and change in summer precipitation. We included quadratic terms to represent potential nonlinear relationships. In addition, we incorporated interaction terms between maximum July temperature and the two disturbance variables to test our second objective. Further, we included interactive terms to represent two potential climate interactions: an interaction between maximum July temperature and change in summer precipitation, and an interaction between drainage area and change in summer precipitation. These interactions were included based on predictions that (1) warmer and wetter regions may experience negative effects due to the higher potential for water quality and substrate degradation following climate-induced sedimentation (e.g., Goudie 2006; Bryant 2009; Goode et al. 2012), and (2) that smaller drainages would be at greater risk to drought, whereas larger drainages may experience detrimental high flows (e.g., Brooks 2009; Leppi et al. 2014; Shanley and Albert 2014). Two potential random effects levels (watershed hydrological codes 4 and 6) were first tested for significance using a log-likelihood test, and if both levels were significant we retained the HUC level that provided the best model fit. As a result, HUC6 was used for all models with the exception of lithophil models which used HUC4. Further, elevation was included as a random

intercept after being categorized into six equal levels. We used the *lme4* package for running mixed models, and the *dredge* function in the *MuMin* (Multi-Model Inference) package for model selection (Barton 2018). The dredge function runs all possible model combinations as potential competing hypotheses and identifies the top model based on the lowest AICc value (Johnson and Omland 2004; Grueber et al. 2011). Models that were within 2 AICc from the lowest score were considered to be equally valid models, following Burnham and Anderson (2002). In the event that a higher order term was selected in the final model, we also retained related lower order terms. All variables were standardized using the function *standardize* in the *arm* package which converts all variables to a comparable, unitless scale (Gelman et al. 2018). Using the partial regression coefficients as indicators of effect size, we interpreted values between 0.1-0.3 as weak, between 0.3-0.5 as moderate, and greater than 0.5 as strong (Nakagawa and Cuthill 2007). Pseudo-R^2 values for mixed models were obtained using the *r.squaredGLMM* function from the *MuMin* package (Barton 2018).

Using fish survey records that had accompanying site-specific habitat quality data (n = 340), we also ran regression tree models to examine any potential important climate or habitat quality thresholds for four community indicators (square-root transformed species richness, log-transformed catch per unit effort, logit-transformed percentage of lithophilic individuals, and the assemblage tolerance index). Regression trees employ a recursive binary partitioning algorithm, minimizing node variability at each subsequent split using the best possible predictor variable (De'ath and Fabricius 2000). Further, regression tree modelling is an effective tool for identifying potential ecological thresholds and interactions within complex ecological datasets. For better alignment with site-specific predictors, we used individual fish survey data records rather than the local catchment summaries used in the land use models described above. However, because some surveys had very low catch data (minimum = 1, median = 10), we were unable to use species rarefication and instead corrected for the influence of effort on species richness using log-transformed electrofishing effort as a model offset.

Results

Fish community indicators demonstrated variable responses to climate and land use variables (Tables 2 and 3). The top species richness models included drainage area, frost free period, and watershed-level linear disturbance (R^2 = 44%; Table 2). However, there was equal support

(ΔAICc < 2) for models that did not retain watershed-level linear disturbance. More species were found in larger drainages (Table 3; std. coefficient = 0.55 ± 0.05, $P < 0.01$), with intermediate growing seasons (quadratic std. coefficient = -0.28 ± 0.09, $P < 0.01$), and intermediate linear disturbance (quadratic std. coefficient = -0.20 ± 0.06, $P < 0.01$; Figure 3). Overall, drainage size was the strongest predictor of species richness, with the frost-free period and linear disturbance demonstrating relatively weak effect sizes. Species richness peaked in watersheds with approximately 1225 m/km^2 of linear disturbance (Figure 3), however few watersheds exceeded disturbance levels greater than 1600 m/km^2. There was no evidence for a climate-land use interaction for species richness.

Total community catch was best explained by maximum July temperature and drainage area (R^2 = 35%; Table 2), with higher abundances found in small catchments (std. coefficient = -0.14 ± 0.05, $P < 0.01$) and with warmer summer temperatures (std. coefficient = 0.39 ± 0.09, $P < 0.01$; Figure 4). Human disturbance variables were unrelated to total catch.

The riparian network disturbance model best explained the proportion of lithophilic spawners (R^2 = 53%; Table 2). More lithophils were found in larger, higher gradient drainages that were receiving more summer precipitation (Figure 5, Table 3). However, lithophils declined sharply in regions experiencing the warmest and wettest climate due to a strong synergistic interaction between July temperature and change in summer precipitation (std. coefficient = -0.84 ± 0.14, $P < 0.01$) (Figure 5). Further, a moderate linear disturbance – climate interaction (std. coefficient = -0.39 ± 0.1, $P < 0.01$) revealed a potential increase in regions with cooler summers, whereas lithophils declined with increasing disturbance in regions with the warmest summers (Figure 5).

The assemblage tolerance index (ATI) was best explained using the watershed-level disturbance model (R^2 = 56%, Table 2). Community tolerance was generally higher in smaller, lower gradient drainages (Figure 6, Table 3). We identified a strong interaction between watershed-level land use and maximum July temperature, with similar trends noted as above for lithophils (std. coefficient = 0.63 ± 0.15, $P < 0.01$; Figure 6). Community tolerance increased in regions experiencing warmer summer temperatures in conjunction with higher land use stress (synergistic), whereas a decrease was observed in regions experiencing cooler summer temperatures. Another strong synergistic interaction was observed between change in summer precipitation and drainage area (std. coefficient = 0.51 ± 0.09, $P < 0.01$; Figure 6), where more

precipitation was associated with lower community tolerance in small streams and higher community tolerance in large streams.

Site-specific regression tree models identified several important climate and habitat quality variables for three of four community metrics (Figure B1). More species were found at warmer sites (> 21 °C), however, richness was similarly high at cooler sites that had lower water conductivity (R^2 = 0.26, CV R^2 = 0.19; Figure B1a). The model for catch per unit effort did not identify any important predictor variables and cross validation error was 100%, indicating very poor model fit. Lithophilic spawners declined in smaller streams receiving less summer precipitation, and in larger drainages that were dominated (>71%) by fine substrates (R^2 = 0.38, CV R^2 = 0.29; Figure B1b). Lastly, intolerant species declined at warmer sites (July air temperatures > 21 °C and water temperatures > 11 °C), and when either fine substrates exceeded 72% or dissolved oxygen levels fell below 7.1 mg/L (R^2 = 0.53, CV R^2 = 0.42; Figure B1c).

Discussion

Results from this study highlight the importance of considering potential climate interactions in real-world environments for the improved conservation and management of freshwater resources. In particular, the significance of cumulative human disturbance variables was often contingent on the inclusion of climate interactions due to opposing, climate-dependent land use effects. We observed unexpected positive associations with human disturbance in cooler regions that may be indicative of a subsidy-stress response, whereas community integrity declined with increasing catchment disturbance stress in warmer regions. Further, climate interactions revealed potential indirect effects on habitat quality as well as the important role of stream type in determining potential drought or flooding risks. Site-specific habitat quality models further supported land use model results, demonstrating the combined negative effect of warming and habitat degradation on sensitive species including highly valued coldwater fishes such as Arctic grayling and rainbow trout. However, overall community richness and productivity were not negatively affected by land use, underscoring the importance of field-based multiple stressor studies that may reveal complex species compensatory responses.

Climate interactions

The potential buffering effect of climate on other stressors has been raised by numerous experimental studies (reviewed in Jackson et al. 2016), however, we observed only partial

evidence for climate antagonisms. In this study, the proportion of sensitive species (lithophilic spawners and intolerant species) increased with greater anthropogenic land use, but only in cooler regions (Figures 5-6). Positive land use effects at low to moderate disturbance levels may be indicative of a subsidy-stress response, possibly due to increased nutrients or water temperatures in these naturally cooler and less productive regions (e.g., Piggott et al. 2012). A potential subsidy-stress response was also noted by Scrimgeour et al. (2008), where increased disturbance area was associated with higher occurrences of Arctic grayling and mountain whitefish in higher elevation regions of west-central Alberta. In contrast, we observed a predominance of synergistic interactions in warmer and wetter regions experiencing greater land disturbance (Figures 5-6). As many lithophilic and intolerant species are sensitive to warming water temperatures (Hasnain et al. 2010), fish in regions experiencing the greatest July air temperatures may be experiencing thermal stress, potentially lowering their abilities to withstand concurrent stress following catchment disturbance (Vinebrooke et al. 2004; Lyons et al. 2015). Further, the synergistic interaction between maximum July temperature and change in summer precipitation may be explained by indirect effects such as increased sedimentation run-off, which would compromise lithophilic spawning habitat (e.g., Goudie 2006; Bryant 2009; Goode et al. 2012). Notably, sites experiencing both high July temperatures and higher rates of summer wetting were also characterized as having lower current summer precipitation regimes, with sites being concentrated in the northern portion of our study area (Fig. A.2d). Despite having naturally lower precipitation regimes, dry regions are disproportionately sensitive to changes in precipitation which may result in increased flooding events (Ashmore and Church 2001). Furthermore, sedimentation impacts may be particularly detrimental in northern boreal streams that are being rapidly altered by permafrost loss (Chin et al. 2016). In agreement with our predictions, the interaction between drainage area and change in summer precipitation identified potential benefits of increasing streamflow in smaller streams that may be increasingly vulnerable to stranding and degraded water quality with ongoing climate change (e.g., Brooks 2009; Leppi et al. 2014; Shanley and Albert 2014).

Findings from the few field-based freshwater multiple stressor studies that have incorporated climate interactions further highlight the importance of considering ecological context, as well as the great need for an improved mechanistic understanding of combined stressors within a natural setting (Radinger et al. 2016; Bruder et al. 2017; Gutowsky et al. 2019). In this study, the higher

prevalence of synergistic climate interactions observed may be specific to northern boreal ecosystems experiencing amplified climate change rates, although future work will be required to substantiate this possibility (Schindler and Lee 2010). In contrast, Radinger et al. (2016) identified predominantly antagonistic climate – land use interactions on freshwater fish distributions which were attributed to the potential for dominance effects (where one stressor greatly outweighs another) commonly found in smaller lotic systems. However, within the same river system, synergistic interactions were observed in larger rivers experiencing higher land use pressures, suggesting the potential for systems to shift from an antagonistic to a synergistic state once certain stressor thresholds are surpassed. An additional example of ecological context comes from observing the interaction between warming and land use degradation on freshwater trophic state, which can produce either dampened or synergistic net effects depending on the original state, the rate of ecological change, and the response of freshwater biota (Smith et al. 1999; Heino et al. 2009; Jacobson et al. 2010; Porter et al. 2013). For instance, Gutowsky et al. (2019) observed an antagonistic interaction between warming and forest cover loss on lake fish biomass, indicating that warming-induced productivity may be partly offsetting concurrent land use effects in regions with naturally lower trophic states. In contrast, climate and land use-mediated eutrophication of freshwaters has been widely observed at lower latitudes, producing devastating consequences for aquatic biodiversity (Heino et al. 2009).

Independent effects of land use, climate, and stream size on overall richness and catch per unit effort

Potential species compensatory dynamics and subsidies at low-moderate disturbance levels may be masking land use effects, particularly for richness and abundance metrics which contain a wider species tolerance portfolio (Vinebrooke et al. 2004; Jackson et al. 2016). Increasingly degraded habitats may favour the success of more tolerant or generalist species over intolerant species, which has been observed in many lotic systems (Bramblett et al. 2005), including watersheds in southern and central Alberta (Stevens et al. 2010; Cantin and Johns 2012). We observed tenuous support for linear disturbance in the top species richness models, and caution that further investigation would be required to confirm this potential relationship. However, we speculate that the observed increase in species richness with low levels of linear disturbance up to a peak of approximately 1225 m/km^2 may be attributed to potential stream subsidies (Figure 3; Allan 2004; Wagenhoff et al. 2011). Another potential explanation for this trend may be the

intermediate disturbance hypothesis, where moderately disturbed ecosystems are theorized to have higher species richness due to a reduction in competitive exclusion (Connell 1978). In this case, systems with intermediate catchment disturbance may produce indirect effects such as flashier flows, increased sedimentation, or altered water quality, that may keep the watershed in a slightly higher state of flux compared to baseline conditions (Townsend et al. 1997).

Species richness and community catch were greater in regions with longer growing seasons, and higher July temperatures, respectively (Figures 3-4). It has been well established that warmer regions generally support greater species diversity and productivity due to higher and more seasonally stable resources (e.g., species energy theory), combined with a lower risk of overwinter mortality (Krebs 2008; Shuter et al. 2012; Rypel and David 2017). Further, warmer regions are closer to recent glacial refugia, facilitating higher species dispersal rates (Abell et al. 2008). Drainage area was an important predictor in all community models, however mixed results were observed (Figures 3-6). In particular, species richness was strongly related to increased drainage area, which is in agreement with the species-area hypothesis and typical of small lotic systems that support increased habitat heterogeneity required for varying fish life stages, including more critical overwintering habitat, in areas further downstream (Gorman and Karr 1978; Connor and McCoy 1979). However, both community catch and the ATI index were higher in smaller catchments, which may be related to sampling methodology or species preferences specific to the dataset used. For example, our finding that more fish are found in smaller catchments is likely an artefact of backpack electrofishing, as it is more effective in smaller drainages where fish are unable to escape (Portt et al. 2006). Further, the positive relationship with the ATI may be explained by the prevalence of small-bodied tolerant species (e.g., brook stickleback) in this dataset that are commonly found in small watercourses with low to moderate flows (Langhorne et al. 2001).

Study limitations

While we selected an extensive human disturbance dataset available for the study region, the dataset still had several potential limitations. First, grouping of all disturbance variables was necessary to avoid low individual gradients, however this removed our ability to distinguish disturbance types that may have yielded differing impacts on watershed integrity (Esselman et al. 2011). The disturbance data may have also been limited due to spatial and temporal constraints,

for example all disturbance data was identified using 2008-2010 satellite imagery yet some of these effects may have been in place for many years prior. Conversely, watershed alteration that occurred after 2010 would not have been accounted for in our analyses, possibly masking the detection of disturbance trends.

We did not have data for several key variables, such as nutrient levels or streamflow, which have been demonstrated as good predictors of land use stress elsewhere (Stevens et al. 2010; Cantin and Johns 2012; Lange et al. 2014). Further, reductions in fishing pressure over time may influence results, as was suggested by Arciszewski et al. (2017) as a possible explanation for a recently observed rise in fish abundance near the Athabasca oil sands. While we used the most up to date hydrology dataset for the region (AEP 2018b), we did not have information regarding any previous instream habitat loss or alterations that may have altered local fish community structure. Lastly, we note that potential stressor mechanisms identified in this study would require testing in controlled, experimental settings to determine causation. Until then, it is possible that relationships observed here are due to correlation with untested variables, for example spatially correlated variables relating to differing species assemblages or disturbance mechanisms, watershed connectivity, or fine-scale processes.

Conservation and management implications

Despite the mounting threat of climate change worldwide, potential climate interactions with other cumulative stressors continue to be overlooked in typical conservation and management planning (Mantyka-Pringle et al. 2016). The inherent risk in ignoring potential climate interactions is likely to accelerate over time, and poorly informed management actions may lead to (at best) ineffective outcomes to (at worst) negative consequences for biodiversity (Côté et al. 2016). Modified solutions may be required for stressors involved in antagonistic interactions, as mitigation of a non-dominant stressor could lead to a net negative outcome. Further, identifying additive or synergistic interactions that may reach detrimental ecological threshold points under future climate and land use scenarios will be critical for prioritizing conservation efforts and thereby minimizing future biodiversity losses.

Regionally specific multiple stressor studies that include field-based validation will help to expedite successful conservation outcomes, particularly if they are designed for integration with current environmental management frameworks. For example, the Government of Alberta,

Canada, has implemented an adaptive cumulative effects management framework that incorporates semi-quantitative dose-response relationships for facilitating informed management decisions (MacPherson et al. 2014). Regional multiple stressor studies such as ours could be used for refining their models, including the consideration of novel stressor interactions, and identifying potential stressor hotspots that could be used for conservation prioritization (Figure B2). For instance, we identified that lower Athabasca River fish populations may be at a higher risk to future warming and oil sands development, possibly warranting more strategic land use planning and/or climate adaptation strategies for this quickly evolving region (Schindler and Lee 2010). The Athabasca watershed supports many highly valued and already threatened coldwater fishes that may be increasingly vulnerable to the combined effects of warming and disturbance, including Arctic grayling (listed as a species of special concern in Alberta; AEP and ACA 2015), rainbow trout (listed as endangered under COSEWIC; COSEWIC 2014), and bull trout (listed as a species of special concern under COSEWIC; COSEWIC 2012). In contrast, potential land use subsidies observed in cooler, higher elevation regions suggest currently low levels of stress, however, this interaction has the potential to tip from antagonistic to synergistic under future warming scenarios.

Conclusion

Our study provides evidence for complex interactions between warming and co-occurring stressors in a northern boreal region experiencing substantial land use and climate changes pressures. In particular, sensitive fish species (e.g. rainbow trout, Arctic grayling) declined owing to synergistic interactions between warming, increased rainfall, and land use intensity. Our use of an extensive field dataset allowed the identification of regions that may be increasingly vulnerable to ongoing climate change and land use impacts (e.g. warmer and wetter regions), versus regions that may be temporarily benefiting from low-moderate land use subsidies (e.g. cooler and less productive regions). Based on our results, we caution that the continued exclusion of mounting climate change effects in standard conservation and management plans may result in detrimental long-term impacts on freshwater biodiversity.

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Tables and Figures

Table 1. Fish assemblage metrics representing the biological integrity of Albertan fish communities

Fish Metric	Description	Predicted Effect	Catchment Mean ±SD
Species richness	Total number of species present in a catchment	Highly stressed watersheds will support less biodiversity	3.1 ±1.5
Fish catch per 100s of electrofishing (CPUE)	Fish catch is an index of relative abundance	Highly stressed watersheds will have a lower carrying capacity	7.0 ±16.0
Percent lithophil[c]	The percentage of individuals requiring coarse unembedded substrate for reproduction	Expected to decline with land use that may increase stream sedimentation (e.g. forestry, agriculture)	44 ±38
Assemblage Tolerance Index (ATI)	An index of the overall community tolerance to disturbance	Expected to increase with land use that may degrade habitat or water quality	5.9 ±2.2

SD=standard deviation

[c] lithophils included Arctic grayling, brook trout, bull trout, burbot, lake chub, lake whitefish, longnose dace, longnose sucker, mountain whitefish, rainbow trout, spottail shiner, trout-perch, walleye and white sucker

Table 2. Linear mixed model results for four community metrics. Disturbance scale indicates the spatial scale of potential disturbance variables (linear disturbance or polygonal land use), ranging from disturbance in the riparian buffer of the local catchment to the entire watershed at the HUC-8 level (AEP 2017). Predictors that contributed to the top models at each scale are reported, along with the AICc, difference in AICc to the best model for each metric, and the conditional pseudo R^2 followed by the marginal R^2 in brackets. Highlighted rows indicate where a single top disturbance scale model was identified for each biological metric (ΔAICc >2).

Biological Metric	Disturbance Scale	AICc	ΔAICc	R^2	Important Predictors[4]
Species richness[1]	watershed	322.3	0	44 (37)	area, FFP, FFP2, linear, linear2
	riparian local	322.7	0.4	46 (35)	area, FFP, FFP2
	local	322.7	0.4	46 (35)	area, FFP, FFP2
	riparian network	322.7	0.4	46 (35)	area, FFP, FFP2
	network	322.7	0.4	46 (35)	area, FFP, FFP2
Total catch[2]	all	389.4	-	35 (12)	area, July
Lithophils (%)[3]	riparian network	292.4	0	53 (42)	area, July, slope, ΔSMPP, ΔSMPP*July, linear, linear*July
	watershed	297.1	4.7	50 (40)	area, July, slope, ΔSMPP, ΔSMPP*July, land
	riparian local	299.6	7.2	49 (39)	area, July, slope, ΔSMPP, ΔSMPP*July
	local	299.6	7.2	49 (39)	area, July, slope, ΔSMPP, ΔSMPP*July
	network	299.6	7.2	49 (39)	area, July, slope, ΔSMPP, ΔSMPP*July
Assemblage Tolerance Index	watershed	284.4	0	56 (45)	area, july, slope, ΔSMPP, ΔSMPP*area, land, land*July
	riparian local	288.6	4.2	51 (44)	area, july, july2, slope, ΔSMPP, ΔSMPP*area
	riparian network	288.6	4.2	51 (44)	area, july, july2, slope, ΔSMPP, ΔSMPP*area
	network	288.6	4.2	51 (44)	area, july, july2, slope, ΔSMPP, ΔSMPP*area
	local	293.4	9.0	55 (43)	area, july, july2, ΔSMPP, ΔSMPP*area, linear, land, land2

[1]Species richness was square-root transformed, [2]Total catch was log-transformed and [3]Lithophils were logit transformed

[4]Area= drainage area, FFP = frost free period, land = land use (%), slope = catchment slope, July = maximum July air temperature, ΔSMPP = change in summer precipitation, linear = linear disturbance (m/km^2); a suffix of "2" indicates a quadratic term and an asterisk indicates an interactive term.

Table 3. Top model standardized coefficients for four community metrics.

Biological Metric	Disturbance Scale	Important Predictors[4]	Standardized Coefficient	SE	*P*-value
Species richness[1]	Watershed	Area	0.55	0.05	<0.01
		FFP	0.04	0.06	0.53
		FFP2	-0.28	0.09	<0.01
		Linear	0.10	0.05	0.04
		Linear2	-0.20	0.06	<0.01
Total catch[2]	n/a	Area	-0.14	0.05	<0.01
		July	0.39	0.09	<0.01
Lithophils (%)[3]	Riparian network	Area	0.34	0.05	<0.01
		Slope	0.14	0.06	0.01
		July	-0.03	0.09	0.7
		ΔSMPP	0.17	0.08	0.04
		July* ΔSMPP	-0.84	0.14	<0.01
		Linear	-0.09	0.04	0.06
		Linear* July	-0.39	0.1	<0.01
Assemblage Tolerance Index	Watershed	Area	-0.15	0.05	<0.01
		slope	-0.17	0.06	<0.01
		July	0.21	0.10	0.04
		ΔSMPP	-0.11	0.08	0.17
		Land	-0.14	0.07	0.05
		Area * ΔSMPP	0.51	0.09	<0.01
		Land* July	0.63	0.15	<0.01

[1]Species richness was square-root transformed, [2]Total catch was log-transformed and [3]Lithophils were logit transformed

[4]Area= drainage area, FFP = frost free period, land = land use (%), slope = catchment slope, July = maximum July air temperature, ΔSMPP = change in summer precipitation, linear = linear disturbance (m/km^2); SE = standard error; a suffix of "2" indicates a quadratic term and an asterisk indicates an interactive term.

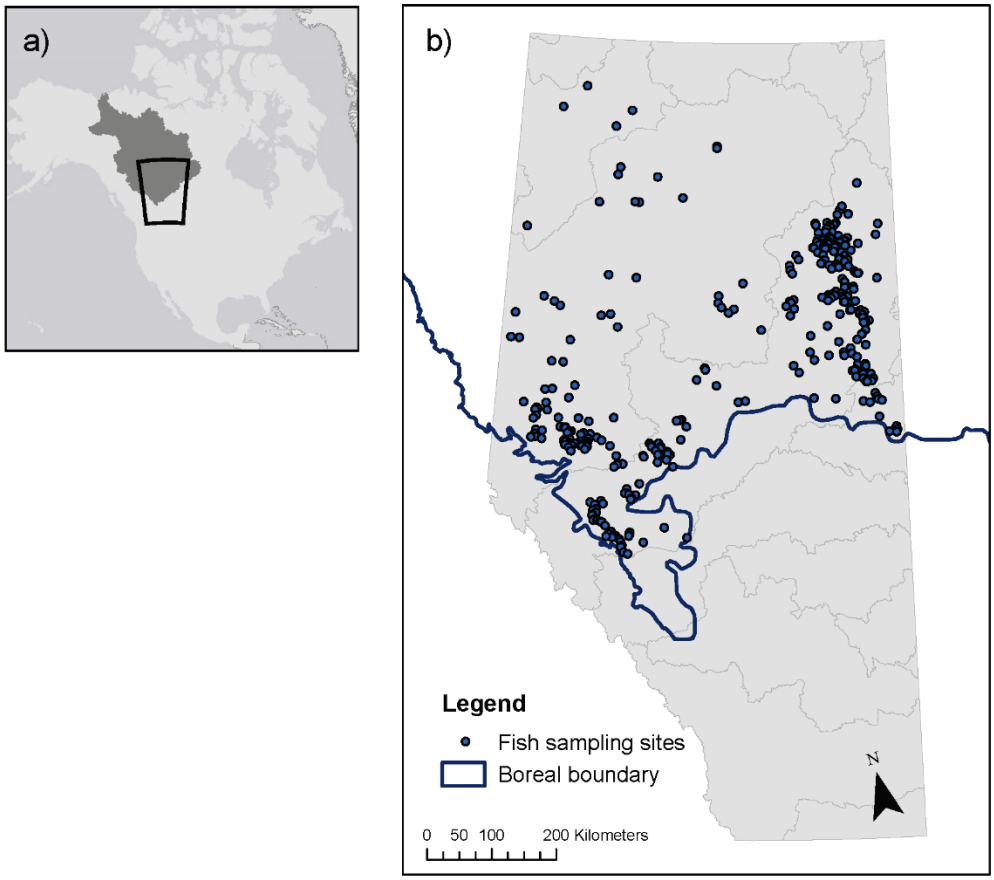


Figure 1. Study area in the boreal region of Alberta, Canada, showing a) the Mackenzie River drainage which flows from its headwaters in the Peace-Athabasca Delta north to the Arctic Ocean and b) zoomed in view of the study area including backpack electrofishing sampling sites and the southern boundary of the boreal disturbance dataset.

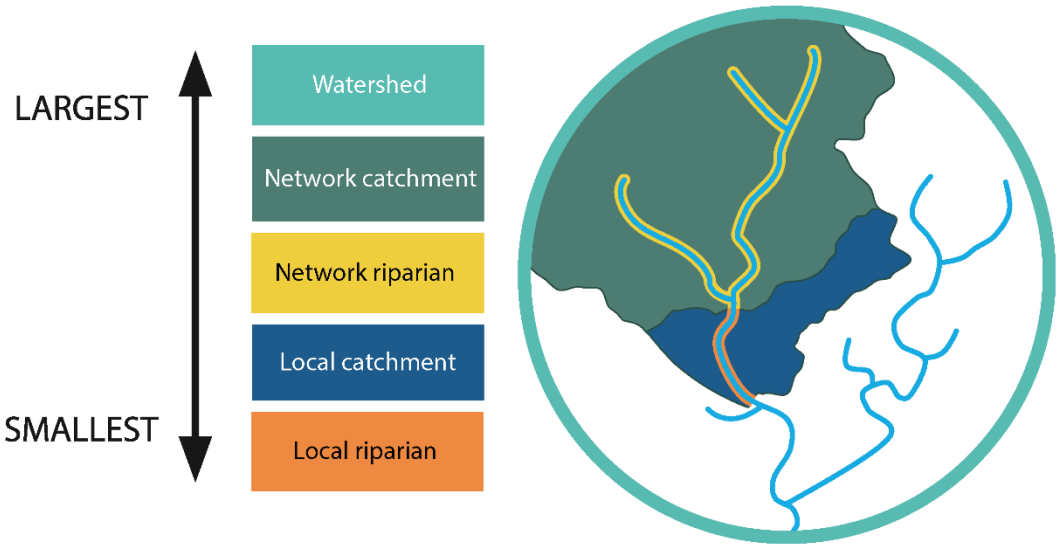


Figure 2. Five spatial scales used for calculating human disturbance variables. Local spatial scales encompass the immediate catchment where the fish survey was conducted. Network spatial scales include the local catchment and the entire upstream catchment. Riparian areas were defined as areas within 30m of the stream line. Watershed-level catchment includes the network catchment, as well as the greater area surrounding it as defined by Alberta's Hydrologic Unit Code 8 (AEP 2017).

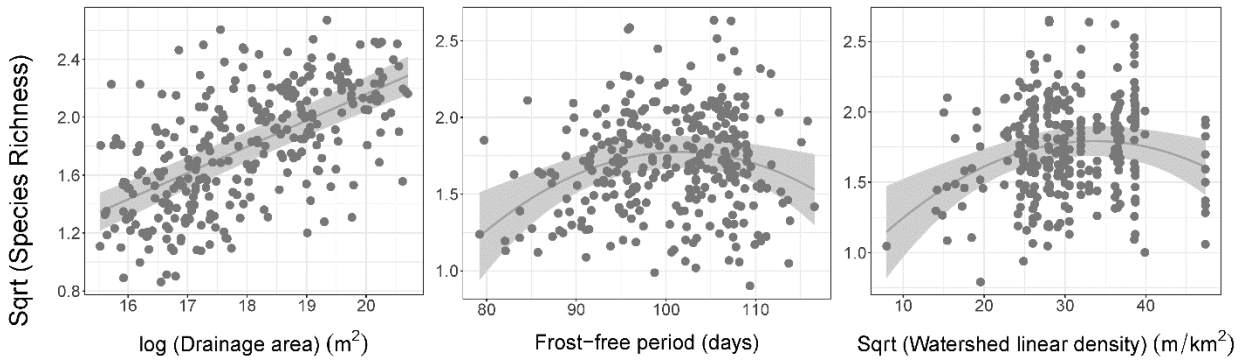


Figure 3. Partial plots for square-root transformed species richness with drainage area, frost-free period and watershed linear density. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

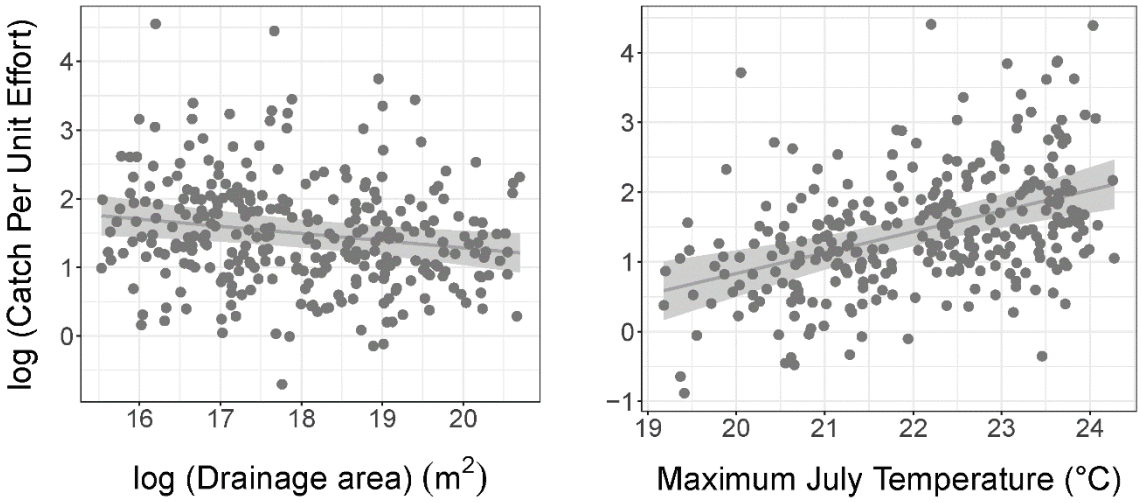
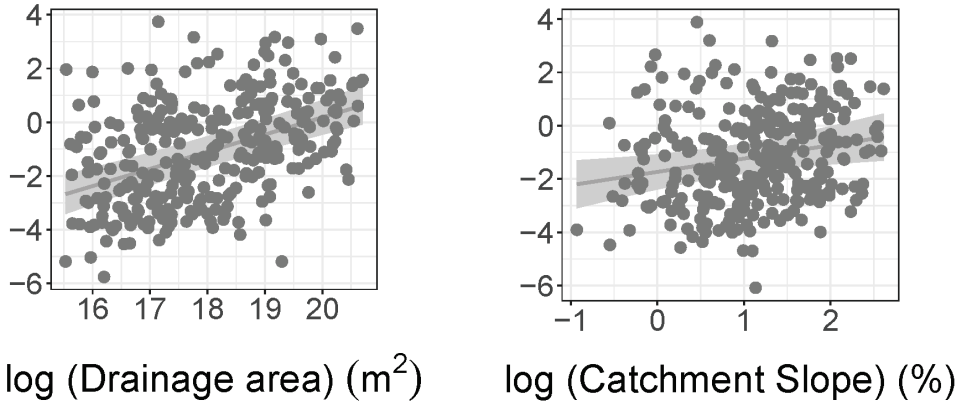
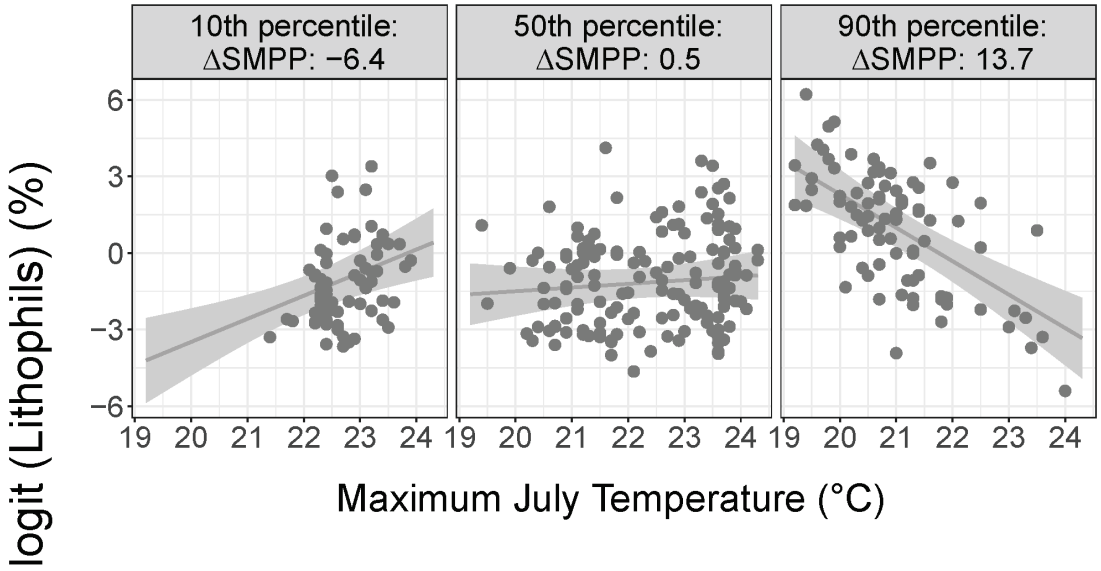


Figure 4. Partial plots for log-transformed catch per unit effort with drainage area and maximum July temperature. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.


log (Drainage area) (m²)
log (Catchment Slope) (%)


10th percentile:
ΔSMPP: −6.4
50th percentile:
ΔSMPP: 0.5
90th percentile:
ΔSMPP: 13.7
logit (Lithophils) (%)
Maximum July Temperature (°C)

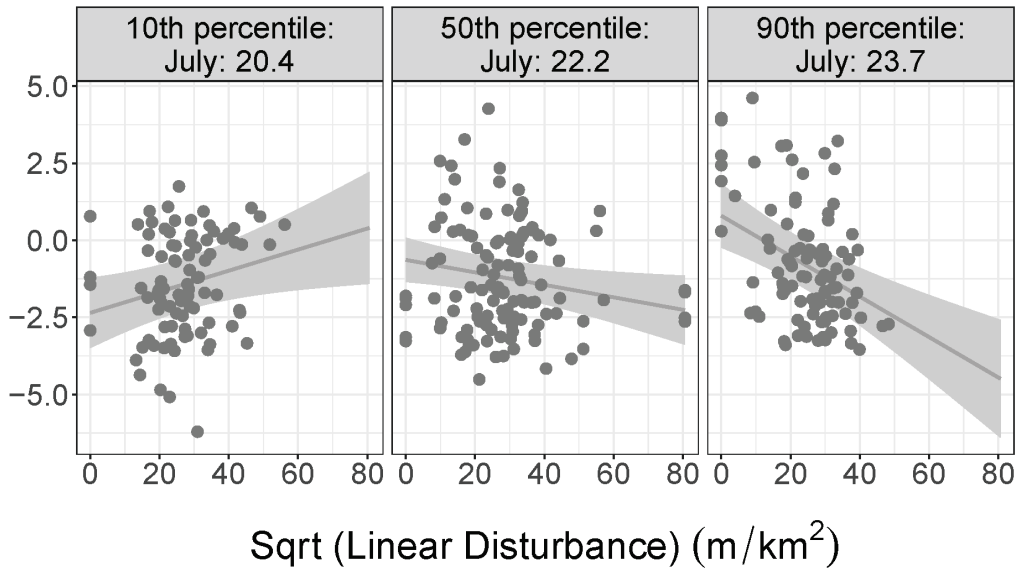

10th percentile:
July: 20.4
50th percentile:
July: 22.2
90th percentile:
July: 23.7
Sqrt (Linear Disturbance) (m/km²)

Figure 5. Partial plots for logit-transformed lithophils (%) with log-transformed drainage area and slope (top), with maximum July temperature by change in summer precipitation (ΔSMPP) (mm) (middle), and with square-root transformed linear disturbance by maximum July temperature (°C) (bottom). Cross sectional plots are shown at the 10th, 50th, and 90th percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence interval.

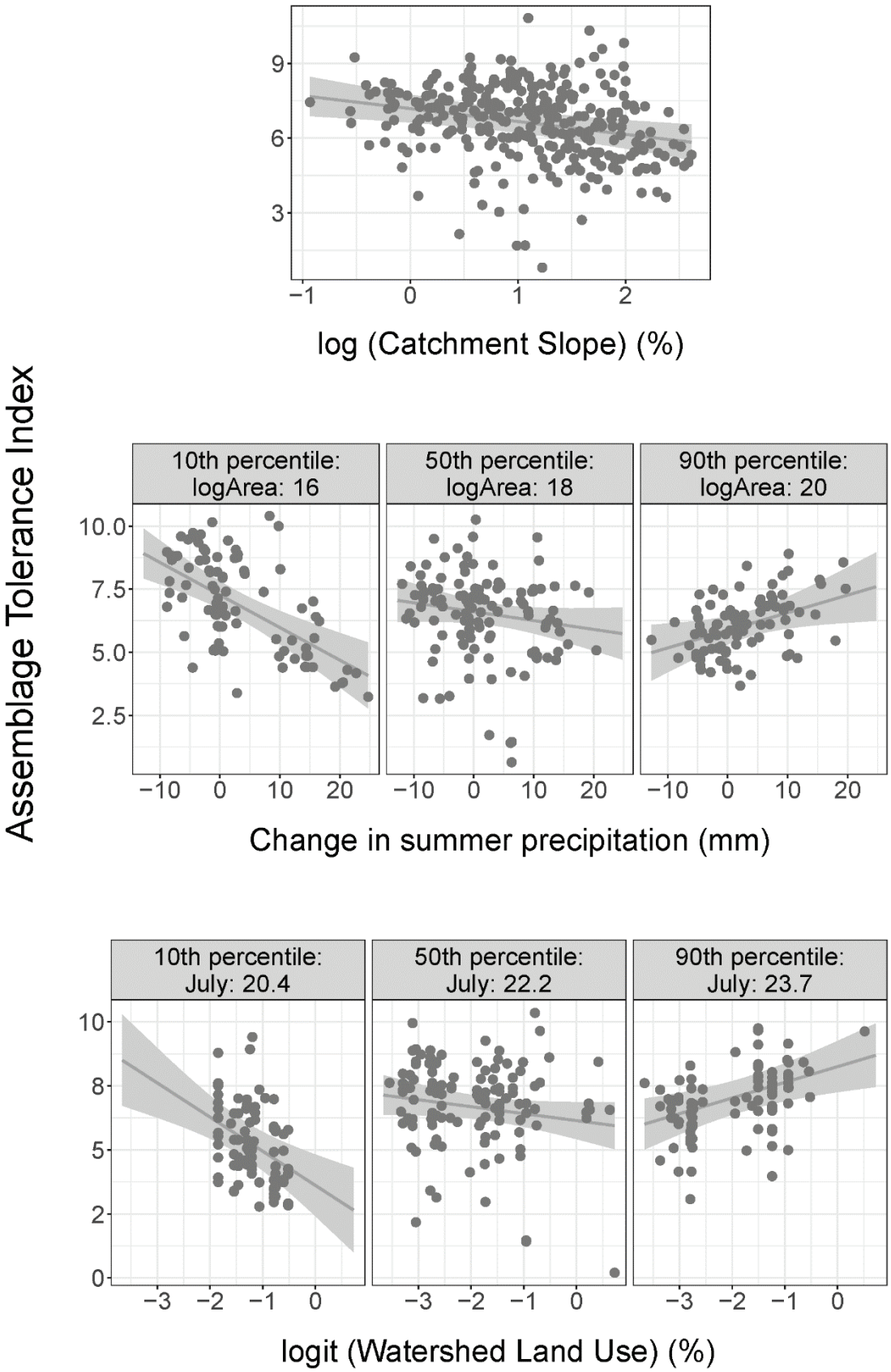

Assemblage Tolerance Index
log (Catchment Slope) (%)
10th percentile: logArea: 16
50th percentile: logArea: 18
90th percentile: logArea: 20
Change in summer precipitation (mm)
10th percentile: July: 20.4
50th percentile: July: 22.2
90th percentile: July: 23.7
logit (Watershed Land Use) (%)

Figure 6. Partial plots for the Assemblage Tolerance Index (ATI) with log-transformed slope (top), with change in summer precipitation by log-transformed drainage area (m^2) (middle), and with logit-transformed land use by maximum July temperature (°C) (bottom). The ATI is a scale from one to ten, with a high value indicating a more tolerant community, and a low value indicating a more sensitive community. Cross sectional plots are shown at the 10^{th}, 50^{th}, and 90^{th} percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

Chapter 3: Drivers of fish biodiversity in a rapidly changing permafrost landscape

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Author's Contributions:

AM, DG, JK, and SS conceived the research ideas; AM, DG, JK, and SS acquired funding; AM, DG, and JK obtained field data; AM analysed the data and led the writing of the manuscript. All authors contributed to sequential drafts and final approval for inclusion in this dissertation.

Summary

Northern ecosystems are undergoing rapid environmental changes and there is a need to document, predict, and mitigate the resulting impacts on biodiversity before new ecological states are reached. Climate change and other anthropogenic stressors have the potential to produce both direct and indirect effects on sensitive northern aquatic species, including reducing preferred thermal habitat, and altering habitat quality via freshwater eutrophication ("greening") and brownification ("browning"). In addition, warming and infrastructure development may amplify permafrost thaw, which can alter water quality and quantity. We investigated the drivers of freshwater fish community health in lakes of the lower Mackenzie River basin, one of the most rapidly warming regions of North America. To do this, we collected ecological data including lake morphometry, water quality, and fish community data from fifty lakes and derived several indicators of aquatic health including fish species richness, relative abundance, and the occurrence of three culturally important fish species. We found that water quality and lake size were significant co-drivers of fish community health whereas relationships with direct warming, as represented by July air temperature, were relatively negligible. Dissolved organic carbon (an indicator for lake browning) emerged as a particularly important driver of fish community structure, and fish community health steeply declined above a threshold point of 17 – 18 mg/L. We suggest potential mechanisms for these declines including light inhibition during summer and a reduced capacity for overwintering in smaller and murkier lakes that may experience faster oxygen depletion rates. Using a more expansive regional water quality database of 203 lakes, we observed potential supporting evidence for the effects of warming and new road development on increased lake browning (increases in dissolved organic carbon) and nutrient enrichment (increases in total phosphorus concentrations), with possible consequences for declining fish habitat in this region. Together, these results highlight the potential vulnerability of fishes that rely on the numerous small and shallow lakes that dominate rapidly warming permafrost landscapes.

Introduction

Rapid climate change in northern regions is leading to unprecedented ecological events, with far-reaching impacts on northern biodiversity and people (Marsh et al. 2009; Carroll et al. 2011; Hovelsrud et al. 2011; Dunmall et al. 2013; Kokelj et al. 2013; DFO 2018; Knopp et al. 2020). Growing concerns shared by northern Indigenous citizens and scientists alike have resulted in an international call for more targeted conservation actions, including more protection for abruptly changing freshwater ecosystems (CAFF 2013; Greaves 2016; Heino et al. 2020). However, predicting northern environmental change remains a great challenge due to inadequate monitoring combined with a backdrop of rapidly shifting baselines (Lento et al. 2019; Laske et al. 2019).

Climate change can produce differential regional impacts on biodiversity, and some of the most complex and substantial changes are occurring in northern regions (CAFF 2013; Meredith et al. 2019). At high latitudes, warming rates are two to three times faster than global levels, leading to widespread permafrost thaw and cascading effects on freshwater ecosystems (Wrona et al. 2013; Bush and Lemmen 2019; Meredith et al. 2019). Much of the climate change research on aquatic biodiversity to-date has focused on direct warming impacts on thermal habitat of species, and it is anticipated that there will be a net loss of habitat for Arctic specialists whereas cold and cool water species will gradually expand their northern range limits as new habitats become thermally suitable (Reist et al. 2006b; Lynch et al. 2016; Poesch et al. 2016). In addition to warmer lakes, climate change can produce marked changes in water quality including the eutrophication ("greening") and brownification ("browning") of subarctic lakes (Hayden et al. 2019; Saulnier-Talbot et al. 2020), mirroring what has been observed for thousands of lakes at lower latitudes (Leech et al. 2018; Mahdiyan et al. 2020). As northern lakes become both warmer and more nutrient-rich it is expected that the diversity and productivity of many biological communities will increase, particularly in many northern lakes that have been previously limited by low nutrients and short growing seasons (Heino et al. 2009; Wrona et al. 2013; Brucet et al. 2013; Hayden et al. 2017). In contrast, increased carbon inputs and associated nutrients such as phosphorus or nitrogen may eventually reach and then surpass optimal states for northern fish communities due to resultant light inhibition, reduced oxygen levels, and altered lake thermal structure (Stasko et al. 2012; Finstad et al. 2014; Karlsson et al. 2015; Creed et al. 2018). As the number of brown and eutrophic lakes appear to be rising worldwide, understanding the unique

ecological consequences of these ‘murky’ lakes (i.e., lakes that are both eutrophic and brown) across different ecosystems including those at higher latitudes will be critical for identifying regional conservation priorities and actions.

An additional growing concern is how permafrost degradation will contribute to rapidly changing lake ecosystems through active layer deepening and thermokarst (i.e., melting of ground ice) processes (Wrona et al. 2013). Across circumpolar Arctic and subarctic regions, thawing permafrost is leading to increased dissolved organic carbon and nutrient delivery to lakes (Vonk et al. 2015; Wauthy et al. 2018; Tank et al. 2020). Although the effects of permafrost thaw on freshwater food webs can be varied and complex, many forms of thaw including active layer thickening, peat subsidence, and lakeshore erosion have been linked to substantial water quality changes that may act to either strengthen or counteract lake greening and browning processes (Lougheed et al. 2011; Korosi et al. 2015; Vonk et al. 2015; Wrona et al. 2016; Morison et al. 2019). One prominent example of permafrost degradation in the western Canadian Arctic occurs when hillslope thermokarst processes lead to retrogressive thaw slumping and other thermo-erosional features, producing large inputs of eroded mineral soils into surface waters that can increase ionic concentrations and decrease nutrients and coloured dissolved organic matter (cDOM) (Kokelj et al. 2005; Vonk et al. 2015; Houben et al. 2016; Wrona et al. 2016). The decrease in water column nutrients and cDOM likely occurs as a result of adsorption to eroded materials and subsequent deposition to the bottom lake sediments (Moquin and Wrona 2015; Vonk et al. 2015). In the uplands east of the Mackenzie Delta, shoreline retrogressive thaw slumps are a common feature on lakes that have been shown to alter lake biological communities, and may have significant consequences for upper trophic levels such as zooplankton or fish with continued warming (Thienpont et al. 2013; Vucic et al. 2020; Cohen et al. 2020).

A warmer and more accessible north has facilitated an increasing interest in northern resource extraction and tourism, and is already leading to a myriad of negative and cascading effects on fragile northern ecosystems (Christiansen et al. 2013; Raynolds et al. 2014; Tonn et al. 2015; Reist et al. 2016; Halliday et al. 2020). In particular, the construction of new roads through previously intact landscapes can lower economic hurdles for other development, provide novel angling access, and disrupt critical fish migrations if crossing structures present barriers

(Chetkiewicz et al. 2017). The predominant use of gravel highways over permafrost terrain can also impact adjacent terrestrial and aquatic ecosystems due to deposits of calcareous road dust and resultant changes in roadside vegetation, snow accumulation patterns, and warmer ground temperatures (Walker and Everett 1987; Gill et al. 2014; Gunter 2017; Ackerman and Finlay 2019; Zhu et al. 2019). Further, historical infrastructure projects across permafrost have demonstrated substantial changes to surrounding terrestrial ecosystems that could be relevant for nearby lakes, including indirect habitat alterations from roadside flooding and thermokarst that were substantially greater than direct habitat loss from the infrastructure footprint alone (Raynolds et al. 2014). However, as most major highway projects in permafrost regions occurred decades ago, there is a growing need to understand how new development projects may combine with concurrent climatic changes to influence lake biodiversity, including higher trophic levels such as fish (Christiansen et al. 2013; Raynolds et al. 2014; Reist et al. 2016).

Our main study question was: what are the current drivers of fish community health in lower Mackenzie River basin lakes? The lower Mackenzie River basin is an ice-rich permafrost region that is experiencing substantial environmental change due to rapid warming, widespread permafrost thaw, and the recent opening of the Inuvik-to-Tuktoyaktuk Highway in 2017, North America's second all-weather highway connection to the Arctic Ocean (Tyson et al. 2016; Bush and Lemmen 2019). Although there have been several previous studies examining lake water quality and lower trophic levels within the context of environmental change in the Mackenzie Delta region (e.g., Kokelj et al. 2005, 2009; Thienpont et al. 2013; Moquin et al. 2014; Houben et al. 2016; Zhu et al. 2019; Vucic et al. 2020; Cohen et al. 2020), comparable work examining lake fishes remains a substantial data gap here and in other ice-rich permafrost regions worldwide (Raynolds et al. 2014; Laske et al. 2016, 2019). The importance of understanding changing fish biodiversity is echoed by Indigenous knowledge holders across the circumpolar north that have reported observations of environmental change directly relevant for their food security and cultural identity (Knopp et al. 2020). To investigate fish community drivers, we collected standardized ecological data (lake morphometry, water quality, and fish community data) for fifty subarctic lakes at the forest-tundra transition. As many of our fish sampling lakes appeared to have degraded water quality, we decided to obtain more limnological data (lake morphometry and water quality) for the region to provide a broader context for ongoing environmental changes. Using available regional limnological data for 203 lakes we asked (1)

Are the physicochemical characteristics of our fish sampling lakes comparable to previously sampled lakes in this region, and (2) Is there any evidence for the effects of climate change or road use on water quality in regional lakes?

Materials and Methods

Study area

Supporting the second largest Arctic delta in the world, the lower Mackenzie River basin is an extremely dynamic ecosystem (Burn and Kokelj 2009; Lesack and Marsh 2010). In addition to providing extensive riverine and estuarine habitats for freshwater and anadromous species, the region contains tens of thousands of generally small and shallow lakes that receive varying inputs from river flooding each year (Ecosystem Classification Group 2007; Emmerton et al. 2007; Lesack and Marsh 2010). The region's climate is classified as subarctic, with historically cold and dry conditions that have experienced considerable warming (> 3°C since 1970), and have led to widespread permafrost degradation including 'mega' thaw slumps, disappearing (draining) lakes, and changes in freshwater biodiversity (Burn and Kokelj 2009; Marsh et al. 2009; Dunmall et al. 2013; Thienpont et al. 2013; Kokelj et al. 2013). There are two major highways that intersect the study area, including the Dempster Highway, opened in 1979, which connects Inuvik to the Klondike Highway 740 km to the south, and the Inuvik-to-Tuktoyaktuk Highway, opened in 2017, which joins Inuvik to the coastal hamlet of Tuktoyaktuk (Figure 1; Zhu et al. 2019; Cohen et al. 2020). The region is further characterized by its position along several steep ecozone gradients including the Peel Plateau located west of Fort McPherson, the intermediate northern taiga plains, and the tundra uplands north of Inuvik (Figure 1).

Our study area spans two traditional territories including the Gwich'in Settlement Area in the south and the Inuvialuit Settlement region in the north. Since time immemorial, Gwich'in and Inuvialuit citizens have been stewards of their lands and have heavily relied upon healthy ecosystems for their food security, culture, and overall well being (Gwich'in Tribal Council and Government of Canada 1992; Inuvialuit Regional Corporation 2011). Gwich'in Peoples of this region predominantly reside in the communities of Fort McPherson, Tsiigehtchic, Aklavik, and Inuvik, whereas the Inuvialuit are more concentrated in Inuvik, Aklavik, and Tuktoyaktuk (Figure 1). Some culturally important fish species for Gwich'in and Inuvialuit citizens in the lower Mackenzie River basin include broad whitefish *Coregonus nasus*, lake whitefish

Coregonus clupeaformis, lake trout *Salvelinus namaycush*, Dolly varden *Salvelinus malma*, burbot *Lota lota*, inconnu *Stenodus leucichthys*, northern pike *Esox lucius*, Arctic grayling *Thymallus arcticus*, Arctic cisco *Coregonus autumnalis*, and least cisco *Coregonus sardinella* (Stewart 1996; Inuvialuit Regional Corporation 2011; Kavik-Stantec Inc. 2012).

Part 1: Examining drivers of fish community health

Conceptual model development and predictions

Based on the literature, we created a conceptual model to understand the potential relationships among variables indicative of environmental change (warming, changes in precipitation, permafrost thaw, and road development and use), physical environmental covariates (lake morphometry and hydrologic connectivity), lake water quality variables, and fish community indicators of health in lower Mackenzie River basin lakes (Figure 2, Table 1). We chose three fish species for investigation due to their relatively high presence in our study lakes (captured in 22 – 50% of lakes). In contrast, other species including lake trout and inconnu were found in less than 10% of our study lakes. We made specific directional predictions for the linkages between each fish community indicator and relevant physical, chemical, and thermal habitat variables, and these expected relationships were then used to inform variable selection for our analyses described below. Briefly, we predicted that overall diversity and abundances would increase with warming and nutrient availability, but that individual species would have varied results (Table 1; Brucet et al. 2013; Poesch et al. 2016; Hayden et al. 2017). Based on prior studies that investigated thermal preferences and requirements of our focal species groups, we predicted that the two coldwater Coregonids (whitefish and least cisco) would decline with increased warming, whereas coolwater northern pike would increase (Christie and Regier 1988; Harvey 2009; Hasnain et al. 2010; Sharma et al. 2011; Jacobson et al. 2012; Van Zuiden et al. 2016; Edwards et al. 2016). Further, we predicted that northern pike would be sensitive to changes in water clarity due to the species' reliance on macrophyte habitats but would also demonstrate a preference for mesotrophic to eutrophic lakes (Casselman and Lewis 1996; Harvey 2009). In contrast, we expected that Coregonid species would prefer lower nutrient and chlorophyll levels as previous studies have linked declines to eutrophication-driven oxythermal habitat degradation (COSEWIC 2005; Jacobson et al. 2010, 2012). With regards to changes in dissolved organic carbon, we predicted that increases would lower overall diversity and abundances in lower Mackenzie River basin lakes that already face potential light limitations in

lake productivity due to highly coloured water (Pienitz et al. 1997; Finstad et al. 2014; Moquin and Wrona 2015; Solomon et al. 2015; Karlsson et al. 2015; Houben et al. 2016). For determining species-specific predictions, we combined lake and broad whitefish due to similar expected lake habitat preferences, and used literature for lake cisco to supplement the smaller body of work dedicated to least cisco (Scott and Crossman 1973; Richardson et al. 2001).

Field sampling methods

Our team sampled 48 lakes over a three-year period (2017-2019) along the Dempster and Inuvik to Tuktoyaktuk Highways (Figure 1). Fish sampling followed a modified version of the Ontario Broadscale Monitoring protocol which incorporates a standardized study design using large and small mesh gillnets spread over representative lake depth strata (Sandstrom et al. 2013). We used Ontario broadscale monitoring nets which target fish over 20 cm with large mesh sizes ranging from 38 – 127 mm, and fish under 20 cm with mesh sizes ranging from 13 – 38 mm. Each fish was identified to species level, and length and weight measurements were recorded. We additionally acquired fish presence/absence data for two lakes from a sampling program conducted by White Mountain Environmental in 2018 (White Mountain Environmental 2018). Although different gillnets were used, the range of mesh sizes was similar for comparing presence/absence data of our main focal species (25 – 76 mm and 76 – 127 mm).

In most lakes, gillnets were set for one-hour periods with an average of 11 net-hours for lakes less than 500 ha and 37 net-hours for lakes over 500 ha (Table C1). However, we also used data collected using overnight sets for two lakes visited in 2017. The difference in lake sampling methods stemmed from community feedback following our 2017 field season, which resulted in moving to short one-hour sets to reduce fish mortality during 2018 and 2019. While most 2017 lakes were re-sampled to ensure comparable data, we were unfortunately unable to revisit every lake. As a conservative measure, we removed these two lakes from analyses examining catch-per-unit-effort trends but retained them when looking at models relying on species presence/absence data, as these indicators are typically more robust to sampling methodology variation (Table C1).

In addition to fish sampling, we collected lake morphometry and water quality data for each lake including mean and maximum lake depth (m), lake area (ha), water temperature (°C), Secchi depth (m), turbidity (NTU), specific conductivity (µS/cm), chlorophyll-a (µg/L), total

phosphorus (TP) (µg/L), total nitrogen (TN) (mg/L), dissolved oxygen (mg/L), pH, and dissolved organic carbon (DOC) (mg/L)(Table 2). Full sampling details have been described previously in Vucic et al. (2020) and Cohen et al. (2020). Briefly, we obtained lake bathymetry data using a Humminbird® Helix 5 chart plotter (Johnson Outdoors Marine Electronics, Inc.) and Reefmaster bathymetry software (Reefmaster Ltd.). Water quality data were collected using a Eureka Manta multiparameter probe (Eureka Water Probes) at a 1 m depth over the deepest point of the lake for water temperature, pH, conductivity, dissolved oxygen, and turbidity. Secchi depth was measured at the same location by lowering the disk over the shady side of the boat. A water sample was collected and analyzed in the laboratory at Wilfrid Laurier University to measure TP, TN, chlorophyll-a, and DOC. Chlorophyll-a measurements were obtained by filtering 250 mL of each sample through Fisherbrand G4 glass fiber filters. We then used methanol to extract the chlorophyll-a from the filters and measured the concentration dissolved in the methanol using a Turner TD700 fluorometer (Symons et al. 2012). While most water quality sampling happened within the same sampling season as fish sampling, sampling year differed for a few lakes when re-sampling was required (Table C1). Zooplankton data were also collected at each lake for an additional project, and we used one indicator species from this dataset (*Chaoborus americanus*) to infer fish absence in six of our study lakes (Table C1; Sweetman and Smol 2006; Vucic et al. 2020).

Additional data acquisition

As our water quality sampling was conducted as one-time events during mid-late summer, we observed a significant negative trend between date of sampling and surface water temperature as lakes began to cool. An additional complication was that there was a wide range of air temperatures during the three different sampling years which had a significant influence on measured water temperatures. To avoid issues relating to differences in sampling timing among sites and years, we instead used mean July air temperature as a surrogate for mean summer water temperature (Sharma et al. 2007). *In situ* water temperatures were significantly related to both sampling date and air temperature during the month and year of sampling in our dataset, indicating that air temperature was a suitable proxy for mean summer water temperature (R^2_{adj} = 0.84). July air temperature was obtained from the ClimateNA program, which uses a 4 km grid spatial resolution (version 6.3; Wang et al. 2016).

Hydrologic connectivity to major perennial habitats was also investigated as a potential binary predictor variable for fish species richness, catch per unit effort, and the presence of migratory Coregonid (whitefish and cisco) species (Table 1). Because we were unable to visit our lakes during spring freshet to assess potential seasonal connections, we instead used a conservative approach and only indicated connectivity if the lake had a close and stable connection that we verified in the field or using a combination of Google Earth imagery and stream crossing assessment information (IMG Golder Corporation 2012). As a result, we noted a total of six lakes that had close and seasonally stable connections to large, perennial habitats including two lakes adjacent to the Mackenzie River East Channel, one lake connected to the Peel River floodplain system, one offline lake on a major Peel River tributary, and two lakes that were closely connected to the Husky Lakes.

Data analyses

Fish community analyses followed a sequential framework that included deriving indicators of fish community health, identifying potentially important environmental drivers of fish community health (Figure 1, Table 1), isolating environmental gradients using a principal component analysis (PCA), performing model selection, interpreting final models, and identifying individual effect contributions using hierarchical partitioning (Figure 3). We chose a PCA approach as many of the environmental variables were related (Figure C1), and PCA allowed a more effective means for separating key environmental gradients while maintaining the overall variability. To provide insight into the relative contribution of individual environmental variables to final models, we additionally completed hierarchical partitioning analyses which allowed us to isolate the sum of the individual and joint effects of related variables (Walsh and Mac Nally 2013).

We calculated three community-level metrics including species richness, catch per unit effort (CPUE) with largemesh nets and CPUE using smallmesh nets. CPUE was calculated as the total number of fish caught per net per hour ("net-hours") and was only calculated for lakes with comparable sampling methods and gillnet mesh sizes (n = 46 lakes, Table C1). Lake and broad whitefish were combined into one 'species' category due to small samples sizes and similar expected lake habitat preferences (Scott and Crossman 1973; Richardson et al. 2001).

Prior to running analyses, we examined variable distributions and applied log-transformations to improve normality for several predictor variables including lake area, turbidity, conductivity, DOC, and chlorophyll. In addition, we applied a log(x+1) transformation to two response variables including largemesh CPUE and smallmesh CPUE. We discovered that the effect of sampling date was significantly and negatively related to chlorophyll ($R^2_{adj} = 0.44$), so we detrended this variable prior to analyses. In addition, DOC appeared to display a wedge-shaped response, i.e., an abrupt and nonlinear response (Baker and King 2010), with several fish community indicators, making its effect potentially less detectable using linear statistical methods. To help further explore these relationships, we performed threshold change-point analyses between DOC and all fish indicators plus overall fish presence using the *TITAN2* package (Baker and King 2010).

A PCA approach was used to determine and isolate the major environmental gradients within our study lakes. PCA scores from the first four axes were used as predictor variables for each fish community indicator. We ran linear models for three community-level metrics (species richness, largemesh CPUE, and smallmesh CPUE) and logistic regression models for the distributions of three species (whitefish, least cisco, and northern pike). All predictor variables were standardized onto a unitless comparable scale prior to model selection using the *arm* package (Gelman et al. 2018). Standardization allowed inference of the relative strength of each predictor variable within models. For model selection, we used the *dredge* function from the multi-model inference package to identify the most parsimonious model with the lowest AICc (Barton 2018). To assess model performance for the logistic regression models we computed classification success, sensitivity (proportion of true positives) and specificity (proportion of true negatives) using 70% of the data as a training dataset and the remaining 30% as a testing dataset. We employed receiver operating characteristic curves to determine the most accurate threshold points for assigning probabilities to either ‘present’ or ‘absent’ (Fielding and Bell 1997).

Hierarchical partitioning analyses were conducted using the package *hier.part* (Walsh and Mac Nally 2013). The model output includes the individual contribution of each predictor variable to the overall explained variance. However, because there is no reporting of relationship direction, we additionally completed pairwise correlations between each predictor variable and fish community indicator for improved interpretation of the hierarchical partitioning results. We

calculated Pearson correlations for community-level indicators and non-parametric Spearman correlations for species presence absence indicators. While all predictor variables with potential importance to fish community indicators were included in the PCA step, we used indicator-specific variable combinations based on empirical relationships found in previous studies for the hierarchical partitioning step (Table 1).

Part 2. Regional water quality patterns

Data sources

We compiled water quality data from five different studies, including our own, that resulted in a database of 203 lakes spanning several ecoregions including the Mackenzie Delta tundra uplands outside of the delta influence, lakes situated within the delta, the taiga plains, and the Peel Plateau (Figure 1; Table 3). Of these lake water quality studies, one examined the effects of retrogressive permafrost thaw slumps (Korosi et al., unpublished), two focused on potential road-related effects (This study and Zhu et al. 2019), and two had no known landscape stressors ("reference studies"; Pienitz et al. 1997; Ogbebo et al. 2009a). In addition to these differences in study design, sampling years greatly varied with the earliest study occurring in 1990 and the remaining studies occurring between 2004 – 2019. Another consideration is that the month of sampling varied from late June to August which could result in water quality differences as solutes may become more concentrated over the course of the open-water season (Houben et al. 2016). Although field sampling methodology was similar across studies, the noted variation in survey year, geographic location, and study design means that we can not fully eliminate potential study-related effects (i.e., unknown variables relating to study differences), and we are therefore cautious with our inferences in the following results and discussion sections.

The results from one study, Korosi et al., have yet to be published, and so we provide additional sampling details here. Fifty-nine lakes were sampled for water chemistry between June 28 and July 5 2017, during the period of 24-h daylight in the Arctic summer. Lakes were accessed by helicopter, and sampling was conducted from the helicopter pontoons as a platform and taken from the centre of the lakes. Water depth was recorded using a hand-held sonar device, and vertical temperature profiles were taken using a Hanna multi-probe. Surface water samples (~0 – 2m depth) were collected using a vertical Van Dorn water sampler and shipped to Taiga

Environmental labs in Yellowknife for water chemistry analysis, which is a CALA accredited facility.

Using our compiled database, we identified lake morphometry and water chemistry parameters that were measured among the majority of studies and that were of potential interest to structuring fish communities. These included lake area, maximum depth, TP, DOC, specific conductivity, and pH (Table C2). To account for potential differences in sampling timing over the season, we additionally assigned each project to broad sampling time categories including early (late June – early July), early-mid (July), mid - late (late July – mid August) and late (mid-late August). Maximum depth values were missing from one study (Ogbebo et al. 2009a), however we estimated them using a quadratic model between mean depth and maximum depth for 105 lakes across northern Canada ($R^2 = 0.95$). Depth data for 50 lakes were from this study in the lower Mackenzie Delta, and an additional 55 lakes were from lakes spanning northern Canada (Campana et al. 2020).

We derived four climate variables including mean annual air temperature, mean annual precipitation, and the long-term change in mean annual air temperature and precipitation from the ClimateNA program (Table C2; Wang et al. 2016). Mean annual air temperature and mean annual precipitation were extracted for each lake location over the five-year period prior to sampling. We opted for a five-year period as some studies did not report which samples were collected in which years, and the longer time period allowed for a more robust estimate of the climate during potential sampling conditions which could vary year to year. To confirm our choice, we ran all models using either one year or five-year averages, which allowed us to verify that all models using the five-year period had greater model fit (increased variation explained and predictive cross validation). The two long-term climate change variables were calculated as the difference between mean annual air temperature from the most recent thirty-year period and the previous thirty-year period. The site locations reported in one study that used older geospatial technology (Pienitz et al. 1997) were georeferenced for accuracy using their published study map for reference, and we used these new estimated locations for climate extraction. Georeferencing was completed in ArcMap Desktop 10.7.1.

To account for other potential sources of variability, we added terms to indicate survey year, road type (0 = no road, 1 = representing the older, pre-existing Dempster Highway, 2 =

representing the newly constructed Inuvik to Tuktoyaktuk Highway), and presence of shoreline retrogressive permafrost thaw. Lakes situated within 1 km of the road were considered "road lakes" following Zhu et al. (2019). Data for shoreline thaw slump presence was provided directly by thaw studies, and we additionally identified that eight of our fish sampling study lakes had shoreline retrogressive thaw slumps using the Northwest Territories Inventory of Landscape Change map viewer, five of which were currently active (Segal et al. 2016b).

Data analyses

We recognize that differences in study design pose limitations to our regional water quality analysis, and that an 'ideal' study would have had a more equal distribution of study lakes across ecoregions, sampling years, impact categories, and morphometric gradients. However, given the lack of historical data to conduct such a study in this region, and the careful analytic framework proposed below, we suggest that useful conclusions may still be drawn surrounding water quality patterns in our study region.

We followed a stepwise analytical framework to address our water quality research questions, which is detailed below (Figure 4). To provide a more general basis for comparison, we first approximated nutrient-colour lake status using the framework described by Leech et al. (2018) that divides lakes into four categories: oligotrophic or 'blue' (TP < 30 µg/L and true colour < 20 PCU), eutrophic or 'green' (TP > 30 µg/L and true colour < 20 PCU), dystrophic or 'brown' (TP < 30 µg/L and true colour >20 PCU), or mixotrophic or 'murky' (TP > 30 µg/L and true colour > 20 PCU). We chose this classification system as many of our fish sampling lakes exhibited both high TP and DOC values, i.e., murky lakes, and this approach recognizes that murky lakes may have different ecological consequences than lake browning or eutrophication alone. However, as we did not have direct measurements of true colour, we approximated them using an unpublished dataset of 66 regional lakes that had a reasonable relationship between DOC and apparent colour, a close proxy for true colour ($R^2 = 0.7$; Korosi et al., unpublished). While approximate, we note that other studies in the region have demonstrated strong relationships between lake colour and DOC (Scruton 1984; Kortelainen 1993; Kokelj et al. 2005, 2009b), and that our approximate threshold value of DOC for 20 PCU was similar to reported DOC – true colour values in a regional study by Houben et al. (2016).

Next, we performed a principal component analysis (PCA) to compare our fish sampling lakes to previous studies, and to identify water quality variables that were potentially related to climate and road use in our study area. PCA is a method that can be used to reduce the complexity of environmental site data, allowing for improved inference of the most important variables structuring the data as well as providing insight into how those variables interrelate (Borcard et al. 2011). A data subset (n = 198 lakes) was used because depth data were missing for five lakes from Korosi et al. (unpublished data), including one lake along the new highway, three reference lakes, and one thaw lake. All variables were inspected for normality which resulted in log-transforming lake area, lake depth, DOC, and conductivity, and square-root transforming TP.

After inspecting the first two PCA axes we then chose two variables, DOC and TP, that were potentially related to road use and/or climate as well as fish community health for further analyses. To examine the potential environmental drivers of DOC and TP we developed boosted regression tree models using previously identified candidate variables (Figure 1, Table 1). The boosted tree method uses boosting, which builds on each successive model output, in combination with regression tree analyses, which aim to group data following a recursive binary partitioning algorithm (Elith et al. 2008; Elith and Leathwick 2017). We were able to use the entire lake database for this step, as the algorithm can accurately impute missing data (Elith and Leathwick 2017). For each tree model, we initially tested ten predictor variables including two morphometric variables (lake area and maximum depth), four climate variables (mean annual temperature, change in mean annual temperature, mean annual precipitation, change in mean annual precipitation), and other potential contributing factors (road type, ecoregion, the presence of thaw slumps, and sampling month). We additionally added DOC as a predictor variable for TP, as it can be a useful metric for inferring the amount of external dissolved organic matter loading to lakes, which includes TP (Eimers et al. 2009; Huser et al. 2018; Isles et al. 2020). Models were simplified to remove variables that did not contribute to predictive performance using the gbm.simplify function in the package *dismo* (Elith and Leathwick 2017).

Results

Drivers of fish community health in lower Mackenzie River basin lakes

1.1 Environmental variability

A principal component analysis was completed as an initial step to determine the main environmental gradients structuring our study lakes that were then used as model predictors for fish community health indicators (Section 1.2). Results from the principal component analysis indicated that our fish sampling study lakes had two main environmental gradients, with the first axis representing a DOC, temperature, and lake size gradient, "browning-warming gradient" (axis variation explained = 30%), and the second axis representing a nutrient and water clarity gradient, "eutrophication gradient" (axis variation explained = 17%; Figure 5, Table C3). Lakes with positive PC1 scores were colder, larger, deeper, and had less DOC, whereas lakes with positive PC2 scores were deeper and less eutrophic (clearer lakes with low TP and chlorophyll). In addition, lake area was strongly and positively related to PCA axis three (axis variation explained = 13%), and lake connectivity was positively related to PCA axis four (axis variation explained = 11%; Figure C1).

1.2 Fish community

Water quality variables collectively explained the most variation in fish community indicators (43%), followed by lake size (40%), connectivity (12%), and July temperature (6%), averaged across all six hierarchical partitioning models (Figure 6). Larger, deeper, clearer, and colder lakes with direct access to larger perennial habitats supported more fish species and higher abundances overall (Figures 6-8, Table 4). Water quality variables including DOC and Secchi depth emerged as important predictors for many fish community indicators. Using change-point threshold analyses, it was found that lakes exceeding 17 - 18 mg/L of DOC demonstrated greatly reduced species richness, CPUE, and overall fish presence (Figure 9; Table C4).

Overall, more species were present in larger, deeper, clearer, colder, and well-connected lakes with low DOC and nutrient concentrations (Figure 7, Table 4). The top multiple linear regression model for species richness contained all four PCA axes, with the browning-warming gradient (std. effect size = 0.5) and eutrophication gradient (std. effect size = 0.4) demonstrating the strongest relationships with richness (R^2_{adj} = 57%; Table 4). Using the hierarchical partitioning results, we observed that lake area, maximum depth, DOC, connectivity, and Secchi

depth had the highest individual contributions, and together these variables made up 77% of the explained variance. When divided by variable type, it was found that lake size and water quality had equally large contributions to the explained variance (each = 41%), followed by connectivity (16%), and July temperature (3%) (Figure 6).

Similar to species richness, larger, deeper, and colder lakes with lower DOC and nutrient values supported the highest relative abundances of both large and small-bodied fish (Figure 7, Table 4). Water quality variables were the most important drivers of overall abundance as they made up 50-65% of the explained variance for largemesh and smallmesh abundances, respectively (Figure 6). The next most important drivers included lake size (24 – 39%, for small and largemesh abundances, respectively), connectivity (7 – 8%), and July temperature (3 – 4%). Relative abundances were best explained in our multiple regression models by the browning-warming gradient (std. effect sizes = 0.6), followed by the eutrophication gradient (std. effect sizes = 0.3 – 0.4; largemesh model R^2_{adj} = 58%; smallmesh model R^2_{adj} = 37%; Table 4). Both models had the same top four variables identified by hierarchical partitioning, including mean depth, Secchi depth, lake area, and DOC, however depth was the primary determinant for large-bodied fish whereas DOC was the top predictor for small-bodied fish.

Water quality variables including DOC, Secchi depth, and TP, were collectively the most important drivers of whitefish and pike presence, but not for least cisco presence (Figure 6, Figure 8). Both whitefish and pike were more likely to be present in larger and clearer lakes with lower trophic states, whereas cisco were found in larger, colder and well-connected lakes with varying water quality. All three species were significantly related to the browning-warming gradient, with smaller, warmer, and browner lakes having lower species occurrences (logistic regression classification success 79-100%; Figure 8, Tables 4 - 5). However, there were some key differences as the two species more reliant on benthic habitats, northern pike and whitefish, were positively related to the eutrophication gradient (=more occurrences in less eutrophic lakes) whereas planktivorous least cisco was unrelated.

The contribution of July air temperature in the two Coregonid species models was greater than what was observed at the community level, or for northern pike, but was still relatively small (Figure 6). Following lake size, connectivity, and Secchi depth (whitefish only), temperature was the fourth most important variable for both Coregonid species, making up 9-

15% of the explained variance in hierarchical partitioning (Figure 8). While cisco demonstrated a clearer decline in warmer lakes (Figure C2), whitefish presence displayed a more complicated relationship as the species presence was more consistently distributed across the July temperature gradient. Based on this uncertain result, we conclude that temperature may be interacting with other important variables that could be mediating the overall effect (i.e., lake depth, connectivity, water clarity), but our small sample size and multicollinearity of several predictor variables precluded further statistical testing (Figure C1).

Examining regional water quality patterns within the context of environmental change

2.1 Are the physicochemical characteristics of our fish sampling lakes comparable to previously sampled lakes in this region?

Results from the PCA indicated that our fish sampling lakes were associated with higher TP and DOC concentrations relative to previous regional studies (Figure 10a). Although the separation on the biplot also suggested that lake sizes (area and depth) were smaller, we note that our lakes were generally larger in area but had similar depths to all other studies with the exception of Ogbebo et al. 2009 (Table C2). The positioning of lake sites on the PCA biplot were strongly related to study source, which may be attributed to environmental and sampling differences captured in our analysis but may also be ascribed to unknown unaccounted sources of variation. The two older studies which occurred during a colder period and without any road influence are clustered in the bottom left quadrant (Pienitz et al. 1997; Ogbebo et al. 2009a), the Peel Plateau road study from 2014 – 2015 is located on the bottom right in association with lower latitude and a warmer and wetter climate (Zhu et al. 2019), and the two most recent studies from 2017 – 2019 that occurred during the warmest period with many sites along the highway corridor are located mainly in the upper half (This study and Korosi et al., unpublished).

Using the colour-nutrient status framework, we observed that lakes in our fish sampling study had a higher proportion (78%) of murky lakes, i.e., being both highly coloured and phosphorus-enriched, in comparison to previous regional studies which ranged from 17 – 39% (Figure 10b). Notably, none of our fish sampling lakes were considered oligotrophic or ‘blue’. While it is difficult to draw direct comparisons among studies based on lake status alone due to differences in lake sizes, ecoregions, and thaw lake presence, some further cautious observations may still be derived. First, it appears that lakes are relatively quite brown or humic in this region,

as brown lakes were prominent in each study including those sampled decades ago by Pienitz et al. (1997). Conversely, the proportion of oligotrophic lakes was relatively low overall, with the largest number of blue lakes observed by Ogbebo et al. (2009a), notably the only study that included much larger and deeper lakes in this region. Another observation is that the number of murky lakes may be increasing over time, as illustrated by differences between the two earlier studies and the most recent three.

2.2 Is there any evidence for the effects of climate change or road use on water quality in regional lakes?

Principal Component Analysis

A few water quality variables emerged as being potentially related to climate change and road use including DOC, TP, and conductivity (Figure 10a). The first PCA axis (38%) was most correlated with geographic location, mean annual air temperature, mean annual precipitation, long-term change in precipitation, lake size, and DOC. The second PCA axis (17%) was most related to survey year, climate warming, road type, total phosphorus, and conductivity. Smaller, warmer, and wetter taiga lakes sampled more recently (2014 – 2019) had the highest DOC values, whereas colder and larger lakes sampled earlier (1990 – 2007) had the lowest DOC values. Lakes with high phosphorus levels were sampled more recently and therefore had experienced greater warmer rates. High phosphorus lakes were also more likely to be located along the newly constructed Inuvik-to-Tuktoyaktuk Highway. Both pH and conductivity were greater in lakes at higher latitudes, with conductivity values being positively correlated with road presence.

Boosted Regression Tree Analyses

DOC values were highest in smaller and warmer lakes that received more annual precipitation and had experienced higher rates of climate warming (Figure C3; $R^2 = 0.68$ CV $R^2 = 0.39$). Lake area and depth were the most important variables, representing approximately 50% of the explained variability. Other variables such as the presence of thaw slumps, road type, designated ecoregion, survey month, and changing precipitation were less important for understanding DOC variability across the entire study area, as their inclusion did not decrease model prediction error.

TP values were elevated in shallower lakes that had experienced more external loading (increased DOC) and higher rates of warming (Figure C4; $R^2 = 0.50$ CV $R^2 = 0.33$). In addition, road type emerged as an important predictor, with lakes along the new highway having the highest TP values relative to lakes along the old highway, and to lakes situated away from the road. Variables that did not contribute to lowering model prediction error included mean annual precipitation, mean annual temperature, change in mean annual precipitation, the presence of thaw slumps, survey month, and ecoregion.

Discussion

Water quality and lake size emerged as the leading co-drivers of fish community health in lower Mackenzie River basin lakes. Smaller lakes with poorer water quality (high DOC, low water clarity) were less likely to support healthy fish communities, and we found that lakes exceeding a DOC threshold of 17 - 18 mg/L had abruptly lower fish diversity, abundance, and overall fish presence. In contrast, direct climate warming had a relatively negligible effect on fish communities in our study lakes. Lake DOC and water clarity may be influenced by multiple interacting pathways of environmental change in this ice-rich permafrost landscape, and we provided potential evidence for increases in regional lake browning (DOC) and nutrient enrichment (TP) over time that were related to current and changing climate variables and road use. Together, these results highlight the potential vulnerability of freshwater fish diversity within the rapidly changing lower Mackenzie River landscape as lakes may become increasingly degraded with additional warming, permafrost loss, and human development. Our finding that water quality effects may be superseding direct climate warming effects on northern fish diversity has important implications for guiding future research at the global scale, as much of the work on climate change to-date has focused on thermal habitat limitations alone rather than incorporating a more comprehensive view of possible outcomes (e.g., Reist et al. 2006; Lynch et al. 2016; Poesch et al. 2016).

Water quality and lake size co-driving fish community health in lower Mackenzie River basin lakes

We observed near-universal declines in fish diversity and abundance in smaller, browner, and more eutrophic lakes, underscoring the importance of water quality and lake size for co-driving fish community health. Based on our hierarchical partitioning results averaged across all six

models, lake size (area and depth) contributed 40%, DOC contributed 17%, water clarity (turbidity and Secchi depth) contributed 16%, and nutrients (TP, TN) and chlorophyll-*a* made up 14%. The environmental PCA of our fish sampling sites revealed that water quality was closely related to lake size, with smaller and shallower lakes generally having lower water clarity and higher concentrations of DOC, nutrients, and chlorophyll-a. This observed relationship between lake size and water quality is an important consideration for understanding fish community health in lower Mackenzie River basin lakes, as many of our study lakes were small, shallow lakes that may be disproportionately sensitive to changes in their catchments including warming, altered runoff, and permafrost thaw (Prowse et al. 2006b; Ogbebo et al. 2009a; Stasko et al. 2012; Read and Rose 2013). Moreover, climate-induced permafrost degradation surrounding lakes is anticipated to accelerate alarming lake drainage trends occurring across the western North American Arctic (Chen et al. 2014; Lantz and Turner 2015; Nitze et al. 2020), which may further reduce the availability of larger lakes that currently provide important fish diversity refugia. Notably, the interplay between lake size and water quality may be enhanced in shallow lakes dominating the lower Mackenzie River basin as they are prone to periodic wind mixing, which can prohibit stratification and facilitate the resuspension of nutrients in the water column (Ogbebo et al. 2009a; Dranga et al. 2018). This potential for increased mixing suggests that typical effects expected via lake browning or eutrophication, such as lowered oxythermal habitat in deeper waters (Jacobson et al. 2010; Stasko et al. 2012; Solomon et al. 2015), are less relevant in our study lakes which maintain relatively high dissolved oxygen levels throughout the water column during summer. Instead, we suggest that the dual and interconnected effects of lake size and water quality may be impacting other key components of fish habitat in our study area, including the light environment during summer, and water quality and quantity during the critical winter period.

Effects of reduced light on fish community health

Murkier water was strongly related to declining fish community health in our study lakes, including declines in species richness, overall abundance, and the presence of northern pike and whitefish, two species that primarily use benthic habitats (Richardson et al. 2001; Harvey 2009). In particular, we observed that higher DOC levels and lower Secchi depths had the strongest individual relationships with declining diversity and abundance metrics. Here, we note that Secchi depth may be interpreted as a composite index of both browning and eutrophication

effects in our murky study lakes as it integrates interrelated components including algal productivity and water column DOC concentrations (Leech et al. 2018). Both DOC and nutrient concentrations are generally expected to have a unimodal relationship with lake productivity, where increases provide beneficial subsidies at low levels but becomes prohibitive of primary production and trophic energy transfer at high levels due to light inhibition (Creed et al. 2018). Murkier lakes (high nutrient and colour) have been associated with specific food web alterations including a shift towards inedible plankton species, leading to lower quality food and possible declines in fish growth, maximum size, functional diversity, and overall nutritional value (Creed et al. 2018; Leech et al. 2018; Hayden et al. 2019). Because lower Mackenzie River basin lakes have relatively high humic properties, and moderate - high nutrient levels, our results may provide important insight into potential ecosystem shifts occurring in murkier lakes. In particular, the steep drop-off in fish diversity and abundance when DOC exceeded ~17 – 18 mg/L in our study lakes suggests that there could be an important light-limiting threshold for supporting higher trophic levels such as fish in lower Mackenzie River lakes. To our knowledge, a light-limiting threshold for subarctic fish diversity has not been specifically identified elsewhere, although gradual declines in fish abundance and biomass were noted over similar or even lower DOC ranges in Scandinavian boreal lakes (Finstad et al. 2014; Karlsson et al. 2015).

Individual fish species demonstrated differing relationships with water clarity variables that could be reflective of their respective habitat preferences and diet. As predicted, we observed that northern pike presence was lower in lakes with higher DOC values, mirroring other studies that have deciphered links between lowered water clarity, reduced pike feeding efficiency, and declining body condition (Craig and Babaluk 1989; Casselman and Lewis 1996; Harvey 2009). Although northern pike can withstand some reductions in light, their close connection to macrophyte habitat for spawning, rearing, and feeding, and strong reliance on visual predation may explain why their presence declined in our exceedingly humic study lakes (Harvey 2009). In contrast, the expected shift toward stronger pelagic pathways with lowered light conditions may help explain why least cisco, a predominantly pelagic species, had the weakest response to water quality variables (Leech et al. 2018; Hayden et al. 2019). Based on this finding, we suggest that cisco may be experiencing trade-offs between increased pelagic food availability and lowered pike predation in larger lakes with low - moderate light conditions.

Water quality implications for winter survival in small, northern lakes

We found that larger, deeper, clearer lakes with lower DOC concentrations and with stronger hydrologic connections represented key habitats for fishes across our study region, revealing potential implications for winter life history strategies and survival. Although lake size and hydrologic connectivity are universally important predictors for northern aquatic diversity (Ryder 1965; Jackson et al. 2001; Hershey et al. 2006; Haynes et al. 2014; Laske et al. 2016), they may be especially important for fishes in the lower Mackenzie River basin where the landscape is dominated by small, shallow lakes that are covered by thick ice for much of the year (Kokelj et al. 2005; Lesack and Marsh 2010). To survive in this landscape over winter, fish must seek lakes and rivers with sufficient water depths and oxygen levels, both of which may track downwards as winter progresses depending on local conditions such as ice formation and snow cover (Hershey et al. 2006; Chambers et al. 2008; Rautio et al. 2011; Haynes et al. 2014; Laske et al. 2016). Importantly, oxygen levels are strongly related to lake depth and trophic state, with depletion occurring faster in shallower and more eutrophic lakes (Mathias and Barica 1980; Ogbebo et al. 2009b; Shuter et al. 2012). Further, previous studies have found that small northern lakes with elevated organic carbon experienced heightened oxygen depletion rates over winter, and were additionally linked to high levels of toxic methane production under ice (Clilverd et al. 2009; Cunada et al. 2018). Together, these potential mechanisms suggest that smaller lakes with poorer water quality could pose a significant limitation for fish diversity and abundance in our study area, particularly if there is no hydrologic connection allowing seasonal habitat use.

Although research examining winter habitat requirements by individual fish species in our study area is lacking, we observed key differences in habitat use that could be reflective of differing winter life history tactics. Large-bodied fishes such as whitefish and northern pike appeared particularly responsive to lake size and water quality variables, , possibly reflecting their greater overwintering needs including more physical space and higher oxygen concentrations in comparison to smaller species (Haynes et al. 2014). Although our sampling gear was not well suited for catching very small species, we did observe several lakes with poor water quality (DOC > 25 mg/L or TP > 100 µg/L) that were able to support ninespine sticklebacks and no other species, suggesting their elevated potential for withstanding low winter oxygen levels. While least cisco, an intermediate-sized species, also declined sharply in smaller lakes, we were surprised that their presence in relatively larger lakes was generally unrelated to

water quality variables considering that eutrophication-driven declines for closely related Coregonid species, including lake cisco, have been documented elsewhere (e.g., COSEWIC 2005; Jacobson et al. 2012). However, we suggest that more information is needed to understand if and how cisco are successfully spawning and/or overwintering in these lakes considering the potentially heightened risk for winterkill (Mathias and Barica 1980). We recommend that further studies examine least cisco seasonal habitat use patterns and whether or not they seek spawning and overwintering habitats elsewhere or are able to withstand relatively low oxygen concentrations compared to other species. Evidence for how least cisco respond to eutrophication is currently lacking, and cisco in our study lakes demonstrated wide morphological diversity including a dwarf non-migratory form, which suggests some unknown potential for local adaptation (Richardson et al. 2001). Further, it is possible that cisco lakes had reliable hydrologic connections that we were unable to ascertain using satellite imagery or during our limited field surveys, which would allow them to exit lakes before oxygen levels decline over winter.

Limited evidence for the effect of direct warming on fish community structure

Considering that the Mackenzie Delta region is experiencing some of the most rapid warming worldwide, the limited evidence for the direct effect of warming on lower Mackenzie River basin lake fish was unexpected. The two coldwater Coregonid species demonstrated relatively weak responses to warming, whereas the effect was negligible for all other indicators. As warmer lakes were linked to higher concentrations of DOC, we suggest that fish fitness, abundance, and survival may have been compromised by rising DOC levels before concurrently rising temperatures reached sufficiently stressful levels in certain lakes. However, water temperatures at the end of July and beginning of August when we began sampling were between 15 - 20°C for many of our study lakes, some of which supported species that we predicted would have lower thermal preferences such as cisco (12.4°C) and lake whitefish (12.7°C; Hasnain et al. 2010). In contrast, the lack of a relationship for northern pike may be due to the wide thermal habitat tolerances observed for this species and its preference for warmer temperatures overall (19-23°C; Harvey 2009). There are a few potential reasons that may help explain why warming appeared to have a minimal influence on fish community health in our study lakes. The first is that many of the warmest lakes in our dataset had connections to major habitats, allowing potential behavioural thermoregulation to avoid rising temperatures (Magnuson et al. 1979). Further, the fish sampling often occurred a few days to a week after the water quality sampling,

and we therefore cannot confirm if coldwater fish were present in connected lakes during the earlier, warmer period. Both least cisco and whitefish display migratory periods during the summer, and it is possible that they were actively moving during our sampling period (Richardson et al. 2001; Tallman 2001). An additional consideration is that some of the warmest lakes contained only juvenile whitefish, which require warmer thermal habitat for growth in comparison to adults (15.5°C - 19.5°C; Edsall 2011). Finally, it is possible that our use of July air temperature as a proxy for mid-summer lake water temperature was insufficient for capturing potential lake thermal variability that could arise due to local geomorphic processes (O'Reilly et al. 2015). Despite the lack of evidence for a warming impact in our specific dataset, we caution that further warming may still be able to impact coldwater fish species once temperature thresholds are surpassed in larger and more isolated tundra lakes.

Potential evidence for changing regional lake water quality

Although our water quality analyses faced some notable limitations, using the available data for this region we presented some potential evidence for increased lake TP, DOC, and conductivity in association with environmental change variables including climate warming (DOC, TP) and road type (TP, conductivity). In particular, our fish sampling study lakes had some of the highest concentrations of TP and DOC that may be explained by various factors including the more recent sampling, positioning along the road corridor, greater area:depth ratios which could enhance lake nutrient mixing (Gorham and Boyce 1989), the low number of lakes with shoreline retrogressive thaw impacts, and the inclusion of lakes in the taiga plains ecoregion. While we recommend that future studies aim for a more balanced study design across lake sizes, ecoregions, and thaw/road impacts to verify these results, we note that our preliminary results do align with many other studies and observations from Indigenous knowledge holders that have reported evidence for declining water quality across the circumpolar north (Wrona et al. 2016; Hayden et al. 2017, 2019; Wauthy et al. 2018; Knopp et al. 2020).

The emergence of warming rate as a potentially important predictor for both DOC and TP is an interesting finding as it suggests that water quality changes may be associated with warming-related impacts on land cover and permafrost thaw. Notably, our fish sampling lakes had experienced some of the greatest warming rates in the regional dataset, including record-high winter temperatures in 2018 and 2019 which may have contributed to permafrost degradation

and resultant changes in water quality (Segal et al. 2016a; van der Sluijs et al. 2018; Nitze et al. 2020). Both tundra and taiga regions have experienced substantial land cover change in northwestern North America over the past several decades due to longer growing seasons and warming-related disturbances such as permafrost thaw and fire (Carpino et al. 2018; Wang et al. 2020). For example, widespread shrub expansion has been documented across previously unvegetated tundra regions, which could be leading to increased dissolved organic matter and nutrient delivery to lakes (Wrona et al. 2016; Myers-Smith et al. 2019). In contrast, impacts in the more southern taiga have varied depending on local disturbances such as permafrost thaw, insect infestations, and fire (Myers-Smith et al. 2019; Wang et al. 2020). One particularly relevant change for lake water quality is the loss of forest cover to fen and bog expansion in the taiga region following permafrost degradation (Wrona et al. 2016; Carpino et al. 2018; Wang et al. 2020). In the Arctic Red Plain of the lower Mackenzie River basin where many of our recently sampled lakes are situated, we calculated that approximately 8% of the forest cover was lost over the 1984 – 2014 period, whereas the areal coverage of fens has expanded by 6% (Wang et al. 2019). Therefore, we suggest that this notable increase in wetland cover over a relatively short period of time could be contributing to the observed elevated nutrients and DOC levels measured in our taiga study lakes. In contrast, lakes in the tundra region of our study area did not demonstrate appreciable increases in fen or bog cover (<1% increase), but increases in shrubland were substantial in certain regions (e.g., +9% in the Tuktoyaktuk Coastal Plain) (Wang et al. 2019). Warming-induced permafrost thaw in the taiga region may be additionally elevating lake nutrient and DOC levels as thermokarst shoreline processes can erode banks and destabilize riparian vegetation, increasing woody debris and soil transport into lakes (Burn and Kokelj 2009). Anecdotally, many of the taiga lakes we visited for our fish surveys contained a substantial amount of shoreline *erosion* with scores of drunken trees and deadfall encroaching the lake perimeter, potential signs of permafrost decay that could be additionally contributing to water quality degradation in this ecoregion. Above the treeline, we also observed signs of permafrost thaw including shoreline bank failure, ice-wedge polygons, methane bubbling, as well as exposed ground ice surrounding various tundra lakes, some of which were highly degraded.

Contrary to other latitudinal studies observing declining nutrients with latitude (Gregory-Eaves et al. 2000; Ruhland et al. 2003; Medeiros et al. 2012), we observed high total phosphorus

values in many of our fish sampling lakes in the tundra uplands that may be partly attributed to new road development. We further noted that conductivity values in road-adjacent tundra lakes were significantly elevated (mean difference = 32 µS/cm; t-test: t_{50} = -2.4, P = 0.02) compared to tundra reference lakes sampled by Korosi et al. during a similar time period (unpublished data), which has been an important indicator of road disturbance elsewhere (Gunter 2017; Zhu et al. 2019). However, we caution that our inferences here are limited as most lakes along the new road corridor were not sampled prior to construction, and it is possible that other unmeasured variables or sampling differences could be responsible for enriched road-adjacent lakes. While there is some previous work looking at the effects of infrastructure and road use over permafrost terrain on ecosystems, few have looked directly at impacts on lakes (Walker and Everett 1987; Raynolds et al. 2014; Zhu et al. 2019). A noted exception is one other study included in our regional analysis which concluded that total phosphorus values did not significantly vary according to road proximity, however they examined effects along the Dempster Highway which has been in operation for 40+ years (Zhu et al. 2019). Further investigations within our dataset of the potential relationships between total phosphorus with catchment road density, and distance between the lake and road, yielded no significant negative relationships (data not shown), suggesting that other unmeasured variables were responsible for the TP variation observed in lakes along the highway. Although there is still much uncertainty surrounding the cascading ecological effects of development over permafrost, other studies have documented substantial impacts on the surrounding landscape including increased flooding and thermokarst (Raynolds et al. 2014; Gill et al. 2014). Based on these observed impacts elsewhere, we speculate that nutrient-rich gravel fill excavated from permafrost and used to build the new highway could have leached into nearby waterbodies during spring flooding events (Ackerman and Finlay 2019; Zhu et al. 2019). Another possibility is that despite best management practises, the road construction itself could have disturbed nearby permafrost, creating a positive feedback mechanism which may have resulted in increased solute delivery to nearby lakes (Gill et al. 2014).

Monitoring northern biodiversity change

Rapid environmental changes in northern ecosystems have prompted international initiatives to document, predict, and mitigate impacts on biodiversity before new, irreversible ecological states are reached (Lento et al. 2019; Heino et al. 2020). In particular, the implementation of standardized methods and long-term assessments of change are still lacking for all biological

levels including freshwater fish (Lento et al. 2019). Our study collected valuable ecological data for 50 lakes using standardized methods suitable for sensitive northern lakes that could be repeated to monitor further biodiversity changes in the quickly evolving lower Mackenzie River basin. We adapted the Ontario Government's broad-scale monitoring approach using shorter gillnet sets which greatly reduced lethality while also providing sufficient data for examining aquatic health (Sandstrom et al. 2013). Given the large number of lakes we sampled, our resulting dataset is one of the most comprehensive overviews of lake ecology in this region, and further makes a significant contribution toward understanding current emerging stressors in sensitive permafrost regions worldwide. However, our field program still faced many necessary trade-offs due to the high cost and logistical challenges associated with northern work. We sampled a large number of lakes along the highway corridor but were limited in our inferences because we did not have comparable reference or control lakes. Several lakes along the new highway corridor displayed anomalously high DOC (three lakes > 50 mg/L) and total phosphorus (seven 'hypereutrophic' lakes > 96 µg/L; Carlson and Simpson 1996) values, and having measurements of these lakes in earlier years would have been key for understanding the relative contributions of climate change, road development, or other local factors. Indeed, the limited monitoring before the new highway went in was perhaps a missed opportunity for understanding how development over sensitive permafrost may impact lakes (Kiggiak-EBA Consulting Ltd 2011), although we note that future paleolimnological studies could be employed as a useful solution for the lack of timely data collection. Moving forward, we recommend that future northern major development projects such as the proposed Mackenzie Valley Highway consider conducting a before-after-control-impact study including potential impacts to fish communities.

Opportunities for biodiversity stewardship

Traditional food activities (hunting, fishing, gathering) are an integral part of the well-being of thousands of Indigenous citizens residing in the Gwich'in Settlement Area and the Inuvialuit Settlement Region (Kavik-Stantec Inc. 2012; Hovel et al. 2020; Hodgson et al. 2020). However, these traditional activities are deeply tied to inter-generational knowledge transfer, which is being increasingly undermined by rapid environmental change (Meredith et al. 2019). Our study results have direct implications for local Gwich'in Peoples and the Inuvialuit as regional lakes provide both seasonal and year-round habitat for culturally important species such as broad

whitefish, lake whitefish, lake trout, inconnu, northern pike, and cisco. The community-based fishing plan developed for lakes along the Inuvik-to-Tuktoyaktuk Highway provides a proactive conservation-focused template for protecting newly accessible fisheries resources, including individualized restrictions to community members and sport fishers (Inuvik and Tuktoyaktuk Hunters and Trappers Committees 2017). Results from this study could directly tie into these ongoing and future conservation planning efforts, including the identification of large and well-connected lakes that may serve as key biodiversity refugia amid continued environmental changes. As these same lakes are likely to garner the most fishing attention, extra preventative measures could be considered to protect them, and their hydrologic connections, from rising regional human pressures (Tyson et al. 2016; Meredith et al. 2019).

To our knowledge, ours is the first study to identify that lake browning and nutrient enrichment could be adversely affecting aquatic diversity in the lower Mackenzie River basin. We conclude that fishes relying on the numerous small lakes that dominate the lower Mackenzie landscape could be disproportionately vulnerable to water quality degradation which was unexpected given the relatively low human influence in the region. However, we note that our findings align with observations made by Indigenous knowledge holders across the circumpolar north that have included permafrost thaw, declining water quality, and changes in fish biodiversity (Knopp et al. 2020). Based on our study results, we advise that future research should aim to understand how projected environmental changes may accelerate water quality degradation and potentially contribute to declining biodiversity in this region, especially for lakes near Fort McPherson and Tsiigehtchic where almost 80% of our sampled lakes exceeded 20 mg/L of DOC. Further, an assessment of the potential link between seasonal water quality and under-ice oxygen would be particularly beneficial for disentangling potential mechanisms at play. Expanded monitoring of lakes in the uplands region that are experiencing a range of potentially counteracting stressors including permafrost thaw and road use will also be useful for mitigating future impacts to biodiversity north of the treeline. As most permafrost studies examining impacts on freshwater lakes in this region have focused on the effects of larger retrogressive thaw slumping on lakes, the inclusion of lakes experiencing different types of thaw into future studies may be useful for understanding a broader range of impacts on regional fish diversity. Finally, as northern climate change and human development pressures are expected to escalate further in the coming decades, building on existing standardized monitoring data while

also prioritizing opportunities for impactful community-based collaborations will be key for addressing this complex conservation challenge (Hovel et al. 2020; Wong et al. 2020; Knopp et al. 2020).

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Tables and Figures

Table 1. Background information describing the predicted linkages in our conceptual model between variables of environmental change (warming, changes in precipitation, permafrost thaw, and road development and use), physical environmental covariates (lake morphometry and hydrologic connectivity), lake water quality (DOC, TP, TN, Chlorophyll-a, dissolved oxygen, and water clarity), and six indicators of fish community health including species richness, relative abundance (catch per unit effort), and the presence of whitefish, least cisco, and northern pike. Numbers in brackets of the second column refer to a specific link in the conceptual model where relevant. Expected moderating variables are included for additional context but are not illustrated in the model.

Environmental variable	Conceptual model link ID and type	Fish community indicators	Predicted relationships with fish community indicators*	Description of linkage in conceptual model
Lake morphometry	(1) Direct	All	↑ Lake surface area (+) ↑ Lake depth (+)	Larger lakes provide more diverse habitat types and facilitate zonation, allowing more species to survive at greater abundances (Mathias and Barica 1980; Post et al. 2000; Jackson et al. 2001); species presence in small high latitude lakes has been linked to maximum lake depth and resultant overwintering capacity (Hershey et al. 2006; Haynes et al. 2014), and mean depth is important for determining overall fish productivity (Ryder 1965; Christie and Regier 1988).
	Moderating	-	Link to water quality sections on changes in nutrients and primary productivity, browning, and permafrost thaw.	Smaller and shallower northern lakes are often associated with higher levels of nutrients and organic carbon due to smaller lake volumes, more lake mixing, and higher relative proportions of littoral habitat (Alexander et al. 1989; Pienitz et al. 1997; Ogbebo et al. 2009a; Paquette-Struger 2011; Dranga et al. 2018).
Hydrologic connectivity	(2) Direct	Species richness, relative abundance, presence of migratory species	↑ Direct seasonal or year-round connection to large, perennial habitats (+)	Close hydrologic connections to larger habitats increase the probability of species establishment (Hershey et al. 2006; Haynes et al. 2014; Laske et al. 2016) and allow for seasonal use of small lakes by migratory species such as whitefish and cisco (Richardson et al. 2001; Lesack and Marsh 2010).

	Moderating	Species richness, relative abundance, presence of migratory species	↑ Direct seasonal or year-round connection to large, perennial habitats (+)	Hydrologic connectivity can facilitate behavioural thermoregulation, reducing the effects of direct warming (Magnuson et al. 1979)
Warming and changes in precipitation	(3) Warming (direct)	All	↑ Water temperature (+/-)	Fish biodiversity and productivity are positively related to warmer temperatures (Abell et al. 2008; Brucet et al. 2013; Rypel and David 2017); individual species exhibit optimal temperatures for growth and reproduction, and are constrained by thermal limits that dictate survival (Magnuson et al. 1979); comparing known species thermal optima and preferences with summer water temperatures observed in lower Mackenzie River Basin lakes, we predicted that northern pike would benefit from increasing temperatures whereas whitefish and cisco would decline (Christie and Regier 1988; Harvey 2009; Hasnain et al. 2010; Sharma et al. 2011; Jacobson et al. 2012; Van Zuiden et al. 2016; Edwards et al. 2016).
	(4) Changes in nutrients and primary productivity (indirect) Eutrophication (sub-category)	All	Δ TN (+/-) Δ TP (+/-) Δ Chl-a (+/-) ↓ Secchi depth (-) ↓ Dissolved oxygen (-)	(4a) Climate – water quality link: Warmer temperatures may enhance terrestrial runoff into lakes as well as increase internal nutrient cycling due to a longer growing season, expected shifts in vegetation, and shorter ice cover; more precipitation can increase catchment mineral weathering and delivery of nutrients including TP (Gregory-Eaves et al. 2000; Ruhland et al. 2003; Jeppesen et al. 2009; Wrona et al. 2016; Huser et al. 2018); in contrast, lake nutrient declines may be expected in association with warmer and/or drier climates due to increases in nutrient sequestration by growing terrestrial vegetation, or increased evapotranspiration (Jeppesen et al. 2009; Huser et al. 2018). (4b) Water quality – fish link: Effects of changing nutrients and primary productivity can vary depending on the original lake trophic state and individual species preferences (Heino et al. 2009; Wrona et al. 2013); prolonged

				nutrient increases may lead to lake eutrophication including substantial reductions in water clarity that can alter fish community structure (Jeppesen et al. 2000; Jacobson et al. 2017); northern pike demonstrate a preference for mesotrophic to eutrophic lakes, but may be sensitive to greater reductions in water clarity that could occur in association with lake eutrophication (Casselman and Lewis 1996; Harvey 2009); Coregonid species (whitefish and cisco) are expected to prefer relatively low nutrient and chlorophyll levels as previous studies have linked declines to eutrophication-driven oxythermal habitat degradation (COSEWIC 2005; Jacobson et al. 2010, 2012); increased eutrophication of lakes may facilitate hypoxic or anoxic conditions either during the open water season or under ice, lowering fish survival at the community level (Mathias and Barica 1980; COSEWIC 2005; Ogbebo et al. 2009b; Jacobson et al. 2010, 2012).
	(5) Browning (indirect)	Species richness, relative abundance, northern pike presence	↑ DOC (-) ↓ Secchi depth (-) ↓ Dissolved oxygen (-)	(5a) Climate – water quality link: Recent lake browning trends have been observed across the northern hemisphere with suggested mechanisms including recovery from acidification, land use change, warming, and changes in hydrology (Solomon et al. 2015; Creed et al. 2018; Leech et al. 2018; Kritzberg et al. 2020; Mahdiyan et al. 2020); although trends are complex and there is substantial regional variation, projected warming and increases in precipitation are generally expected to lead to additional browning of northern lakes due to longer growing seasons, changes in vegetative cover, and resultant increases in terrestrial runoff (Stasko et al. 2012; Creed et al. 2018; Leech et al. 2018; Kritzberg et al. 2020); latitudinal studies in northern regions provide additional insight into browning trends, as lakes situated within relatively warmer, more vegetated areas with greater wetland coverage typically have higher DOC concentrations that lakes located further north (Pienitz et al. 1997; Gregory-Eaves et al. 2000; Ruhland et al. 2003).

				(5b) Water quality – fish link: Further browning of lower Mackenzie River basin lakes is expected to adversely affect freshwater food web diversity as many lakes have relatively high levels of DOC and low water clarity already (Pienitz et al. 1997; Moquin and Wrona 2015; Houben et al. 2016; Cohen et al. 2020); reduced water clarity can lower food availability, fish feeding efficiency, growth, and survival, leading to altered community composition and eventual productivity declines once high concentrations are reached (Stasko et al. 2012; Finstad et al. 2014; Solomon et al. 2015; Karlsson et al. 2015; van Dorst et al. 2019); lowered water clarity has been shown to negatively affect northern pike growth and reproduction due to a decline in important macrophyte vegetation (Craig and Babaluk 1989; Casselman and Lewis 1996; Harvey 2009); increases in DOC can enhance oxygen depletion and increase toxic methane production under ice which could limit fish survival in small, northern lakes (Clilverd et al. 2009; Cunada et al. 2018).
(6)	Permafrost thaw (indirect)			(6a) Climate – permafrost link: Warmer and wetter conditions have led to increased permafrost degradation over the past several decades (Kokelj et al. 2015; Segal et al. 2016a; Douglas et al. 2020). (6b) Permafrost – water quantity link: Permafrost degradation may lead to changes in lake size including declining water levels or entire lake drainage, lake subsidence, increased lake levels with flooding, or changes in hydrologic connections between habitats (Marsh et al. 2009; Kokelj et al. 2009a; Lantz and Turner 2015; Wrona et al. 2016; Nitze et al. 2020).
		All	Δ Lake size (+/-) Δ Lake connectivity (+/-)	
	Shoreline retrogressive thaw slumps		↓ DOC (+) ↑ Secchi depth (+) ↓ Turbidity (+) ↓ TN (+/-) ↓ TP (+/-) ↓ Chl-a (+/-)	

	Other types of thaw including active layer thickening, peat subsidence, and other forms of lake shoreline erosion		Δ DOC (+/-) Δ Secchi depth (+/-) Δ Turbidity (+/-) Δ TN (+/-) Δ TP (+/-)	(6c) Permafrost – water quality link: Lakes with shoreline retrogressive thaw slumps are linked to lower DOC, nutrients, and chlorophyll-a in the Mackenzie Delta uplands region; other types of permafrost thaw have been associated with variable changes including increases in nutrients and DOC in freshwaters (Hobbie et al. 1999; Kokelj et al. 2005, 2009b; Burn and Kokelj 2009; Lougheed et al. 2011; Reyes and Lougheed 2015; Korosi et al. 2015; Vonk et al. 2015; Houben et al. 2016; Wrona et al. 2016; Wauthy et al. 2018; Morison et al. 2019). (6d) Water quality – fish link: Dependent on thaw type and resultant water quality changes. Lake DOC is naturally high in many lower Mackenzie River basin lakes and we therefore predict that decreases could benefit freshwater food web diversity including fish (Pienitz et al. 1997; Moquin and Wrona 2015; Houben et al. 2016; Cohen et al. 2020); Link to sections on browning and changes in nutrients and primary productivity for further detail.
	Ecoregion (moderating)	-	Link to sections on changes in nutrient and primary productivity, browning, and permafrost thaw.	Ecoregions are defined using a combination of climate, vegetation, permafrost, and surficial geology properties, all of which may contribute to the transport of nutrients and DOC into waterbodies; higher DOC and nutrient levels are found in forested regions in comparison to tundra regions, and are strongly related to differences in vegetation and peatland coverage; TP concentrations are highly influenced by weathering processes which may differ by ecoregion (Pienitz et al. 1997; Gregory-Eaves et al. 2000; Ruhland et al. 2003; Ogbebo et al. 2009a; Eimers et al. 2009).
Road development and use	(7) Indirect	-	Link to permafrost thaw section.	Roads and other infrastructure development over ice-rich permafrost have been associated with increased flooding, road dust deposition, and thermokarst (Walker and Everett 1987; Raynolds et al. 2014; Zhu et al. 2019).

*Arrows or delta symbols represent the direction of the environmental variable (↑ = increasing, ↓ = decreasing, or Δ = changes in either direction possible), whereas symbols in brackets indicate the response of the fish community

indicator, where "+" is a positive response, "-" is a negative response and "+/-" means either direction could occur depending on the context described.

Table 2. Summary statistics of predictor variables used to model indicators of fish community health in fifty lower Mackenzie River basin lakes

Variable Type	Variable	Units	Mean	Min	Max	SD
Temperature	mean July air temperature	°C	13.1	10.8	15.3	1.6
Lake morphometry	lake area	ha	126	0.4	1310	285
	maximum lake depth	m	4.8	0.6	13.1	2.8
	mean lake depth	m	1.6	0.6	3.1	0.5
Water quality	dissolved organic carbon	mg/L	21.2	6.0	54.5	12.0
	total phosphorus	µg/L	59	0	165	37
	total nitrogen	mg/L	0.7	0.1	1.8	0.4
	chlorophyll-a*	µg/L	4.4	0.3	24.2	5.0
	dissolved oxygen	mg/L	10.2	8.0	12.6	1.1
	Secchi depth	m	1.7	0.5	3.7	0.8
	turbidity	NTU	5.9	0.1	38.3	6.0

*Chlorophyll-a values are uncorrected raw data and may not reflect maximum summer values (see methods); SD = standard deviation

Table 3. Regional water quality studies compiled into a database of 203 lakes.

Study	Year(s) sampled	Month(s) sampled	Ecoregion(s)	Reference lakes	Thaw lakes	Road lakes
Pienitz et al. 1997	1990	July	taiga, tundra	36	0	0
Ogbebo et al. 2009	2004, 2006, 2007	July - August	taiga, tundra, delta	30	0	0
Zhu et al. 2019	2014, 2015	August	Peel Plateau	12	4	12
Korosi et al. unpublished	2017	June - July	tundra	29	26	4
This study	2017, 2018, 2019	July - August	taiga, tundra, delta	0	0	50
			Totals	107	30	66

Eight lakes from this study were assigned to being thaw lakes in addition to road lakes (see methods). Information from an additional source, Gunter (2017) was used to assign thaw lakes for Zhu et al. 2019.

Table 4. Top model results for fish community and species indicators. The first three metrics were examined with multiple linear regression whereas species presence were examined with logistic regression.

Biological indicator	AICc	Classification Success*	Adj. R^2	Predictor variable	Std. coefficient	SE	P-value
Species richness	36.99	n/a	57	PC1 (Browning-warming)	0.51	0.09	<0.01
				PC2 (Eutrophication)	0.42	0.09	<0.01
				PC3 (Lake area)	0.25	0.09	0.01
				PC4 (Connectivity)	0.32	0.09	<0.01
Largemesh CPUE	32.46	n/a	58	PC1 (Browning-warming)	0.62	0.10	<0.01
				PC2 (Eutrophication)	0.46	0.10	<0.01
				PC4 (Connectivity)	0.19	0.10	0.06
Smallmesh CPUE	47.77	n/a	37	PC1 (Browning-warming)	0.56	0.12	<0.01
				PC2 (Eutrophication)	0.31	0.12	0.01
Least Cisco presence	38.79	87 (100, 80)	n/a	PC1 (Browning-warming)	6.13	2.10	<0.01
				PC3 (Lake area)	3.48	1.91	0.07
				PC4 (Connectivity)	2.49	1.03	0.02
Northern pike presence	60.95	79 (86, 71)	n/a	PC1 (Browning-warming)	2.31	0.89	0.01
				PC2 (Eutrophication)	1.49	0.76	0.04
				PC3 (Lake area)	1.73	0.81	0.03
Whitefish species presence	25.23	100 (100, 100)	n/a	PC1 (Browning-warming)	3.23	1.37	0.02
				PC2 (Eutrophication)	5.55	2.10	0.01
				PC4 (Connectivity)	3.25	1.57	0.04

CPUE = catch per unit effort, Adj. R^2 = adjusted R^2, Std. coefficient = standardized coefficient, SE = standard error; *Model sensitivity (%) and specificity (%) indicated in brackets

Table 5. Habitat suitability models using logistic regression for the three most dominant fish species: whitefish, least cisco, and northern pike

	Whitefish	Least Cisco	Northern Pike
Classification Success (%)	100	87	79
Sensitivity (%)	100	100	86
Specificity (%)	100	80	71

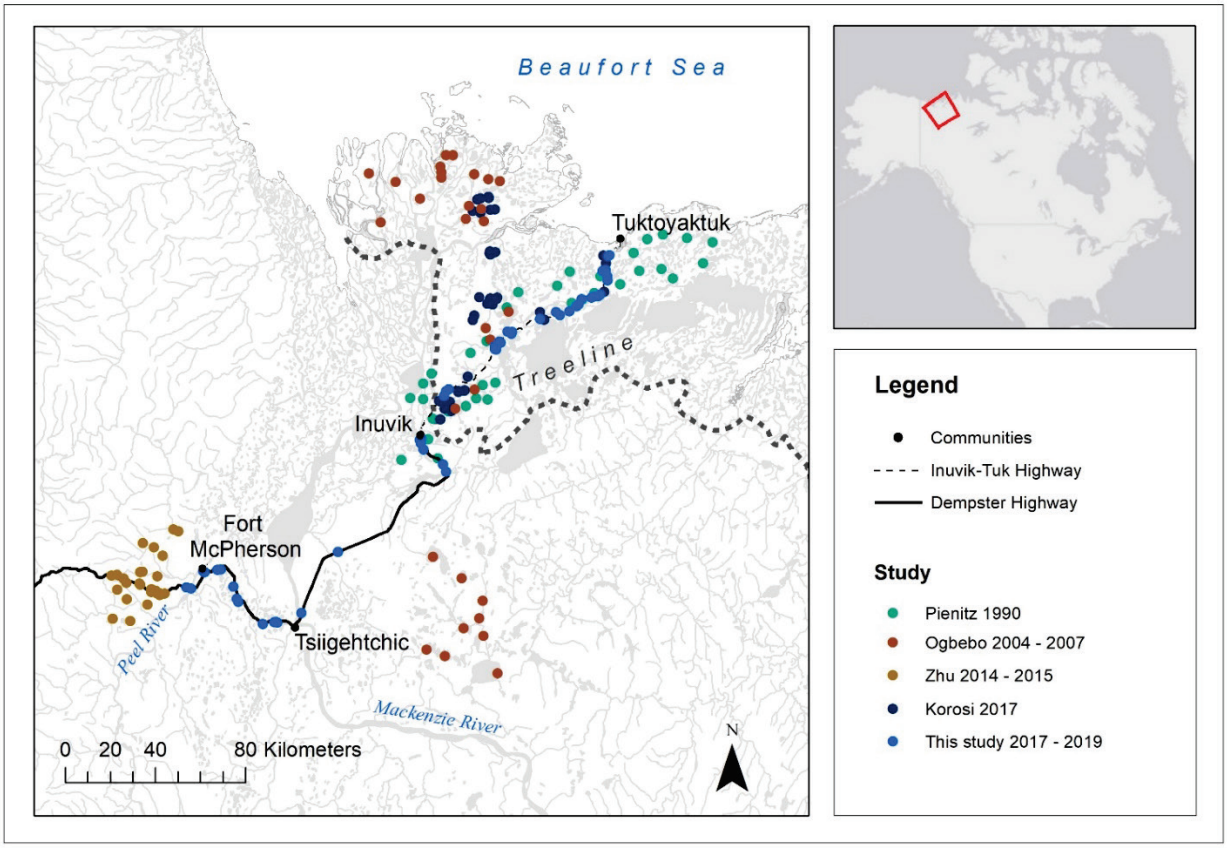


Figure 1. Study area in the lower Mackenzie River basin, Northwest Territories, Canada. Sites used for the regional water quality analysis of 203 lakes are coloured by study source, with sampling years indicated in brackets. Sampling lakes from this study include both water quality and fish sampling.

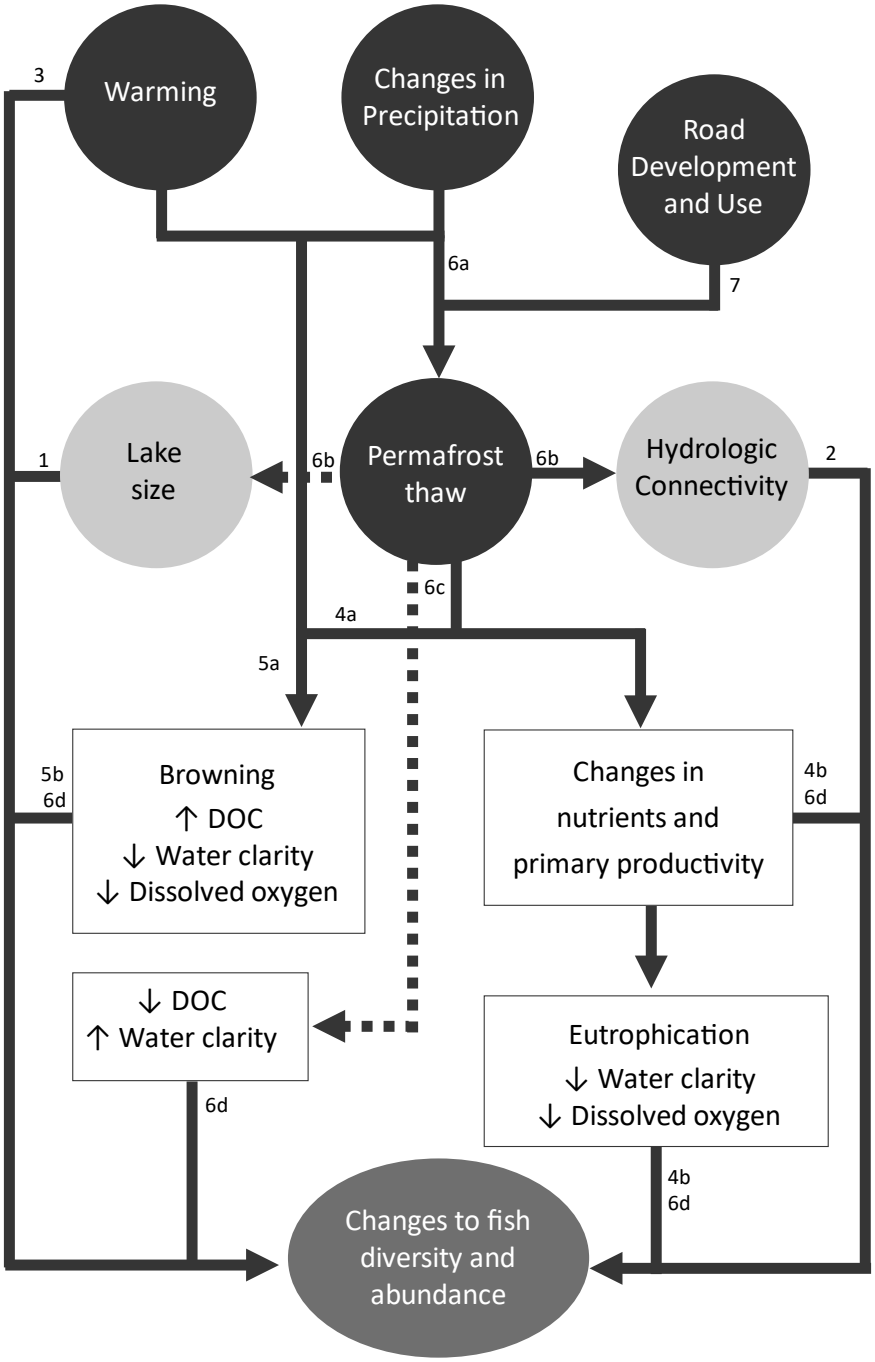


Figure 2. Conceptual model demonstrating the predicted linkages between variables of environmental change (black circles), physical environmental covariates (light gray circles), lake water quality (white boxes), and fish diversity and abundance in lower Mackenzie River basin lakes. Dashed lines are used to illustrate linkages that do not connect to overlaying solid lines. Refer to Table 1 for further details behind each numbered linkage.

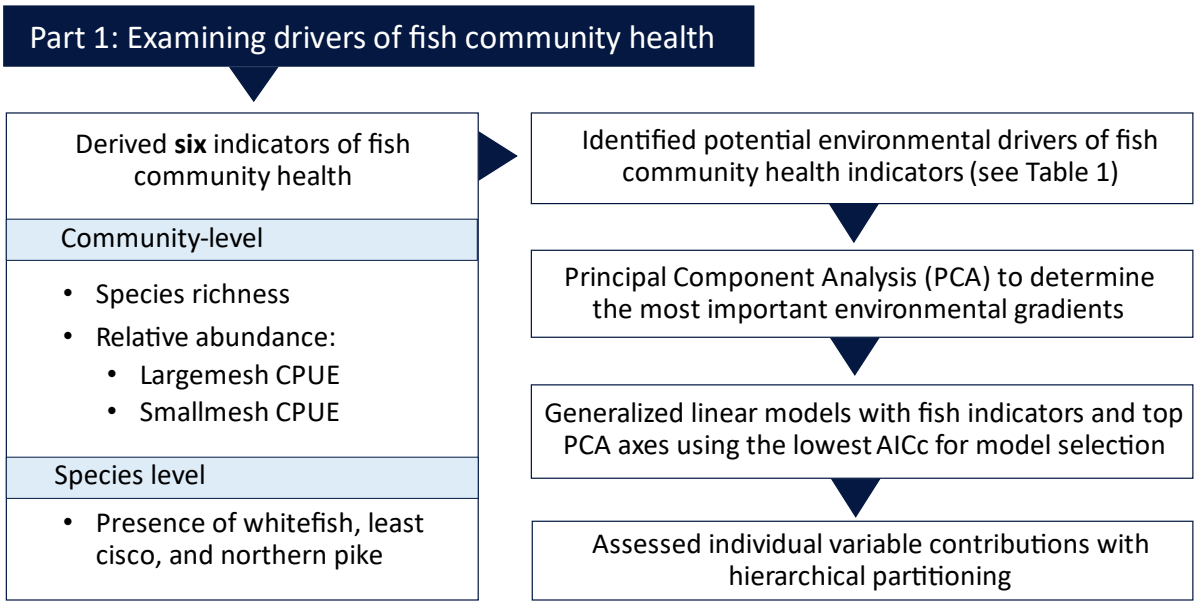


Figure 3. Stepwise framework used to investigate drivers of fish community health. CPUE = catch per unit effort.

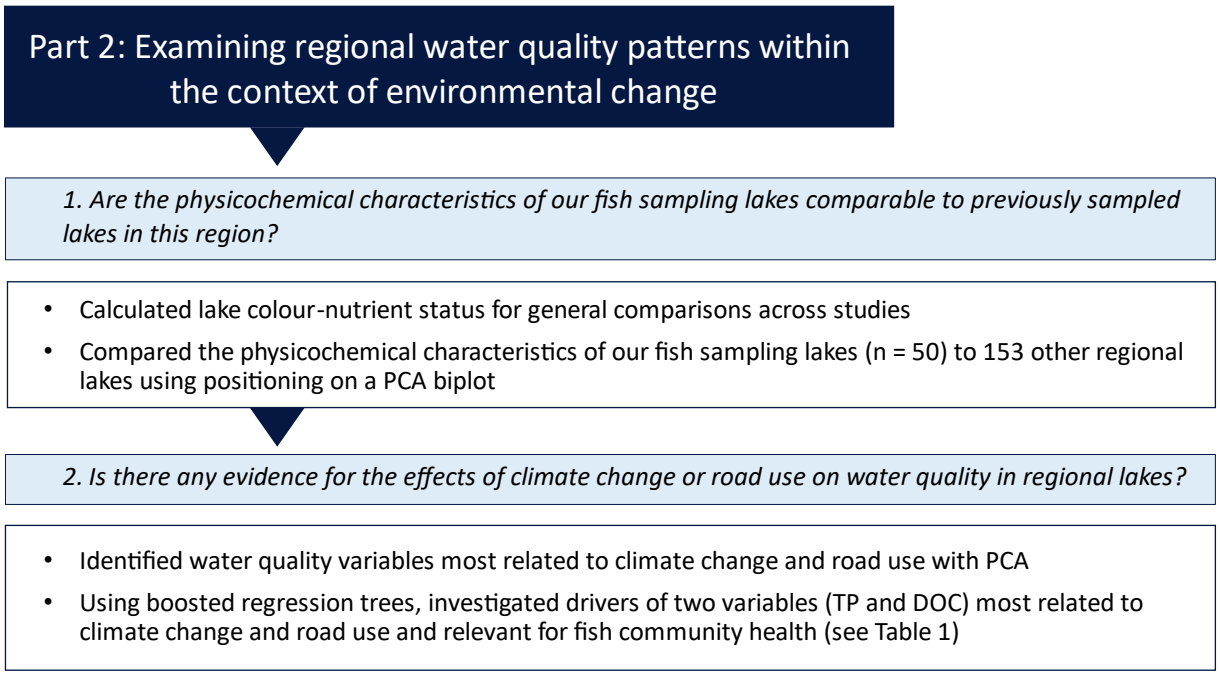


Figure 4. Stepwise framework used to investigate regional water quality patterns in the lower Mackenzie River basin. PCA = principal component analysis.

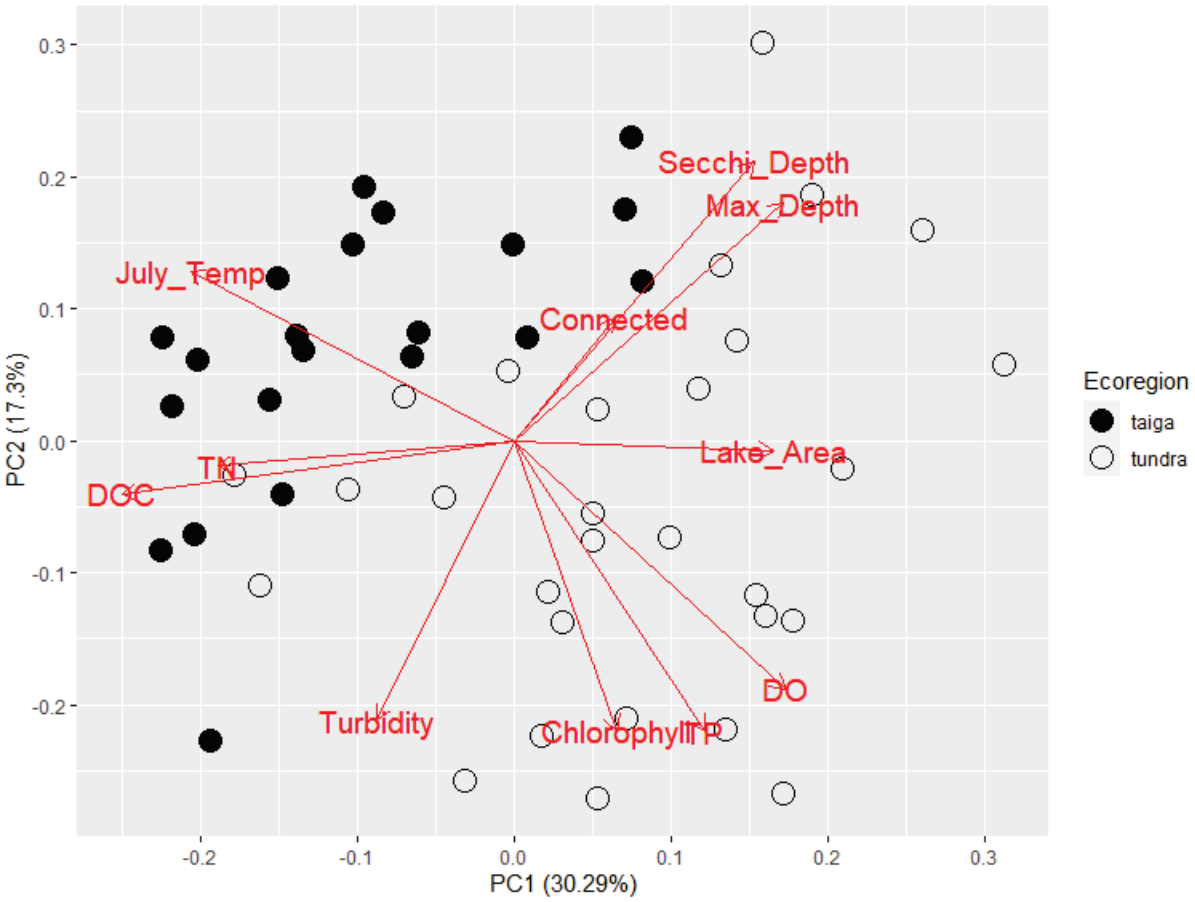


Figure 5. Principal component analysis examining the environmental variability at fish community sampling lakes. PC1 is characterized as a browning-warming gradient and PC2 as a eutrophication gradient. Abbreviations include DOC = dissolved organic carbon, TN = total nitrogen, TP = total phosphorus, and DO = dissolved oxygen.

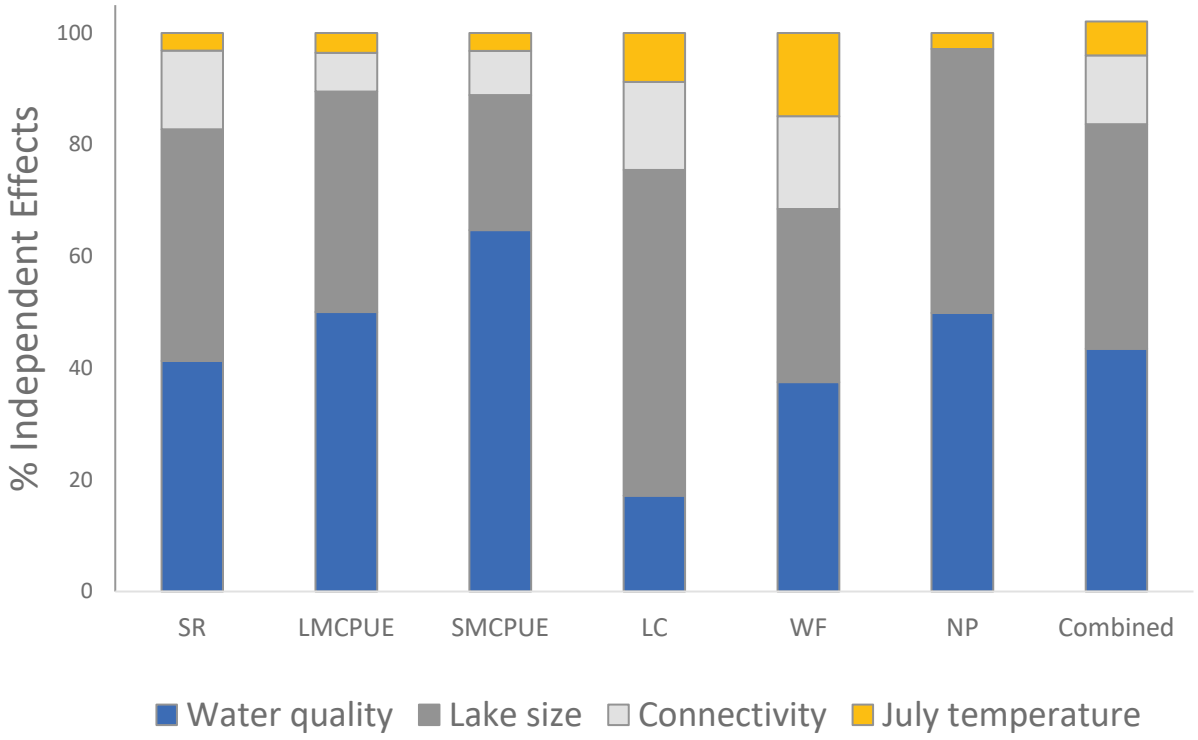
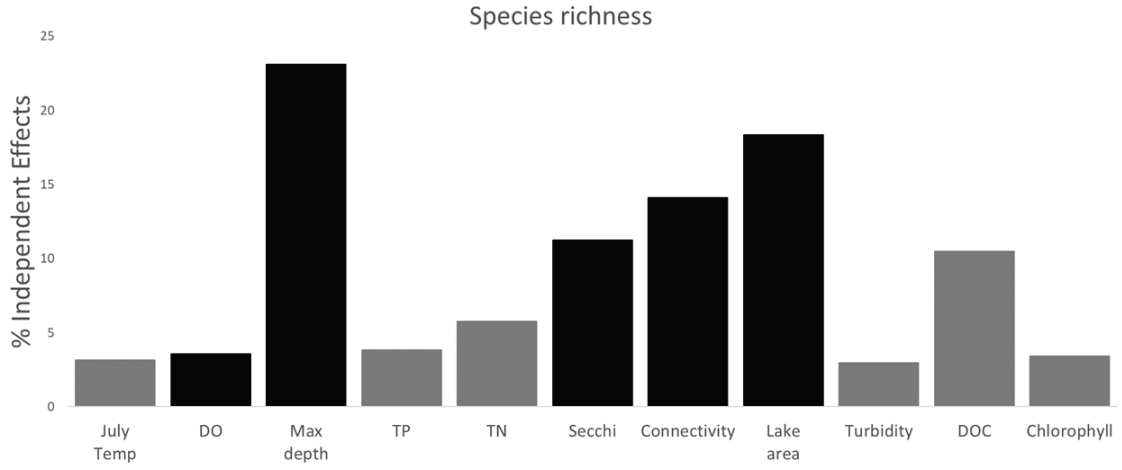
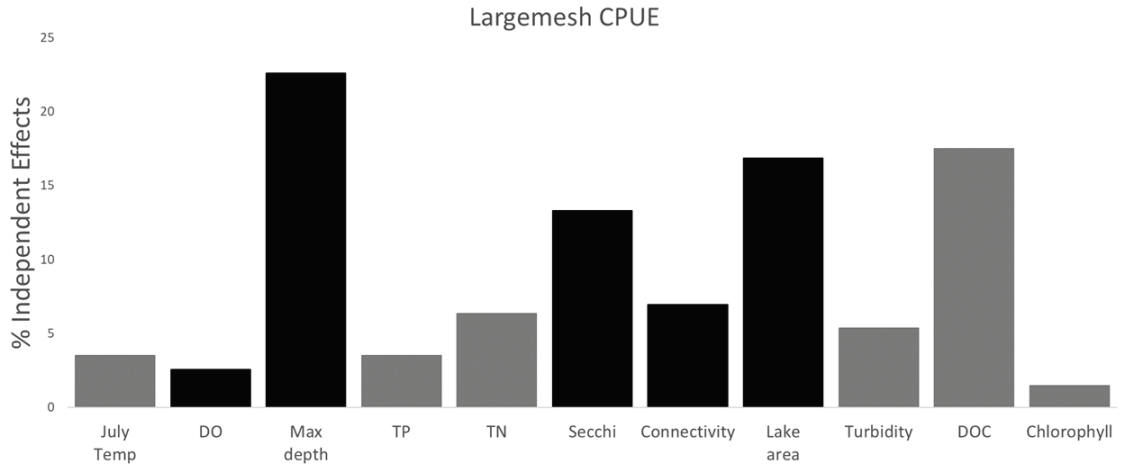


Figure 6. Hierarchical partitioning results summarized by variable category for all six fish community indicators. Indicator codes include SR = species richness, LMCPUE = largemesh catch per unit effort, SMCPUE = smallmesh catch per unit effort, LC = least cisco, WF = whitefish and NP = northern pike. The water quality category includes the total sum of independent effects for dissolved organic carbon, Secchi depth, total phosphorus, total nitrogen, chlorophyll-a, and dissolved oxygen. The lake size category includes the sum of independent effects for lake area and lake depth. The combined total does not add up to 100% because different models had different variable inputs (see methods).


Species richness
% Independent Effects
25
20
15
10
5
0
July Temp
DO
Max depth
TP
TN
Secchi
Connectivity
Lake area
Turbidity
DOC
Chlorophyll


Largemesh CPUE
% Independent Effects
25
20
15
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5
0
July Temp
DO
Max depth
TP
TN
Secchi
Connectivity
Lake area
Turbidity
DOC
Chlorophyll

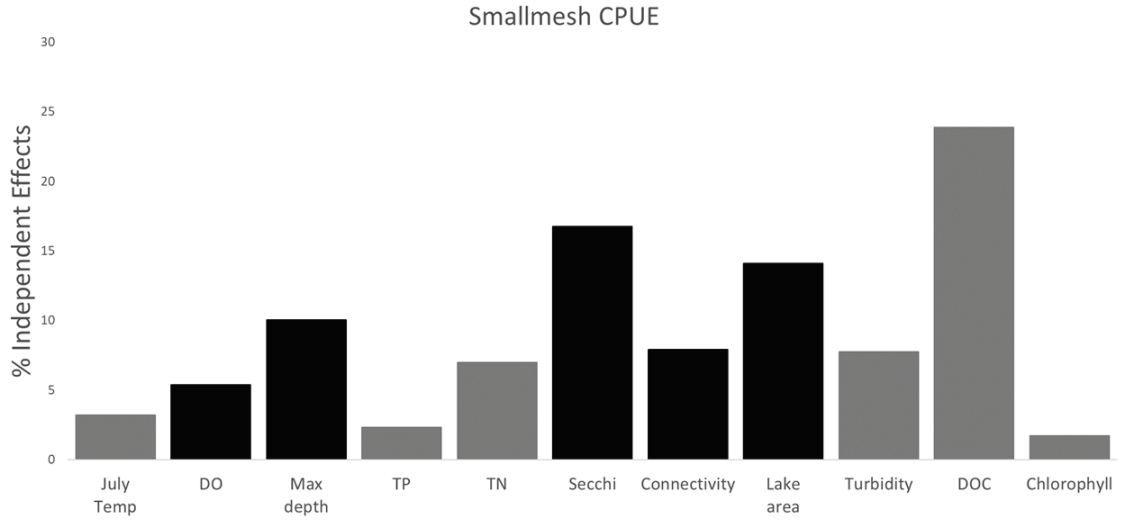
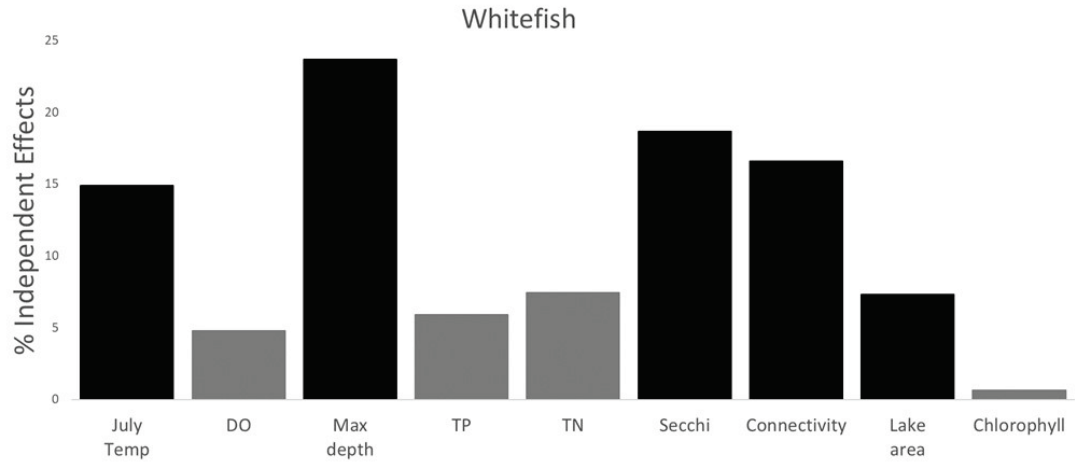
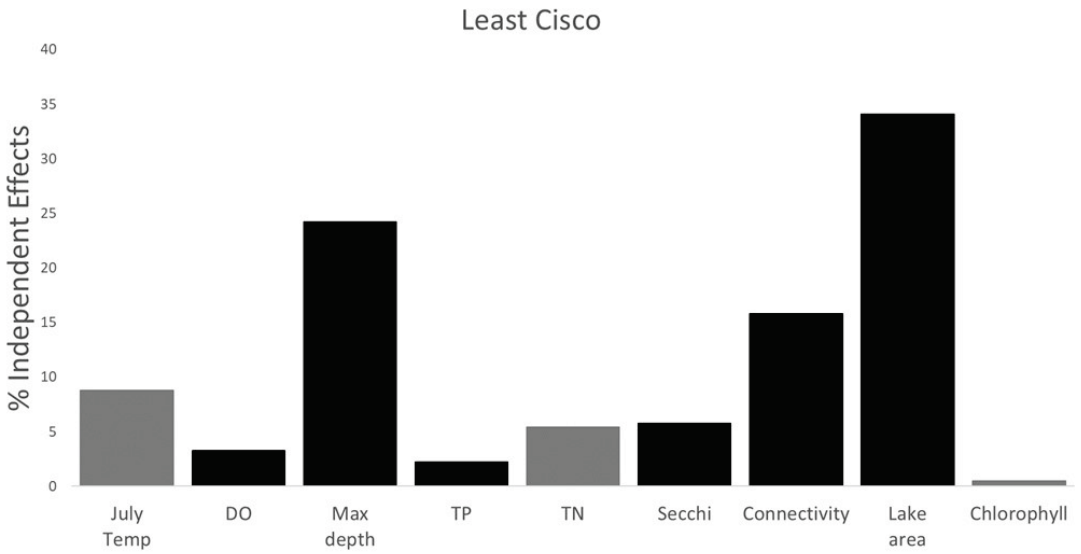

Smallmesh CPUE
% Independent Effects
30
25
20
15
10
5
0
July Temp
DO
Max depth
TP
TN
Secchi
Connectivity
Lake area
Turbidity
DOC
Chlorophyll

Figure 7. Hierarchical partitioning results for species richness, largemesh catch per unit effort (CPUE), and smallmesh catch per unit effort. Black bars indicate positive relationships and gray bars indicate negative relationships using pairwise Pearson correlation tests.


Whitefish
% Independent Effects
25
20
15
10
5
0
July Temp
DO
Max depth
TP
TN
Secchi
Connectivity
Lake area
Chlorophyll


Least Cisco
% Independent Effects
40
35
30
25
20
15
10
5
0
July Temp
DO
Max depth
TP
TN
Secchi
Connectivity
Lake area
Chlorophyll

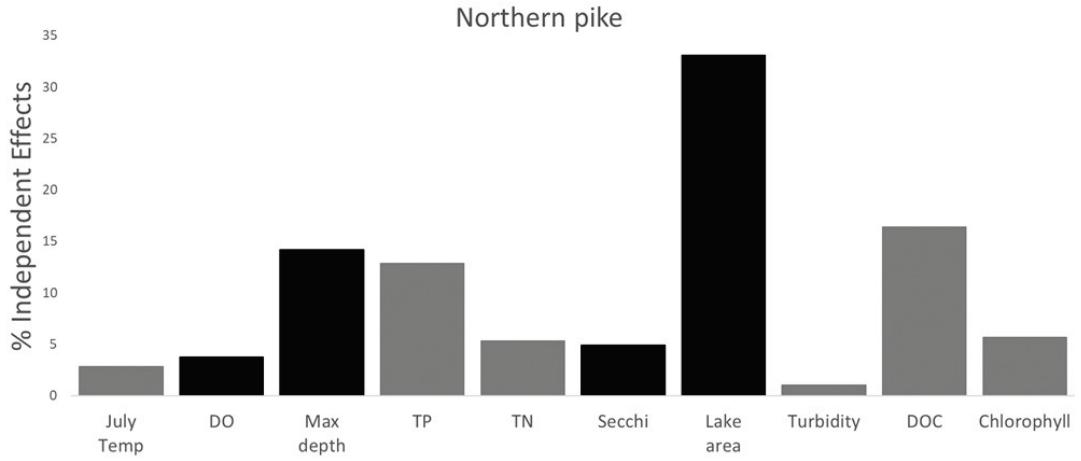

Northern pike
% Independent Effects
35
30
25
20
15
10
5
0
July Temp
DO
Max depth
TP
TN
Secchi
Lake area
Turbidity
DOC
Chlorophyll

Figure 8. Hierarchical partitioning results for whitefish species, least cisco, and northern pike presence. Black bars indicate positive relationships and gray bars indicate negative relationships using pairwise spearman correlation tests.

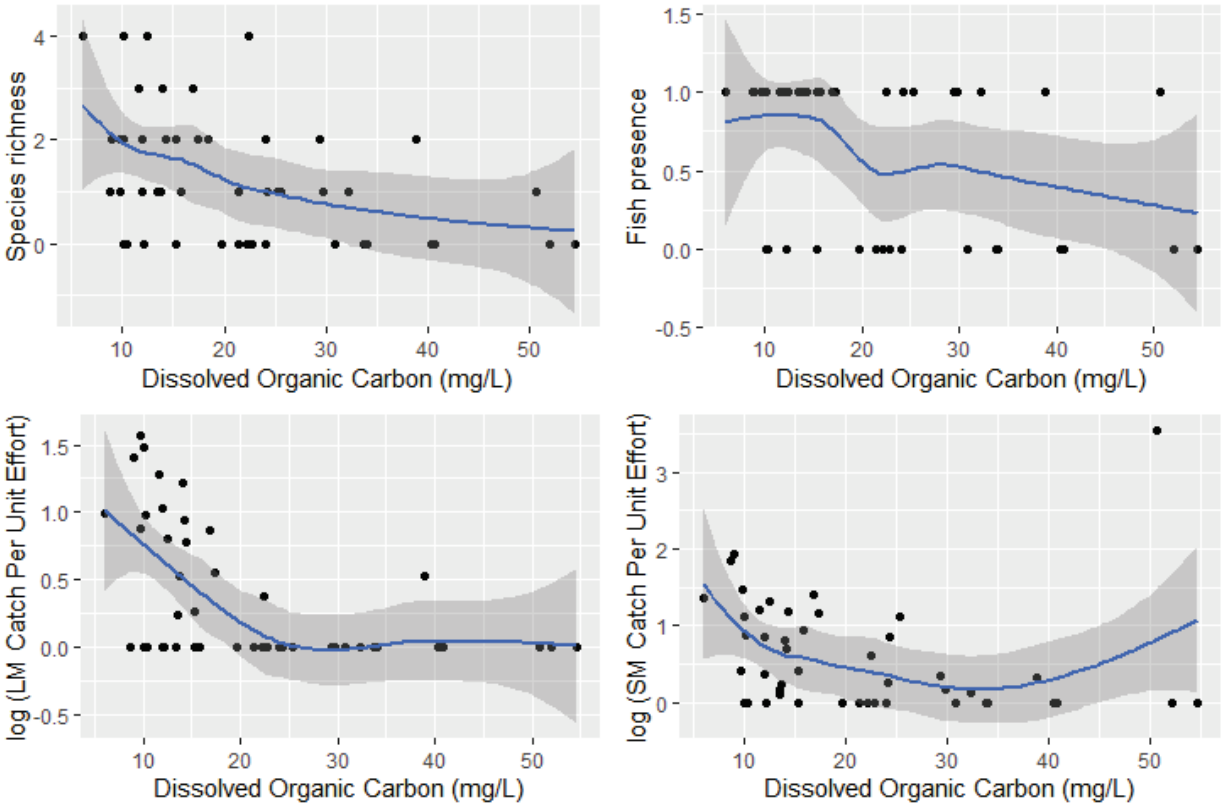


Figure 9. Species richness, fish presence, log-transformed total largemesh (LM) catch per unit effort, and log-transformed total smallmesh (SM) catch per unit effort with dissolved organic carbon (mg/L). Gray shading indicates 95% confidence interval.

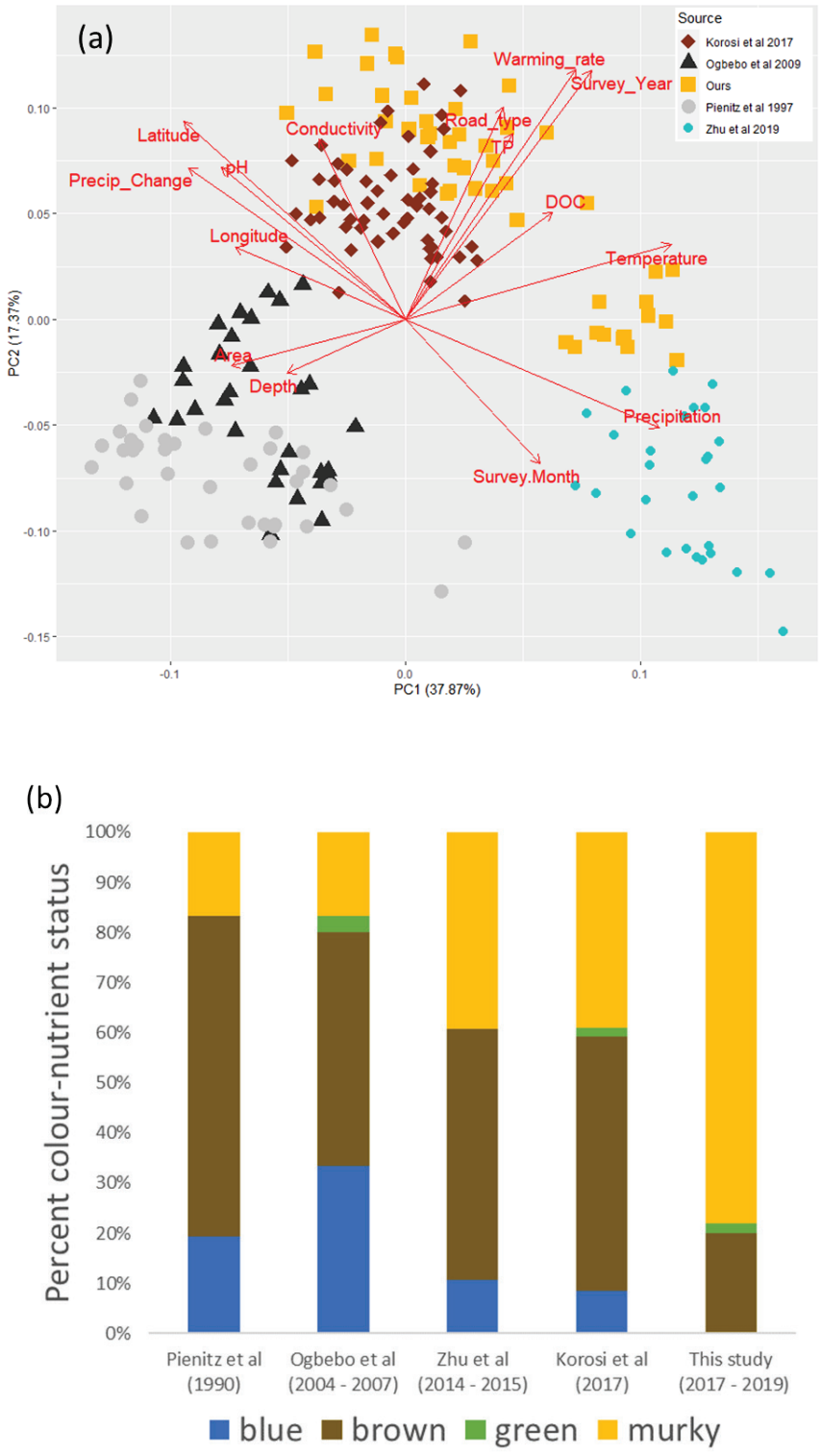


Figure 10.(a) Principal Component Analysis biplot demonstrating the relationship between water quality variables (DOC = dissolved organic carbon, TP = total phosphorus, specific conductivity, pH), study source, geographic location (latitude, longitude), climate (mean annual

air temperature, mean annual precipitation, warming rate, change in annual precipitation), lake size (maximum depth, lake area), sampling timing (survey year and survey month), and road type (0 = no road, 1 = old highway, 2 = new highway), and **(b)** the proportion of lakes in each colour-nutrient status category by study source, with sampling year(s) indicated in brackets. Blue lakes are considered oligotrophic, brown lakes are humic, green lakes are eutrophic, and murky lakes have high TP and DOC concentrations.

General Conclusion

My dissertation research consisted of three studies that examined how northern fish biodiversity is being impacted by cumulative environmental changes including climate change, water quality, and land use (summary provided in Table 1). These studies encompassed three broad northern regions including: (1) the boreal region of central-northern Alberta, (2) further downstream at the taiga-tundra boundary in the Mackenzie River Delta, and (3) across a wide variety of Alaskan ecoregions. Given the diverse set of landscape factors and climatic conditions found in these three study areas, each project setting provided a different angle for understanding how cumulative environmental effects may be impacting northern fish diversity (Table 1).

As global biodiversity continues to decline, research considering cumulative real-world impacts is greatly needed to inform improved evidence-based conservation and management planning (Nõges et al. 2016; WWF 2018). Through this dissertation work, we identified several key threats to northern North American fish species across broad geographic scales that have received minimal documentation to-date, and provided recommendations for how we may safeguard northern fish diversity given this improved understanding. We note that the range and complexity of climate change impacts observed in this research often supported long held and widely discussed expert predictions for northern North American freshwater diversity (Reist et al. 2006b, 2016; Christiansen et al. 2013), and therefore provided an essential link between scientific theory and application. In particular, we observed evidence for the dominant role of climate change in structuring northern fish diversity, including direct and indirect climate effects, as well as highlighted the potential for key interactive effects with local factors such as anthropogenic land use or local environmental conditions (e.g., stream size, elevation, weather). In two of my dissertation chapters, we provided evidence for the potential increase of northern fish diversity and overall abundance in association with climate warming, confirming predictions based on ecological theory. However, this trend was not observed for fish communities in small subarctic lakes at the taiga-tundra boundary, where water quality degradation appeared to have a stronger role in regulating fish community health than direct warming. In all cases, we observed evidence for localized gains and losses of individual fish species in association with mounting environmental changes that included warming (both direct and indirect effects), changes in precipitation, and land use.

Despite the heightened risk of climate change in northern regions, anthropogenic activities (i.e., setting fisheries management goals, conducting environmental assessments for proposed development projects) do not explicitly consider potential climate impacts (e.g., Samis et al. 2005; Kiggiak-EBA Consulting Ltd 2011; Joint Technical Committee of the Yukon River U.S./Canada Panel 2020). Throughout these dissertation chapters, we have outlined several specific climate change adaptation and mitigation strategies that could be readily adopted into management and stewardship planning for northern fishes. One central recommendation across all three studies was to directly incorporate climate sensitivity information into land use planning and fisheries management. Different approaches may be taken depending on regional conservation priorities and the suite of available options, for example, regions that contain relatively intact watersheds may choose to protect these areas as increasingly important climate refugia for freshwater biodiversity. In contrast, regions that have experienced greater direct anthropogenic effects may choose to limit further pressures in the most climatically sensitive watersheds, and/or undergo more active restoration activities such as riparian restoration or new habitat creation that aims to offset prior impacts. Climate risk information may also be used to inform improved fisheries management, for example, harvest pressure on migratory species could be reduced in years where fish may be experiencing additional stress from warmer water temperatures, higher velocities, or low-flow barriers.

Throughout my dissertation research, we have identified key information gaps that could be used to guide future monitoring and research programs. A common theme that emerged was the importance of overwintering habitat for northern species, and the need to understand how the rapidly changing winter period may be structuring fish communities. Warmer winters may have direct impacts on critical groundwater-fed overwintering habitats in streams and could also reduce the potential for winterkill in small northern rivers or lakes over time. However, the role of degraded winter water quality was also raised as a potential mechanism in this dissertation for lowering fish diversity in small northern lakes in the Mackenzie Delta. Based on these varied results, future studies that focus on changes to winter habitat including groundwater quality and quantity, ice conditions, and under-ice physicochemical habitat will be particularly useful for forecasting changes in northern fish diversity.

Creating more open and accessible northern data will be a key component for facilitating an 'all hands on deck' approach that is urgently needed to adequately address rapid northern environmental change (Lento et al. 2019; Heino et al. 2020). This dissertation aimed to address this issue by using large, previously unanalyzed governmental datasets, and by collecting new data that can be used as an important baseline for detecting further changes in a rapidly warming ice-rich permafrost region. Many further opportunities exist for using the Alaskan and Albertan governmental databases employed in this dissertation for future research questions, and there is also a huge untapped potential for combining data from numerous northern environmental assessments. Many of these assessment reports are publicly available but remain underutilized as they are difficult to locate and often do not contain data in a usable format. However, we note that large multi-source databases do come with their limitations which have been described within each of my research chapters, including typically coarser measurements of environmental change, and the inability to fully control for differences in study design. Despite these noted limitations, studies using large multi-source datasets for northern regions remain rare and are therefore still extremely useful for identifying potential impacts on northern fish diversity on large spatial scales, particularly as coordinated standardized datasets for broad spatial regions currently do not exist in subarctic and Arctic regions of North America (Lento et al. 2019).

As expressed by Heino et al. (2020), multiple tactics including more coordinated efforts for largescale standardized monitoring programs, enhancing the role of Indigenous knowledge and stewardship, and increasing modelling predictions to include multiple stressors, are greatly needed to safeguard northern diversity amid rapid environmental change. Results from this dissertation echoed these sentiments and further suggested that strategic monitoring and research within northern North America could be useful for maximizing our conservation impact. For example, northern regions with escalating development pressures could be targeted for future work examining the combined and interactive effects of climate change and direct human pressure on freshwater diversity, including Ontario's Ring of Fire, expanding hard-rock mining regions in Nunavut and NWT (i.e., the diamond district), and the Mackenzie River Valley which is slated for northern Canada's next new major highway route, the Mackenzie Valley Highway (Chetkiewicz et al. 2017; Government of Northwest Territories 2020). There are also examples of declining northern migratory fish populations, such as Yukon River Chinook salmon and Western Arctic Dolly Varden, that could be examined as valuable case studies for understanding

rapid environmental change across broad geographic regions (COSEWIC 2010; JTC - Joint Technical Committee of the Yukon River U.S./Canada Panel 2020). In other cases, current government-led standardized monitoring programs in provinces such as Alberta and Ontario could be expanded to examine cumulative and interacting effects in their northern jurisdictions where more sensitive coldwater species assemblages are experiencing heightened climatic changes. Although the rapid trajectory of northern environmental change is likely to continue in the foreseeable future, these outlined opportunities for more targeted, evidence-based research have the chance to make a difference in protecting northern biodiversity and people in an increasingly developed, warmer, and unpredictable world.

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Table 1. Thesis summary including study questions, predictions, main findings, and overall implications

#	Study Area and Data		Question	Prediction	Main Findings	Overall Implications
1	Fish community data from 1587 sites in small streams and rivers across the state of Alaska Environmental variables: Seasonal current weather and climate change variables, water temperature, landscape factors (drainage area and elevation), anthropogenic land use, pollution, fire disturbance	(1)	Which key environmental variables are influencing Alaskan stream fishes?	Climate variables including warmer and wetter winters, and warmer summers with varying precipitation changes were expected to yield the greatest influence on Alaskan stream fishes (See Chapter 1, Table 1)	• Fish distributions were most accurately predicted using a combination of climate and landscape variables • The effects of land use and fire appeared relatively inconsequential	Positive: fish diversity, overall abundances, and select species may benefit from climate change across their northern ranges Negative: local losses of fish species of economic and cultural importance may be detrimental for Alaskan communities with limited fishing portfolios
		(2)	Is climate interacting with other environmental variables to produce non-additive effects (i.e. antagonistic or synergistic interactions)?	Climate interactions would reveal important context-dependence for effects depending on local conditions (i.e., local climate and landscape factors) and species life history (See Chapter 1, Table 2)	• A mixture of antagonistic and synergistic interactions was observed between current weather, climate change, and landscape variables • Warmer water temperatures had varying relationships with species depending on other local climate factors • The inclusion of landscape variables was important for understanding the relationship between winter air temperature and species richness	
		(3)	Is the overall effect of climate change positive or negative?	Positive effects were expected at the community level; differing effects were expected at the species level (See Chapter 1, Table 1)	• Warming temperatures were linked to increased community fish diversity and overall abundance • Arctic specialists appeared the most vulnerable to warming • Pacific salmon demonstrated complex interacting relationships that suggested an overall distribution gain across Alaska, with the potential for local losses depending on local climate and landscape factors	

2	Fish community data from 301 stream and small river catchments in the boreal region of Alberta, Canada Environmental variables: Maximum July air temperature, change in summer precipitation, frost free period, landscape factors (drainage area, elevation, slope), anthropogenic land use and related habitat quality variables	(1)	How are cumulative land use pressures influencing boreal stream fish community structure?	Sensitive species would decline in response to rising land use impacts, whereas overall community metrics would be more robust (at low-mid disturbance levels) owing to species compensatory dynamics	• Fish diversity and overall abundance were not negatively related to land use changes • Sensitive fish species declines were observed in association with increasing land use in warmer regions	As many northern regions are expected to become warmer, wetter, and more developed over time, we advised that preparing for negative long-term effects on valued fish species will be essential despite the potential for any small, short-term benefits
		(2)	Is climate is producing a buffering (antagonistic) or amplified (synergistic) effect on concurrently acting stressors across a broad, real-world landscape?	Warming would dampen the effects of co-occurring stressors on boreal fishes owing to its stimulatory effect, whereas amplified (synergistic) species declines would be observed when stressors interacted with changes in summer precipitation.	• Amplified declines of sensitive fish species were observed owing to the combined and interacting effects of warming, increased precipitation, and increased land use stress • Some sensitive species living in cooler and less productive watersheds increased with low-level development, possibly due to increased nutrient releases following minor disturbance	
3	Fish community data from fifty lakes at the taiga-tundra boundary in the lower Mackenzie River basin Environmental variables: July air temperature, lake morphometry, water quality variables (total phosphorus, total nitrogen, chlorophyll-a, dissolved oxygen, Secchi depth, dissolved organic carbon, turbidity), hydrologic connectivity	(1)	What are the current drivers of fish community health in lower Mackenzie River basin lakes?	Warmer and more productive lakes would support more species at higher abundances; differing effects were expected at the species level (See Chapter 3, Table 1); further lake browning (increases in dissolved organic carbon) was predicted to negatively affect fish diversity and abundances in lower Mackenzie River basin lakes that already face potential light limitations due to highly coloured water	• Water quality and lake size were the dominant co-drivers of fish community health, whereas direct warming had a relatively weak relationship with fish community indicators • Fish diversity, overall abundance, and individual species declined in smaller, more eutrophic, and browner lakes • Lakes below the treeline had high dissolved organic carbon levels that were associated with dramatic declines in fish diversity, illustrating a potentially important ecological threshold for supporting higher trophic levels in subarctic lakes	Future environmental changes including warming, development, and interrelated permafrost thaw may lead to additional degradation of fish habitat in lower Mackenzie River basin lakes, with potentially negative implications for fish diversity in the numerous small lakes that dominate this region. These results have important implications for guiding future research and for informing conservation management in permafrost regions across the circumpolar north.
	Supplementary analysis using regional water quality records for 203 lakes	(2)	Is there any evidence for the effects of climate change or road use on water quality in regional lakes?	Warmer and wetter climate combined with increased road development may lead to increased permafrost thaw, which in turn could impact water quality including increases in nutrients and water colour	• Lakes that had experienced greater warming rates and were situated by the new highway had more degraded water quality including higher dissolved organic carbon and total phosphorus values	

= Chapter number

Appendices

Appendix A: Supplementary Information for Chapter 1

Table A1. Summary of simplified boosted tree model results including predictor variable importance by type for community metrics (species richness, total catch per unit effort) and population metrics (presence absence) for three species groups.

Response Variable Type	Species Richness	Total CPUE	Arctic grayling	Dolly Varden	Juvenile salmon	Total Average
current weather	62	49	59	37	71	56
climate change	9	39	18	35	21	24
habitat	29	12	24	28	8	20
land use and fire	0	0	0	0	0	0
Overall Model Performance	58 (35)[1]	48 (32)[1]	78 (74,90)[2]	77 (81,74)[2]	77 (79,72)[2]	

Note: Refer to Table 3 for variable types. Total CPUE = Catch Per Unit Effort, measured as number of fish per 100s of electrofishing

[1]Overall model deviance explained is reported, followed by deviance explained using cross validation in brackets

[2]Classification success (%) is reported, followed by sensitivity (%) and specificity (%) in brackets

Table A2. Mixed model results for community metrics (species richness, total catch per unit effort) and population metrics (presence absence) for three species groups. A suffix of "2" indicates a quadratic term.

	Species	Predictor Variables	Standardized Coefficient Estimate	SE	*P*-value
Species richness	All	winter temp	0.17	0.05	<0.01
		water temp	0.17	0.03	<0.01
		water temp2	-0.12	0.03	<0.01
		drainage area	0.30	0.03	<0.01
		elevation	-0.31	0.03	<0.01
		winter temp x drainage area	0.28	0.05	<0.01
		winter temp x elevation	-0.31	0.06	<0.01
Total Catch Per Unit Effort	All	winter temp	0.18	0.05	0.01
		change in winter precip	0.13	0.04	<0.01
		change in summer precip	-0.16	0.05	<0.01
		water temp	0.10	0.03	<0.01
		water temp2	-0.16	0.03	<0.01
		elevation	-0.01	0.04	0.81
		elevation2	-0.17	0.04	<0.01
Presence Absence	Arctic grayling	winter temp	-2.73	0.47	<0.01
		change in fall precip	-1.20	0.36	<0.01
		change in fall precip2	-1.40	0.61	0.02
		water temp	1.30	0.25	<0.01
		water temp2	-1.03	0.25	<0.01
		drainage area	0.77	0.20	<0.01
		elevation	-1.38	0.31	<0.01
		winter temp x water temp	2.09	0.41	<0.01
	Dolly Varden	winter temp	2.21	0.50	<0.01
		winter precip	0.37	0.31	0.23
		change in winter temp	-0.68	0.38	0.08
		change in winter temp2	-0.96	0.30	<0.01
		change in winter precip	1.90	0.39	<0.01
		water temp	-1.37	0.20	<0.01
		elevation	4.36	0.36	<0.01
		elevation2	-2.60	0.33	<0.01
		winter precip x change in winter precip	-1.38	0.34	<0.01
	Juvenile salmon species	change in winter temp	-0.80	0.28	<0.01
		spring temp	1.86	0.50	<0.01
		summer precip	1.22	0.39	<0.01
		summer precip2	-0.92	0.30	<0.01

fall temp	1.90	0.43	<0.01
change in fall precip	-0.65	0.31	0.04
water temp	0.23	0.18	0.22
water temp2	-0.83	0.23	<0.01
drainage area	0.99	0.17	<0.01
water temp x summer precip	1.32	0.38	<0.01

Table A3. Summary of interaction types. The direction of each coefficient is indicated by (+) positive, (-) negative, or (+/-) mixed/unimodal.

Interaction type	Biological metric	Interaction	a	b	a:b	Interaction Classification
Current Weather × Current Weather	Arctic grayling presence	a) winter air temperature b) water temperature	-	+/-	+	antagonistic in warmer waters
	salmon presence	a) water temperature b) summer precipitation	+/-	+	+	antagonistic in warmer waters
Current Weather × Climate Change	Dolly Varden presence	a) winter precipitation b) change in winter precipitation	+/-	+	-	antagonistic
Current Weather × Habitat	species richness	a) winter air temperature b) log drainage area	+	+	+	positive synergistic
	species richness	a) winter air temperature b) elevation	+	-	-	negative synergistic at higher elevations

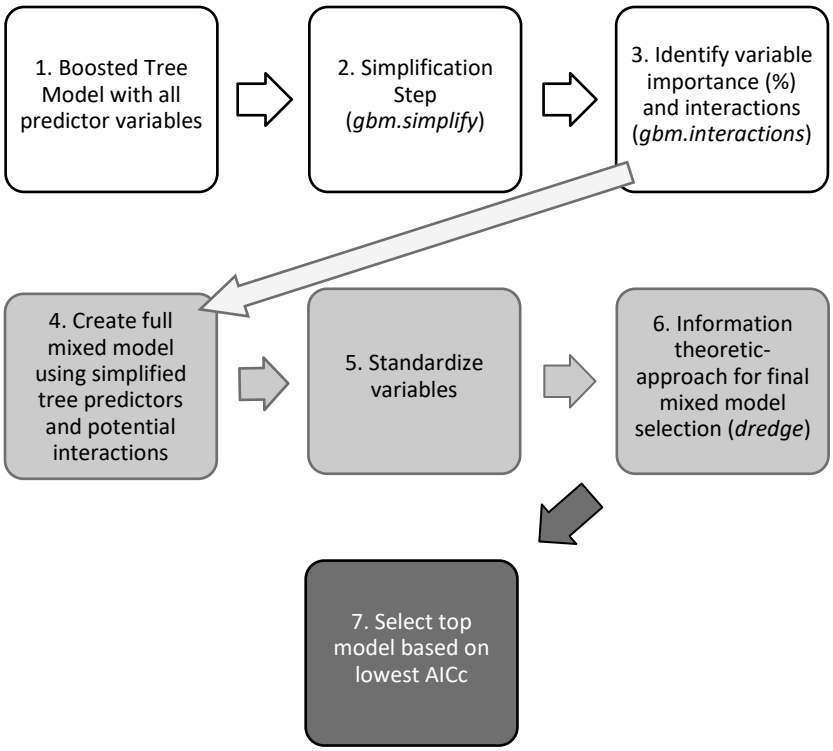
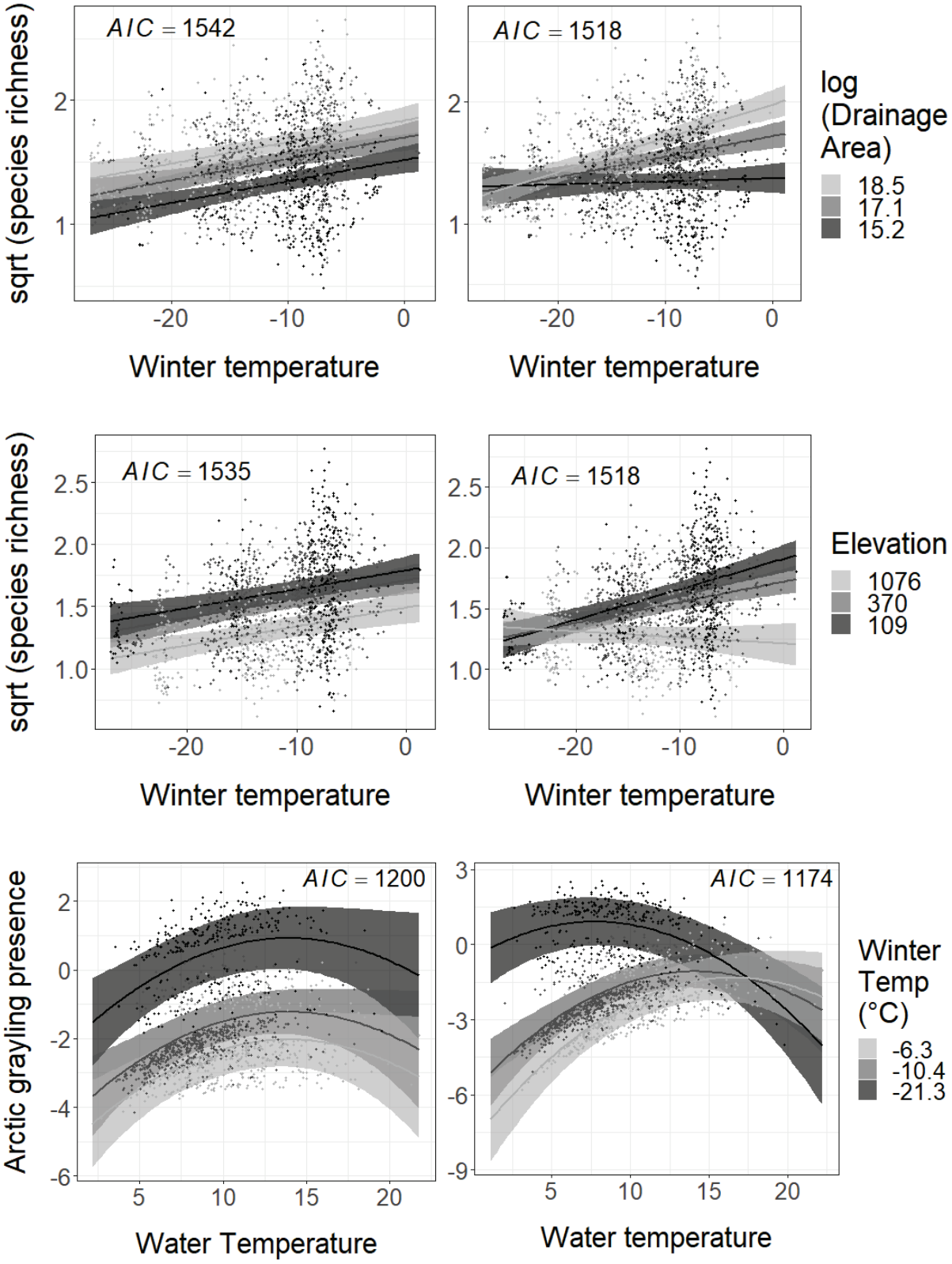


Figure A1. Analysis workflow adapted from Feld, Segurado, & Gutiérrez-Cánovas (2016). Boosted tree models are used to identify important variables and interactions following the simplification step, which removes variables that do not contribute to the model's predictive performance (Elith and Leathwick 2017). Mixed models go through a secondary selection step using *dredge* from the *MuMin* package (Barton 2018).


AIC = 1542
AIC = 1518
sqrt (species richness)
Winter temperature
log (Drainage Area)
18.5
17.1
15.2
AIC = 1535
AIC = 1518
Elevation
1076
370
109
AIC = 1200
AIC = 1174
Arctic grayling presence
Water Temperature
Water temperature
Winter Temp (°C)
-6.3
-10.4
-21.3

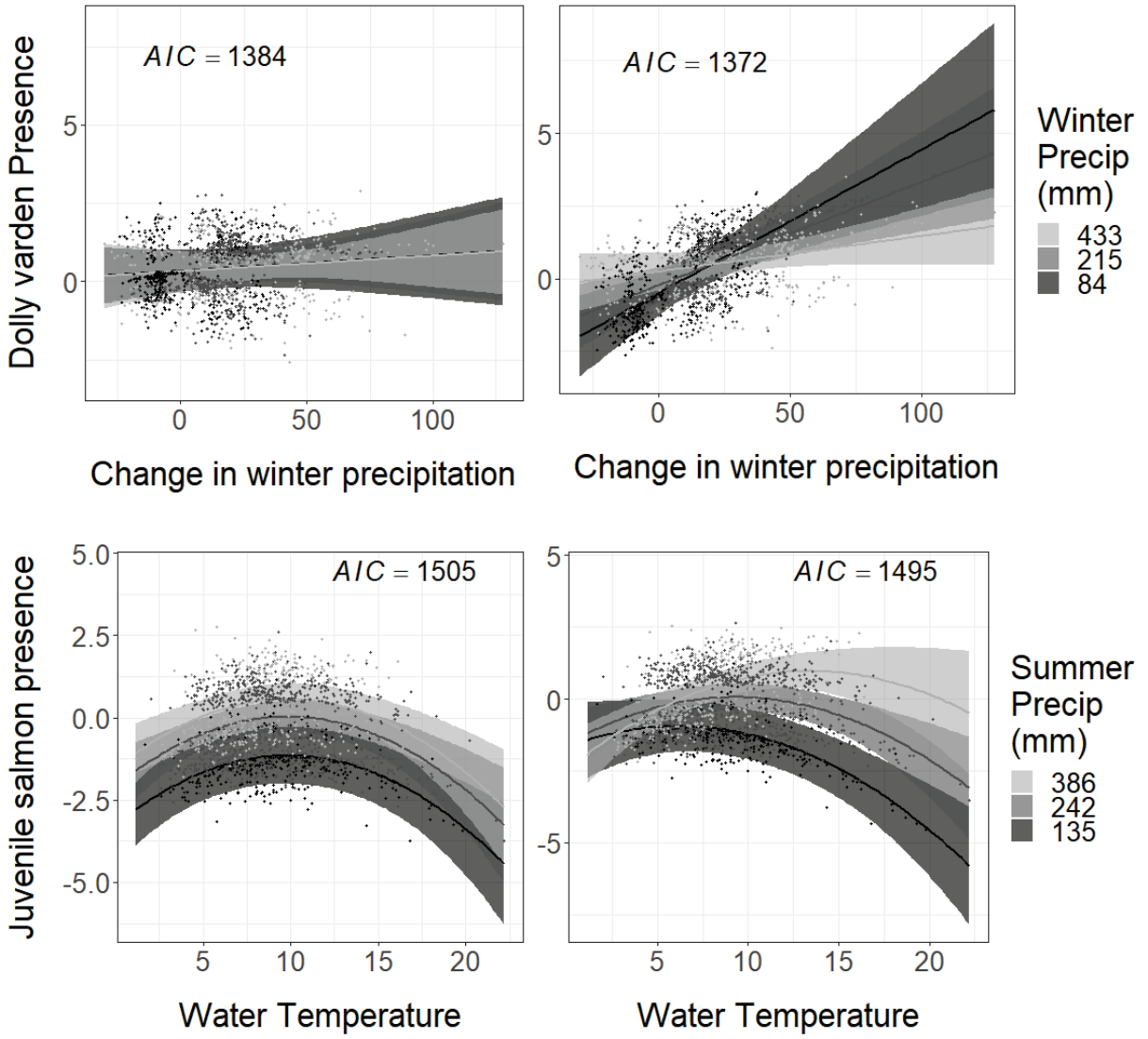


Figure A2. Partial plots used for interaction interpretation, illustrating the difference between the additive model (left) and interactive model (right). Shading indicates 95% confidence intervals and y-axes of species models are plotted on the linear predictor (logit) scale.

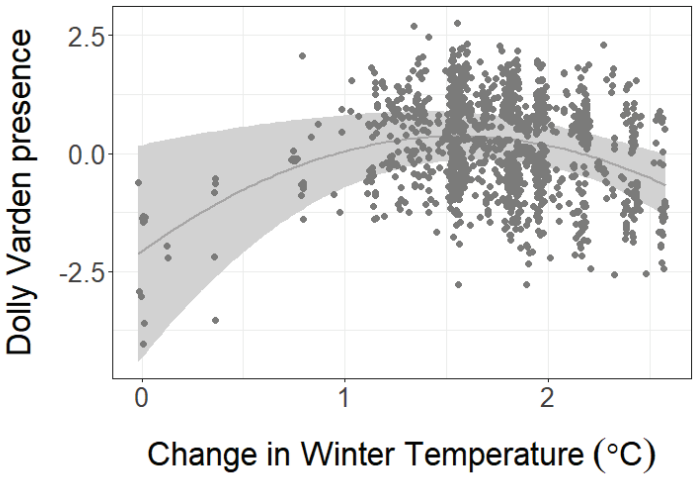


Figure A3. Generalized linear mixed model partial plot demonstrating the relationship between Dolly Varden presence and change in winter temperature. Change in temperature is the difference between the current 30-year mean and the previous 30-year mean. All additional model variables have been corrected to their mean values for improved model interpretation. Shading indicates the 95% confidence interval and Dolly Varden presence is plotted on the linear predictor (logit) scale.

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Appendix B: Supplementary Information for Chapter 2

Table B1. Fish species occurrence in 301 local catchments

Species common name	Species scientific name	Family	# Catchments Present	Presence (%)
lake chub	*Couesius plumbeus*	Cyprinidae - Minnows	158	52
brook stickleback	*Culaea inconstans*	Gasterosteidae - Sticklebacks	147	49
white sucker	*Catostomus commersoni*	Catostomidae - Suckers	119	40
longnose sucker	*Catostomus catostomus*	Catostomidae - Suckers	108	36
pearl dace	*Margariscus margarita*	Cyprinidae - Minnows	91	30
finescale dace	*Phoxinus neogaeus*	Cyprinidae - Minnows	88	29
slimy sculpin	*Cottus cognatus*	Cottidae - Sculpins	83	28
longnose dace	*Rhinichthys cataractae*	Cyprinidae - Minnows	61	20
burbot	*Lota lota*	Lotidae - Cuskfishes	57	19
trout-perch	*Percopsis omiscomaycus*	Percopsidae - Trout-perches	56	19
spoonhead sculpin	*Cottus ricei*	Cottidae - Sculpins	42	14
northern redbelly dace	*Phoxinus eos*	Cyprinidae - Minnows	39	13
rainbow trout	*Oncorhynchus mykiss*	Salmonidae - Salmons and trouts	38	13
Arctic grayling	*Thymallus arcticus*	Salmonidae - Salmons and trouts	36	12
fathead minnow	*Pimephales promelas*	Cyprinidae - Minnows	28	9
northern pike	*Esox lucius*	Esocidae - Pikes	17	6
mountain whitefish	*Prosopium williamsoni*	Salmonidae - Salmons and trouts	16	5
redside shiner	*Richardsonius balteatus*	Cyprinidae - Minnows	15	5
brook trout	*Salvelinus fontinalis*	Salmonidae - Salmons and trouts	13	4
flathead chub	*Platygobio gracilis*	Cyprinidae - Minnows	8	3
spottail shiner	*Notropis hudsonius*	Cyprinidae - Minnows	8	3
walleye	*Sander vitreus*	Percidae - Perches and darters	7	2
Iowa darter	*Etheostoma exile*	Percidae - Perches and darters	6	2
bull trout	*Salvelinus confluentus*	Salmonidae - Salmons and trouts	5	2
yellow perch	*Perca flavescens*	Percidae - Perches and darters	5	2
emerald shiner	*Notropis atherinoides*	Cyprinidae - Minnows	3	1
largescale sucker	*Catostomus macrocheilus*	Catostomidae - Suckers	2	1
brassy minnow	*Hybognathus hankinsoni*	Cyprinidae - Minnows	1	0
log perch	*Percina caprodes*	Percidae - Perches and darters	1	0
lake whitefish	*Coregonus clupeaformis*	Salmonidae - Salmons and trouts	1	0
northern redbelly dace x finescale dace	*Phoxinus eos x Phoxinus neogaeus*	Cyprinidae - Minnows	1	0
river shiner	*Notropis blennius*	Cyprinidae - Minnows	1	0

Table B2. Pearson correlation coefficients between predictor variables. Pink and green highlights indicate correlations greater than or less than 0.7 and -0.7, respectively.

	Δ MSMT	Δ SMPP	FFP	MX JULY	Area	SMPP	LDens-L	LDens-RipL	LDens-N	LDens-RipN	LDens-H	Land-L	Land-RipL	Land-N	Land-RipN	Land-H
ΔSMPP	-0.60															
FFP	-0.17	0.01														
MXJULY	0.77	-0.51	-0.06													
Area	0.27	-0.08	0.08	0.38												
SMPP	-0.82	0.48	0.17	-0.90	-0.33											
LDens-L	0.04	-0.25	-0.04	0.01	-0.03	0.08										
LDens-RipL	-0.03	-0.20	-0.10	-0.10	-0.16	0.13	0.77									
LDens-N	0.12	-0.28	-0.18	0.08	0.00	-0.02	0.77	0.64								
LDens-RipN	0.03	-0.19	-0.15	-0.02	-0.02	0.05	0.66	0.77	0.82							
LDens-H	0.02	-0.17	-0.23	-0.04	-0.03	0.15	0.52	0.44	0.63	0.55						
Land-L	-0.31	0.30	0.34	-0.26	-0.18	0.25	-0.37	-0.22	-0.36	-0.26	-0.19					
Land-RipL	-0.20	0.20	0.22	-0.12	-0.21	0.10	-0.37	-0.28	-0.33	-0.30	-0.20	0.73				
Land-N	-0.47	0.43	0.41	-0.40	-0.23	0.43	-0.24	-0.17	-0.40	-0.27	-0.19	0.78	0.55			
Land-RipN	-0.25	0.26	0.35	-0.13	-0.14	0.16	-0.30	-0.27	-0.41	-0.35	-0.22	0.69	0.76	0.78		
Land-H	-0.51	0.56	0.35	-0.41	-0.16	0.41	-0.15	-0.08	-0.24	-0.11	-0.17	0.52	0.33	0.68	0.51	
Slope	-0.51	0.37	0.05	-0.64	-0.10	0.62	-0.14	-0.04	-0.17	-0.07	-0.11	0.19	0.02	0.34	0.13	0.32

Variable codes: ΔMSMT = change in summer temperature, ΔSMPP = change in summer precipitation, FFP = frost free period, MXJULY = maximum July temperature, Area = drainage area, SMPP = current summer precipitation, LDens = linear density, Land = land use. Suffixes to linear density and land use are defined as L = local, RipL = local riparian, N = network, RipN = network riparian, and H=HUC8-level.

Table B3. Comparison of linear mixed models using either change in summer precipitation or current summer precipitation as predictor variables during model selection. Predictors that contributed to the top models are reported, along with the AICc, difference in AICc to the best model for each metric, and the conditional pseudo R^2 followed by the marginal R^2 in brackets. Highlighted rows indicate the top models for each biological metric according to the lowest AICc values.

Biological Metric	Precipitation variable	AICc	ΔAICc	R^2	Important Predictors[4]
Species richness[1]	ΔSMPP	322.3	0	44 (37)	Area, FFP, FFP2, linear, linear2
	SMPP	322.3	0	44 (37)	Area, FFP, FFP2, linear, linear2
Total catch[2]	ΔSMPP	389.4	0	35 (12)	Area, July
	SMPP	389.4	0	35 (12)	Area, July
Lithophils (%)[3]	ΔSMPP	292.4	0	53 (42)	Area, July, slope, ΔSMPP, ΔSMPP*July, linear, linear*July
	SMPP	323.9	31.5	42 (21)	Area, July, slope, linear, linear*July
	ΔSMPP	284.4	0	56 (45)	Area, july, slope, ΔSMPP, ΔSMPP*area, land, land*July
Assemblage Tolerance Index	SMPP	302.2	17.8	53 (40)	Area, july, slope, SMPP, SMPP*area, land, land*July

[1]Species richness was square-root transformed, [2]Total catch was log-transformed and [3]Lithophils were logit transformed; [4]Area= drainage area, FFP = frost free period, land = land use (%), slope = catchment slope, July = maximum July air temperature, ΔSMPP = change in summer precipitation, SMPP = current summer precipitation, linear = linear disturbance (m/km^2); a suffix of "2" indicates a quadratic term and an asterisk indicates an interactive term. Spatial scales used for disturbance variables (linear disturbance and land use) were HUC-8 level for species richness and the Assemblage Tolerance Index models and riparian network for lithophils.

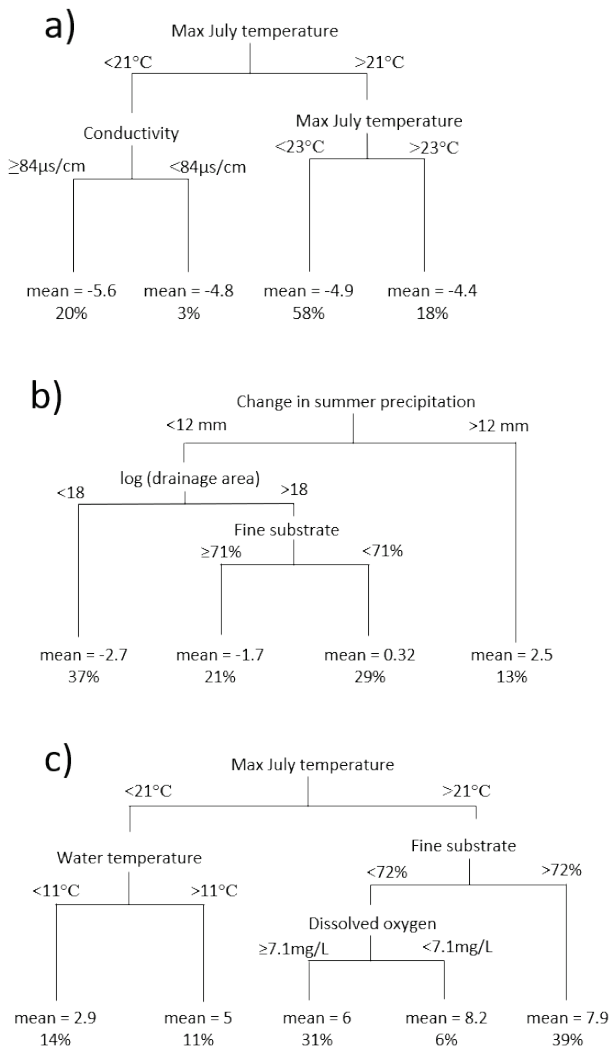


Figure B1. Regression tree models for a) square-root transformed species richness corrected using an electrofishing effort offset, b) logit-transformed lithophils (%), and c) the assemblage tolerance index. Important predictor variables included maximum July temperature (°C), water conductivity (µs/cm), change in summer precipitation, log-transformed drainage area (m), the proportion of fine sediment (%), water temperature (°C), and dissolved oxygen (mg/L). Values at terminal nodes indicate the mean response value and the percentage of sites within that node.

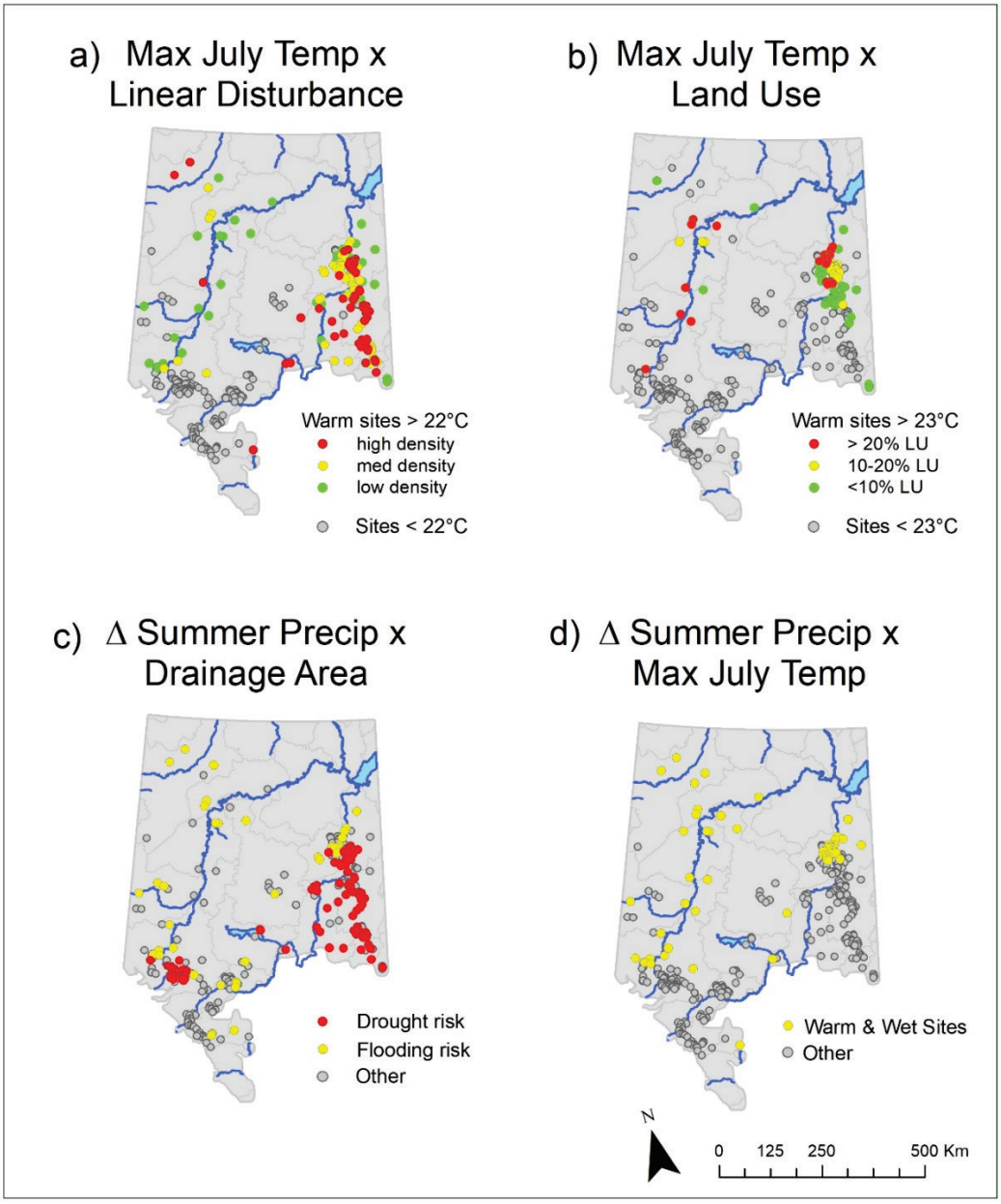


Figure B2. Maps based on stressor interactions identified in Figures 5-6 demonstrating **a)** warm sites (> 22°C) with potential lithophil species declines when riparian network linear disturbance is high (> 955 m/km^2) or moderate (480 - 955 m/km^2). Warm sites with low linear disturbance (< 480 m/km^2) have the potential for future declines with increased development; **b)** warm sites (> 23°C) with potential intolerant species declines when HUC-8 land use is high (> 20%) or moderate (10-20%). Warm sites with low (< 10%) land use have the potential for future declines with increased development; **c)** potential intolerant species declines at sites with heightened

drought risk (change in summer precipitation < 0 mm and drainage area < 18,000 ha), and at sites with potential flooding risk (change in summer precipitation > 0 mm and drainage area > 18,000 ha), and **d)** potential lithophil species declines at sites experiencing warm (>22°C) and wetter summer weather (> +0.5 mm).

Appendix C: Supplementary Information for Chapter 3

Table C1. Fish and water quality sampling dates, locations, fish sampling method, and fishing effort in net-hours

Lake	Latitude	Longitude	Fish sampling date	Water quality sampling date	Fish sampling method[1]	Net-hours
CIMP2017-1	68.35	-133.70	15-Aug-17	17-Aug-17	Overnight Gillnet	151.6
CIMP2017-19	68.31	-133.35	n/a	21-Aug-17	n/a	n/a
CIMP2017-25	67.42	-133.93	n/a	28-Jul-19	n/a	n/a
CIMP2017-27	67.42	-133.94	n/a	28-Aug-17	n/a	n/a
CIMP2017-28	67.38	-134.04	n/a	28-Jul-19	n/a	n/a
CIMP2017-3	68.32	-133.62	19-Aug-17	19-Aug-17	Overnight Gillnet	345.8
CIMP2017-43	67.50	-133.77	n/a	01-Sep-17	n/a	n/a
CIMP2017-ZOO3	67.79	-133.79	n/a	01-Sep-17	n/a	n/a
CIMP2018-1	68.55	-133.74	09-Aug-18	31-Jul-18	Short Set Gillnet	16.7
CIMP2018-10	68.90	-133.54	16-Aug-18	08-Aug-18	Short Set Gillnet	7.8
CIMP2018-11	68.90	-133.49	16-Aug-18	06-Aug-18	Short Set Gillnet	6.1
CIMP2018-12	69.01	-133.31	18-Aug-18	05-Aug-18	Short Set Gillnet	11.1
CIMP2018-15	69.07	-133.15	18-Aug-18	04-Aug-18	Short Set Gillnet	10.9
CIMP2018-16	69.07	-133.20	12-Aug-18	11-Aug-18	Short Set Gillnet	25.1
CIMP2018-17	69.10	-133.08	11-Aug-18	04-Aug-18	Short Set Gillnet	13.6
CIMP2018-20	69.17	-133.04	14-Aug-18	07-Aug-18	Short Set Gillnet	5.2
CIMP2018-21	69.19	-132.95	19-Aug-18	13-Aug-18	Short Set Gillnet	40.8
CIMP2018-22	69.20	-132.94	25-Aug-18	15-Aug-18	Short Set Gillnet	9.3
CIMP2018-23	69.21	-132.90	14-Aug-18	11-Aug-18	Short Set Gillnet	5.7
CIMP2018-24	69.22	-132.89	24-Aug-18	13-Aug-18	Short Set Gillnet	24
CIMP2018-27	69.30	-133.01	21-Aug-18	14-Aug-18	Short Set Gillnet	46.4
CIMP2018-28	69.31	-132.98	23-Aug-18	14-Aug-18	Short Set Gillnet	14.4
CIMP2018-3	68.58	-133.74	25-Aug-18	01-Aug-18	Short Set Gillnet	10.5
CIMP2018-30	69.37	-133.04	23-Aug-18	16-Aug-18	Short Set Gillnet	14.5
CIMP2018-4	68.81	-133.54	17-Aug-18	05-Aug-18	Short Set Gillnet	8.8
CIMP2018-5	68.81	-133.55	17-Aug-18	08-Aug-18	Short Set Gillnet	10.2
CIMP2018-6	68.82	-133.57	10-Aug-18	03-Aug-18	Short Set Gillnet	15.4
CIMP2018-8	68.85	-133.54	15-Aug-18	02-Aug-18	Short Set Gillnet	9.7
CIMP2018-9	68.85	-133.55	15-Aug-18	02-Aug-18	Short Set Gillnet	8.9
CIMP2019-1	67.34	-134.91	16-Aug-19	29-Aug-17	Short Set Gillnet	13.6
CIMP2019-10	67.41	-134.41	14-Aug-19	29-Jul-19	Short Set Gillnet	10.3
CIMP2019-11	67.40	-134.38	04-Aug-19	08-Aug-19	Short Set Gillnet	9.7
CIMP2019-13	67.42	-133.95	05-Aug-19	02-Aug-19	Short Set Gillnet	16.8
CIMP2019-19	68.29	-133.28	03-Aug-19	20-Aug-17	Short Set Gillnet	13
CIMP2019-22	68.33	-133.68	08-Aug-19	18-Aug-17	Short Set Gillnet	15.1
CIMP2019-23	68.34	-133.71	03-Aug-19	05-Aug-19	Short Set Gillnet	12.6
CIMP2019-25	68.56	-133.75	07-Aug-19	30-Jul-19	Short Set Gillnet	9.1
CIMP2019-26	68.82	-133.56	09-Aug-19	30-Jul-19	Short Set Gillnet	13.7

CIMP2019-27	68.91	-133.50	04-Aug-19	03-Aug-19	Short Set Gillnet	7.9
CIMP2019-28	69.28	-132.90	10-Aug-19	09-Aug-19	Short Set Gillnet	10.9
CIMP2019-29	69.30	-132.93	11-Aug-19	03-Aug-19	Short Set Gillnet	34.3
CIMP2019-3	67.34	-134.87	16-Aug-19	29-Aug-17	Short Set Gillnet	9.7
CIMP2019-30	69.37	-133.04	10-Aug-19	01-Aug-19	Short Set Gillnet	8
CIMP2019-4	67.43	-134.86	17-Aug-19	30-Aug-17	Short Set Gillnet	11.4
CIMP2019-6	67.43	-134.85	15-Aug-19	30-Aug-17	Short Set Gillnet	14.4
CIMP2019-7	67.47	-134.75	02-Aug-19	24-Aug-17	Short Set Gillnet	10.6
CIMP2019-8	67.47	-134.72	15-Aug-19	04-Aug-19	Short Set Gillnet	11.6
CIMP2019-9	67.44	-134.51	02-Aug-19	05-Aug-19	Short Set Gillnet	8.1
WhiteMountain1	69.14	-133.04	09-Aug-18	31-Jul-19	Short Set Gillnet[2]	3.7
WhiteMountain2	69.13	-133.04	10-Aug-18	31-Jul-19	Short Set Gillnet[2]	3.7

[1]Six lakes were not sampled for fish

[2]Differences in gillnet mesh sizes used by White Mountain Consulting

Table C2. Summary statistics for regional water quality analyses by study source

Variable	Units	Source	n	mean	min	max	SD
Lake area	ha	Pienitz (1990)	36	75	1	547	93
		Ogbebo (2004 - 2007)	30	1518	18	11321	2371
		Zhu (2015)	28	3	0.2	9	3
		Korosi (2017)	59	8	1	77	12
		This study (2017 - 2019)	50	126	0.4	1310	285
Maximum lake depth	m	Pienitz (1990)	36	4.9	1.2	18.5	4.2
		Ogbebo (2004 - 2007)*	30	35.2	5.1	210.0	44.6
		Zhu (2015)	28	3.3	0.8	9.8	2.2
		Korosi (2017)	54	4.8	0.9	11.3	2.9
		This study (2017 - 2019)	50	4.8	0.6	13.1	2.8
Conductivity	µS/cm	Pienitz (1990)	36	119.7	35.0	343.0	60.2
		Ogbebo (2004 - 2007)	30	177.3	63.5	342.3	97.3
		Zhu (2015)	28	137.3	11.3	598.0	166.4
		Korosi (2017)	59	252.8	33.5	1380.0	249.0
		This study (2017 - 2019)	50	171.0	52.0	542.6	91.7
Dissolved Organic Carbon	mg/L	Pienitz (1990)	36	11.5	4.6	29.9	5.5
		Ogbebo (2004 - 2007)	30	9.9	3.6	20.6	4.8
		Zhu (2015)	28	13.8	5.8	20.0	3.7
		Korosi (2017)	59	14.3	4.3	31.6	5.9
		This study (2017 - 2019)	50	21.2	6.0	54.5	12.0
pH	-	Pienitz (1990)	36	7.8	6.9	8.6	0.5
		Ogbebo (2004 - 2007)	30	8.2	7.8	8.5	0.2
		Zhu (2015)	28	6.7	5.2	8.2	0.8
		Korosi (2017)	59	7.7	6.3	8.4	0.5
		This study (2017 - 2019)	50	7.9	6.1	10.7	1.0
Total Phosphorus	µg/L	Pienitz (1990)	36	18	3	55	13
		Ogbebo (2004 - 2007)	30	15	2	42	14
		Zhu (2015)	28	35	4	127	34
		Korosi (2017)	59	34	7	154	27
		This study (2017 - 2019)	50	59	0	165	37
Mean annual temperature	˚C	Pienitz (1990)	36	-9.5	-10.5	-7.0	0.9
		Ogbebo (2004 - 2007)	30	-8.8	-9.5	-7.7	0.6
		Zhu (2015)	28	-6.5	-6.9	-5.6	0.3
		Korosi (2017)	59	-7.7	-8.5	-7.2	0.4
		This study (2017 - 2019)	50	-6.9	-8.0	-5.7	0.7
Mean annual precipitation	mm	Pienitz (1990)	36	189	142	343	45
		Ogbebo (2004 - 2007)	30	204	173	248	23
		Zhu (2015)	28	341	287	383	20
		Korosi (2017)	59	205	149	250	33
		This study (2017 - 2019)	50	252	162	364	59

Change in mean annual temperature**	˚C	Pienitz (1990)	36	-0.01	-0.05	0.07	0.04
		Ogbebo (2004 - 2007)	30	1.01	0.97	1.08	0.04
		Zhu (2015)	28	1.43	1.40	1.46	0.01
		Korosi (2017)	59	1.64	1.53	1.72	0.06
		This study (2017 - 2019)	50	1.63	1.51	1.78	0.07
Change in mean annual precipitation**	mm	Pienitz (1990)	36	4.2	2.8	7.0	0.9
		Ogbebo (2004 - 2007)	30	2.8	-18.0	18.4	12.4
		Zhu (2015)	28	-24.7	-31.2	-15.1	3.9
		Korosi (2017)	59	2.0	-2.2	5.1	1.5
		This study (2017 - 2019)	50	-1.7	-16.7	10.0	7.2

*Depths for Ogbebo are estimated (see methods); **Change in mean annual air temperature and precipitation variables refer to the long-term temperature and precipitation trends over time and were calculated as the difference between the current thirty-year period and the previous thirty-year period; Sampling years for each study source are indicated in brackets. SD = standard deviation

Table C3. Principal component scores for each environmental variable for the top four axes. Top variables for each axis are bolded and variance explained is reported in brackets.

	PC1 (30%)	PC2 (17%)	PC3 (13%)	PC4 (11%)
July temperature	**-0.39**	0.24	-0.26	0.23
DO	0.33	-0.35	0.29	-0.12
Max_depth	0.32	0.34	0.09	0.01
Secchi	0.29	**0.40**	-0.05	-0.03
Connected	0.12	0.18	-0.02	**0.82**
TP	0.23	**-0.41**	-0.45	0.06
TN	-0.36	-0.04	0.38	-0.15
loglake_area	0.31	-0.01	**0.57**	0.15
logturbidity	-0.16	**-0.40**	0.27	0.46
logDOC	**-0.47**	-0.08	0.15	0.02
logchlorophyll	0.12	**-0.41**	-0.26	0.06

Table C4. Dissolved organic carbon (DOC) change-point threshold analysis results. Reliability and purity scores greater than 0.95 indicate robust results (Baker and King 2010)

Biological Indicator	DOC threshold (mg/L)	Reliability	Purity
species richness	17	0.98	1.00
largemesh CPUE	18	1.00	1.00
smallmesh CPUE*	18 (10)	1.00 (0.93)	1.00 (0.96)
fish presence	17	0.95	0.99

CPUE = catch per unit effort

*Model results in brackets include an outlier for smallmesh CPUE (see Figure 8)

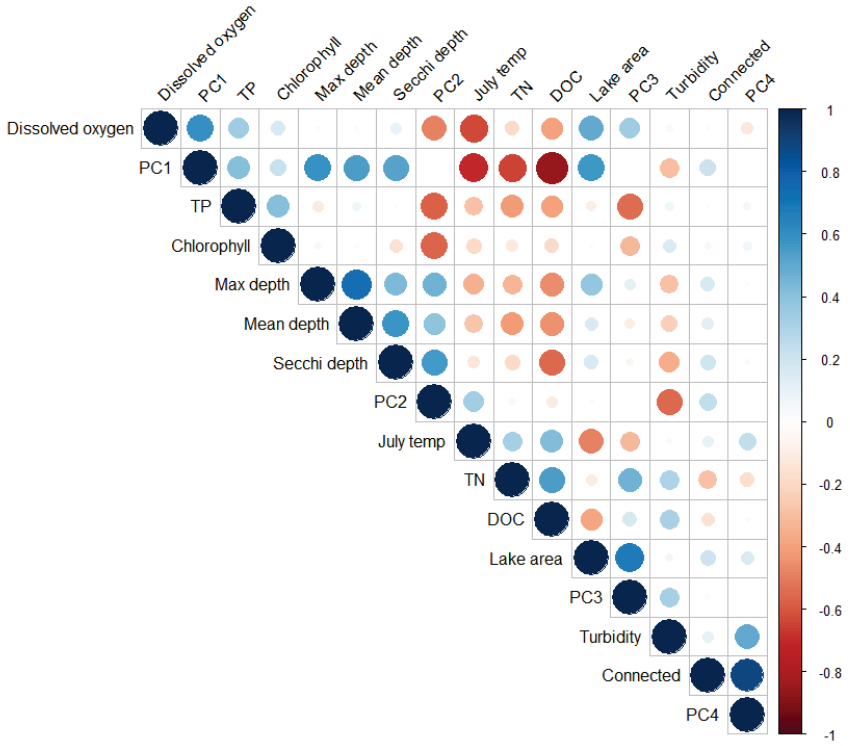
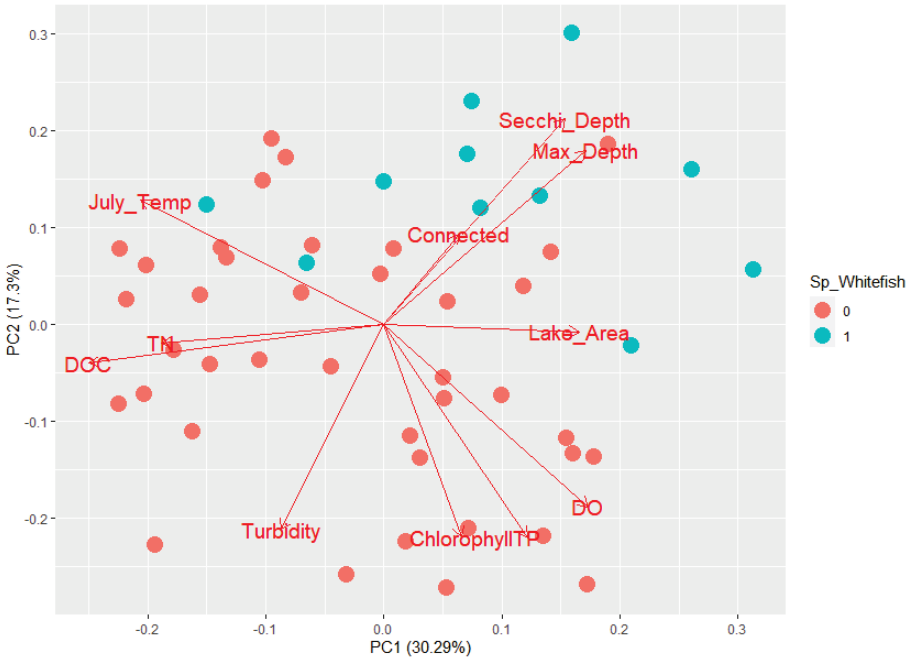
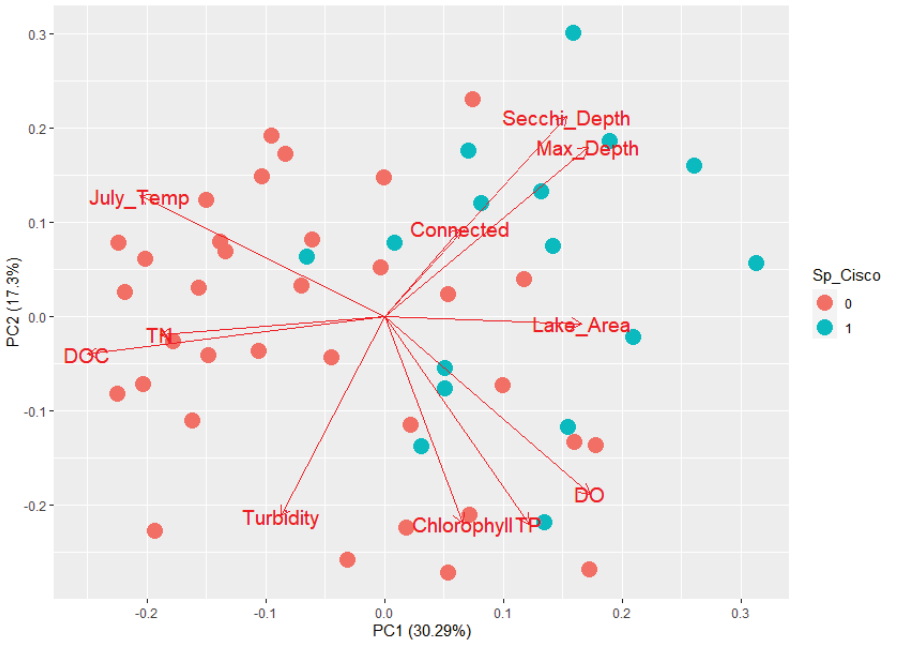


Figure C1. Correlation table for potential environmental drivers of fish community indicators.


Secchi_Depth
Max_Depth
July_Temp
Connected
Lake_Area
TN
DOC
DO
Turbidity
Chlorophyll
TP
PC2 (17.3%)
PC1 (30.29%)
Sp_Whitefish
0
1


Secchi_Depth
Max_Depth
July_Temp
Connected
Lake_Area
TN
DOC
DO
Turbidity
Chlorophyll
TP
PC2 (17.3%)
PC1 (30.29%)
Sp_Cisco
0
1

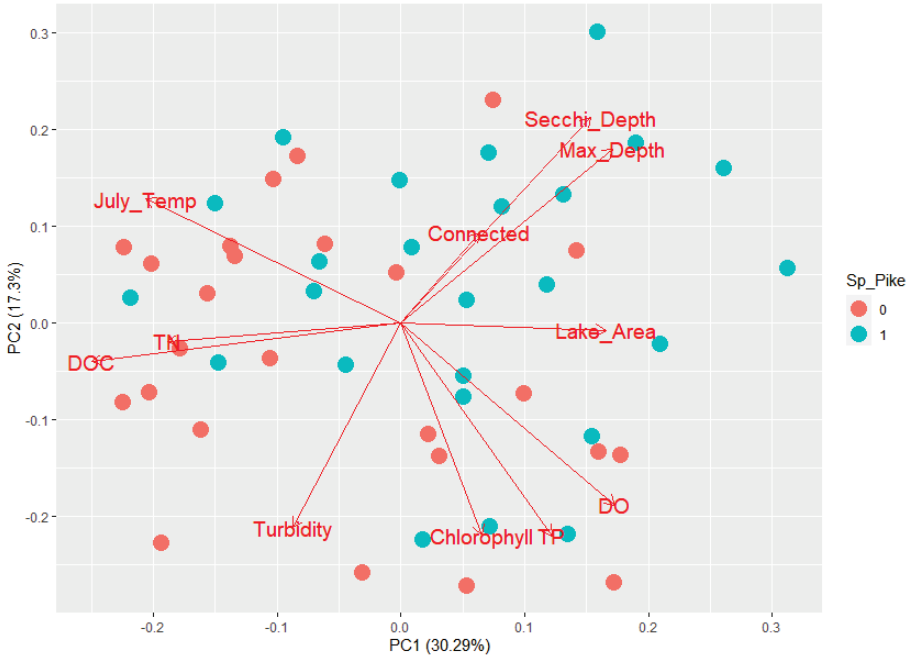


Figure C2. Principal component analysis of the sampled fish lakes demonstrated the environmental characteristics of lakes with whitefish presence (top) least cisco presence (middle) and northern pike presence (bottom). Blue circles indicate species presence and red circles indicate species absence.

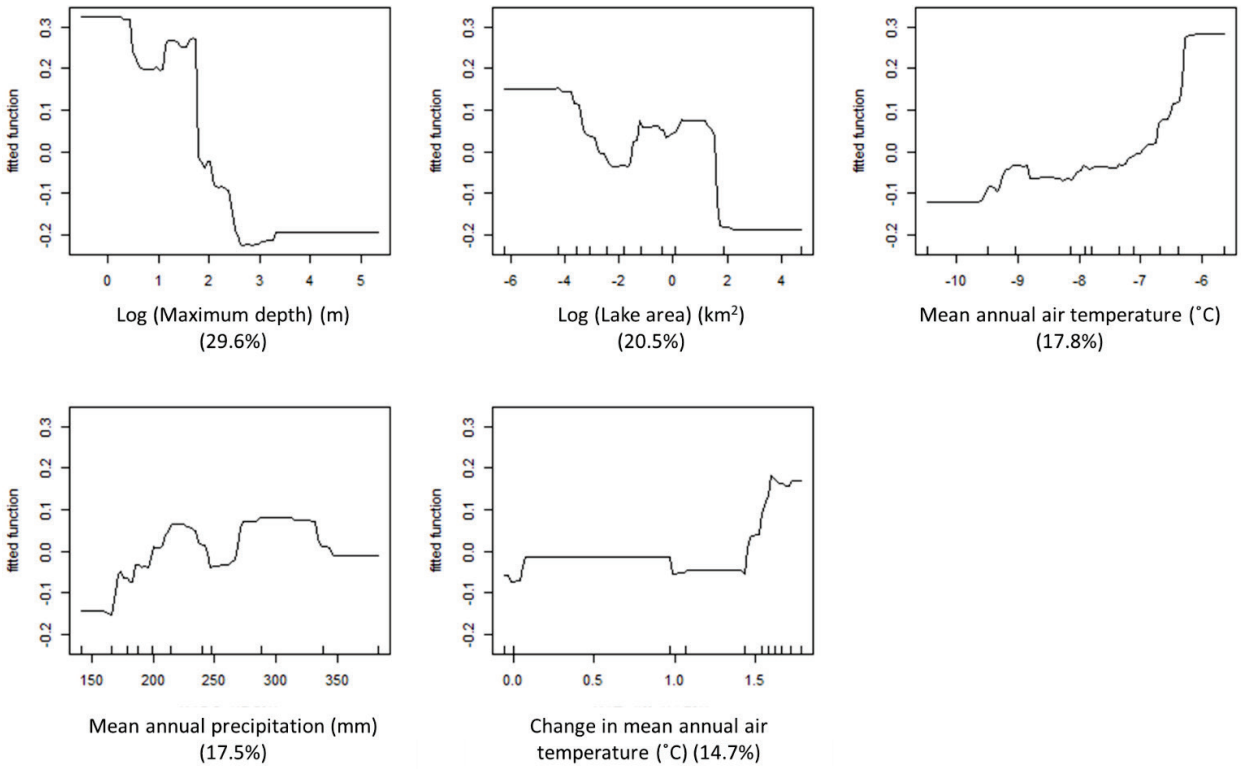


Figure C3. The relationship between log-transformed dissolved organic carbon (y-axis) and log-transformed lake depth, log-transformed lake area, mean annual air temperature, mean annual precipitation, and change in mean annual air temperature using boosted regression tree partial plots. The contribution of each predictor variable to the model fit is provided in brackets.

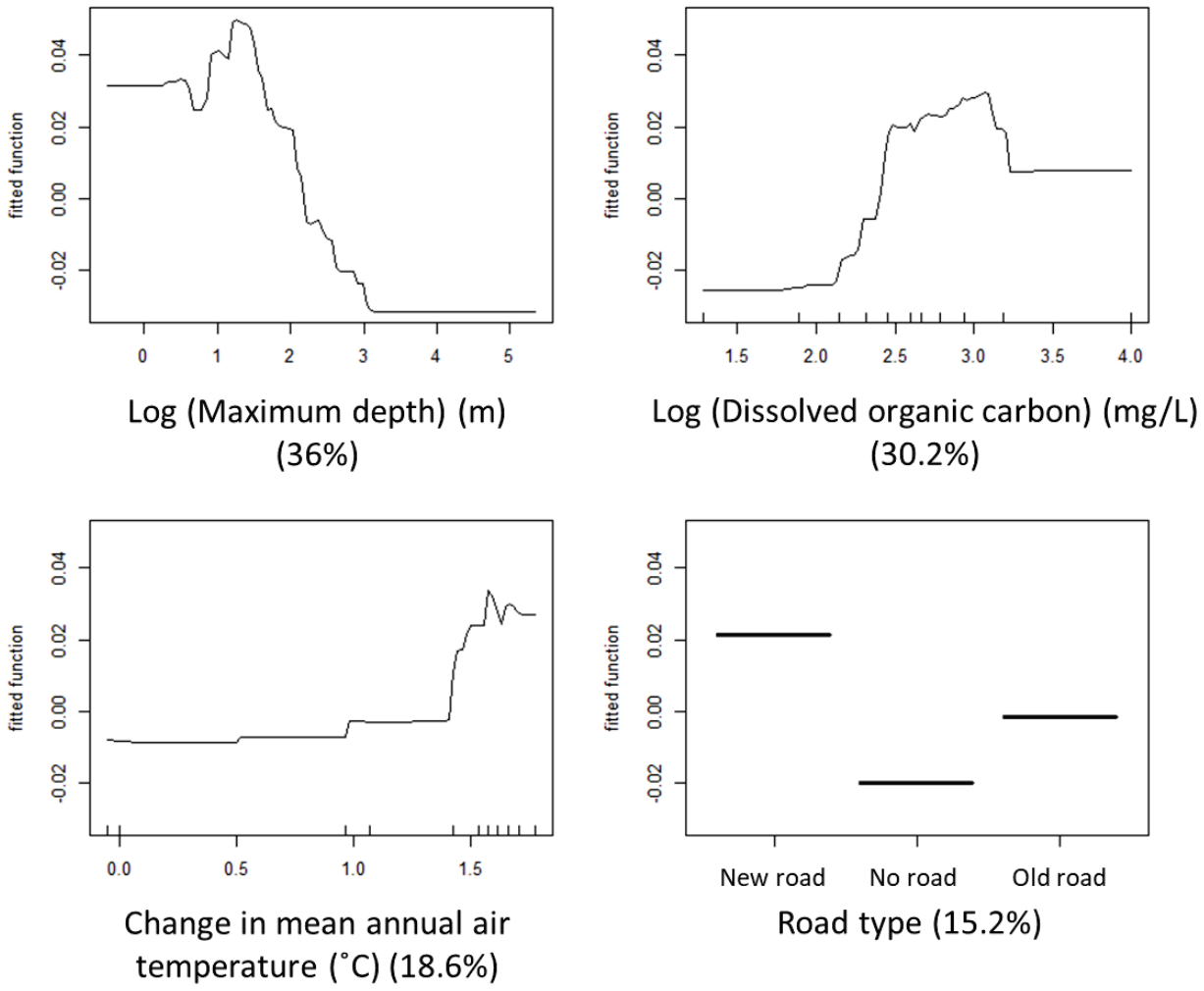


Figure C4. The relationship between square-root transformed total phosphorus (y-axis) and log-transformed lake depth, log-transformed dissolved organic carbon, change in mean annual air temperature, and road type using boosted regression tree partial plots. The contribution of each predictor variable to the model fit is provided in brackets.

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Gmail **Alyssa Murdoch <alyssamurdoch@gmail.com>**

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Permissions Helpdesk <permissionshelpdesk@elsevier.com> Wed, Oct 7, 2020 at 11:03 AM
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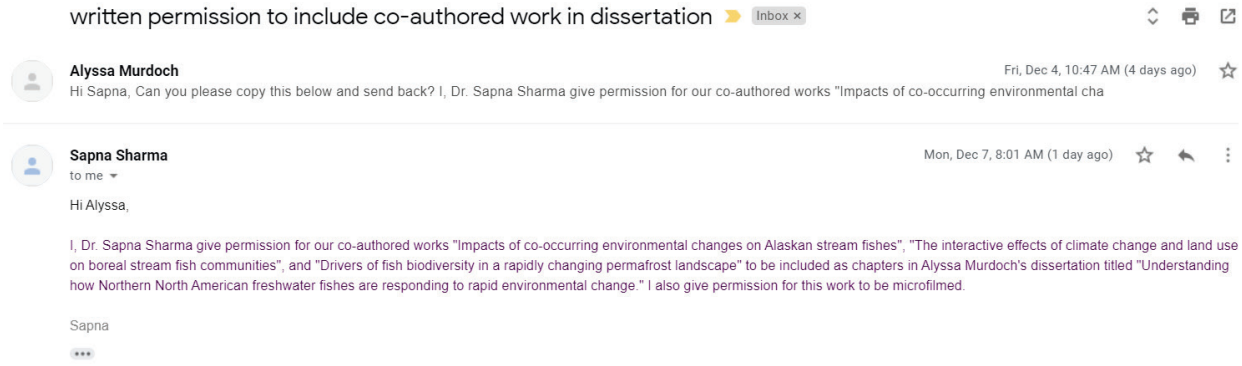

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Alyssa Murdoch Fri, Dec 4, 10:47 AM (4 days ago)
Hi Sapna, Can you please copy this below and send back? I, Dr. Sapna Sharma give permission for our co-authored works "Impacts of co-occurring environmental cha

Sapna Sharma Mon, Dec 7, 8:01 AM (1 day ago)
to me

Hi Alyssa,

I, Dr. Sapna Sharma give permission for our co-authored works "Impacts of co-occurring environmental changes on Alaskan stream fishes", "The interactive effects of climate change and land use on boreal stream fish communities", and "Drivers of fish biodiversity in a rapidly changing permafrost landscape" to be included as chapters in Alyssa Murdoch's dissertation titled "Understanding how Northern North American freshwater fishes are responding to rapid environmental change." I also give permission for this work to be microfilmed.

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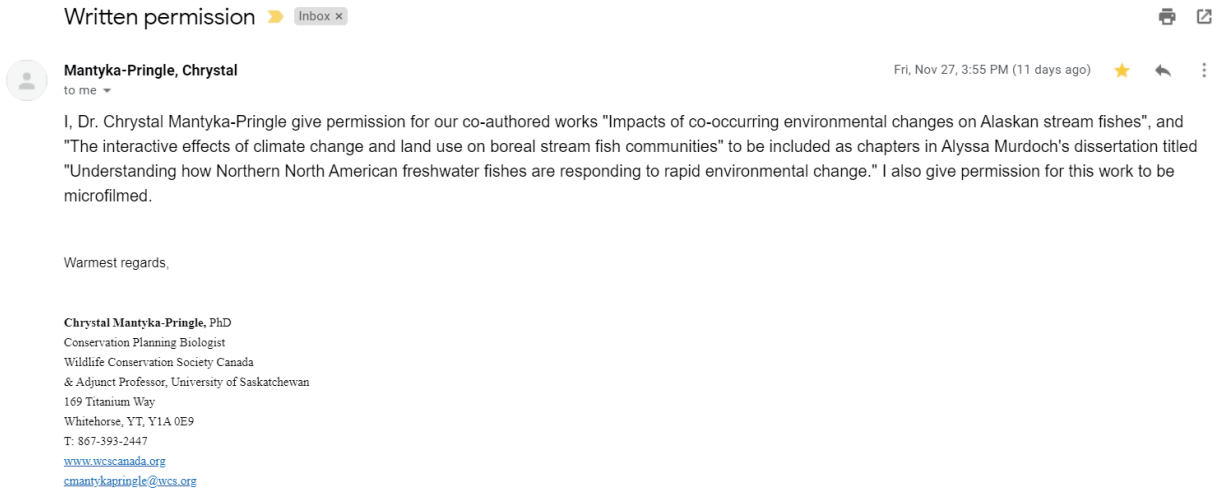

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Mantyka-Pringle, Chrystal Fri, Nov 27, 3:55 PM (11 days ago)
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Warmest regards,

Chrystal Mantyka-Pringle, PhD
Conservation Planning Biologist
Wildlife Conservation Society Canada
& Adjunct Professor, University of Saskatchewan
169 Titanium Way
Whitehorse, YT, Y1A 0E9
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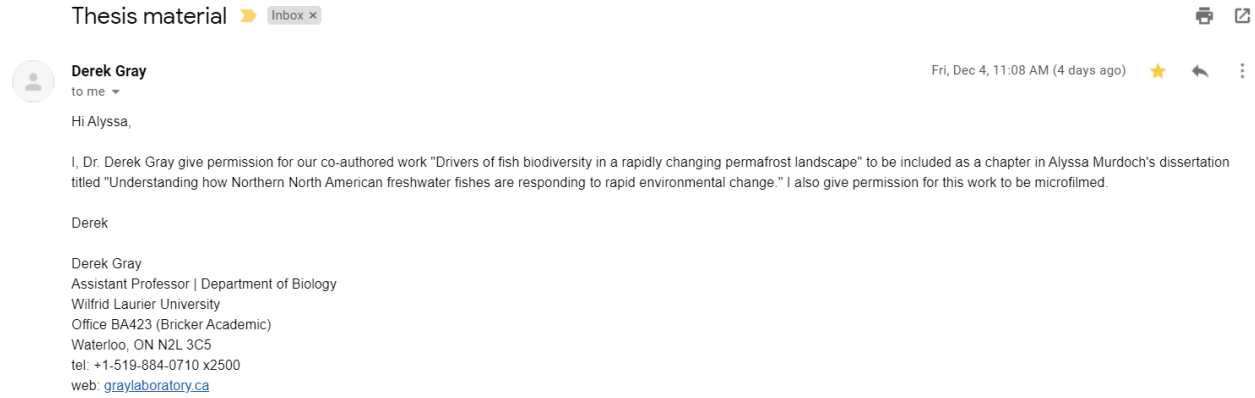
Chapter 3: Dr. Derek Gray



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Derek

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Chapter 3: Dr. Jennifer Korosi

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Jennifer B. Korosi Thu, Dec 3, 9:00 AM (5 days ago)
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Best
Jennifer

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Appendix G: Candidate's contribution to co-authored work

Statement of Alyssa Murdoch's contribution to co-authored works included in the dissertation titled "Understanding how northern North American freshwater fishes are responding to rapid environmental change"

Chapter 1: Impacts of co-occurring environmental changes on Alaskan stream fishes

Alyssa Murdoch, Chrystal Mantyka-Pringle, Sapna Sharma

This chapter has been published in Freshwater Biology as Murdoch A, Mantyka-Pringle C, Sharma S. Impacts of co-occurring environmental changes on Alaskan stream fishes. *Freshwater Biology*. 2020;65:1685–1701. https://doi.org/10.1111/fwb.13569.

Candidate's Contribution:

Alyssa Murdoch, Dr. Mantyka-Pringle, and Dr. Sharma conceived the research ideas; Alyssa Murdoch acquired funding and data, analysed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Freshwater Biology.

Chapter 2: The interactive effects of climate change and land use on boreal stream fish communities

Alyssa Murdoch, Chrystal Mantyka-Pringle, Sapna Sharma

This chapter has been published in Science of the Total Environment as Murdoch A, Mantyka-Pringle C, Sharma S. The interactive effects of climate change and land use on boreal stream fish communities. *Science of the Total Environment*. 2020;700:134518. https://doi.org/10.1016/j.scitotenv.2019.134518

Candidate's Contribution:

Alyssa Murdoch, Dr. Mantyka-Pringle, and Dr. Sharma conceived the research ideas; Alyssa Murdoch acquired funding and data, analysed the data, and led the writing of the manuscript. All authors contributed to sequential drafts and gave final approval for publication in Science of the Total Environment.

Chapter 3: Drivers of fish biodiversity in a rapidly changing permafrost landscape

Alyssa Murdoch, Derek Gray, Jennifer Korosi, Sapna Sharma

Candidate's Contribution:

AM, DG, JK, and SS conceived the research ideas; AM, DG, JK, and SS acquired funding; AM, DG, and JK collected field data; AM analysed the data and led the writing of the manuscript. All authors contributed to sequential drafts and final approval for inclusion in this dissertation.

December 8, 2020

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December 8, 2020

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