Climate change and glacier retreat in salmon watersheds

by

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Abstract

Global air temperatures are projected to rise over the next century following the continued increase and amplification of greenhouse gas emissions, mainly due to human activity. This rise in air temperature will pose significant changes to the landscape, most notably glacier retreat. Salmon watersheds beheaded by glaciers will undergo drastic changes as ice melts from the landscape changing downstream river flow, water temperature, and channel morphology, and shifting nutrients and availability of prey resources. Broadly, my thesis provides insight on how the effects of climate change, particularly from glacier retreat, may present challenges and benefits to Pacific salmon. In chapter 2, I explore the ways in which glacier retreat impacts salmon habitat by reviewing and constructing a conceptual model that defines glacier retreat across four distinct phases, from a landscape blanketed by ice to complete deglaciation. I describe each of these pathways of impact and how they will affect Pacific salmon across the four phases. In chapter 3, I quantify how much new Pacific salmon habitat will be created by glacier retreat over the next century. I found that glacier retreat will create hot spots of future habitat gains within glacierized regions of western North America, while other areas will experience no habitat gain. In my fourth chapter, I assessed how water temperatures along an important Pacific salmon migratory river are associated with landscape features of tributary systems. I placed temperature loggers at all major tributary rivers and determined how they play a role in cooling a major salmon migratory corridor. Glacier and snowpack fed tributaries from larger watersheds cooled a major salmon migratory river more than other tributaries. Collectively, this thesis provides insight into how climate change and glacier retreat impact river systems and their salmon. This work illuminates the need for forward-looking conservation and management to aid in the protection and preservation of important and iconic species, such as Pacific salmon.

Keywords: climate change; glacier retreat; Pacific salmon; Babine River; water temperature

To Iris

Thank you for your patience.

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Chapter 1.

General Introduction

1.1. Climate change impacts on the physical world

Global air temperatures have increased by ~0.85°C since the industrial revolution in the 1880s, and are projected to exceed another 1.5°C over the next century following the continued increase and amplification of greenhouse gas emissions (IPCC 2013). Global air temperature rise has caused glaciers to retreat and sea level to rise (Zemp et al. 2019), reduced winter snowfall (Huss et al. 2017), and changed annual precipitation patterns (Trenberth 2011), causing ecological changes to both flora and fauna (Walther et al. 2002). These changes to the physical world have posed many challenges to human societies and other species (IPCC 2013). It is agreed that global air temperatures will continue to rise for decades to come due to greenhouse gas emissions produced by human activities. Thus, it is integral to understand how climate change is altering the physical world, and how this will impact species of cultural or economic importance.

One important visible indicator of climate change is glacier retreat. Mechanistically, glaciers retreat when the mass accumulation (via snowfall) is less than the mass ablation (via melting) (Martini et al. 2001). Glaciers around the world are typically ablating, or retreating, and forecasts expect this loss to continue (Clarke et al. 2015; Huss et al. 2017; Zemp et al. 2019). For example, between 2006 and 2016, glaciers in western Canada have lost an average of 1.3% of their ice mass each year (Zemp et al. 2019), and are projected to lose up to 80% of their ice volume by 2100 in some regions (Clarke et al. 2015). Ice loss from mountain glaciers is contributing to the rise in global sea level (Zemp et al. 2019), changing seasonal patterns of streamflow (Bliss et al. 2014), and increasing geohazards (Marzeion et al. 2014). Additionally, glacier retreat is changing downstream rivers (Bliss et al. 2014) and creating new habitat that could be colonized by important species such as Pacific salmon (*Oncorhynchus* spp.) (Milner et al. 2011).

Rising global air temperature and landscape features such as glaciers will change the thermal regime of river systems. There is a strong relationship between air and water temperature (Caissie 2006) that can be modulated by landscape features such as glacier cover, snowpack, watershed elevation, and presence of lakes (Webb et al. 2008; Garner et al. 2014; Lisi et al. 2015). Thus, characteristics of landscapes will filter the impacts of rising air temperatures. For example, climate change is accelerating the rate of glacier melt, transforming solid ice into water, which is altering water temperatures downstream (Jansson et al. 2003). Over longer timescales, persistent declining spring snowpack and retreating glaciers could lead to a decline of glacier meltwater contribution to downstream rivers (Bliss et al. 2014; Huss and Hock 2018), a processes that will increase water temperatures. Thus, the interaction of air temperature rise, and glacier retreat will alter thermal dynamics in river systems.

1.2. Pacific salmon responses to climate change and glacier retreat

Climate change will present challenges and benefits to freshwater species, such as Pacific salmon. In some instances, climate change is warming rivers and lakes, threatening cold-water freshwater fishes, such as Pacific salmon (Schindler 2001; Strayer and Dudgeon 2010). For example, water temperature in the Fraser River, British Columbia, has risen 1.5°C since the 1950s, causing severe mortality of some Pacific salmon populations (Patterson et al. 2007b; Martins et al. 2011). More broadly, with air temperatures rise, there will be changes in stream flow patterns and increases in water temperatures contributing to the decrease in Pacific salmon survival (Martins et al. 2011). Glacier retreat is also creating new salmon frontiers. In heavily glacierized watersheds, the loss of glacier ice may actually improve downstream habitat for freshwater fishes via increases in summer water temperature, river channels stabilizing, and stream flow dampening (Pitman et al. 2020). Additionally, as glaciers retreat, new rivers and lakes will form that Pacific salmon can rapidly colonize (Milner et al. 2011). For example, new pink salmon populations grew to over 10,000 individuals within ~15 years following extensive glacier retreat in Glacier Bay, Alaska (Milner et al. 2011). Thus, while climate change poses many risks, it also presents opportunities for species of cultural importance, such as Pacific salmon.

1.3. Pacific salmon in glacierized watersheds

Salmon within the Pacific regions of North America are iconic and foundational to coastal ecosystems and cultures. In western North America, there are six species of anadromous Pacific salmon, including steelhead trout (*O. mykiss*), that support subsistence fisheries, as well as commercial and recreational fisheries worth billions of dollars annually (Clark et al. 2006; Gislason et al. 2017; Johnson et al. 2019a). The North American range of Pacific salmon spans from southern California through to northwestern Alaska, and 85% of major salmon watersheds have at least some glacier coverage (Pitman et al. 2020). Additionally, within Canadian rivers, 25 to 50% of the total annual river flow occurs as meltwater from previous winter snowpack (Schindler 2001). Thus, most North American salmon watersheds are being influenced by some degree of snowpack or glacier ice.

This thesis aims to understand how climate change will present challenges and benefits to freshwater species, such as Pacific salmon. In chapter 2, I explore the ways in which glacier retreat impacts salmon habitat by reviewing and constructing a conceptual model that defines glacier retreat across four distinct phases, from a landscape blanketed by ice to complete deglaciation. I describe the pathways of impact glacier retreat will have on the landscape, such as changes to channel morphology, shifts in seasonal water temperature and stream flow patterns, and the creation of new rivers and lakes. I describe each of these pathways of impact and how they will affect Pacific salmon across the four distinct phases. In chapter 3, I build off the theory established in chapter 2 to quantify how much new Pacific salmon habitat will be created by glacier retreat over the next century. I built a model that links glacier mass change, forced by five different Global Climate Model projections, with a simple model of salmon stream habitat. I projected across the Pacific mountain ranges of western North America the gains in future stream kilometers by applying stream gradient thresholds constraining salmon migration, and spawning and juvenile rearing for the years 2050, 2100, and potential complete deglaciation. In chapter 4, I assessed how water temperatures along an important Pacific salmon migratory river are associated with landscape features of tributary systems. I placed temperature loggers at all major tributary rivers and determined how tributaries fed from varying landscape features play a role in cooling a major salmon migratory corridor. In the appendix, I assessed how salmon watersheds are embedded in socio-ecological systems. I examined the relationships between fish, anglers, and management interventions on six rivers within the Skeena River watershed, British Columbia, to understand if angler satisfaction was attributed to fish abundance, angler crowding, or management implementations. The six rivers I examined support steelhead, a highly sought-after species for recreational fishers.

My thesis contributes fundamental research on the impacts that glacier retreat will have on Pacific salmon watersheds with implications for conservation and management. By building a conceptual model of glacier retreat and Pacific salmon, forecasting future habitat gains for Pacific salmon, and examining river temperatures along mainstem and tributary rivers, my thesis provides a foundation for understanding how salmon systems my shift over the next century. This thesis provides insight on how the effects of climate change, particularly from glacier retreat, may present challenges and benefits to Pacific salmon. While it is crucial to curb our greenhouse gas emissions to reduce the consequences of climate change, I hope that my thesis may help inform forward-looking management and conservation to predict where salmon populations may flourish and where they will many be challenged over the next century will help in the protection and preservation of our salmon futures.

1.4. Contributions

The body of this work (chapters 2,3,4, and Appendix A) was collaborative in nature, and each chapter is either published or a prepared manuscript with co-authours. Therefore, these chapters are written in first-person plural. I was responsible for writing the initial draft conducting the spatial analyses, collecting, and analyzing data, but benefited greatly from feedback by co-authours and colleagues. Chapters 2 and 3 were conceived during a working group – Glacier Retreat and Pacific Salmon – held in Vancouver in November in 2017. These works were built from ideas and insights from scientists present at the meeting. Chapter 4 was developed out of discussions with Jonathan Moore who was instrumental in the writing. Appendix A was conceived during a Salmon Watersheds lab retreat with contribution from Samantha Wilson and Elissa Sweeney-Bergen that was brought to completion with contributions from Patty Hirshfield, Mark Beere, and Jonathan Moore. The general introduction and conclusion are works of my own and are written in first-person singular.

Chapter 2.

Glacier retreat and Pacific salmon[1]

2.1. Abstract

Glaciers have shaped past and present habitats for Pacific salmon (Oncorhynchus spp.) in North America. During the last glacial maximum, ~45% of the current North American range of Pacific salmon was covered in ice. Currently, most salmon habitat occurs in watersheds where glacier ice is present and retreating. This synthesis examines the multiple ways that glacier retreat can influence aquatic ecosystems through the lens of Pacific salmon life cycles. We predict that the coming decades will result in: (1) areas where salmon populations will be challenged by diminished water flows and elevated water temperatures; (2) areas where salmon productivity will be enhanced as downstream habitat suitability increases, and (3) areas where new river and lake habitat will be formed that can be colonized by anadromous salmon. Effective conservation and management of salmon habitat and populations should consider the impacts of glacier retreat and other sources of ecosystem change.

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[1] A version of this this chapter appears as Pitman KJ, Moore JW, Sloat MR, Beaudreau AH, Bidlack AL, Brenner RE, Hood EW, Pess GR, Mantua NJ, Milner AM, Radić V, Reeves GH, Schindler DE, Whited DC. 2020. Glacier retreat and pacific salmon. BioScience 7:220–236.

2.2. Introduction

Glaciers are retreating rapidly across Pacific salmon (Oncorhynchus spp.) landscapes, driven in large part by anthropogenic climate change (Figure 2.1; Marzeion et al. 2014). In western North America, glaciers are predicted to lose up to 80% of their ice volume by 2100 (Radić et al. 2013) and have already lost up to 3% per year between 2006–2016 (Zemp et al. 2019). This rapid contemporary ice loss follows longer-term glacier retreat — most glaciers in North America have been retreating since the 1600s–1800s Little Ice Age maxima (Menounos et al. 2009).

Glacier retreat can increase or decrease wild Pacific salmon productivity by modifying downstream habitat conditions and by creating new habitat. Changes in glacier runoff (i.e., all water discharged from the glacier terminus) have important downstream effects on hydrology, sediment transport, water temperature, and biogeochemical fluxes, which alter conditions for salmon in freshwater and nearshore marine habitats (O'Neel et al. 2015; Milner et al. 2017). For example, a significant decrease of glacier contribution to total watershed runoff generally increases downstream water temperature, which could be either beneficial or stressful to salmon. In cold rivers (<5°C), increases in water temperature could increase juvenile salmon growth potential (Fellman et al. 2014), whereas in warm rivers (>15°C), increases in water temperature could increase stress and mortality rates of adult salmon as they migrate upstream (Martins et al. 2012).

Glacier retreat can also directly create new habitat for salmon. For example, in Glacier Bay, Alaska, tidewater glacier retreat created new river systems that were colonized by pink salmon (*O. gorbuscha*) within 30 years of formation (Milner et al. 2011). Thus, glacier change can impact salmon ecosystems through a variety of mechanisms (Moore et al. 2009; O'Neel et al. 2015; Milner et al. 2017). Overall, the net effects of glacier retreat on salmon will likely depend on the phase of glacier retreat, the life-history traits of salmon species, and a suite of local environmental, geographic, and ecological characteristics of watersheds.

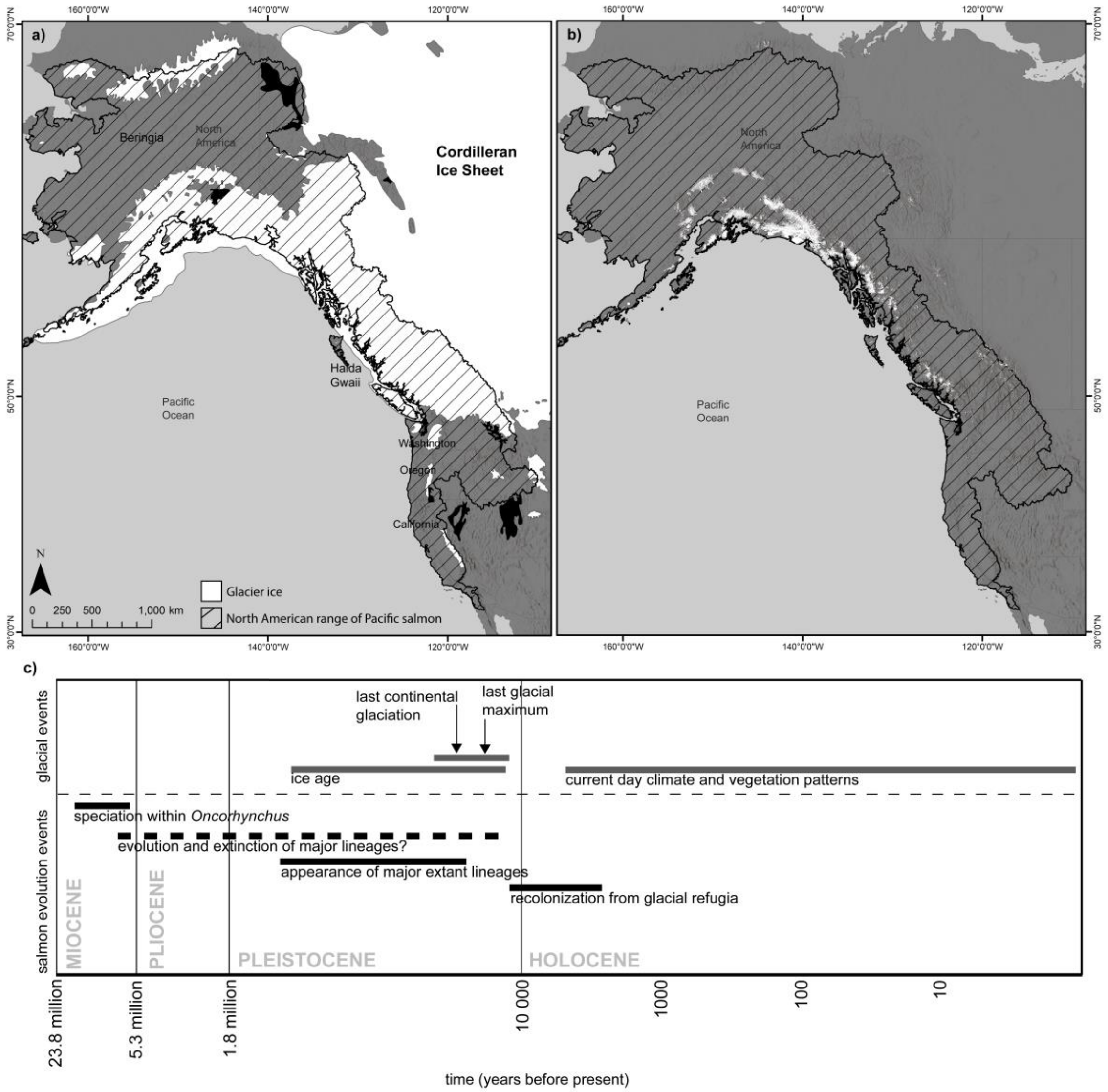


Figure 2.1 The North American range of Pacific salmon, ice extents (historic and present), and the evolution of Pacific salmon in North America. (a) Approximate ice extent from the Cordilleran Ice Sheet around 16,000 years ago (Dyke 2004), including regions of ice-free refugia (i.e., Haida Gwaii, Beringia, and parts of the Washington, Oregon and California coasts). The core range of current-day salmon is shown in black hatched lines, following (http://www.stateofthesalmon.org/resources/sosdb.php). We acknowledge that there are some peripheral populations beyond this hatched region (e.g., Mackenzie River). (b) Approximate current day ice extent from the Randolph Glacier Inventory 6.0 (Pfeffer et al. 2014) overlapping with the North American range of Pacific salmon. Note that there are small high elevation glaciers present in conterminous United States. (c) Timeline of major glacial changes and evolutionary history of Pacific salmon (from 23.8 million years ago – present), adapted from (Waples et al. 2008).

Understanding how glacier retreat will affect Pacific salmon will help inform the management and conservation of these economically- and culturally-important species. There is growing understanding of the pathways by which glacier retreat alters aquatic environments (O'Neel et al. 2015, Milner et al. 2017), and a large body of research on how environmental variables influence salmon across their life cycle (Quinn 2018). By integrating these two fields of study, we offer a conceptual synthesis of how glacier retreat may affect Pacific salmon populations in North America and how these effects may vary by species and watershed context. Specifically, we review the historical interaction of glaciation and Pacific salmon in North America over geological time scales, propose a conceptual model for the evolution of salmon watersheds in response to glacier retreat, quantify the current status of glaciers in salmon watersheds, propose research frontiers, and highlight implications of glacier loss for salmon management and policy.

2.3. Glaciation and Pacific salmon watersheds over geological time scales

To provide context for the response of Pacific salmon to contemporary glacier retreat, we briefly review Pacific salmon and glacier dynamics over geological time scales. Over time, the advance and retreat of glaciers are controlled by the difference between rates of ice accumulation (via snowfall on the glacier) and ice ablation (via melting, sublimation, and glacier calving). Such advance and retreat of glaciers have been driven by shifts in global and local climate patterns (Menounos et al. 2009), with rapid glacier retreat occurring in the recent decades due to climate change (Zemp et al. 2019). For example, with recent glacier ice-loss rates being up to 3% per year, most of today's glacier volume in western Canada and conterminous USA will vanish by the second half of this century (Zemp et al. 2019).

Pacific salmon evolved over millions of years during the Miocene epoch, a time of warmer global temperature and relatively little glacier coverage (Figure 2.1; Stearley 1992). The Miocene radiation, 6 – 20 million years ago (mya), resulted in the species of anadromous Pacific salmon in North America (hereafter "salmon") that are present today (Waples et al. 2008, table 2.1). In this paper, we focus on six species: Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), pink salmon, sockeye salmon (*O. nerka)*, and steelhead trout (anadromous *O. mykiss;* table 2.1) due to their ecological and economic importance and the extensive body of related scientific research. During the late Pliocene and early Pleistocene, 1.8 mya to 17 thousand years ago (kya), glaciers repeatedly advanced and retreated, reworking the surface of the northwestern North American landscape. These repeated ice sheet expansions covered large portions of Alaska and British Columbia. Salmon survived in ice-free refugia, including Beringia and along the coasts of British Columbia (e.g., Haida Gwaii), Washington, Oregon, and California (Figure 2.1; Smith et al. 2001). Based on the maximum spatial extent of ice (Dyke 2004), we estimate that approximately 45% of the current North American range of salmon was covered by ice at some point in the past (Figure 2.1).

The late Pleistocene and Holocene brought the onset of deglaciation (beginning ~17 kya) (Figure 2.1; Booth et al. 2003), which shifted and increased the spatial distribution of freshwater habitats available to salmon (Smith et al. 2001; Waples et al. 2008). During this time, rapid glacier retreat opened major river valleys, land rebounded as a result of post-glacier isostatic adjustment, and sea level rose (Beechie et al. 2001, Waples et al. 2009). Deglaciation led to a range of landscape disturbances, from high-magnitude catastrophic glacier lake outburst floods (e.g., Lake Missoula, Benito and O’Connor 2003) to low-magnitude events such as landslides and annual floods. Retreating glaciers left behind landscape features, such as characteristic deep and wide U-shaped valley bottoms, that set the stage for development of high-quality salmon habitat (Benda et al. 1992; Beechie et al. 2001). Thus, much of the current range of salmon bears the legacy of glaciers past.

Table 2.1 Trends in Pacific salmon life cycles across species. We note that there is enormous variation in salmon life cycles within species and use this table as a simplifying construct to compare different species. Information for this table was predominantly obtained from Quinn (2018).

			SPAWNING		FRESHWATER REARING	
species	years to maturity	winters at sea	spawning location	spawning timing	length of freshwater rearing	rearing location
Chinook	3-8	1-5	Medium-to large-sized rivers, sometimes downstream of lakes.	summer – fall	depends whether ocean or stream type[3]	rivers, estuaries
chum	3-5	1-4	Lower reaches of rivers[1]	late summer – fall	none, but sometimes stay in streams for a few days/weeks	None
coho	4-5	1-2	Often in smaller tributaries.	late summer – winter	weeks-2 years	small streams, off-main channel habitats, beaver ponds, lake margins, estuaries.
pink	2	1	Rivers, generally close to ocean	late summer – fall	none, but sometimes stay in streams for a few days/weeks	None
sockeye	3-6	1-4	Rivers, creeks, lake beaches[2]	late summer – fall	weeks-2 years	usually lakes[2]
steelhead	1-12	1-5	Small- to medium-sized rivers.	late winter – spring	1-5 years	high gradient reaches

[1] Some chum salmon populations are long-distant migrants.
[2] there are also “ocean-type”: populations that migrate to sea in their first year of life, and “river-type”: populations that rear in rivers for a year before going to sea
[3] *“Ocean-type”:* migrate downstream right after emergence (few months in river), *“stream-type”:* spend full year in river. Ocean-type” are almost exclusively south of 56 degrees

Historical landscape disturbances, such as those associated with glacier dynamics, are thought to have shaped many of the life-histories and traits of salmon that we see today (Waples et al. 2008, 2009). For example, some salmon species (e.g., Chinook and sockeye salmon, and steelhead trout) have considerable diversity in age-at-maturity that can buffer populations against freshwater disturbances (Waples et al. 2008, 2009), such as glacier outburst floods that might eradicate a generation of spawning adults or rearing juveniles. While most salmon return to spawn in their natal stream, some fraction of the population disperses or strays, enabling salmon to colonize new habitats (Pess et al. 2014), such as watersheds opened following glacier retreat (Milner et al. 2011). Additionally, for species with freshwater juvenile rearing (e.g. Chinook and coho salmon, and steelhead trout), dispersal within freshwater may further enable salmon to take advantage of newly opened and shifting habitat conditions (Reeves et al. 1995). Overall, a low but substantial level of dispersal may maximize population resilience in dynamic landscapes by enabling salmon to both maintain local adaptations but also enable meta-population processes (Yeakel et al. 2018). Thus, current salmon life histories and traits reflect adaptations to dynamic landscapes, such as those with a legacy of glacier disturbances (Waples et al. 2008, 2009).

Salmon life cycles are complex and vary across and within species (table 2.1). Salmon migrate a range of distances in freshwater, from river deltas to more than 1000 km upriver, to spawn in diverse habitats that include the mainstem river, river side-channels, small headwater streams, groundwater-fed sloughs, and littoral zones of lakes (Quinn 2018). Subsequently, salmon dig depressions (known as redds) where they deposit their eggs in sediments that are generally pebbles to small cobbles (around 5-80 mm in diameter; Kondolf and Wolman 1993) that enable sufficient subsurface flow past the eggs, thus providing oxygen and removing nitrogenous wastes. Steelhead trout are iteroparous (i.e., can undergo multiple reproductive cycles) and generally spawn in the spring (Kendall et al. 2015), whereas the other species of Pacific salmon are semelparous (i.e., undergo a single reproductive episode before death) and spawn in the summer to fall (Quinn 2018). Depending on the species and population, juvenile salmon may migrate immediately to the ocean (e.g., chum and pink salmon) or stay in freshwater for months to several years (e.g., Chinook, coho, and sockeye salmon, and steelhead trout; table 2.1). During this freshwater phase, juvenile salmon may rear in the main river channel or off-main channel habitats (e.g., Chinook salmon and steelhead trout), ponds (e.g., coho salmon), or lakes (e.g., sockeye salmon). Once young salmon migrate to the marine environment, survival can be strongly influenced by food web interactions and ocean conditions (Beamish et al. 2016). Thus, life-history variation between and within each salmon species will influence how they respond to glacier retreat.

2.4. Evolution of salmon habitat across phases of glacier retreat

Here we describe a conceptual model for the evolution of salmon habitat during the process of glacier retreat (Figure 2.2). Our model describes general biophysical phases as glaciers retreat from the coast to higher elevations. Because of the overriding effect of local topography and climate on the rate of glacier retreat, we structure the model across four phases corresponding to glaciers covering distinct components of the salmon landscape rather than by discrete time periods. Therefore, different watersheds or regions can be in different phases of glacier retreat. “Phase 1” refers to the beginning of glacier retreat from the coast, when new lakes and streams are being formed, but most of the watershed remains covered by ice. During “phase 2”, glaciers continue to retreat up-valley, further exposing new rivers and proglacial lakes, as well as a mosaic of lateral valley-bottom and hillslope tributary habitats. “Phase 3” begins when glaciers have retreated to higher elevations, above the extent of accessible salmon habitat, with glacier runoff still influencing downstream river evolution. “Phase 4” considers the continued evolution of salmon habitats after glaciers have disappeared. We suggest that these four generalized phases of glacier retreat are characterized by a unique set of processes that influence the biological and physical characteristics of downstream ecosystems (Figure 2.2; Milner et al. 2001). We consider how these biophysical changes will affect salmon life stages across species and their habitats. Specifically, we assess the following watershed changes associated with glacier retreat: river and lake creation, channel morphology and form, annual and seasonal hydrology, water temperature, turbidity, and, nutrients and prey resources.

2.4.1. Phase 1: Ice-dominated watersheds

As glaciers begin to retreat from the coast, freshwater habitats emerge (Figure 2.2). However, during this initial phase of glacier retreat, much of the watershed is under ice. River systems are “beheaded” by glaciers and have relatively low quantity of salmon habitat due to the high glacier coverage. In addition, new rivers can be quite inhospitable to salmon due to high sediment loads, channel instability, and frigid temperatures, but do represent new habitat that salmon can colonize (Milner et al. 2011). As glaciers retreat, they leave behind large unconsolidated glacial deposits in a vegetation-free landscape carved by new proglacial streams. Because of the high sediment load, low bank cohesion, and high specific discharge (i.e., discharge per unit watershed area), young proglacial streams are typically braided, wide, and shallow with shifting and dynamic stream channels (Figure 2.2; Milner and Petts 1994). Young proglacial lakes may also form in these landscapes, such as those dammed by glacial moraines. Moraine-controlled lakes commonly breach and may drain completely if their dams of unconsolidated sediments erode (Carrivick and Heckmann 2017). Consequently, new habitats created during the early phase of glacier retreat are often ephemeral, and those that persist are initially highly unstable.

Unstable habitats pose many challenges to salmon spawning, egg incubation, and rearing. For example, all species of salmon construct redds in stream sediments where eggs incubate for several months over the winter prior to emergence (Quinn 2018). During incubation in these young glacier streams, high sediment mobility can lead to streambed scour, entraining or destroying developing embryos (Jensen et al. 2009), or channel avulsions that can lead to dewatering of stream reaches resulting in the desiccation of eggs. High channel instability and widely-fluctuating flow regimes can limit food resources for juvenile salmon that rear months to years in freshwater, such as Chinook and coho salmon, and steelhead trout (table 2.1, Figure 2.3), by reducing the abundance and diversity of aquatic macroinvertebrates (Figure 2.3; Death and Winterbourn 1995). Within-season channel movement may also strand juveniles in abandoned stream channels. Thus, channel instability of young proglacial streams can initially limit successful salmon reproduction and juvenile rearing during early phases of glacier retreat (Murphy et al. 1989), particularly for stream-rearing species (Figure 2.3).

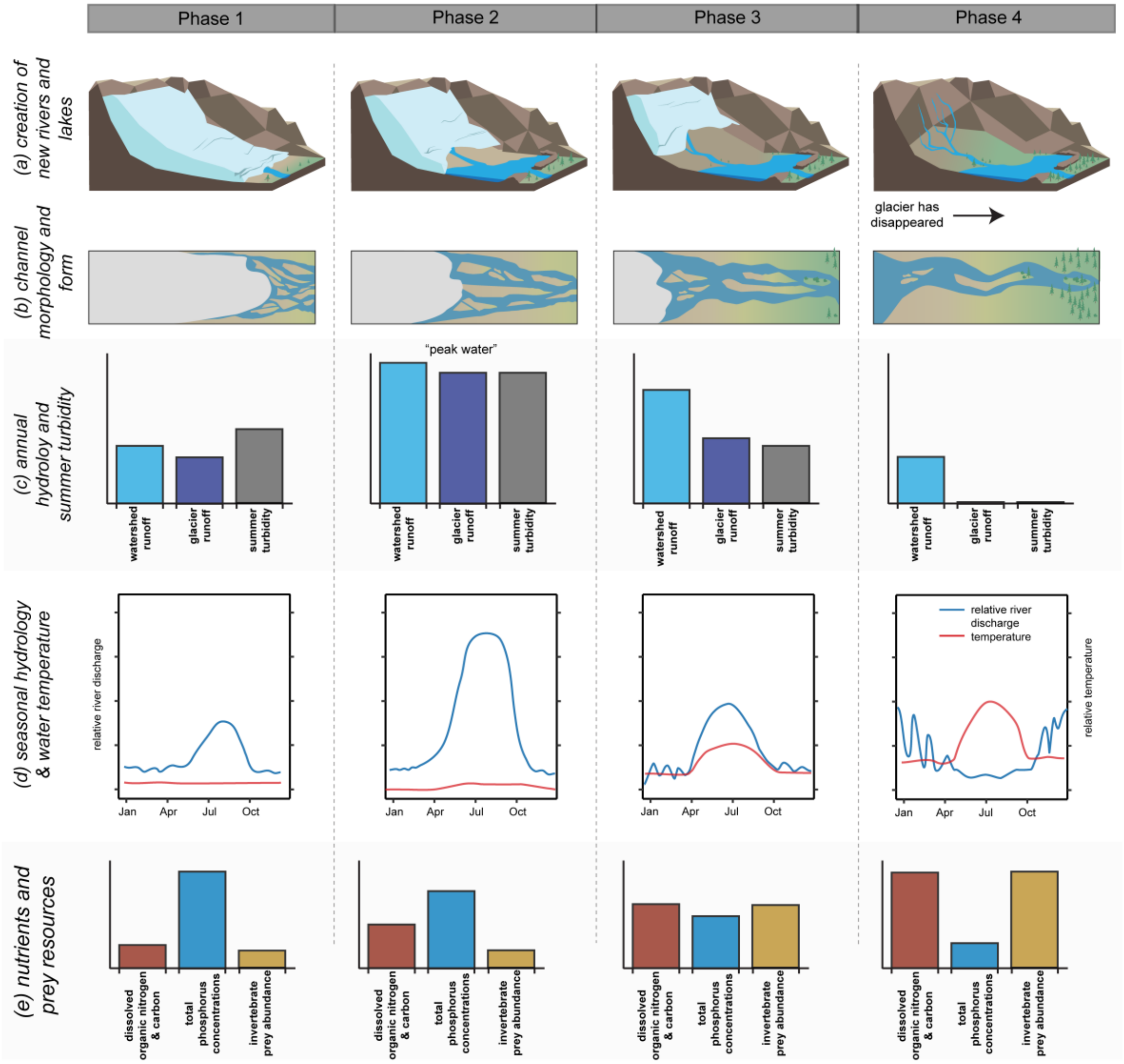


Figure 2.2 Predicted effects of glacier retreat (phases 1-4) on: (a) river and lake habitats, (b) channel morphology and form, (c) total annual watershed runoff, glacier runoff, and summer turbidity, (d) seasonal hydrology and temperature relationships, and (e), predicted stream water organic matter and nutrient concentrations and prey availability.

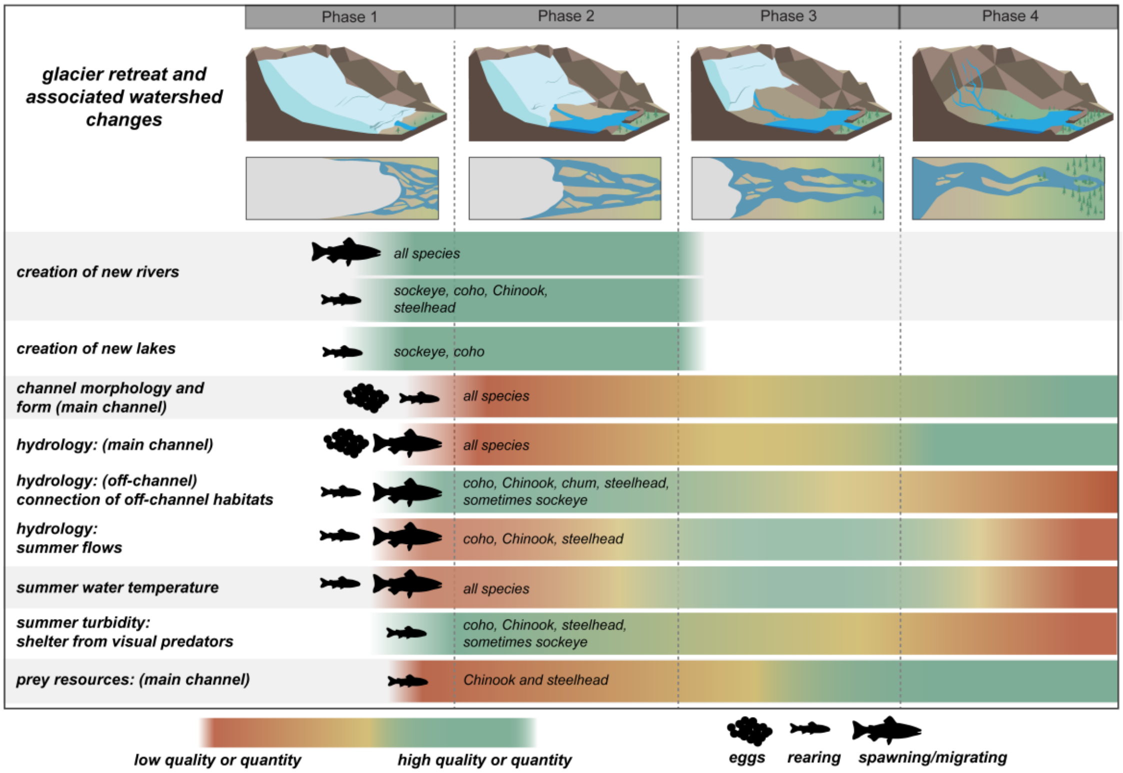


Figure 2.3 **Predictions of how glacier retreat and its associated watershed changes will affect salmon species across life phases during the different phases of glacier retreat.**

Cold temperatures in young streams may present obstacles to salmon success when the landscape is dominated by glacier ice. In heavily glacierized watersheds (e.g., >40% glacier coverage), river temperatures remain very cold (<5°C) throughout the year because discharge is dominated by glacier meltwater (Figure 2.2; Fellman et al. 2014). For example, in a comparative study of watersheds that ranged from 0% to 65% glacier coverage, average summer water temperature was ~1°C colder for every 10% increase in glacier coverage (Fellman et al. 2014). Water temperature plays a critical role in regulating the metabolism and development of embryos and juvenile salmon (Brett 1971). Cold water temperatures in heavily glacierized streams challenge the thermal performance of salmon egg and juvenile development (Brett 1971). However, cold water temperature does not necessarily preclude salmon embryo and juvenile survival and growth (Adelfio et al. 2018). For example, recent work by Campbell et al. (2019) suggests that coho salmon in a cold stream (4°C) grew at the same rate as those in a warmer stream (10-12°C) that is closer to the assumed optimum temperature for the species (Richter and Kolmes 2005). Thus, local adaptation or physiological compensation may potentially allow salmon to persist in what are presumed to be less-than-ideal thermal conditions. Regardless, when acting in combination with other features of young proglacial streams such as channel instability and low prey abundance, cold temperatures in young streams can limit salmon productivity (Murray and McPhail 1988).

Despite these limitations, salmon can colonize highly dynamic and very cold rivers. Salmon straying combined with high population growth rate potential (20% to 100% per generation; Pess et al. 2014) can lead to rapid population expansion in newly deglaciated habitat. Estimated salmon stray rates range from approximately 1–20%, depending on study, species and life histories, and environmental factors (Keefer and Caudill 2014). The amount of straying is also positively related to proximity—most straying individuals return to within 30 km of their origin (Pess et al. 2014). Accordingly, salmon colonization is affected by four key factors that vary across species: (1) the size and distance of nearby (donor) populations; (2) species' presence in the same or nearby watershed(s); (3) the suitability of newly available habitat for the species; and (4) the presence of life-history variants in the donor population that facilitate colonization of newly opened habitats (Pess et al. 2014). For example, in Stonefly Creek, Alaska, pink salmon were the first salmon to establish populations following deglaciation and river habitat creation (Milner et al. 2011), likely because pink salmon tend not to have extended juvenile rearing phases, stray at high rates, and are in high abundance in this region. Thus, different species of salmon will likely colonize river habitats created by recent deglaciation at different rates given their life-history traits and location of the deglaciated area (Table 2.1).

2.4.2. Phase 2: Rivers and lakes fed by ice

During phase 2 of glacier retreat, substantial portions of the valley floor are revealed and reorganized by physical processes that affect the geomorphic evolution of potential salmon habitat (Figure 2.2). During this phase, there is an increase in the diversity of habitats formed and therefore expanded opportunities for different salmon life histories. However, continued fluxes of water and sediments from the upstream glacier may limit salmon and prey productivity in mainstem river channels. Glaciers are effective agents of erosion and carve characteristically broad U-shaped valleys with large volumes of excavated sediment (Montgomery 2002). The valley bottoms left behind are typically organized into three linked hydrogeomorphic domains: canyons, gravel-bedded floodplains, and lakes (Hauer et al. 2016). Canyons occur where valleys are narrowly constrained by shallow resistant bedrock. Gravel-bedded floodplains occur where valleys are broad and may be filled with glacier sediment (i.e. silt, clay, sand, and gravel) of a range of sizes. Lakes form by dammed bedrock, landslide formations, or moraines (Hauer et al. 2016). These hydrogeomorphic domains can alternate and reappear as glaciers retreat up-valley depending on watershed-specific lithography and topography (Hauer et al. 2016). Streams confined by canyons have low physical complexity, and when combined with high river discharge, may even create salmon migration barriers or offer limited opportunities for salmon habitat development during glacier retreat (Murphy et al. 1989; Bellmore and Baxter 2014; Hauer et al. 2016).

In contrast, broad unconfined floodplains provide opportunities for the development of complex and diverse river habitats (Bellmore and Baxter 2014; Hauer et al. 2016). Riverbanks still have low cohesion because terrestrial vegetation remains in early successional stages. Increased stream discharge and high sediment loads can maintain unstable braided channels (Figure 2.2). Glacier runoff is typically at its highest, known as “peak water”, during this phase of glacier retreat before declining in later phases as glacier melt declines (Figure 2.2; Jansson et al. 2003, Huss and Hock 2018). This peak in glacier runoff typically leads to watershed runoff also being at its maximum during this phase of glacier retreat (Figure 2.2). High summer air temperature can also intensify runoff from the glacier, resulting in increases in seasonal glacier meltwater that decreases downstream water temperature (Fellman et al. 2014). Due to this high glacier and watershed runoff, glacier-fed rivers during this phase can have high sediment loads. Included in these high sediment loads are suspended sediments that are formed as the glacier grinds against rock resulting in fine silt or glacier flour. In watersheds dominated by glaciers, more than 500 mg l^{-1} of glacier flour are typical and up to 2000 mg l^{-1} occur frequently (Gurnell et al. 1987), primarily during the summer months. For example, more than 29 x 10^6 tons of suspended sediment are deposited annually into Cook Inlet, Alaska, from the heavily glacierized Susitna River watershed (Brabets et al. 1999). Comparatively, the Kenai River watershed, which is less glacierized and contains large lakes that trap sediment, is about 1/20th the size of the Susitna River watershed but deposits about 1/300th the amount of suspended sediment (~1 x 10^4 tons) into the Cook Inlet (Brabets et al. 1999).

High turbidity can act in concert with cold temperature and channel instability to limit food resources and growth of juvenile salmon (Milner et al. 2001; Brown and Milner 2012). The high turbidity can limit visual foraging success by juvenile salmon such as Chinook and coho salmon, and steelhead trout (Lloyd et al. 1987). However, juvenile salmon may shift to forage on benthic prey or move to more productive off-channel habitats that are typically lower in turbidity levels (Tippets and Moyle 1978). Further, some degree of glacially derived turbidity may benefit juvenile salmon during rearing and outmigration by sheltering them from visual predators (Figure 2.3; Gregory and Levings 1998).

Side channels and other off-main channel habitats may be particularly important salmon habitat in unconstrained floodplains during this phase of glacier retreat. As braided streams cut new paths across broad floodplains, their abandoned channels remain as preferential flow paths for clearwater side channels often fed by groundwater (Lorenz and Eiler 1989; Curran et al. 2011; Hauer et al. 2016). In combination with other lateral habitats, such as precipitation-fed tributaries, side channels can provide important habitats for some salmon species to spawn (e.g., Chinook, chum, and coho salmon) or rear (e.g., coho and sockeye salmon, steelhead trout; table 2.1; Figure 2.3) because they are often warmer, less turbid, have higher prey production, and have lower velocities than the mainstem channel dominated by glacier meltwater (Murphy et al. 1989; Curran et al. 2011; Rine et al. 2016). For example, in the heavily glacierized Taku River in Alaska and BC, where sockeye salmon rear within the river rather than in lakes, juvenile Chinook, coho and sockeye salmon were found at extremely low densities or not at all in the mainstem during the summer, but instead were found rearing in tributaries or side channel habitats (Murphy et al. 1989). Typically, in heavily glacierized watersheds, groundwater-fed valley margin habitats can receive disproportionately high use by salmon for spawning and rearing (Lorenz and Eiler 1989; Murphy et al. 1989; Curran et al. 2011). Thus, during this phase of glacier retreat there is a mosaic of habitat conditions produced that salmon can utilize across their life phases.

As glaciers retreat, they leave behind moraines that can result in the formation of ice marginal or proglacial lakes (Figure 2.2). Immediately after formation, these unstable moraine-dammed lakes are typically cold and have shallow euphotic zones due to high levels of suspended glacier flour (Lloyd et al. 1987), rendering them relatively unproductive. Regardless, sockeye salmon may spawn and rear in young proglacial lakes, even those with actively calving glaciers and high turbidity (Ramstad et al. 2004; Barouillet et al. 2019). Other salmon species do not typically spawn in lakes; however, newly created lakes can provide rearing habitat for juvenile coho salmon (Milner et al. 2011). Thus, the creation of lakes from glacier retreat can directly increase salmon spawning and rearing habitat, particularly for sockeye salmon (Figure 2.3).

Glacially created lakes can also have substantial downstream effects on salmon habitats and their suitability (Dorava and Milner 2000). Proglacial lakes modify downstream conditions by attenuating peak flows, sustaining base flow through the drier summer months, settling bedload and suspended sediment, and increasing stream temperature (Dorava and Milner 2000). Consequently, stream channel stability is much higher below proglacial lakes, and turbidity and thermal regimes are more hospitable to salmon reproduction and juvenile rearing (Dorava and Milner 2000, Schoen et al. 2017). For example, Chinook salmon in many regions spawn extensively downstream of large lake systems presumably because of the suitability of these habitats for egg incubation due to lake-moderation of flow, temperature, and sediment transport (table 2.1; Roni and Quinn 1995, Brabets et al. 1999, Schoen et al. 2017). Thus, lakes can be a key mediating factor that influences the downstream effects of glacier retreat.

2.4.3. Phase 3: High elevation glaciers with downstream effects

As glaciers recede, they retreat up valley to steeper terrain that is inaccessible to salmon. Therefore, during this phase, there is no creation of additional accessible river habitat to salmon, but glacier retreat affects salmon habitat via downstream effects and continual river evolution despite lower levels of watershed and glacier runoff than the previous “peak water” phase 2 (Figure 2.2). Decreased summer river discharge and lower sediment transport lead to increased stabilization of downstream mainstem channels and floodplains. Riparian forests have typically matured to the point of stabilizing stream banks, corresponding with a more general transition from strict physical control of the deglaciated landscape to a period of increasing biotic influence (Figure 2.2; Milner et al. 2007). Riparian forests also begin to influence habitat quality as wood is recruited to stream channels. Wood accumulations trap suitably sized spawning gravel (Buffington et al. 2004) and causes local hydraulic forcing that sorts sediment, and scours pools, thus increasing size and number of areas available for juvenile rearing, particularly for Chinook and coho salmon (Mossop and Bradford 2004).

Increases in channel stability may also improve conditions for species that spawn in the mainstem, such as Chinook salmon and steelhead trout.

Overall, at this later phase of glacier retreat, the proportional contribution of glacier meltwater to total watershed runoff will be lower, and therefore downstream water temperatures will be warmer (Figure 2.2). However, glacier runoff from relatively small high elevation glaciers can still play an important role in regulating downstream water temperature. During periods of warm weather, glaciers will provide more cold meltwater and thus decrease climate sensitivity of downstream river water temperatures (Jansson et al. 2003). For example, during late summer months, glacier runoff can contribute up to 25% of total watershed runoff even in watersheds that are only 1% glacierized (Huss and Hock 2018). Given that summer water temperatures have been shown to decrease by ~1°C for every 10% increase in glacier coverage (Fellman et al. 2014), in regions where water temperatures may otherwise reach high levels (e.g., >15 °C), high elevation glaciers may be an important source of cold water by stabilizing or buffering stream temperatures.

Increased water temperature during this phase of glacier retreat will generally increase development and growth rates of salmon, but the overall effects on salmon populations are complex. Warmer temperatures can accelerate embryo development, potentially resulting in smaller (Beacham and Murray 1990) and less well-developed fish (Fuhrman et al. 2018) that emerge earlier (Adelfio et al. 2018). Increased temperatures can also increase juvenile growth rates (Bailey et al. 2018), which could lead to increased marine survival due to escaping size-selected mortality (Ward and Slaney 1988). However, warmer freshwater temperatures could also induce juvenile salmon to complete freshwater rearing in fewer years, which could decrease marine survival (Cline et al. 2019). Therefore, salmon responses to changing temperatures are complex and will depend on how effects cascade over their life cycles.

Total fluxes and concentrations of suspended sediments are predicted to be lower in phase 3 systems compared to the previous phase of glacier retreat (Figure 2.2; Milner et al. 2017). Increased water clarity could increase prey production and foraging success of mainstem-feeding juvenile salmon (Milner et al. 2001). With stream temperatures increasing in phase 3, prey species for juvenile salmon may shift from cold-water adapted macroinvertebrates, such as a restricted set of chironomids, to a more diverse benthic invertebrate assemblage (Milner et al. 2008). Terrestrial invertebrates associated with riparian vegetation may also increase the diversity of prey available for juvenile salmon (Wipfli and Baxter 2010). Downstream lake habitats will also likely have greater juvenile salmon growth potential with increases in summer temperature and light penetration, which is particularly important for increasing the prey available to lake-rearing species, such as sockeye salmon. However, lower turbidity could also increase predation rates on rearing and outmigrating salmon (Figure 2.3).

Continued river system evolution and decreased contributions from glacier melt during phase 3 will also shift downstream river physiochemistry (Figure 2.2). For example, watersheds in southeast Alaska with less than 10% glacier coverage typically have substantially higher summer dissolved organic carbon concentration, suggesting that terrestrial ecosystem processes play an increasingly important role in determining stream water nutrient concentrations as glaciers recede (Hood and Berner 2009). Large watersheds with high elevation glaciers may contain a wide range of aquatic habitats including clearwater, brownwater, or glacially fed tributaries that feed into the mainstem (Schoen et al. 2017). These complex habitats offer diverse habitat mosaics and food webs that can support different species and life histories of salmon.

2.4.4. Phase 4: Watersheds without permanent ice

The complete loss of glaciers during phase 4 eliminates the effects of glacier meltwater on downstream salmon habitat (Figure 2.2). Most notably, the loss of high elevation glaciers eliminates an important source of stored water that would otherwise be released as cold meltwater during the summer season, increasing the risk of detrimental low summer flows, which can further exacerbate sensitivity to warm air temperature (Fellman et al. 2014). Thus, the loss of glaciers results in a fundamental change in seasonal patterns of hydrology and temperature (Figure 2.2).

The effects of these shifts in hydrology and temperature on salmon will likely vary depending on environmental context. For example, in warm regions with low summer precipitation, warm summer water temperature and low stream flows could negatively impact salmon by decreasing survival of migratory adult salmon (Figures. 2.3 and 2.5; Eliason et al. 2011, Martins et al. 2012), or by restricting juvenile rearing across habitats (Sloat and Osterback 2013) or seasons (Munsch et al. 2019) due to reduced or changed stream flow patterns. In temperate coastal regions, the loss of glacier ice and shifts in precipitation from snow to rainfall can cause higher streamflow stochasticity that may increase winter flooding risks to salmon (Sloat et al. 2018). Additionally, low summer stream flows and warm temperatures could result in increased frequency of hypoxic events in streams with high salmon abundance (Sergeant et al. 2017). Finally, as glaciers are removed from watersheds there may be microclimatic effects, such as local temperature and rainfall pattern changes, influencing salmon habitat on a smaller scale (Oerlemans 2010). Generally, the loss of glaciers and their meltwater may pose challenges in some regions for salmon in terms of habitat quality and quantity, but such impacts will be strongly influenced by local context and local adaptations.

The effects of glaciers on salmon ecosystems are evident for centuries or millennia after glaciers have disappeared. For example, thousands of years ago, glaciers shaped large lakes and linked river systems in watersheds of southwest Alaska. Presently, these watersheds are now devoid of glaciers, but are thriving and dynamic salmon ecosystems (Hilborn et al. 2003; Brennan et al. 2019). Gravel-bedded river floodplains are another prominent relict feature that can represent highly productive ecosystems (Hauer et al. 2016). Comparative studies of the evolution of deglaciated landscapes suggest an increase in salmon habitat quality as watershed stability increases, but a gradual decrease in salmon habitat quantity over time with continued channel incision and decreased lateral groundwater-fed habitats over thousands of years (Benda et al. 1992). Thus, glaciers have a long-lasting legacy of influence on salmon ecosystems.

2.5. Contemporary glaciers in salmon watersheds

North Americas major salmon watersheds currently have varying degrees of glacier coverage that roughly correspond to different phases of the conceptual model (Figure 2.2). We obtained glacier data from the Randolph Glacier Inventory v6.0 (Pfeffer et al. 2014) — a global inventory of glacier outlines — throughout the current North American range of salmon to quantify percent glacier cover in regions that are either major salmon watersheds or aggregate coastal regions that contain numerous smaller watersheds (Figure 2.4). For example, we estimated glacier coverage in the 50,000 km^2 Susitna River watershed draining into Cook Inlet, Alaska, as well as the “Central Gulf of Alaska Region” that contains an aggregate of small coastal watersheds, some completely covered by glacier ice. Therefore, this analysis of glacier coverage is on the scale of larger watersheds and drainage regions. Collectively these watersheds and regions cover the North American range of salmon (Figures. 2.1 and 2.4).

Salmon watersheds and regions have vastly different extents of current glacier coverage. For instance, 9% of watersheds or regions (3 of 34 watersheds or regions) have high glacier coverage (>20% of watershed area), particularly in southcentral Alaska (Figure 2.4). About 32% of watersheds or regions (11 of 34) have significant glacier coverage (5% to 20%), such as in southeast and southcentral Alaska and along the British Columbia coast. Watersheds or regions with high to significant glacier coverage are likely to contain habitats that are in the earlier phases (phase 1 and 2) of our conceptual model of glacier retreat (Figure 2.2). Similarly, 35% of watersheds or regions (12 of 34) have low glacier coverage (0.1% to 5%), spanning from the Columbia River to the Yukon River and Alaska. These watersheds or regions are generally expected to exhibit characteristics of phase 3 of our conceptual model. Lastly, 24% of watersheds or regions (8 of 34) have minimal or no glacier coverage (<0.1%), corresponding to phase 4 of our conceptual model. These watersheds or regions primarily occur at the southern and northern range extent for salmon, such as the Klamath and Sacramento watersheds and northeast Alaska, respectively (Figure 2.4). Collectively, 85% of watersheds or regions (29 of 34) that we consider have at least some glacier coverage (Figure 2.4). Thus, most of North American salmon watersheds or regions are being influenced by contemporary glacier retreat.

Larger watersheds or regions included in our analysis contain many smaller watersheds within them that all have varying degrees of glacier coverage. For example, our analysis indicates that the large Susitna River watershed has significant glacier coverage (Figure 2.4). However, the Susitna River watershed also contains many small sub-watersheds, some that have no glacier coverage (i.e., phase 4; Figure 2.2) and other catchments that have high glacier coverage and are better represented by phase 1. Thus, watersheds or regions contain many smaller sub-watersheds at different phases of glacier retreat.

2.6. Research frontiers

2.6.1. Mediating factors and context-dependency

The effects of glacier retreat on salmon and their habitat will likely be context-dependent and influenced by mediating factors such as lakes, watershed size, river valley form, and geographic location (Figure 2.5). As discussed above, lakes trap sediments, store water, and alter hydrology; through these processes, lakes mediate the downstream effects of glacier retreat (Dorava and Milner 2000, Schoen et al. 2017). Watershed size and complexity may also be key mediating factors. For example, the downstream hydrology and physiochemistry of large watersheds such as the Copper River in Alaska integrates subwatersheds with different climates across the phases of glacier retreat (Figure 2.5). Larger and more complex watersheds have broader portfolios of glacier recession, climate variability, and habitat types, and thus may have more muted responses (Moore et al. 2015; Chezik et al. 2017). In contrast, in watersheds that have linear topology (few tributaries) or are smaller, runoff from a single glacier may be the main driver of downstream hydrology (Figure 2.5). The location of the watershed and its associated climate will be another key mediating factor. Coastal watersheds with more moderate climates, higher mean annual precipitation may be less at risk of warm summer water temperature and low summer flows following glacier loss. Generally, there is a need for long-term studies that address how landscape features modulate the impacts of glacier retreat.

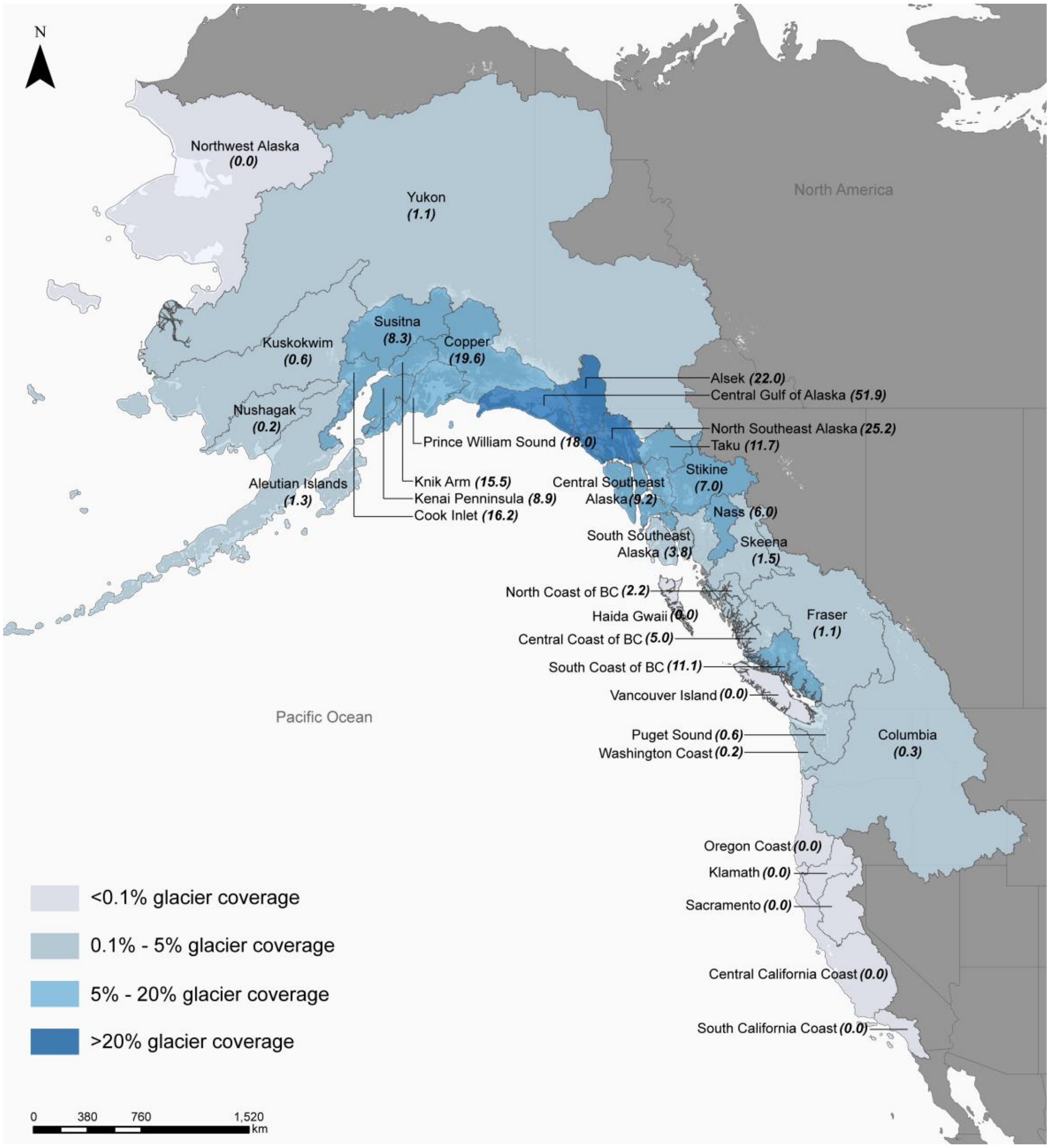
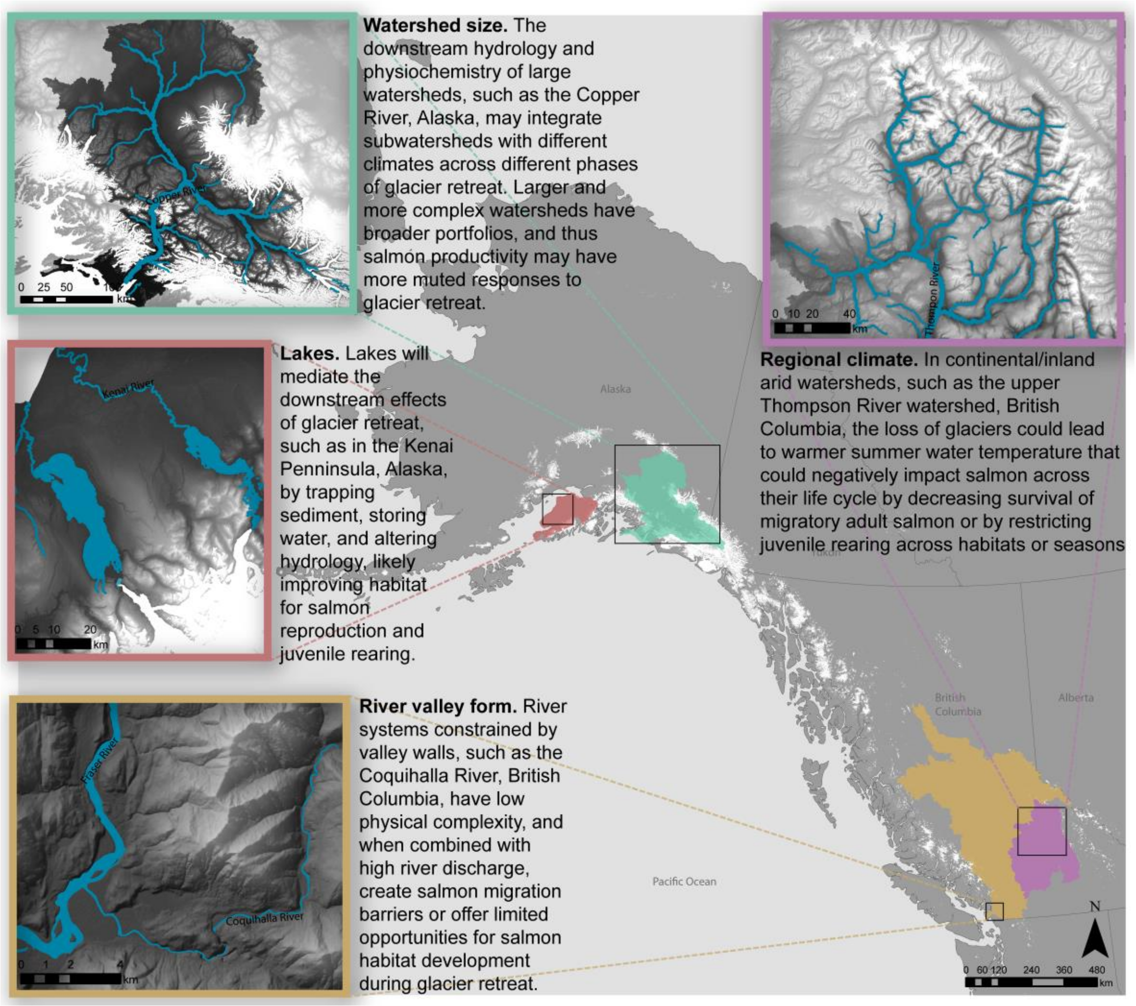


Figure 2.4 **Map showing the percent glacier cover for watersheds or regions between California and Alaska. The numbers in parentheses following the watershed or region names refer to percent cover of glaciers in the watershed or region.**

2.6.2. Plastic and evolutionary responses to glacier retreat

Salmon have remarkable capacity for both plastic and adaptive responses to rapid environmental change (Crozier and Hutchings 2014). Accordingly, rapid evolution and phenotypic plasticity will likely mediate the population-level responses of salmon to glacier retreat. For example, while adult Chinook salmon may be physiologically sensitive to warm water temperature (Muñoz et al. 2015), adaptive or plastic changes in migration phenology could drastically reduce their exposure to periods of warm water (Mantua et al. 2015). For instance, an eco-evolutionary model predicted that evolution may shift sockeye salmon migration timing by approximately 10 days over the next century in a warming river, which could increase the probability of population persistence (Reed et al. 2011). Yet there is great uncertainty in such predictions, and these remain important key research frontiers. For example, can salmon evolve at a rate that keeps pace with climate-driven habitat change (Reed et al. 2011)? What are the limits and cues of their adaptive plasticity (Crozier and Hutchings 2014)?



Watershed size. The downstream hydrology and physiochemistry of large watersheds, such as the Copper River, Alaska, may integrate subwatersheds with different climates across different phases of glacier retreat. Larger and more complex watersheds have broader portfolios, and thus salmon productivity may have more muted responses to glacier retreat.

Lakes. Lakes will mediate the downstream effects of glacier retreat, such as in the Kenai Penninsula, Alaska, by trapping sediment, storing water, and altering hydrology, likely improving habitat for salmon reproduction and juvenile rearing.

River valley form. River systems constrained by valley walls, such as the Coquihalla River, British Columbia, have low physical complexity, and when combined with high river discharge, create salmon migration barriers or offer limited opportunities for salmon habitat development during glacier retreat.

Regional climate. In continental/inland arid watersheds, such as the upper Thompson River watershed, British Columbia, the loss of glaciers could lead to warmer summer water temperature that could negatively impact salmon across their life cycle by decreasing survival of migratory adult salmon or by restricting juvenile rearing across habitats or seasons

Figure 2.5 **Map highlighting the mediating factors such as watershed size, presence of lakes, river valley form, and regional climate influencing the effects of glacier retreat on salmon and their habitat. Watershed boundaries (various colors), and rivers and lakes (blue) data were obtained from the National Hydro Database (www.usgs.gov/products) for Alaska and the Freshwater Atlas (www2.gov.bc.ca/gov/content/data/geographic-data-services/topographic-data/freshwater) for British Columbia. Glacier outlines (white), were obtained from the Randolph Glacier Inventory v6.0 (Pfeffer et al. 2014).**

2.6.3. Fish community responses to glacier retreat

Glacier retreat will not only impact anadromous Pacific salmon, but also other fishes. For example, Dolly Varden (*Salvelinus malma*) and their close relative, bull trout (*S.*

confluentus), are char with extremely flexible and diverse life histories that may be particularly well-suited for utilizing glacier-fed rivers. With both migratory and resident life histories, these fish can use coastal ocean habitats and migrate among river basins (Brenkman and Corbett 2005). Further, these species are particularly adapted to cold waters, such as those found in rivers that are heavily glacierized (e.g., phase 2; Figure 2.2). For example, Milner et al. (2008) discovered that Dolly Varden were the first fish to colonize a new river following glacier retreat. Cutthroat trout (*O. clarkii*) also have flexible and diverse life-histories, including frequent movements within and between watersheds (Trotter 1989, Saiget et al. 2007). Thus, the behavior and life-histories of cutthroat trout may allow them to capitalize on opportunities offered by glacier retreat. Another fish species that may be particularly impacted by glacier retreat are eulachon (*Thaleichthys pacificus*) that are found in many large river systems in the region with high glacial influence (Moody and Pitcher 2010). Eulachon are remarkably lipid-rich anadromous smelt whose late-winter/early-spring migration to rivers is of critical importance to wildlife and human harvesters. These fish migrate and broadcast spawn in the lower reaches of rivers during the late winter and early spring, and their planktonic larvae drift out to estuaries shortly thereafter (Moody and Pitcher 2010). While these elusive fish remain relatively understudied, their spawning timing and survival may be extremely sensitive to changes in the hydrology and sediments of the lower reaches of rivers that could be modified greatly by rapid glacial retreat. Other fishes, such as sculpins (*Cottus* aleuticus) and stickleback (*Pungitius pungitius*), while not of direct cultural importance, may also colonize glacier rivers and play roles in their food webs (Milner et al. 2011). These shifts in other components of the fish communities may play important roles in the ecology of salmon watersheds through the phases of glacier retreat.

2.6.4. Ocean and estuary conditions

Glacier retreat from either marine- or land-terminating glaciers can affect ocean and estuary conditions, by changing the amount and timing of sediment, nutrients, and freshwater inputs (O’Neel et al. 2015). On an ocean-basin scale, increased variability in glacier runoff patterns is expected to affect the strength of the Alaska Coastal Current (ACC), the dominant coastal circulation pattern in the Central Gulf of Alaska, and therefore the cross-shelf transport of organisms and nutrients (O’Neel et al. 2015). Glacier meltwater is also an important source of bioavailable carbon and nutrients such as phosphorus and iron to downstream habitats (Fellman et al. 2010, Schroth et al. 2011), and transport terrestrial and riverine organic matter and nutrients downstream where they are incorporated into estuarine food webs (Arimitsu et al. 2018). However, relatively little is known about how changes in magnitude and timing of freshwater, organic matter, and nutrient fluxes from glacier rivers will affect estuaries and oceans. Thus, glacier retreat could have profound effects on the ocean basin as well as for coastal ocean populations (O'Neel et al. 2015).

Outmigrating juvenile salmon in estuaries and coastal oceans may also be impacted by glacier retreat via different potential pathways of impact. For example, substantial changes in the ACC could affect primary production or the spatial-temporal overlap of salmon with their prey. For example, interannual variability in the abundance of juvenile chum salmon, sampled in July via surface trawl in southeast Alaska, was positively correlated to freshwater runoff in the spring (Kohan et al. 2017). This relationship was attributed to primary production resulting from stronger water column stratification. Changes in environmental conditions arising from shifts in glacier runoff could also structure the distribution of salmon and other marine organisms, as in the heavily glacierized Glacier Bay, Alaska, where variation in community structure was associated with turbidity, water temperature, stratification, and distribution of icebergs from calving glaciers (Arimitsu et al. 2016). Similarly, a study of Greenland fjords found that rising subsurface meltwater plumes from marine-terminating glaciers bring nutrient-rich water to the surface that sustains high phytoplankton productivity during the summer (Meire et al. 2017). Changes in turbidity in nearshore marine habitats could also affect the vulnerability of juvenile salmon to predators and the feeding success of smolts during their outmigration (Gregory and Levings 1998; De Robertis et al. 2003). Indeed, estuaries can function as both transitional and rearing habitat for all species of juvenile salmon during smolt outmigration to the ocean (Weitkamp et al. 2014). Overall, the net effect of glacier retreat on the productivity of estuaries and the ocean for salmon remains relatively unknown.

2.6.5. Multiple stressors and glacier retreat

Contemporary glacier retreat in salmon ecosystems is occurring in concert with a host of additional anthropogenic stressors, such as ocean acidification, habitat loss, warming ocean and freshwater temperatures, shifting precipitation regimes, and hatchery influences. For example, in many regions, glacial meltwater contributions to runoff will decrease as air temperatures increase (Bliss et al. 2014; Huss and Hock 2018), processes that could act additively or multiplicatively to rapidly increased water temperatures. Further, some climate precipitation models also predict drier summers in the study region (Mote and Salathé 2010), which when combined with losses of summer glacier meltwater, could collectively decrease low summer flows. However, precipitation climate models are generally highly uncertain and spatially variable (Mote and Salathé 2010). Shifts in water temperatures could also lead to an increase in invasive or exotic species that could reduce or negatively impact salmon (Lawrence et al. 2014). Thus, the impacts of glacier retreat on salmon should be considered through the lens of cumulative effects. It is also likely that stressors will influence the response of salmon to glacier retreat. For example, if the capacity of the ocean to support thriving salmon populations is compromised by climate change, then salmon may be slower to colonize new habitats. Alternatively, losses of salmon genetic diversity, such as due to habitat loss, over-harvest, or hatcheries, may compromise their capacity for rapid evolution (McClure et al. 2008). Thus, it is unknown how these multiple processes will interact and impact salmon and their ecosystems, as glacier retreat is only one of these many on-going stressors.

2.7. Salmon management in an era of rapid glacier retreat

Glacier loss may pose challenges and opportunities for effective management and conservation of salmon and their habitats. Salmon productivity will likely shift across space and time depending on a watershed’s various phases of glacier retreat. Over the coming decades, we predict that there will be areas where salmon populations will be disadvantaged due to glacier retreat and associated loss of predictable water flows and increased water temperature (Mantua et al. 2010), such as some watersheds or regions in phase 4 of glacier retreat (Figures. 2.2 and 2.4); areas where glacier retreat will enhance salmon productivity as downstream habitat suitability increases (Milner et al. 2008; Fellman et al. 2014), such as watersheds or regions in phases 2 and 3 of glacier retreat (Figures. 2.2 and 2.4); and areas of completely new habitat that can be colonized by significant numbers of salmon as glaciers retreat and river and lake habitats form (some watersheds or regions in phase 1 of glacier retreat; Figures. 2.2 and 2.4; Milner et al. 2011). Thus, glacier retreat, as well as other drivers of global change, will shift salmon production capacity and challenge current management systems. Below we highlight key challenges to salmon management associated with glacier retreat.

Predictive population models, management plans, forecasts, and sustainable harvest rates will need to be revisited and revised as salmon productivity shifts within and between watersheds with glacier retreat. Relationships between salmon returns and environmental conditions may shift as past relationships are pushed beyond their historically enumerated bounds and as other processes become dominant drivers. In other words, glacier retreat may expedite non-stationarity in relationships between environmental factors and salmon (Litzow et al. 2018). As glacier retreat shifts salmon productivity, it would be beneficial to frequently revisit management goals such as escapement targets and sustainable fishing levels. It is also possible that temporary decreases in harvest levels during the expansion phase of salmon colonization may expedite the establishment of thriving salmon populations. For instance, in areas where glacier retreat enhances salmon production, new salmon harvest opportunities may be created, such as on the Kenai Peninsula, southcentral Alaska, where the establishment of sockeye salmon populations supported a commercial fishery (Milner 1997). In addition, complex and differential responses to glacier retreat within regions may differentially shift the productivity of particular locations or populations of salmon. Such response diversity, if untracked, may exacerbate risks of accidental mixed-stock overharvest. Terminal or carefully managed fisheries may be more robust to such shifts in productivity. Alternatively, in regions where glacier loss will degrade salmon habitat, such as in some of the southern portion of salmon’s range where glaciers have or are nearly retreated from the landscape, fisheries may need to be managed more conservatively. For example, in British Columbia’s warming Fraser River, salmon managers restrict fisheries in years when the river becomes too warm for migrating sockeye (Martins et al. 2011). Effective monitoring will enable adaptive management responses to the shifting landscape of salmon.

Salmon restoration activities should be designed and undertaken with a forward-looking outlook (Beechie et al. 2013) that considers how landscapes may change due to glacier retreat. It may be tempting to employ major engineering and infrastructure approaches to mitigate the effects of lost glaciers. In the European Alps, it has been proposed that new reservoirs could be constructed to mitigate projected changes in seasonal water availability from melting glaciers by offsetting up to 65% of the expected summer-runoff changes from presently glacierized basins (Farinotti et al. 2016). However, such engineering approaches would take massive financial investment, mitigate only one of the important potential pathways of connection between glaciers and salmon, and would likely pose major risks to salmon. Thus, we suggest that in most cases, such engineering approaches to mitigating lost glaciers for salmon may not be appropriate. Instead, process-based restoration will likely be more effective in this era of rapid global change. Process-based restoration enables the fundamental processes that generate and maintain habitat and thus will be more robust to a changing world. This approach to restoration should include targeting the root cause of ecosystem change, tailoring restoration actions to the local potential, matching the scale of the restorative action to the scale of the biological or physical process, and being explicit about outcomes and recovery time frames (Beechie et al. 2010). Typical actions such as restoring floodplain connectivity, protecting river floodplains from encroaching human infrastructure (Johnson et al. 2019b), maintaining or restoring wetlands and beaver ponds (Weber et al. 2017), decreasing human water withdrawals to maintain stream flow regimes, and re-aggrading incised channels are most likely to ameliorate stream flow and temperature changes and increase habitat diversity and population resilience (Beechie et al. 2013). Such process-based restoration and habitat protection would represent substantial investment, but large-scale analyses have suggested that such approaches may be cost-effective and provide multiple benefits (Johnson et al. 2019b).

Proactive protection of future salmon habitat also is likely a wise investment. Regions with high glacier coverage (e.g., the Central Gulf of Alaska, Figure 2.4) might have substantial gains in salmon habitat and associated returns over the next century, and salmon are already growing in importance to commercial fishing portfolios (Beaudreau et al. 2019). However, glacier retreat may also expose substantial mineral deposits, and choices will need to be made about fostering salmon production versus extracting mineral resources. Environmental decision-making is often based on current estimates of risks to important species like salmon. For example, mines in the transboundary region of British Columbia and Alaska have been recently approved in part because they are in heavily glacierized areas and, at present, have presumed low value for salmon (Canadian Environmental Assessment Agency 2018). Such environmental decision-making fails to incorporate the risk of lost future salmon production. Meanwhile, tools such as the intrinsic potential models can be used to quantify the potential value of future salmon habitat (Bidlack et al. 2014). There is a need for proactive decision-making and conservation that incorporates the potential values and benefits of future salmon habitat.

The future states of resources will always be extremely difficult to forecast (Schindler and Hilborn 2015). Preserving the genetic diversity and evolutionary potential of salmon will be of foundational importance towards enabling the adaptive capacity of salmon systems (Schindler et al. 2008, Waples et al. 2008). Protecting diverse and connected salmon watersheds is also essential for supporting sustainable fisheries (Hilborn et al. 2003). The story of glaciers and salmon goes back millions of years. In the present phase, there is a key role for management and conservation that are robust to rapid glacier retreat and an uncertain future of salmon stocks.

2.8. Acknowledgments

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Chapter 3.

Glacier retreat creating new Pacific salmon habitat in western North America

3.1. Summary

Rapid glacier retreat poses risks but also potential benefits for species of cultural and economic importance. One example is Pacific salmon (*Oncorhynchus* spp.) (O'Neel et al. 2015; Milner et al. 2017; Schoen et al. 2017; Pitman et al. 2020), which support subsistence harvests as well as commercial and recreational fisheries worth billions of dollars annually (Clark et al. 2006; Gislason et al. 2017; Johnson et al. 2019a). Although decreases in summer streamflow and warming of freshwaters is reducing Pacific salmon habitat in many parts of their range (Moore et al. 2009; Mantua et al. 2010), glacier retreat is creating new rivers and lakes that salmon can rapidly colonize (Milner et al. 2008, 2011). However, potential gains in future salmon habitat associated with glacier loss have yet to be quantified across the range of Pacific salmon. Here we project the extent of future gains in Pacific salmon freshwater habitat by linking a model of glacier mass change for almost 600 glaciers, forced by five different Global Climate Models (GCMs), with a simple model of salmon stream habitat potential across a 623,000 km^2 study region throughout the Pacific mountain ranges of western North America. Based on conservative estimates of the swimming performance and habitat requirements of Pacific salmon, we project that by the year 2100 glacier retreat will create ~6,000 km of new streams accessible to be colonized by Pacific salmon, of which ~1,900 km have the potential to be used for spawning and juvenile rearing. These increases in accessible stream kilometers represent 0 to 27% gains within the 18 sub-regions we studied. Identifying these potential hotspots of future Pacific salmon habitat within glacierized regions of western North America can inform proactive management and conservation of Pacific salmon in this era of rapid climate change.

Climate change is altering Earth's ecosystems at an accelerating rate, providing new challenges and opportunities for effective management and conservation of important resources such as Pacific salmon. Abundance of pacific salmon shift substantially from region to region over decades to centuries (Rogers et al. 2013). Currently, ocean heat waves, low summer water flows, and excessively warm river temperatures are negatively affecting many wild salmon populations (Crozier et al. 2019). However, the warming of Arctic and subarctic freshwaters (Nielsen et al. 2013) and contemporary glacier retreat (Milner et al. 2008, 2011) are creating potential new frontiers for salmon. While glacier retreat can have a variety of direct and indirect impacts on salmon ecosystems (O'Neel et al. 2015; Milner et al. 2017; Schoen et al. 2017; Pitman et al. 2020), the retreat of glacier ice will create new streams that, if not too steep for salmon migration, can provide future salmon habitat. For example, new pink salmon populations grew to over 10,000 individuals within ~15 years following extensive glacier retreat in Glacier Bay, Alaska (Milner et al. 2011).

Although salmon colonization of recently deglaciated streams has been well documented in individual watersheds (Milner et al. 2011), predicting future shifts in the distribution of productive salmon habitat remains a challenge, and there are no regional projections for the creation of new salmon habitat in response to retreating glaciers. Forecasting the location of emerging salmon habitat is imperative because while declining glacier ice can present local opportunities for salmon it is also creating new prospects for large-scale resource extraction industries such as mining or oil and gas, which, if developed without adequate environmental risk management, have the potential to degrade these climate frontiers (Casper 2009; Harsem et al. 2011; Kronenberg 2013; Sexton et al. 2020). Here we project the amount, location, and timing of salmon habitat that will be created throughout the Pacific mountain ranges of western North America as glaciers retreat. Understanding the timing and location of emerging salmon habitat frontiers can inform forward-looking management decision-making and conservation planning.

The ~46,000 North American glaciers in the Pacific mountain ranges cover an area of ~81,000 km^2 (RGI Consortium 2017), of which 80% falls within the range of Pacific salmon (Figure 3.1a). These glaciers are rapidly declining in volume and area, accelerated by recent anthropogenic climate warming (Marzeion et al. 2014, 2020). For example, between 2006 and 2016, glaciers in western Canada have lost an average of

1.3% of their ice mass each year (Zemp et al. 2019), and are projected to lose up to 80% of their ice volume by 2100 in some regions (Clarke et al. 2015).

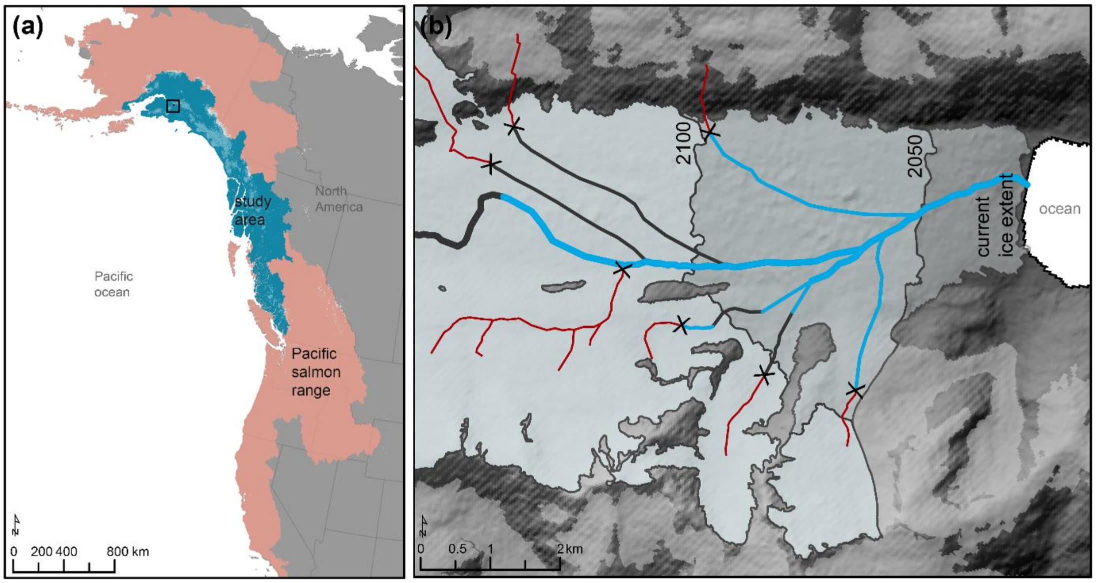

Figure 3.1 Current Pacific salmon range in glacierized watersheds and how glaciers will create new streams. (a) Map showing the Pacific salmon range in North America (pink), and our study region (blue). Glacier outlines are in grey. The black box indicates the location of example focal area, shown in panel (b), Harriman Glacier, Prince William Sound, Alaska, showing glacier retreat (for the benchmark years 2050 and 2100), future salmon-accessible streams (<10% stream gradient threshold over ~500 m; blue and black), and suitable habitat below a 2% stream gradient over ~500 m (blue). Streams >10% stream gradient threshold are marked with an X and colored in red.

To quantify emerging salmon streams created from glacier retreat, we used Digital Elevation Models within a Geographic Information Systems framework to derive a synthetic stream network for glacierized watersheds in the 623,000 km^2 region extending from southern British Columbia to southcentral Alaska (Figure 3.1a). Synthetic stream networks included both present-day and future salmon streams (Methods). Using stream gradient-based salmon migration thresholds, we identified which glaciers are accessible to salmon (Methods). For the accessible glaciers within the 18 sub-regions of our study region, we modelled the timing of glacier retreat (Huss and Hock 2015) and derived future stream networks based on sub-glacial terrain (Figure 3.1b). Modelled glacier retreat was driven by temperature and precipitation projections from an ensemble of five Global Climate Models (GCM; Methods) forced by two climate emission scenarios

(Representative Concentration Pathways, RCP), RCP 4.5 and 8.5, under which global emissions are expected to peak at ~2050 and after 2100, respectively. We present both scenarios but focus on the more moderate RCP 4.5.

We quantified future salmon-accessible stream kilometers (kms) by applying stream gradient thresholds constraining salmon migration, and spawning and juvenile rearing. First, we quantified the extent of the stream network that could be colonized by adult migrating salmon based on two stream gradient thresholds inhibiting adult salmon migration. These gradient thresholds were guided by an analysis of salmon presence records and stream network geomorphology in the Susitna River, a large watershed (53,000 km^2) within our study region with extensive data on the spatial extent of different salmon species (Figure 3.4; Methods). In the Susitna River watershed, the presence of most salmon species occurred in reaches that were accessible at a gradient threshold of ≤10% and the occurrence of all species was rare in reaches above a gradient of 15% (Figure 3.4). This range of gradient thresholds is supported by past studies (Methods) (Cooney and Holzer 2006; Burnett et al. 2007; Sheer et al. 2009); gradient thresholds vary with body size and salmon species due to differences in salmon leaping and burst swimming capabilities. Thus, we selected the conservative (10%) and a more inclusive (15%) stream gradient thresholds for our salmon accessibility analysis. Second, we estimated the extent of new salmon habitat within future salmon-accessible streams that were larger in size (i.e., greater than first order; Methods) with gradients ranging from 0-2% and 0-4% bracketing less and more inclusive bounds of preferred salmon spawning and juvenile rearing habitat, respectively (Methods) (Montgomery et al. 1999). Salmon generally rely on lower stream gradients (i.e., ≤ 4%; Table 3.1) and do not access small mountainous tributary streams for spawning and juvenile rearing habitat (Beechie et al. 1994; Burnett et al. 2007; Bidlack et al. 2014). Thus, this second step defined the extent of newly accessible streams within gradient ranges associated with productive salmon habitat. While a variety of factors, such as changing hydrology, water temperature, and sediment dynamics will continue to change following glacier retreat that ultimately determine habitat productivity (O'Neel et al. 2015; Milner et al. 2017; Schoen et al. 2017; Pitman et al. 2020), here we quantify for the first time the lengths of new salmon-accessible streams and potentially productive salmon habitat that will be available following glacier retreat by 2050, 2100, and under potential complete deglaciation.

3.2. Glaciers creating future salmon-accessible streams

We identified 300 retreating glaciers at the headwaters of present-day streams that will create salmon-accessible streams assuming a 10% stream gradient threshold for upstream salmon migration, and ~600 glaciers assuming a 15% stream gradient threshold. Although the number of glaciers currently covering salmon-accessible streams is proportionally low, given that there are ~46,000 glaciers in the study region, these glaciers are particularly large representing ~50% of the total glacier area in the study region regardless of which stream gradient threshold is used to define salmon accessibility. The total number of accessible glaciers doubles when assuming the 15% stream gradient versus the 10%; however, the glaciers are small and represent a negligible increase in total glacier area.

Over the entire study region, we estimate an increase of between ~6,000 km and ~9,500 km of future salmon-accessible streams by 2100 using the RCP 4.5 climate scenario under the 10% (Figure 3.2) and 15% (Figure 3.5) gradient thresholds, respectively. The projected increase in salmon-accessible streams was not evenly distributed evenly across the 18 sub-regions of our study region, both in terms of absolute and proportional habitat gains. For example, our analysis indicates that seven out of 18 sub-regions show negligible to no gains in salmon habitat because most contemporary glaciers in these sub-regions have already retreated above the limits of upstream salmon migration (Figure 3.2). In contrast, we project that the Gulf of Alaska will have an additional ~2,600 km (27% increase) of salmon-accessible streams under the conservative stream gradient threshold of 10% (Figure 3.2). In some sub-regions, we project substantial absolute gains in salmon-accessible stream kms even though the proportional increase is relatively small. For example, the Copper River will gain a projected ~1,000 salmon-accessible stream km, but this represents only a 2% increase within this large stream network (Figure 3.2). In general, our analysis indicates that the greatest salmon-accessible stream gains will occur in areas where large glaciers occupy low gradient terrain near the coast.

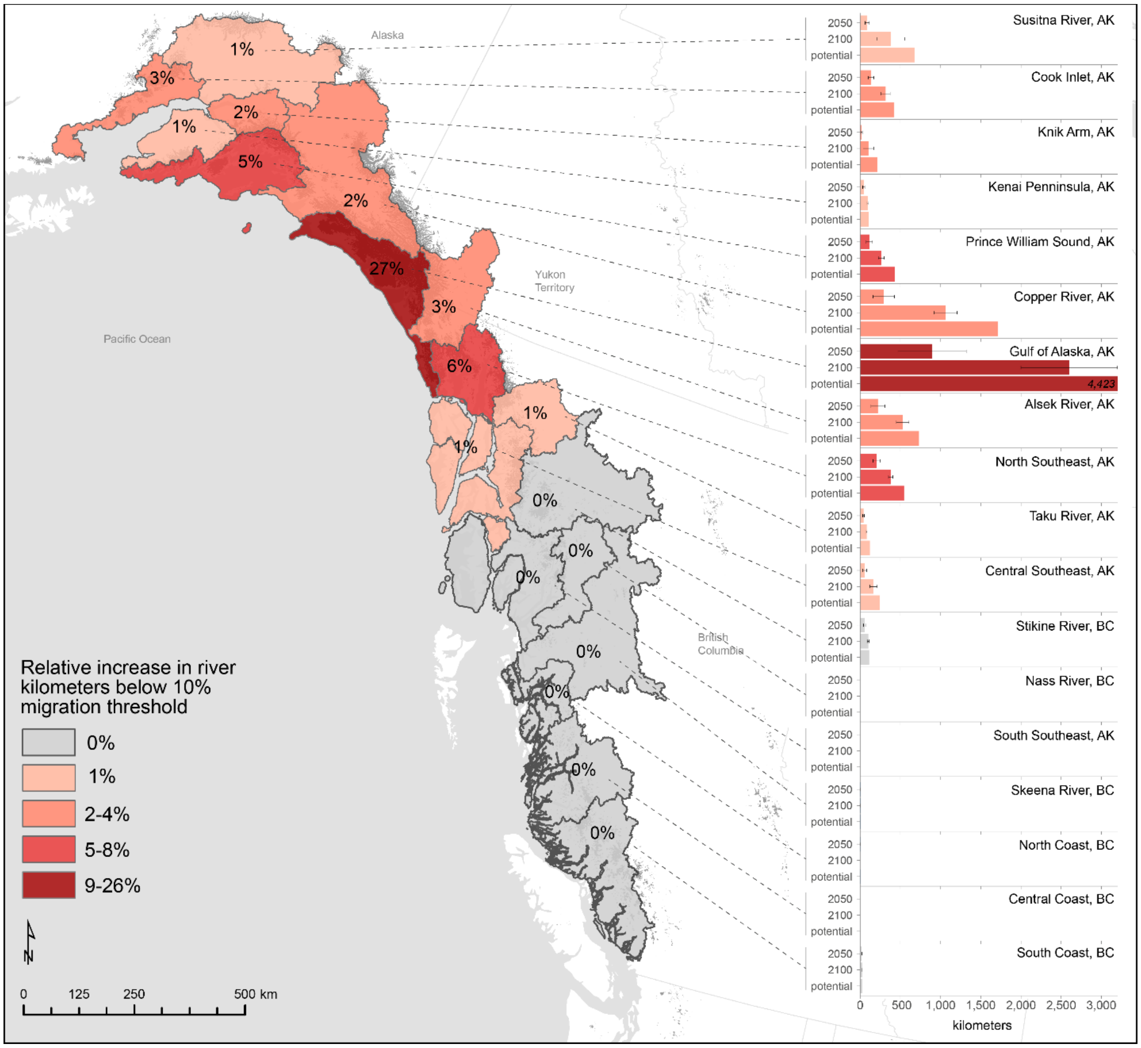

Figure 3.2 **Projected future salmon-accessible stream kms with <10% stream gradient migration threshold. Map shows the projected percent increase in future salmon-accessible stream kms, below a 10% stream gradient threshold for 2100, relative to present-day stream kms summed for each of the 18 sub-regions. Glacier retreat projections, in response to five GCMs with RCP4.5 emission scenario, are used as an ensemble-mean. Bar plots represent the projected future salmon-accessible stream kms with <10% stream gradient threshold for the years 2050, 2100, and complete potential deglaciation (i.e., once glaciers have retreated completely from the landscape) for each of the 18 sub-regions. Projections are computed from 10-year averages centred around these years. Error bars represent + one standard deviation of projected stream kms derived from the ensemble of glacier retreat projections for RCP4.5.**

The timing of when future salmon-accessible streams are exposed depends on the modelled rate of glacier retreat across the 18 sub-regions investigated (Figure 3.2). Of the total salmon-accessible stream kms that could be gained with potential complete deglaciation, 22% will be gained by 2050, and 62% by 2100. Although few, all the salmon-accessible stream gains projected for the Skeena River watershed and North Coast of BC will be created by 2050. In contrast, in the Gulf of Alaska sub-region, which contains some of the largest remaining icefields in North America, only ~20% of new stream kms will be created by 2050. The different climate scenarios affect the projected rates of new stream creation, with the RCP8.5 scenario projecting faster rates of glacier retreat, and thus earlier potential salmon-accessible stream gains in all 18 sub-regions.

3.3. Creation of Pacific salmon habitat for spawning and juvenile rearing

A subset of the created future salmon-accessible streams will possess geomorphic conditions associated with favorable salmon spawning and juvenile rearing habitat. We conservatively estimate that glacier retreat will create a total of ~1,900 kms of future salmon habitat (gradient threshold <10%, 0-2% gradient for spawning and rearing habitat) by 2100 under RCP 4.5 (Figure 3.3). However, it will likely take additional time for further habitat evolution, such as channel stabilization, in order for newly accessible and appropriate salmon habitat to become productive for some salmon species (O'Neel et al. 2015; Milner et al. 2017; Schoen et al. 2017; Pitman et al. 2020). The Gulf of Alaska and Copper River sub-regions have the largest projected increase in salmon spawning and rearing habitat, with ~760 and ~410 kms, respectively, by 2100 (Figure 3.3). However, watershed topography exerts a strong control on future habitat expansion. For example, projections for the Alsek River watershed using lower accessibility (<10%) and habitat (0-2%) gradients show an increase of ~160 km of spawning and rearing habitat by 2100, whereas projections using steeper accessibility (<15%) and habitat (0-4%) gradients show over two times (~385 km) more habitat gained (Figure 3.3). Thus, future increases in salmon habitat will vary depending on the swimming abilities of the particular species and the specific topography of each watershed.

(a) conservative projections of new habitat

(b) projected new habitat with steeper river accessibility

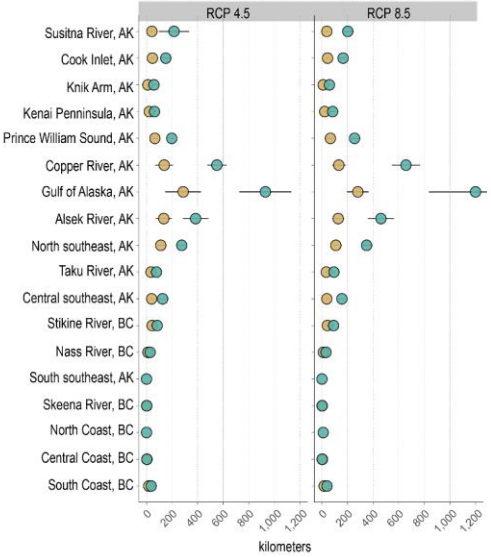

Figure 3.3 Projected kms suitable for salmon spawning and juvenile rearing habitat by 2050 and 2100 for each of the 18 sub-regions. Habitat kms for the 18 sub-regions were computed from a glacier projection model for the years 2050 (yellow) and 2100 (green), based on 10-year averages centred around these years. The glacier projections are shown as an ensemble-mean ± one standard deviation for each of the two emission scenarios (RCP4.5, RCP8.5). The 18 sub-regions are listed from higher to lower latitude. (a) Projected kms of spawning and juvenile rearing habitat (0-2% gradient) from salmon-accessible (<10% gradient) streams larger than first order. (b) Projected kms of spawning and juvenile rearing suitable habitat (0-4% gradient) from salmon-accessible streams with steeper accessibility (<15% gradient).

Gains in salmon habitat are substantial enough that they could lead to emerging salmon fisheries in some locations. For example, one km of suitable stream habitat can produce ~500–1,500 juvenile coho salmon (Table 3.2) (Bradford et al. 1997). Thus, with hundreds to thousands of kms of new habitat being created from glacier retreat there is a potential to produce hundreds of thousands to millions of additional juvenile salmon, depending on species (Quinn 2018). These estimates of suitable salmon habitat are measured from stream gradient and accessible stream length. Despite potentially interacting freshwater conditions that can influence salmon productivity such as water temperature and flow, sediment supply, and stream morphology, juvenile salmon production is strongly and positively related to available stream length across diverse watersheds (Bradford et al. 1997). Thus, as the extent of stream habitat increases, the number of salmon in those streams will generally increase, assuming adequate water quality and supply. Unless overshadowed by larger-scale declines in salmon productivity, such as due to decreased ocean survival (Mantua et al. 1997; Mueter et al. 2002), these forecasted increases in stream kms could lead to emerging salmon fisheries of local importance when the adults return to spawn. For example, over the last century, glacier retreat in the Kenai Peninsula, Alaska, led to the establishment of sockeye salmon populations that supported a local commercial fishery (Milner 1997). While salmon populations are controlled by many factors across their life-cycles that are shifting with climate change (Crozier et al. 2019), areas with increases in the extent of freshwater habitat represent new hotspots of potential increased salmon production.

3.4. Downstream effects of glacier retreat and broader context

Approximately 50% of the glacier area within the study region occurs in steep, mountainous terrain that is inaccessible to migratory salmon, particularly in British Columbia, Canada (Figures 3.2 and 3.3). However, the decrease of runoff from these perched alpine glaciers will impact the quality of downstream salmon habitat (Martins et al. 2012; Milner et al. 2017; Pitman et al. 2020). Across the range of Pacific salmon, southern arid regions will be challenged as glacier meltwater diminishes. This meltwater can sustain water flow and provide cool well-oxygenated water for salmon during the summer months, and its loss could decrease the quality and quantity of salmon habitat (Sergeant et al. 2017; Fellman et al. 2018; Pitman et al. 2020). In contrast, southcentral

Alaska regions, such as the Copper River, will experience substantial increases in glacier meltwater during the summer months over the coming years due to the extensive network of glaciers that contribute flow to pro-glacial rivers (Huss and Hock 2018). Thus, retreat of inaccessible glaciers will have contrasting impacts on downstream salmon habitats across an extensive region via a variety of mechanisms (Pitman et al. 2020).

More broadly, rapid contemporary glacier retreat is only one consequence of anthropogenic climate change; the realized effects of glacier retreat on Pacific salmon populations will depend on interactions with other climate-induced stressors such as ocean heat waves, sea level rise, warming air temperature, and extreme flood events or droughts, all of which could cause widespread declines in salmon abundance (Crozier et al. 2019). Nevertheless, our results indicate that the next century of rapid climate change will cause shifts in both the amount and location of potential salmon habitat.

Understanding future shifts in suitable habitat for Pacific salmon and other species of importance (Morley et al. 2018) can support forward-looking management and conservation. For example, glacial retreat may not only represent a frontier for salmon habitat, but also for mining opportunities. The heavily glacierized ‘transboundary region’ of southeast Alaska/British Columbia, which has substantial forecasted gains in salmon habitat, is concurrently experiencing a modern-day gold rush with potentially far-reaching and long-lasting environmental impacts (Sexton et al. 2020). Mineral claims have been staked in regions currently covered by ice, and mines have been approved in recently deglaciated areas. Our findings indicate that effective protection of Pacific salmon from mining and other watershed developments will entail conserving current salmon habitat while also avoiding the degradation of their future habitat. Whether the climate frontiers in the Arctic ocean, or glacier-covered watersheds, there is an urgent need for science to inform the conservation and management of Pacific salmon and the future distributions of their freshwater habitat (Standal 2003; MacNeil et al. 2010; Gross 2018; Pirotta et al. 2018).

3.5. Methods

3.5.1. Sub-regions.

The study region focuses on 18 sub-regions within the Pacific mountain ranges of North American overlapping with the North American range of Pacific Salmon with more than 1.5% glacier cover (Figures 3.1 and 3.2). The term "sub-region" here refers to either a single major salmon watershed or aggregates of small coastal watersheds, which range in area from ~13,000 to ~68,000 km^2. For sub-regions within Alaska, USA, we accessed boundary data from the Watershed Boundary Database at the USGS (https://www.usgs.gov/). For sub-regions within British Columbia, Canada, we accessed boundary data from the Freshwater Atlas of British Columbia (https://catalogue.data.gov.bc.ca/). Pacific salmon range data were from the National Center for Ecological Analysis and Synthesis (Figure 3.1). The study region covers ~623,000 km^2 across the British Columbia, Canada and Alaska, USA and approximately 20% of the total North American range of Pacific salmon.

3.5.2. Glacier outlines.

Outlines for the 45,963 glaciers within the study region were obtained from the Randolph Glacier Inventory v6.0 (https://www.glims.org/RGI/), which provides a globally complete dataset of glacier outlines outside of Greenland and Antarctic ice sheets (RGI Consortium 2017). These glaciers cover a total area of ~81,000 km^2, which corresponds to 80% of total glacier area in the Pacific mountain ranges within North America. The glacier outlines refer roughly to the years 2009 ± 2 for Alaska, and 2004 ± 5 for Western Canada (Pfeffer et al. 2014; RGI Consortium 2017). Glacierization for each of 18 sub-regions ranges from 1.5% to 52%.

3.5.3. Present-day streams.

Synthetic stream networks were constructed from Digital Elevation Models (DEMs) for each of the 18 sub-regions using Geographic Information Systems (GIS; ArcGIS 10.6 and QGIS 2.18) hydrology tools to represent present-day streams and rivers throughout the study region. Specifically, we used Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) global DEMs v2.0 with a spatial resolution of ~30 m

(Tachikawa et al. 2011), and vertical resolution of ~± 5 m (Elkhrachy 2018). Open access synthetic stream network datasets such as the National Hydrography Dataset (NHD) from the USGS and the Freshwater Atlas from British Columbia government are available but were not used due to inconsistencies in spatial resolution across the study region. From our synthetic stream networks, we eliminated all stream segments that overlapped with the RGI glacier outlines because the ASTER global DEMs used to create the synthetic stream networks represent glacier surface elevation rather than estimated deglaciated terrain. Our analysis required estimated deglaciated terrain values to create newly formed streams following glacier retreat.

3.5.4. Identifying salmon migration barriers in present-day streams.

There is a large body of literature that estimates the stream gradient suitability for migrating Pacific salmon (Cooney and Holzer 2006; Burnett et al. 2007; Sheer et al. 2009; Bidlack et al. 2014). Based on the literature suggesting particular stream gradients suitable for salmon migration (e.g., ranging from <10% - 20%), and our own validation results (see below), we applied a conservative stream gradient threshold of 10%, and more inclusive alternative of 15%, to the synthetic present-day stream networks representing streams suitable for migrating adult salmon. The 15% gradient threshold represents accessibility for salmon that are capable of swimming up steeper gradients (e.g., Chinook salmon). To measure stream gradient, we broke the synthetic stream network in ~500 m segments, calculated the slope of each stream segment by extracting elevation values from the ASTER global DEMs for both ends of each segment, then divided the elevation difference by the segment length. The ~500 m stream segment length was the minimum distance possible given the spatial resolution of our study region (see Uncertainties). The upper limits of salmon migration within present-day streams were then identified by selecting contiguous stream segments in the direction from river mouth to headwaters (i.e., glacier tongue) that were below the different stream gradient thresholds (10% and 15%). The synthetic present-day stream network was used to identify which glaciers would be accessible to migrating adult salmon below the identified migration thresholds.

To verify the migration stream gradient thresholds presented in the literature, we used Pacific salmon presence data, containing a spatial reference (latitude and longitude), obtained from the Anadromous Waters Catalogue (AWC;

www.adfg.alaska.gov/sf/SARR/AWC) for a sample watershed, the Susitna River watershed, that supports good coverage of all five species of Pacific salmon (Figure 3.4). Using GIS, we ran a network analysis on our present-day stream networks that were segmented into ~500 m stream lengths containing slope values for each of these segments. We used the slope value associated with each ~500 m segment representing the maximum stream gradient that salmon could pass, between river mouth and observed location for each Pacific salmon species (Figure 3.4). The values show that apart from coho, all species of Pacific salmon can migrate in stream sections with gradients of 10%, with Chinook, chum, and pink salmon being identified in stream segments ≥ 15% (Figure 3.4). Thus, we selected the migration stream gradient thresholds of 10% and 15% based on maximum rather than median values as it is likely that there are salmon present in the upper more difficult reaches of streams that are not identified in this dataset. The AWC is maintained by the State of Alaska and contains all known anadromous streams based on fish surveys. However, given the difficulties inherent in surveying for fish throughout Alaska, the AWC is incomplete, and Pacific salmon are likely present in many unsurveyed streams. Thus, this analysis of fish presence represents a minimum of the extent of fish occurrence and therefore is conservative.

3.5.5. Future salmon-accessible streams created from estimated deglaciated bedrock.

We selected glaciers that were within 100 m of the present-day stream network below adult salmon migration stream gradient thresholds of 10% and 15%. We define these glaciers as “accessible”. From each of the accessible glaciers, we created future synthetic stream networks from estimated deglaciated bedrock (see below). We joined the present-day stream network with the future stream network creating one continuous stream that salmon could access once deglaciated.

We estimated the deglaciated bedrock terrain by subtracting gridded ice thickness data from ice surface DEMs for every accessible glacier within our study region. Ice thickness distribution was calculated at a grid resolution of 25 to 200 m (depending on glacier area) using a simple dynamic model that considers glacier mass turnover and ice flow mechanics, and by inverting the glaciers’ surface topography (Huss and Farinotti 2012). The data set was updated to RGI v6.0 and is in close agreement with the recently released global consensus glacier ice thickness product (Farinotti et al. 2019). Inferred ice thickness was validated against a set of ice-penetrating radar observations (Huss and Farinotti 2012). Surface DEMs were obtained from the Shuttle Radar Topography Mission (SRTM) DEMs for glaciers below 60°N, and from ASTER global DEMs for glaciers above 60°N.

We built a future synthetic stream network derived from estimated deglaciated bedrock terrain beneath accessible glaciers using the ArcGIS hydrology toolbox. As with the present-day stream network, we split the future synthetic stream network into ~500 m segments, extracted the elevation value from both ends of each segment, applied the rise/run equation, and eliminated all segments above 10% or 15% from the stream network. We assigned stream order to each stream segment using the program RivEX to determine each stream segments size. Stream order is a metric used to measure the relative size of streams, where the smallest tributaries are referred to as first-order streams, which flow into larger streams that combine to form streams of higher order. All future stream segments derived from deglaciated bedrock terrain beneath accessible glaciers below the adult migration thresholds (<10% and 15%) of all sizes (stream orders 1-4) were termed “future salmon-accessible streams”. The absolute future salmon-accessible stream kms were summed for each of the 18 sub-regions (including stream order; Table 3.3) to determine the extent of new streams suitable for migrating adult salmon. Last, we calculated the relative increase in stream kms for each of the 18 sub-regions by dividing the total future salmon-accessible stream kms, projected to be created in 2100, by the total present-day stream kms below either a 10% (Figure 3.2) or 15% (Figure 3.5) stream gradient threshold.

3.5.6. Glacier retreat modelling and exposure of future salmon-accessible streams.

To project the retreat of glaciers, we applied the Global Glacier Evolution Model (GloGEM) to each of the accessible glaciers (Huss and Hock 2015). GloGEM computes glacier mass balance and associated geometry changes for each individual glacier in the study region (Huss and Hock 2015). To calculate glacier surface mass balance, as a difference between accumulation (snowfall and refreezing) and ablation (glacier surface melting), GloGEM was forced with a monthly timeseries of near-surface air temperature and precipitation. Glacier geometry changes (e.g. thinning and/or shrinking) were assessed from the surface mass balance coupled with the empirically derived functions of glacier thinning along the glacier centerline (Huss et al. 2010). For annual mass losses at marine- or lake-terminating glacier fronts, glacier retreat was approximated by accounting for glacier front height and width (Oerlemans and Nick 2005). The total mass changes for each glacier were used to adjust surface elevation and extent on a yearly basis. Previous work gives further details of the model, its calibration, and downscaling procedures (Huss and Hock 2015, 2018).

To project the glacier retreat for the benchmark years 2050 and 2100, we forced the glacier model with temperature and precipitation time series from an ensemble of five GCMs. The five GCM models were selected as they showed better performance in simulating climatology over North America relative to other Coupled Model Intercomparison Project 5 GCMs (Radić and Clarke 2011): CanESM2, CSIRO-Mk3-6-0, GFDL-CM3, MIROC-ESM, and MPI-ESM-LR. The GCMs are subjected to a range of specified climate forcings that correspond to plausible scenarios for the rate of change in the concentration of atmospheric CO_2 and other greenhouse gases. For the IPCC AR5 these scenarios are referred to as Representative Concentration Pathways (RCPs) and the standard emission scenarios are RCP2.6, RCP4.5, RCP6.0, RCP8.5 (Meinshausen et al. 2011). For several of the GCMs we used, the RCP6.0 was omitted, and the RCP2.6 is likely to not be reached (Sanford et al. 2014), therefore we selected the RCP4.5 and RCP8.5 for the glacier modelling. The glacier model is forced by each GCM in the ensemble, while the projections of glacier retreat are presented as the ensemble-mean for each RCP.

We use the glacier retreat projections to assess how many future salmon-accessible stream kms would come available by the years 2050, 2100, and in the case of total potential deglaciation for each of our 18 sub-regions (Figure 3.1b). We considered when each future salmon-accessible stream segment, below either the 10% or 15% stream gradient thresholds, would become exposed from glacier ice based on 10-year averages of modelled glacier extent centered around the years 2050 and 2100 for both the RCP 4.5 and RCP 8.5 and each of the five GCMs, and the ensemble-mean. We then summed the stream kms that would be available by the projected 2050 and 2100 years for each of the 18-sub regions.

3.5.7. Defining salmon habitat requirements using stream gradient and order.

We determined how many of the future salmon-accessible stream kms could be used specifically for salmon spawning and rearing habitat by selecting stream segments with stream orders greater than first order, and with gradients ranging from either 0-2% or 0-4%. While we acknowledge that salmon can use first-order streams, we focus on streams greater than first order, which includes second-, third-, and fourth-order streams. Thus, our analysis indicates that suitable spawning and rearing habitat from the future salmon-accessible stream networks had segments with stream orders that ranged from second to fourth, with stream gradients ranging from either 0-2% or 0-4%.

From the future salmon-accessible streams, we determined the amount of salmon habitat by summing the stream kms based on two scenarios (i.e., 0-2% spawning/rearing with a <10% stream gradient threshold; and, 0-4% spawning/rearing with a <15% threshold), then determined when the stream habitat would become available for the years 2050 and 2100 for each of the 18 sub-regions (Figure 3.3). The two scenarios help capture the fact that different salmon species have different tendencies in terms of stream gradients associated with spawning and rearing (Figure 3.6) (Quinn 2018).

3.5.8. Uncertainties

Given that our study integrated models, data inputs, and analytical approaches for salmon habitat across a large study region, it is important to consider potential uncertainties and sensitivities. These potential sources of uncertainty include the selected segment lengths used for the stream gradient thresholds, glacier model forecasts, and glacier ice thickness estimates. Below we examine these sources of uncertainty. While there are important assumptions and uncertainties, our analysis provides reasonably robust predictions across a 623,000 km^2 region containing almost 50,000 glaciers.

The stream gradient thresholds applied were based on a segment length of ~500 m and a DEM with a 30 m resolution. We chose the ~500 m segment length because shortening the segment length created streams that were dissimilar to established stream networks (such as the NHD USGS), and the 30 m DEM resolution was the finest resolution available across the study region. These segment length and resolution limit the accuracy and precision of the synthetic stream networks, and thus how we derived our stream gradient thresholds. For example, in a ~500 m segment it is impossible to know the exact stream characteristics present (e.g., longer series of riffles vs. a single large waterfalls), and Pacific salmon upstream migration is generally restricted by certain stream features such as waterfalls. Therefore, some segments with 10% stream gradient may contain a migration barrier whereas others may not. For comparison, other studies have used similar reach lengths of 200 m (Beechie and Imaki 2014) and 500 m (Klett et al. 2013).

We could not validate our stream gradient thresholds for adult salmon migration against known barriers (e.g., waterfalls) because there are no known datasets of salmon migration barriers between southern British Columbia and Alaska. Therefore, to determine if the number of accessible glaciers would vary under different stream segment lengths used for determining stream gradient thresholds, we ran a sensitivity analysis on the present-day streams using ~250 m, ~400 m, ~600 m, and ~750 m segment lengths and a 10% stream gradient threshold. We ran this analysis for two sample sub-regions, North Southeast, AK, and Taku River, AK. For the North Southeast, AK, watershed the number of salmon-accessible glaciers changed within the range of -16% to 9% (~90- ~350 ha), depending on the segment length (Table 3.4). For the Taku River, AK sub-region there were the same number of salmon-accessible glaciers in all segment length scenarios (Table 3.4). Thus, given the available resolution of the DEM, the application of ~500 m segment lengths did not strongly influence the results. We also acknowledge that some migration barriers depend on river flows. Our analysis covering 623,000 km^2 should be viewed as the best-available predictions that require field validation at specific locations.

We also ran a sensitivity analysis on future salmon-accessible streams using ~250 m and ~750 m segment lengths and a 10% stream gradient threshold for each of the 18 sub-regions to understand variations in total future salmon-accessible stream kms given different segment lengths (Table 3.5). The difference in future salmon-accessible stream kms when applying a ~250 m versus the ~500 m segment length ranged from -27% to +3% depending on sub-region, whereas the difference in future salmon-accessible stream kms ranged from -2% to +51% when applying a ~750 m segment length. With the ~250 m segment length there are more opportunities for the slope calculation to be above the 10% stream gradient because there are more segments in the stream network, whereas the opposite is true of the ~750 m segment length. In addition, there are more salmon-accessible stream kms when using the ~750 m segment lengths as the segments extend further into the upper reaches of the stream network, whereas the opposite is true of the ~250 m segment length. Thus, the total future salmon-accessible stream kms are greater when using the ~750 m segment length versus the ~250 m. On average between all 18 sub-regions, the total future salmon-accessible stream kms when using the ~250 m segment length is 14% less, and when using the ~750 m segment length is 11% more. Given that the uncertainties in the DEM become more relevant for shorter versus longer lengths, and the small amount of variation in our sensitively analysis results, we chose to use the ~500 m segment length, which was a good trade-off between capturing the accuracy and precision of the stream network and data limitations.

We were unable to measure or estimate the many landscape variables (e.g., channel width and confinement, stream flow, stream temperature, riparian forest development) that are important to Pacific salmon throughout their life cycle (Beechie et al. 2001; Pess et al. 2002; Steel et al. 2004; Firman et al. 2011; Bidlack et al. 2014). Moreover, field measurements of variables such as sediment supply, grain size, bankfull discharge, and channel slope are not readily available over large geographic areas (Beechie et al. 2006; Davies et al. 2007), and impossible to obtain for sub-glacier environments. Many studies have determined ways to extract important environmental variables for salmon using DEMs (Beechie and Imaki 2014; Sloat et al. 2018). However, this type of analysis was not possible given the uncertainties in estimating the deglaciated bedrock topography, which was generated from ice surface DEMS and gridded ice thickness data, some that had a resolution of up to 200 m for the largest glaciers. Therefore, only stream order and gradient were used in determining salmon streams and suitable habitat for spawning and rearing (Lunetta 1997). However, these metrics are useful and accurate in identifying suitable habitat for Pacific salmon, as shown by other studies (Lunetta 1997; Sharma and Hilborn 2001; Burnett et al. 2003).

There are uncertainties in the IPCC climate model projections (IPCC 2013), and therefore, in the projected 2050 and 2100 deglaciated terrain beneath accessible glaciers. However, climate models similar to those used in this analysis have shown to be quite accurate at predicting future temperature changes (Hausfather et al. 2020). To illustrate the uncertainty in the climate models, for each of the 18 sub-regions, we display variation due to the choice of GCM by calculating the future glacier extents as the ensemble-mean + one standard deviation in both Figures 3.1 and 3.2.

There is known error in modelled ice thickness distribution based on a comparison of ice thickness models. Farinotti et al. (2017) estimate deviations on the order of 10 ± 24% of the mean ice thickness for 21 glaciers relative to in situ measurements. Thus, there could be some error in the inferred elevation estimates for the estimated deglaciated bedrock topography. However, ice thickness models show a good performance regarding the patterns of thickness distribution (thin/thick parts of the glacier), even when the average estimated ice thickness of an individual glacier may be high or low. Moreover, errors in estimated elevation of the bedrock are likely similar at either end of a ~500 m reach (Farinotti et al. 2017). Hence, the errors in calculation of slopes are likely reduced due to spatial correlation of errors in the ice thickness estimates.

The stream gradient analysis is based on the deglaciated bedrock topography, estimated from the bedrock beneath the glacier ice, and does not account for any sediment accumulation, or valley fill. Therefore, our stream gradients analyses are likely to be conservatively estimated for larger, less steep streams. In these streams, sediment will accumulate on the bedrock surface, making their overall stream gradient less steep (May and Gresswell 2003), whereas in relatively small and steep streams that typically originate in high elevation mountain slopes, sediment accumulation will occur less frequently, and our projections may be more accurate.

3.6. Acknowledgements

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3.7. Supplementary Material

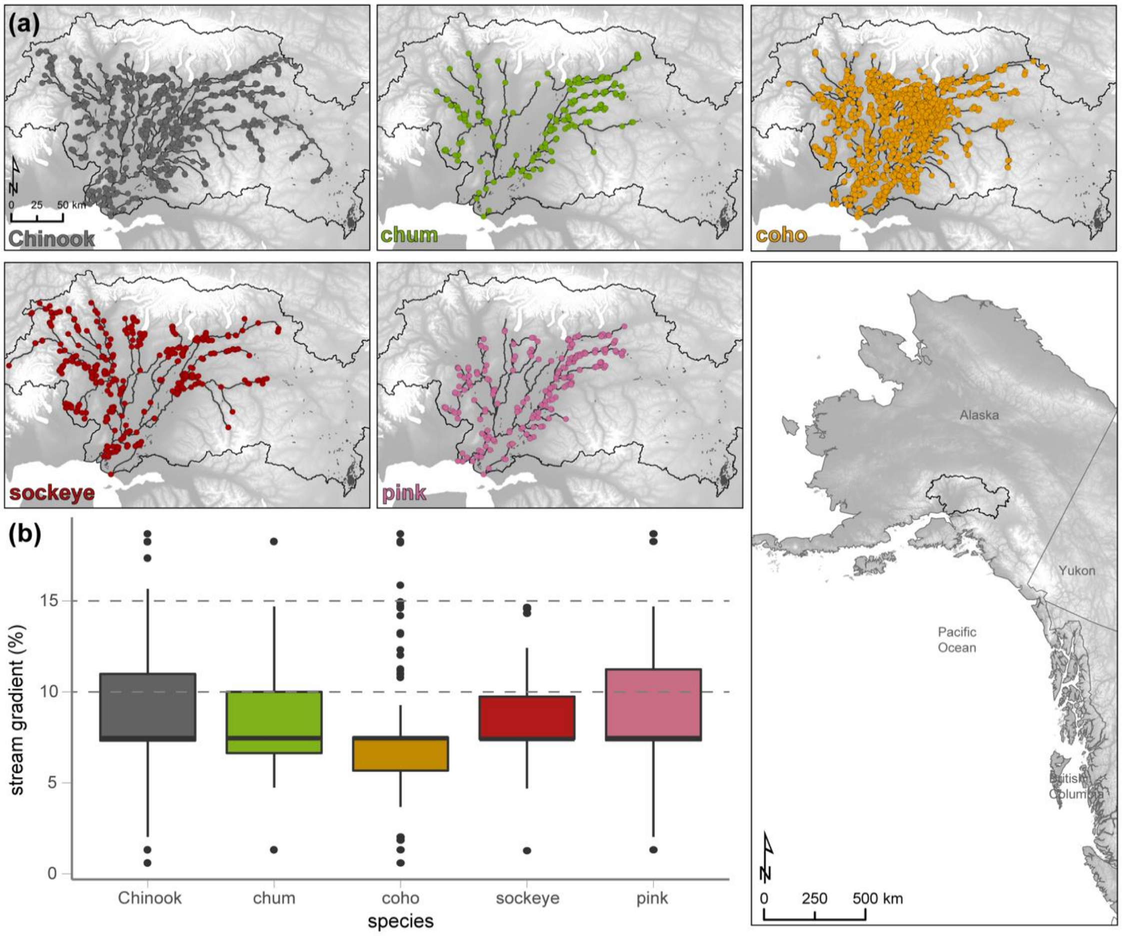

Figure 3.4 Migration stream gradient thresholds for each Pacific salmon species in the Susitna River, Alaska. (a) points represent Pacific salmon presence obtained from the Anadromous Waters Catalogue (AWC; www.adfg.alaska.gov/sf/SARR/AWC), maximum stream gradient value that a salmon would cross along stream segments (~500 m lengths), between stream outlet and observed location. (b) box plot showing median stream gradient along stream segments from stream outlet to point data. Upper quartiles of the boxplot are maximum gradient each Pacific salmon species can access. Dotted lines represent the 10% and 15% stream gradient thresholds.

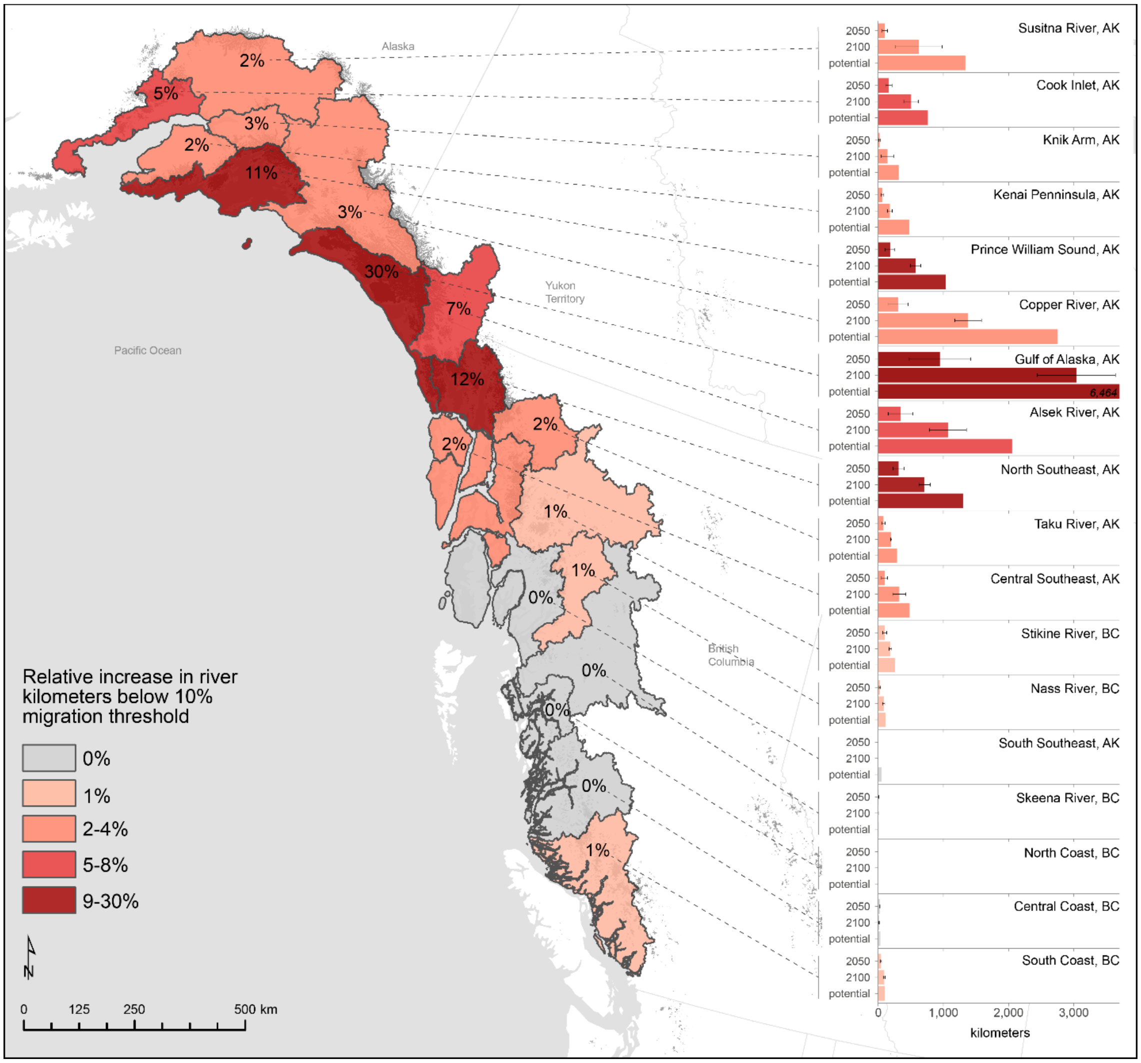

Figure 3.5 **Projected future salmon-accessible stream kms with <15% stream gradient migration threshold. Map shows the projected percent increase in future salmon-accessible stream kms, below a 15% stream gradient threshold for 2100, relative to present-day stream kms summed for each of the 18 sub-regions. Glacier retreat projections, in response to five GCMs with RCP4.5 emission scenario, are used as an ensemble-mean. Bar plots represent the projected future salmon-accessible stream kms with <15% stream gradient threshold for the years 2050, 2100, and complete potential deglaciation (i.e., once glaciers have retreated completely from the landscape) for each of the 18 sub-regions. Projections are computed from 10-year averages centred around these years. Error bars represent + one standard deviation of projected stream kms derived from the ensemble of glacier retreat projections for RCP4.5. Note that x-axis is different from Figure 3.2.**

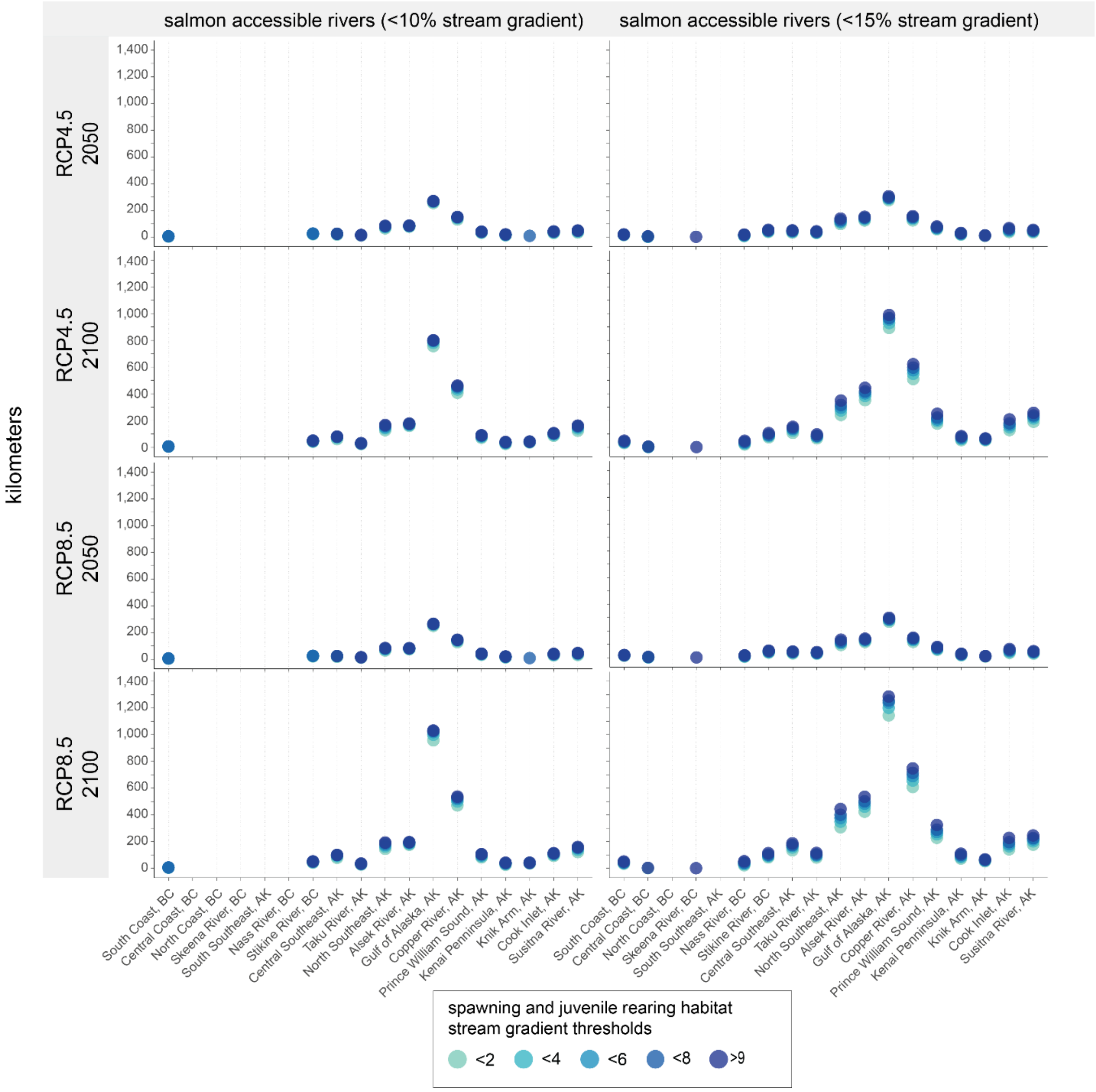

Figure 3.6 **Projected salmon spawning and rearing habitat kms over stream gradients ranging from 0-10% for different RCP scenarios in 2050 and 2100. The results refer to the summed stream kms by habitat (spawning and rearing) slope thresholds (light – dark blue) for the 18 sub-regions based on either 10% or 15% stream gradient migration thresholds. Results are derived from the ensemble-mean of glacier retreat projections in response to five GCMs for each of the two emission scenarios (RCP4.5, RCP8.5) for the years 2050 and 2100. The 18 sub-regions are listed from higher to lower latitude.**

Table 3.1 Stream gradient representing habitat suitability for spawning and rearing for different Pacific salmon species including referenced literature.

species	value	location	life phase	resource
coho	0 – 4%	South Fork Stillaguamish River, USA	spawning and rearing	(Benda et al. 1992)
coho	0 – 4%	Skagit River, WA	spawning	(Beechie et al. 1994)
coho	0 – 4.8%	Washington State, USA	rearing	(Beechie and Sibley 1997)
coho	0 – 3%	Regional	rearing	(Bradford et al. 1997)
coho	0 – 7%[1]	western Oregon	rearing	(Burnett et al. 2007)
coho	0 – 7%	Pacific Northwest	spawning and rearing	(Sheer et al. 2009)
coho	0 – 4.5%	southeast Alaska	spawning	(Sloat et al. 2018)
chum	0 – 3%	Pacific Northwest	spawning and rearing	(Sheer et al. 2009)
chum	0 – 4.5%	southeast Alaska	spawning	(Sloat et al. 2018)
pink	0 – 4.5%	southeast Alaska	spawning	(Sloat et al. 2018)
sockeye	0 – 7%	Pacific Northwest	spawning and rearing	(Sheer et al. 2009)
Chinook	0 – 1.5%	Puget Sound	rearing	(Cooney and Holzer 2006)
Chinook	0 – 7%	Pacific Northwest	spawning and rearing	(Sheer et al. 2009)
Chinook	<4%[2]	Copper River, AK	spawning and rearing	(Bidlack et al. 2014)
steelhead	0 – 4%	South Fork Stillaguamish River, USA	spawning and rearing	(Benda et al. 1992)
steelhead	0 – 4.8%	Washington State, USA	rearing	(Beechie and Sibley 1997)
steelhead	0.5 – 7%[3]	Puget Sound	rearing	(Cooney and Holzer 2006)
steelhead	2 – 3%[4]	western Oregon	rearing	(Burnett et al. 2007)
steelhead	0 – 8%	Pacific Northwest	spawning and rearing	(Sheer et al. 2009)

[1] rear mostly in low gradients and decrease in density as slope increases, nothing upstream of 7. [2] Highest intrinsic potential between 0.5 – 1.5%. [3] densities remained high as gradients increased >4%. Low density at gradients <0.5%, increasing as gradients rose to ~4%. [4] 2 – 3% are optimal, no use upstream of reaches with gradients exceeding 10%.

Table 3.2 Smolt productions/km for coho salmon including referenced literature.

species	value	location	life phase	resource
coho	600 smolts/km	Skagit River, WA	smolts	(Beechie et al. 1994, 2001)
coho	2,732 smolts/km	Big Qualicum River, BC	smolts	(Johnson 1986)
coho	1,367 smolts/km	glacially fed streams	smolts	(Zillges 1977)
coho	250 smolts/km	Baker River, WA	smolts	(Chapman 1981)
coho	457-1,476 smolts/km	Regional	smolts	(Bradford et al. 1997)

Table 3.3 Total kms by stream order once the glaciers have reached potential complete deglaciation.

	<10% stream gradient					<15% stream gradient				
	stream order									
	1st	2nd	3rd	4th	5th	1st	2nd	3rd	4th	5th
Susitna River, AK	404	151	93	15	0	723	269	196	18	0
Cook Inlet, AK	268	94	50	0	0	374	177	100	0	0
Knik Arm, AK	127	38	44	0	0	155	66	65	0	0
Kenai Peninsula, AK	58	29	13	0	0	208	107	39	32	22
Prince William Sound, AK	265	105	48	0	0	486	245	137	12	0
Copper River, AK	1,008	452	219	12	0	1,406	678	396	37	0
Gulf of Alaska, AK	2,918	954	299	179	52	3,883	1,375	527	320	62
Alsek River, AK	493	171	57	0	0	1,077	471	235	94	4
North Southeast, AK	297	167	56	16	0	579	330	203	46	0
Taku River, AK	69	41	8	0	0	125	102	29	0	0
Central Southeast, AK	121	61	32	26	0	219	123	64	26	0
Stikine River, BC	56	32	21	0	0	105	88	31	0	0
Nass River, BC	0	0	0	0	0	45	26	24	0	0
South Southeast, AK	0	0	0	0	0	26	18	0	0	0
Skeena River, BC	2	1	0	0	0	5	1	0	0	0
North Coast, BC	2	0	0	0	0	2	0	0	0	0
Central Coast, BC	0	0	0	0	0	18	5	0	0	0
South Coast, BC	18	7	0	0	0	44	30	18	0	0

Table 3.4 **Total number (and area) of glaciers that salmon can access modelled from present day streams based on the 10% stream gradient threshold using four different stream segment lengths for two sample sub-regions, North Southeast, AK, and Taku River, AK. Bolded is the ~500 m segment length used in this analysis.**

	North Southeast, AK		Taku River, AK	
	number of glaciers	area (HA)	number of glaciers	area (HA)
250m	27	3593.7	8	1241.9
400m	32	3889.0	8	1241.9
500m	**32**	**3505.0**	**8**	1241.9
600m	33	3821.5	8	1241.9
750m	35	3857.5	8	1241.9

Table 3.5 **Total future salmon-accessible stream kilometres using the 10% stream gradient threshold for two different segment length scenarios, ~250 m and ~750 m for once the glaciers have reached potential complete deglaciation summed by sub-region. Included is the % change from the ~500 m segment length used in our analysis**

	500 m	250 m	% change	750 m	% change
Susitna River, AK	675	596	-12	707	5
Cook Inlet, AK	423	387	-8	459	9
Knik Arm, AK	212	183	-14	229	8
Kenai Peninsula, AK	104	76	-27	102	-2
Prince William Sound, AK	429	301	-30	424	-1
Copper River, AK	1713	1284	-25	1878	10
Gulf of Alaska, AK	4423	4134	-7	4932	11
Alsek River, AK	721	578	-21	807	10
North Southeast, AK	546	433	-21	662	21
Taku River, AK	120	94	-22	124	3
Central Southeast, AK	243	204	-16	367	51
Stikine River, BC	111	91	-18	111	0
Nass River, BC	0	0	0	0	0
South Southeast, AK	0	0	0	0	0
Skeena River, BC	3	3	3	3	14
North Coast, BC	2	2	-2	2	-10
Central Coast, BC	0	0	0	0	0
South Coast, BC	25	24	-6	25	-1

Chapter 4.

The role of tributaries in cooling an important salmon migratory corridor.

4.1. Abstract

Climate change and its associated symptoms, such as warming temperatures, glacier retreat, reduced snowpack, and increased variability in precipitation, are warming rivers and lakes. Such warming water temperatures are harming cold-water fishes. For instance, warm water temperatures may kill or harm important populations of anadromous Pacific salmon as they migrate upstream to spawning grounds. In this study we assessed how tributaries, and their relative watershed properties, shape the temporal and spatial dynamics of temperatures in salmon migratory rivers. We focused on the Babine River of British Columbia, an important migratory corridor for steelhead and the five eastern Pacific salmon species, but particularly for sockeye salmon that spawn in stream reaches above the Babine Lake, at the river's headwaters. We discovered that large glacier- and snowpack- fed tributaries cooled the Babine River by approximately 2°C over its 96 km length. Different tributaries played different temperature functions. Cooler and more glacierized rivers showed a bigger change in temperature between the upstream and downstream sites. Understanding the spatial and temporal dynamics of water temperatures in riverscapes, especially those on the edge of potentially harmful levels, can help inform management options in a warming world. While climate change requires a global effort in reducing greenhouse gas emissions, there are options for localized land use management actions to try to mitigate the effects of oncoming climate warming.

4.2. Introduction

Climate change is warming rivers and lakes and threatening cold-water freshwater fishes (Schindler 2001; Strayer and Dudgeon 2010). For example, the mean summer water temperature of the Fraser River in British Columbia, Canada, has increased by ~1.5°C since the 1950's (Patterson et al. 2007a). This warming has caused mass mortality to some populations of migrating Pacific salmon (*Oncorhynchus* spp.) in particularly hot years, and is predicted to drive a 9-16% decrease in Pacific salmon survival by the end of the century (Martins et al. 2011). More broadly, increasing air temperatures due to climate change (IPCC 2013), as well as associated decreases in glaciers (Zemp et al. 2019), decline in annual mountain snowpack (Mote et al. 2005), earlier spring snowmelt (Rauscher et al. 2008; Islam et al. 2017), and changes in annual distribution of precipitation, are all affecting stream flow and temperature (Hartmann et al. 2013). Climate warming is an urgent threat to freshwater biodiversity, thus it is imperative to understand the landscape processes driving temperature regimes in important Pacific salmon rivers (Isaak et al. 2010; Mantua et al. 2010; Martins et al. 2011).

The impacts on fishes of climate warming in river systems will be influenced by the spatial configuration of aquatic habitats (Fullerton et al. 2017; Steel et al. 2017). River systems, with their branching network structure and potentially high connectivity, are particularly interesting thermal landscapes (Isaak et al. 2010; Peterson et al. 2013; Fullerton et al. 2015). While the diverse climate portfolios of each tributary watershed can buffer downstream flow patterns (Chezik et al. 2017), climatic changes may lead to stream flow and temperatures changes within tributary catchments that may alter the thermal profile of downstream rivers (Fullerton et al. 2015; Steel et al. 2017). In mountainous watersheds, like many in British Columbia, tributary rivers are commonly fed from glacierized and snow-covered mountains, with stream runoff from these landscapes acting as “air conditioners” to downstream rivers, many of which are major migratory corridors for Pacific salmon (Islam et al. 2017; Milner et al. 2017). However, the cooling power of these tributaries may be increasingly compromised by rapid glacier retreat (Clarke et al. 2015) and diminishing persistent spring snowpack (Islam et al. 2017). The spatial distribution of temperatures in river networks influences the management options for effective conservation of cold-water fishes in a warming world (Ebersole et al. 2020).

Stream temperature is a product of local climate, landscape features, and human land-use (Lisi et al. 2013; Steel et al. 2017). While water temperatures generally track air temperatures (Caissie 2006), this relationship may be modulated by multiple complex processes that operate at different scales to ultimately control stream temperature (Webb et al. 2008; Garner et al. 2014; Lisi et al. 2015). Landscape features and characteristics such as glacier cover, snowpack, watershed elevation, and presence of lakes can all influence temperature dynamics. For example, during periods of warm weather glaciers and persistent snowpack experience a significant amount of melt, contributing cold water to downstream water temperatures (Jansson et al. 2003), which can decouple the air and water temperature relationship. Over longer timescales, persistent declining spring snowpack and retreating glaciers will lead to a decline of glacier meltwater contributions to stream runoff (Bliss et al. 2014; Huss and Hock 2018), a processes that would inevitably increase water temperatures. Additionally, large lakes can stabilize and in some instances warm downstream water temperatures depending on the lake-feeding water source (Dorava and Milner 2000; Schoen et al. 2017). Forest harvest also can increase stream temperatures (Pollock et al. 2009). Thus, the local climate and landscape characteristics of the sub-catchments will influence tributary temperatures, and thus control whether tributaries act to cool, or warm, rivers (Bellmore and Baxter 2014; Fullerton et al. 2015).

Pacific salmon populations are increasingly adversely impacted by warming water temperatures in rivers throughout North America (Eliason et al. 2011; Martins et al. 2011; Barnett et al. 2020). High water temperature can alter the rate of physiological processes of migrating Pacific salmon, which depletes their energy reserves increasing mortality rates (Rand et al. 2006; Martins et al. 2011). Generally, water temperatures exceeding 18°C can lead to a reduction in aerobic scope or mortality for sockeye salmon (*O. nerka*) (Naughton et al. 2005; Keefer et al. 2008; Martins et al. 2011), although this may vary based on population and their local adaptions (Eliason et al. 2011; Martins et al. 2011). While salmon have capacity for plastic and adaptive responses to environmental change (Crozier and Hutchings 2014), such as by migrating at different times to avoid excessively warm waters (Reed et al. 2011), quantifying the thermal landscapes of key migratory corridors is of timely importance.

The Babine River, British Columbia, Canada, is an important migratory corridor for steelhead(*O. mykiss*) and the five eastern Pacific salmon species, but particularly for sockeye salmon that spawn in stream reaches above the Babine Lake, at the river’s headwaters (Gottesfeld and Rabnett 2008). The Babine River is the origin of most of the sockeye salmon (80-94%) in the Skeena River Watershed and supports commercial, recreational, and cultural fisheries (Gottesfeld and Rabnett 2008). In some years with warmer temperatures and higher flows, it appears that migration by sockeye salmon may be challenged or delayed through this steep river (Stiff et al. 2015). Water temperature at the outlet of the Babine Lake draining into the Babine River has increased by 1.5°C since the 1900's (Stiff et al. 2015). Unlike other major salmon migratory rivers such as the Fraser River (Patterson et al. 2007a; Martins et al. 2011), there is little understanding of the thermal regime for the Babine River and its tributaries.

Here we investigated the role of tributaries in controlling the water temperatures of an important sockeye salmon migratory river. More specifically, we quantified the monthly and daily temperature profiles along the Babine River mainstem and its major tributaries, determined if tributary rivers entering the Babine River provided cool water inputs, and assessed potential relationships between climate and landscape characteristics of the tributary rivers. We hypothesized that the size and watershed characteristics of each tributary would correlate with its cooling power. We also hypothesized that the tributaries and Babine River mainstem seasonal temperature patterns would vary, driving asynchronous contributions to downstream temperatures. These analyses provide insight into the thermal landscape of the Babine River to inform forward-looking management and conservation of a culturally- and economically- important river and fishery.

4.3. Methods

4.3.1. Babine River watershed

This study was conducted in the Babine River watershed, which drains 10,477 km^2 from the Nechako Plateau through the southern Skeena mountains (Figure 4.1). The Babine River watershed is broken into an upper and lower portion, with the upper watershed being situated in the low-relief Nechako Plateau composed mainly of the Babine Lake, the largest natural lake in British Columbia. The lower watershed, draining from the Babine Lake, consists of the 96 km-long Babine River and other major tributaries, including the Nichyeskwa, Nilkitkwa, Shelagyote, and Shedin drainages (Figure 4.1). The elevation at the Babine Lake outlet is ~700 m, and ~320 m at the Skeena River confluence with a ~380 m loss in elevation along the river's profile. The Babine River is predominantly in a canyon, high gradient, and contains falls and rapids rated up to class IV. Major tributaries, some of which originate from high-elevation snow-capped mountains and glaciers, are steep with widely fluctuating water temperatures, flows, and sediment supply (Gottesfeld and Rabnett 2008). There is presently, and a long history of, extensive forestry within the watershed with some areas such as the Nilkitkwa drainage being more heavily impacted than others (de Groot 2014). In 1999, the Babine River was protected from future development activities by designating the river as the Babine River Corridor Provincial Park (Gottesfeld and Rabnett 2008). The upper part of the Babine River watershed is within Lake Babine Nation territory and the lower portion is within Gitxsan territory.

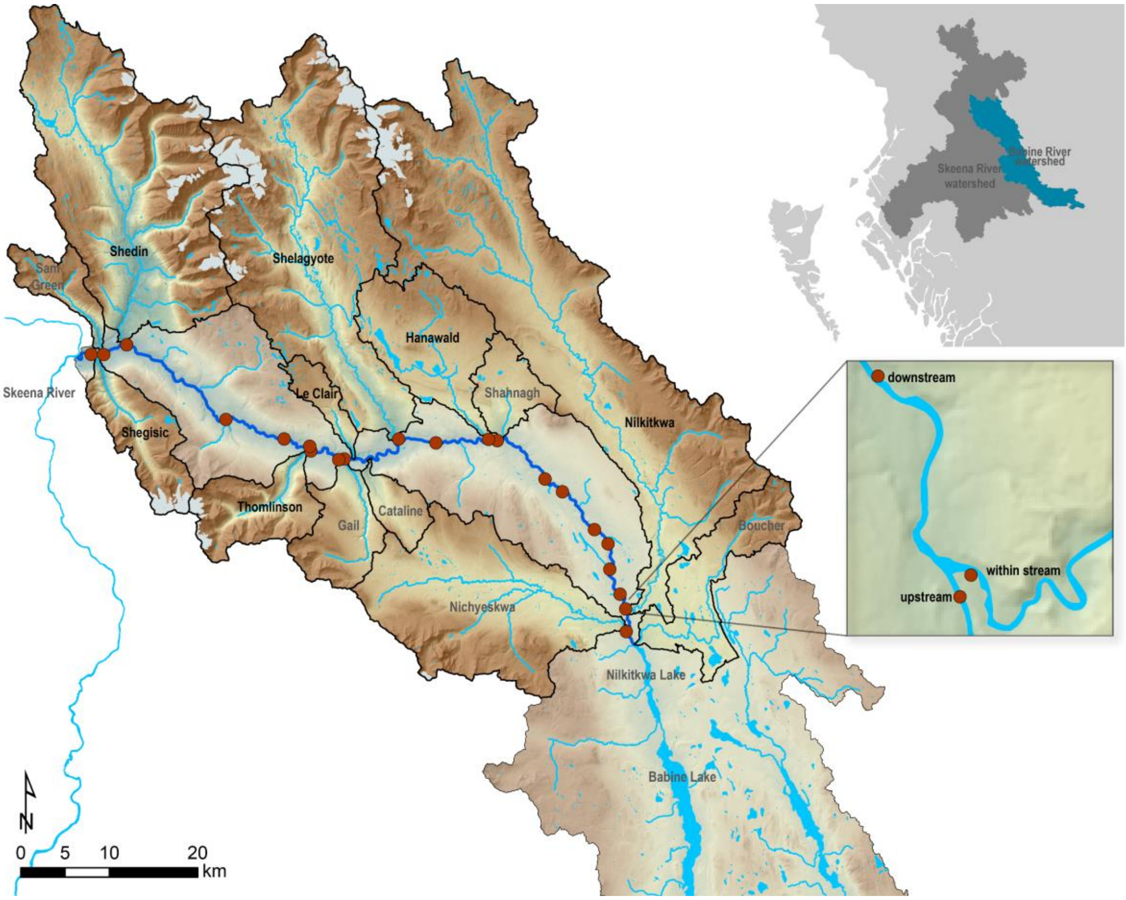

Figure 4.1

Figure 4.1 Babine River watershed and its major tributary watersheds overlaid on a digital elevation model in British Columbia, Canada. Red points represent location of temperature logger sites. Inset map shows temperature logger placement at upstream, within stream and downstream tributary sites. Tributary watersheds identified in bold are those used in our analyses. The Babine River flows northwest from Babine and Nilkitkwa Lake downstream to the Skeena River.

The Babine River watershed is a major producer of all five species of eastern Pacific salmon, including Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), and sockeye salmon fished by

Indigenous, commercial, and recreational fisheries. The Babine River supports the largest sockeye salmon population in Canada, with enhancement channels above Babine Lake; the Babine River produces 90% of the sockeye salmon within the Skeena River watershed. Sockeye salmon typically migrate up the Babine River mainstem between mid-July and the end of August (Gottesfeld and Rabnett 2008). The Skeena River downstream of the Babine River is generally cool (Stiff et al. 2015); thus, the Babine River represents the warmest portion of the arduous migration of these important fishes.

4.3.2. Stream temperature data

We deployed temperature loggers in the Babine River watershed with the goal of understanding how major tributaries influence the Babine River mainstem temperature. Loggers were placed upstream, within, and downstream of major tributaries to capture the relative contribution of each stream to the subsequent downstream temperatures (Marsha et al. 2018). In 2015, we deployed 32 temperature loggers (HOBO Pendants®) upstream, within, and downstream (~1 km) the Nichyeskwa, Nilkitkwa, Hanawald, Shelagyote, Gail, Thomlinson, Shedin, and Shegisic rivers (major tributaries) and along the mainstem of the Babine River (Figure 4.1). In 2016, we obtained, downloaded, and redeployed the loggers, and added 15 additional loggers to the Babine River mainstem and at Boucher, Cataline, Shanagha, Le Claire, and Sam Green tributaries (Figure 4.1). We retrieved all temperature loggers from the Babine River in October 2017. The Babine River is largely inaccessible due to its remoteness and Class IV whitewater rapids. Thus, we accessed and navigated the length of the Babine River by raft, entering the river at the Babine fish weir and exiting at the Skeena River confluence. This project was developed with full recognition of Aboriginal Rights, and all research was conducted with permission to access the territories of Lake Babine and Gitxsan Nations.

Stream temperatures were monitored at two-hour intervals from August 2015 to October 2017. At each site, we anchored the loggers by attaching cable to large healthy trees on the riverbank beyond predicted extreme river flows levels. The loggers were cased with white PVC shields and attached to the cable protecting them from debris and solar radiation that may bias temperature readings (Isaak and Horan 2011). To protect the loggers from de-watering events or being torn out from debris, we attached weights to the loggers and sunk them in deep pools outside of the rivers thalwag. Upon retrieval and downloading of the data, we cleaned the temperature data via manual inspection and removed data believed to be associated with de-watering events (e.g., Sowder & Steel 2012), and averaged remaining raw temperature readings to the daily level. All 2017 data were eliminated from our analysis due to a large flood in early May that destroyed 44% of the data loggers via de-watering events, wedging them beneath boulders, or ripping them off anchored trees. In addition, the Gail River temperature logger data were eliminated from 2016 due to a de-watering event. Thus, our analysis of stream temperature considers July 1 – August 31, 2016, which is typically the period of warmest annual water temperatures and when most Babine River sockeye salmon populations migrate upstream (Stiff et al. 2015).

We assessed the thermal dynamics of the Babine River mainstem and tributaries throughout July and August 2016 (hereafter “summer”) to understand how the temperatures change during the warmest annual period and when adult sockeye salmon typically migrate within the Babine River watershed (Gottesfeld and Rabnett 2008; Stiff et al. 2015). First, we averaged July/August stream temperatures from the 15 sites along the Babine River, and six tributary sites to determine if tributaries that had various watershed sizes played a role in cooling the Babine River during peak summer temperature months. Second, we assessed the mean daily temperature from July 1 – August 31, 2016 for each of the tributary upstream, within stream, and downstream sites to understand how the varying seasonal temperature patterns of the tributaries would affect Babine River temperatures. Last, we calculated the difference in summer temperature between upstream and downstream temperatures to determine how much each tributary impacted the mainstem Babine River water temperature.

4.3.3. Climate and landscape variables associated with tributary water temperature

Many climate and landscape (hereafter “watershed”) variables are known to contribute to stream temperatures (e.g., Isaak et al. 2010). Using Geographic Information Systems (GIS), we obtained watershed data from several sources. Climate data were calculated using the open-source tool ClimateBC (Wang et al. 2016), which extracts and downscales PRISM climate normal data and extrapolates to any location within British Columbia (Daly et al. 2008). We used climate data averages for each of the six tributary watersheds by sampling at a 1 km resolution across the Babine River watershed, then used ClimateBC to estimate the mean summer air temperature and precipitation in 2016, and previous winter precipitation as snow (Table 4.1). Landscape variables included glacier coverage obtained from the Randolf Glacier Inventory (v6.0) (RGI Consortium 2017), watershed and lake areas calculated from polygons within the Freshwater Atlas of British Columbia, and elevation values extracted from a 25 m digital elevation model (DEM). We extracted forest harvest data from the National Forest Information System, derived from Landsat images, identifying yearly forest harvest activity at a 30 m resolution. We calculated the total area of forest harvest within each tributary watershed over a 30-year (1985-2015) period. To characterize the contribution of glaciers and forest harvest relative to the size of each tributary watershed, we divided these variables by their watershed area to calculate their proportional coverage. Similarly, to characterize how much each tributary watershed contributed to the Babine River watershed, we calculated the proportion watershed area relative to Babine River watershed.

We used a Pearson's correlation analysis to identify relationships between watershed characteristics of each tributary, with emphasis on how watershed characteristics are associated with summer stream temperature. We were limited in the number of tributaries (*n* = 6) and therefore did not conduct further statistics. The watersheds and their characteristics are included in our correlation analyses listed in Table 4.1.

Table 4.1 Characteristics of tributary watersheds.

tributary	mean summer water temp. (°C)	watershed area (ha)	percent glaciers (%)	lake area (ha)	mean elevation (m)	mean summer air temp. (°C)	summer precip. (mm)	previous winter precip. as snow (mm)	percent harvest 30-year (%)	prop. tributary size to Babine (%)
Nilkitkwa	12.4	82,642	3.6	528.8	693	11.8	61.5	219.7	5.9	7.9
Hanawald	15.0	17,433	0.0	521.4	591	12.7	54.8	203.5	0.1	1.7
Shelagyote	10.5	57,746	10.8	537.0	542	12.0	66.7	253.6	0.1	5.5
Thomlinson	10.3	10,635	8.2	5.6	484	11.7	49.3	243.2	0.2	1.0
Shedin	9.8	55,635	7.5	321.9	342	12.2	70.7	264.4	1.0	5.3
Shegisic	8.2	9,818	8.6	61.2	333	11.7	55.3	258.7	0.2	0.9

4.4. Results

4.4.1. River temperature patterns

Mean summer stream temperature of the Babine River decreased by ~2.0 °C from Babine Lake outlet site (15.79 °C ± 0.80 °C) to the Skeena River confluence site (13.76 °C ± 1.13 °C) (Figure 4.1). The large and glacierized tributary rivers – Nilkitkwa, Shelagyote, and Shedin – contributed cold water (mean summer temperatures of 12.4 °C, 10.5 °C, 9.8 °C, respectively), which appeared to reduce the summer stream temperature of the Babine River mainstem (Table 4.1; Figure 4.2). The smaller tributary watersheds, Thomlinson and Shegisic, with cold mean summer temperatures of 10.3 °C and 8.2 °C (Table 4.1), and the warmer Hanawald River (15.0 °C mean summer temperature) appeared to have very little effect in changing the Babine River mainstem temperatures (Figure 4.2). The Babine River mainstem water temperature warmed between the major glacierized watersheds, with summer stream temperature increasing by 1.2 °C between the downstream Nilkitkwa tributary and upstream Shelagyote tributary, and 0.2 °C between the downstream Shelagyote tributary and upstream Shedin tributary.

Seasonal dynamics of temperatures in the different tributaries and mainstem were similar. Apart from Hanawald, all tributary sites had mean daily stream temperatures colder than the Babine River mainstem (upstream and downstream) sites between July 1 and August 31, in 2016 (Figure 4.3). Throughout the summer months, the mean daily temperatures of the Nilkitkwa, Shelagyote, and Shedin within stream sites appeared to reduce the Babine River downstream mean daily temperatures (Figure 4.3a,c,e). Meanwhile the Hanawald, Thomlinson, and Shegisic within-stream temperature sites had little to no effect on the Babine River downstream sites. All sites had the warmest mean daily temperature on July 19, 2016, with the peak temperature varying by site. For each within stream tributary site, the warmest mean daily temperature on July 19, 2016 was 17.7 °C for Nilkitkwa, 18.9 °C for Hanawald, 17.6 °C for Shelagyote, 16.7 °C for Thomlinson, 17.0 °C for Shedin, and 16.2 °C for Shegisic. The warmest mean daily water temperature within the Babine River was 17.7 °C on July 20, 2016. Thus, counter to predictions, seasonal patterns of water temperatures were coherent among tributaries and the mainstem.

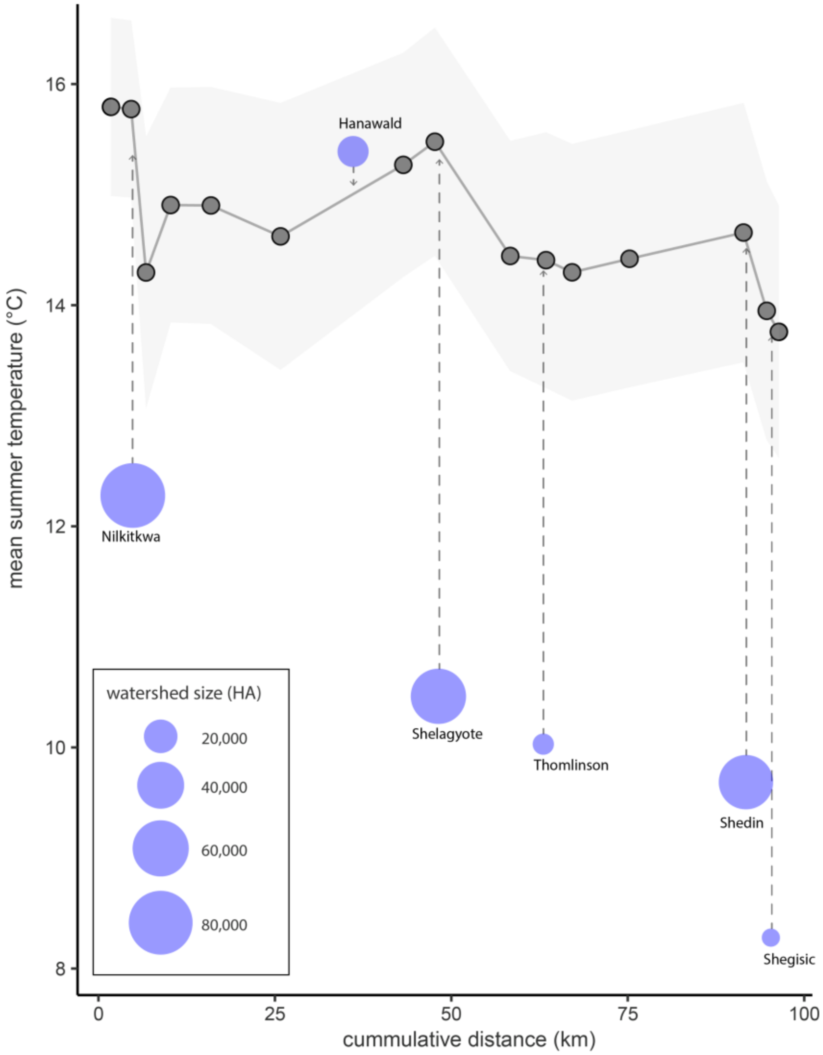

Figure 4.2 Mean summer temperature (°C) ± one standard deviation (shown in grey shading) from temperature sites located within the Babine River, from Babine Lake (distance = 0) to the Skeena River (distance = 96). Blue points represent mean summer temperature (°C) for each tributary that feeds into the Babine River, scaled to watershed size. Note: Hanawald Creek drains from a small watershed with no glaciers, and Shedin and Shegisic are in close proximity and therefore share the same upstream and downstream temperature loggers.

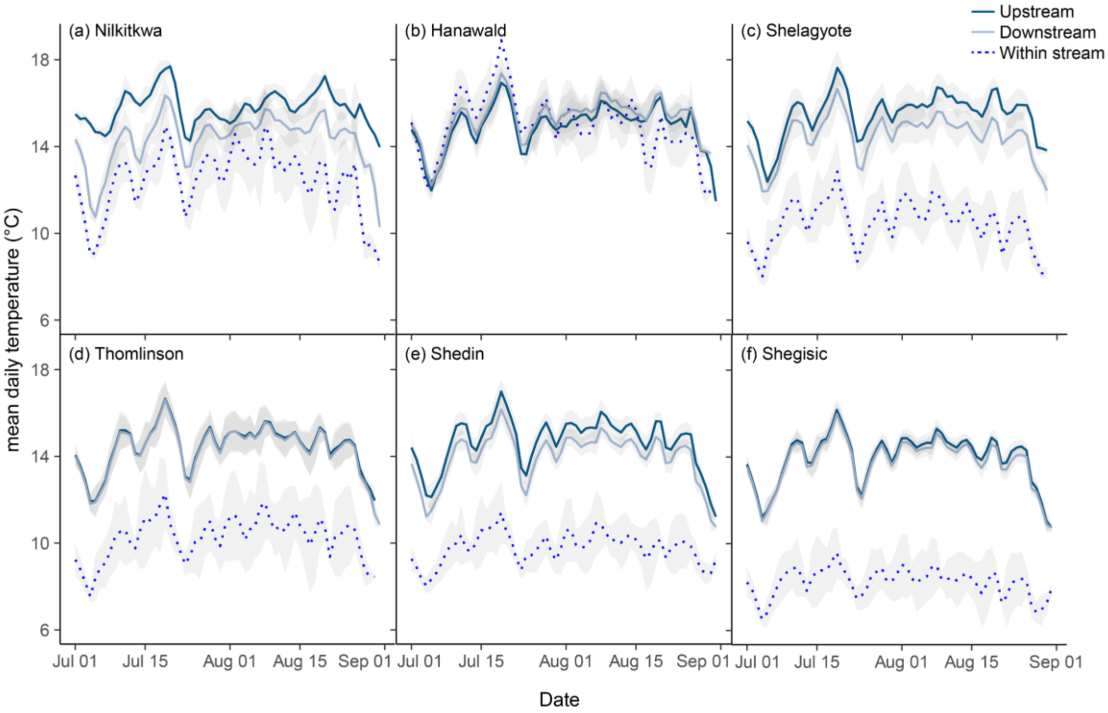

Figure 4.3 **Mean daily temperatures (°C) ± one standard deviation (shown in grey shading) for upstream, within stream, and downstream tributary sites from July 1 – August 31, 2016.**

The contribution of stream temperature from each tributary site to the Babine River was different, with cooler and more glacierized rivers causing bigger change in temperature between the upstream and downstream sites. The change in temperature between upstream and downstream sites at the Nilkitkwa, Shelagyote, and Shedin tributaries was -1.5 °C, -1.03 °C, and -0.71 °C respectively (Figure 4.4). The temperature change at Hanawald was positive (0.63 °C), with changes at the Thomlinson (-0.06 °C) and Shegisic (-0.19 °C) tributaries being trivial. Thus, stream temperatures from large glacierized watersheds appear to be the major contributors to temperature changes within the Babine River mainstem.

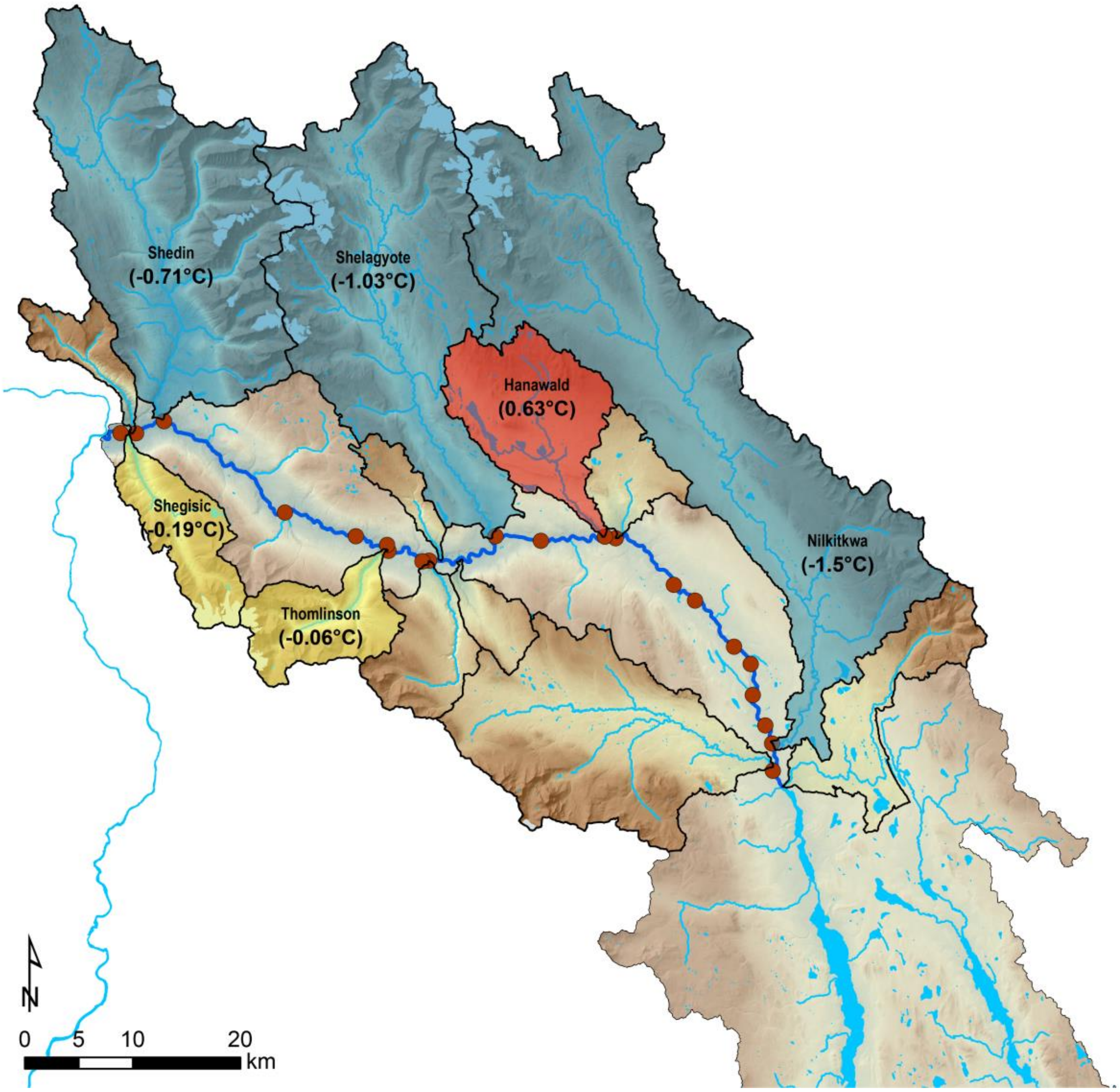

Figure 4.4 **Map showing the temperature (°C) change between upstream and downstream sites at each tributary site. Blue shading represents a cooling of the Babine River mainstem temperature, red represents a warming of the Babine River mainstem, and yellow represents a mimimal change. Red points represent location of temperature logger sites.**

4.4.2. Watershed characteristics associated with tributary stream temperature

There were strong relationships between some of the six watershed characteristics and tributary temperatures (Figure 4.5). Mean summer water temperature were inversely related to previous winter precipitation as snow (r = -0.93; *p* = 0.01) and percent glacier cover (r = -0.87; *p* = 0.02). Not surprisingly, these two variables were strongly correlated with each other (r = 0.9, *p* = 0.02). Mean summer water temperature had a positive association with mean elevation (r = 0.76), mean summer air temperature (r = 0.74), and lake area (r = 0.67), although insignificant (*p* > 0.05; Figures 4.5 and 4.6). There was no relationship between mean summer water temperature and summer precipitation (r = -0.15), watershed area (r = 0.13), percent harvest (30-year) (r = 0.24), and proportion tributary to Babine River watershed (r = 0.14; all *p* > 0.05). Thus, watershed variables vulnerable to the effects of climate change that have the strongest effect on mean summer stream temperature are previous winter precipitation as snow or percent glacier and mean summer air temperature.

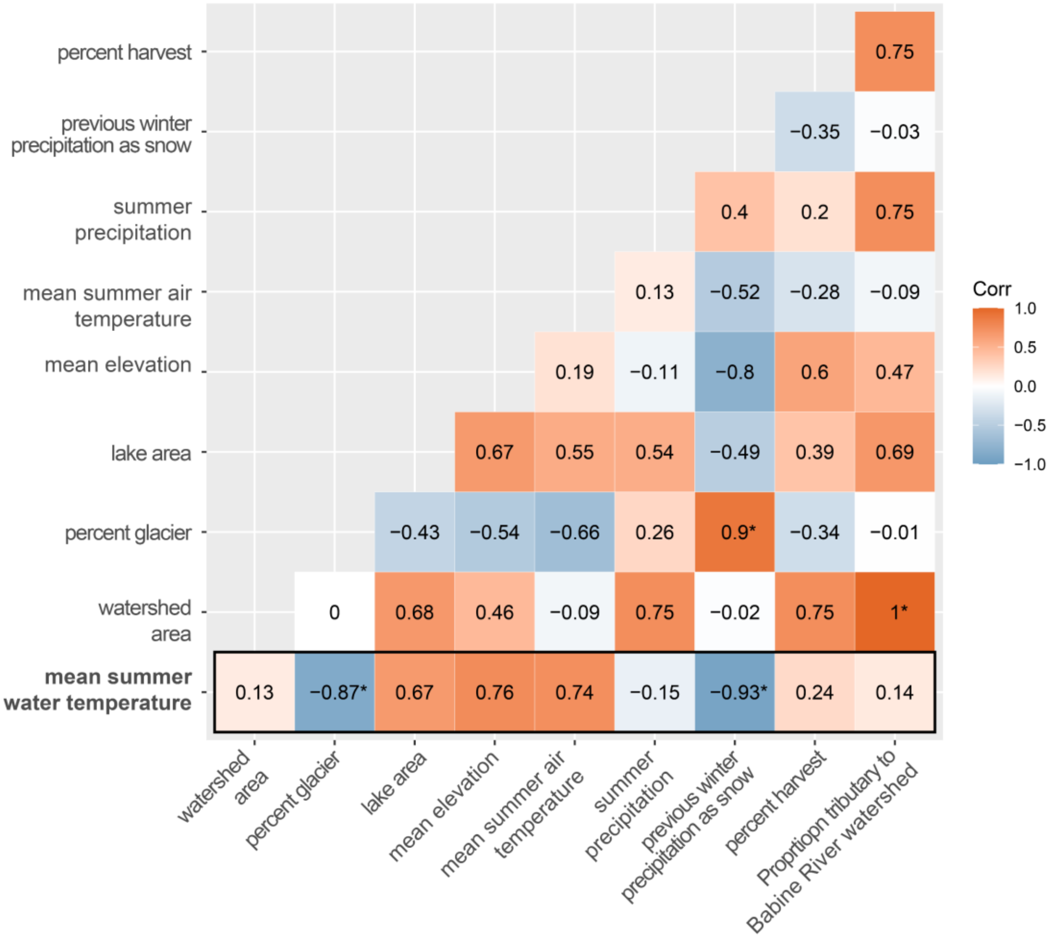

Figure 4.5 Correlations watershed landscape characteristics. Black box represents correlations between mean summer water temperature and watershed characteristics. Values represent Pearson’s correlation coefficients, with higher values shown by increasingly intense colours; blue indicates negative correlations and orange, positive. Asterixis represent statistically significant correlations. N = 6 throughout.

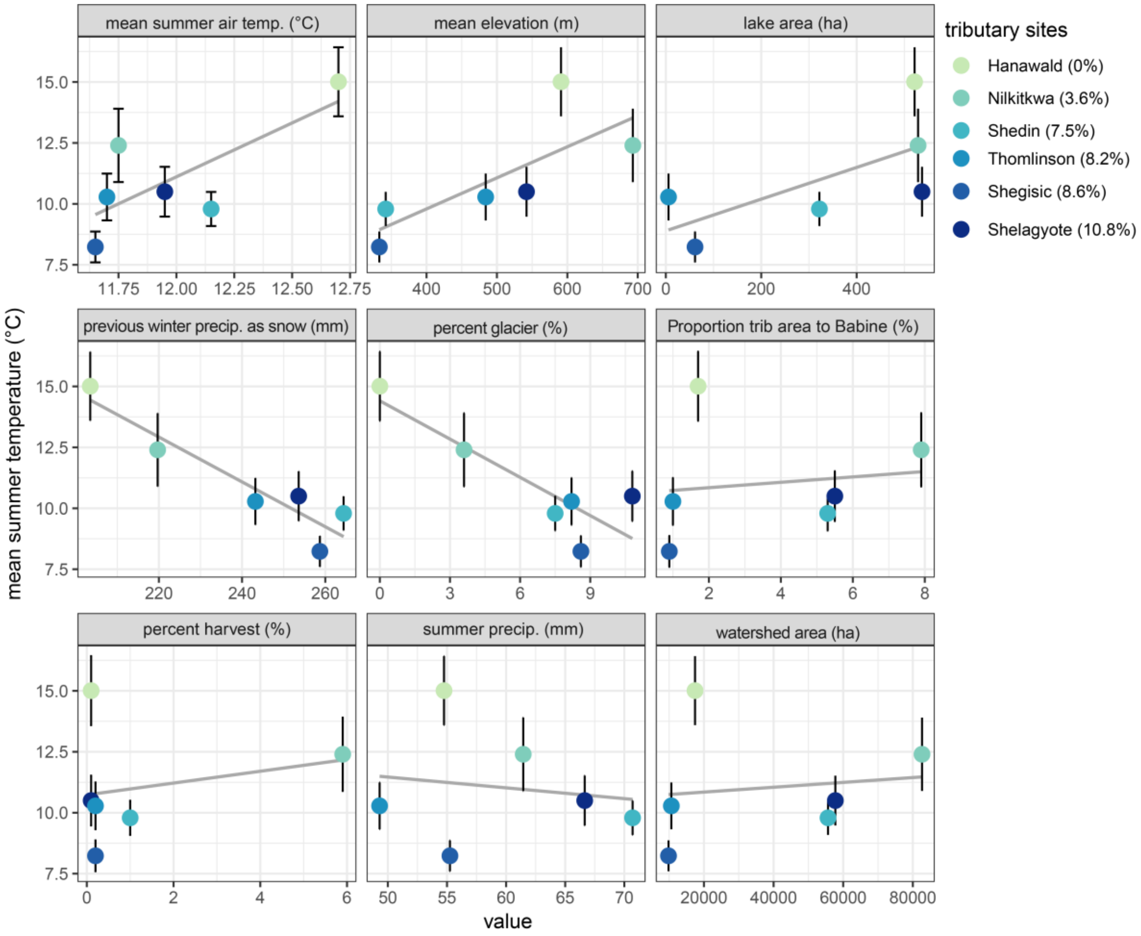

Figure 4.6 **Relationship between watershed characteristics and summer stream temperature for the six tributaries. Tributary sites are listed and colored by percent glacier, with values indicated in parenthesis. The x-scales vary depending on the watershed characteristic. Regression lines (in grey) are for visual purposes only.**

4.5. Discussion

We assessed the role of tributaries in cooling a major salmon migration corridor. While water temperatures often increase as watershed size increases due to cumulative thermal loading (Lisi et al. 2013), here we showcase how large tributaries can decrease mainstem river temperatures. Particularly, tributaries with more snowpack throughout the previous winter and glaciers in their catchment had cooler water temperatures. These glacier- and snowpack- fed tributaries cooled the Babine River by approximately 2 °C over its 96 km length. Specifically, the large and cold Nilkitkwa, Shelagyote and Shedin rivers, with mean summer water temperatures of 12.4 °C, 10.5 °C, and 9.8 °C respectively, provided the most cooling to the Babine River mainstem, and reduced the

Babine River by -1.5 °C, -1.0 °C, and -0.71 °C, respectively. Other studies have also found that glaciers have a cooling effect on summer stream temperature, where water temperatures are reported to decrease by ~1 °C for every 10% increase in glacier cover (Moore 2006; Fellman et al. 2014). Meanwhile, the Thomlinson and Shegisic rivers, which are also cold and glacierized, contributed very little to cooling the Babine River mainstem temperatures. This lack of cooling impact is likely because they contributed less water given their smaller watershed area, even though there was no relationship between mean summer water temperature and the proportion of tributary watershed to the Babine River watershed. Surprisingly, the seasonal temperature dynamics across sites, both mainstem and tributaries, were synchronous. Regardless, cold meltwater from mountainous tributaries is currently decreasing thermal stress to migrating salmon, which agrees with previous work on thermal riverscapes in mountainous region (Fellman et al. 2014).

The Babine River is currently on the edge of posing thermal challenges to sockeye salmon. The Babine River summer water temperatures are approaching those that could potentially harm sockeye salmon, depending on the thermal tolerance of the Babine River sockeye salmon population. For example, sockeye salmon survival declined when water temperatures exceeded 15 °C in the Koeye River, a small watershed on the central coastal of British Columbia (Atlas et al. 2020), whereas some sockeye salmon populations in the Fraser River appear to be adapted to tolerate warmer water temperatures (Eliason et al. 2011). While there are no population-specific studies of Babine River sockeye thermal tolerance, there is some evidence suggesting that when water temperatures near the Babine Lake outlet exceed ~18 °C, sockeye salmon delay migration and stay in cooler waters downstream (Stiff et al. 2015). Thus, while the Babine River may be on the edge of suitable water temperatures, it appears that cold water inputs from major tributaries currently play a key role in maintaining suitable water temperatures for migratory salmon.

The longitudinal thermal profile of rivers can be complex (Fullerton et al. 2015), but all migratory Pacific salmon accessing headwater streams and lakes for spawning must transit through the entire thermal regime. In the Babine River watershed, we discovered that the upstream section is warmer than the downstream portion. This downstream portion is also the location of waterfalls, canyons and steep sections that could present migratory challenges (Gottesfeld and Rabnett 2008). Maximum aerobic scope is required to ascend through difficult portions of upstream migration (Eliason and Farrell 2016), and sockeye salmon have been observed recovering in pools or back eddies, sometimes fed from cold upwelling groundwater (Ebersole et al. 2001), while migrating through challenging river sections (Brett 1995). In addition, the lower sections of the Babine River have been reported to act as a temperature refugium where migrating sockeye salmon delay migration until waters cool down before continuing their migration (Stiff et al. 2015). Thus, the major tributaries of the Babine River are essential in cooling the more challenging lower sections, providing more suitable conditions for migrating sockeye salmon. However, the cold tributaries do not cool the entire river, such as the upper portion, which is still required for transit to spawning grounds.

Like rivers across western North American and beyond (Isaak et al. 2012; Luce et al. 2014), Babine River water temperatures will likely continue to warm. Glacier- and snow-fed rivers maintain cool water temperatures in the Babine River, and projections show a 70% decline of glaciers in British Columbia over the next century (Clarke et al. 2015), and 20% decline in winter snowpack levels by 2050 (Islam et al. 2017), thus impacting the cold water runoff from snow and ice. In addition, the Babine Lake surface water temperatures has increased in recent years (Stiff et al. 2015), and forest harvest has continued to rise (de Groot 2014). Thus, warming temperatures are a potentially pending problem for Babine River and its migratory sockeye salmon.

Understanding the spatial and temporal dynamics of water temperatures in riverscapes can help inform management options in a warming world (Ebersole et al. 2020). While many aspects of climate change require a global effort in reducing greenhouse gas emissions (IPCC 2013), there are options for localized management actions to try to mitigate climate impacts (Johnson and Jones 2000; Pollock et al. 2009). Here we identify that tributaries do measurably cool a major salmon migratory corridor. Land use in the major tributary catchments will influence their ongoing role as effective “air conditioners” for the downstream river. For example, forest harvest increases stream temperatures (Mellina et al. 2002; Pollock et al. 2009), and some of these catchments have already been substantially harvested (e.g., Nilkitkwa River watershed, 5.9% forest harvest). Although our findings did not indicate a relationship between forest harvest and mean summer water temperature, likely due to consequences of the large scale of our analysis. We suggest further research on the impacts forest harvest is having on major important tributary water temperatures, such as the Nilkitkwa River. Further restriction of forest harvest within important tributaries that cool downstream Babine River sections would likely help maintain the cold-water refugia during upstream migration. Spatial heterogeneity in river temperatures, whether it is small-scale groundwater seepages or tributaries that act as cold-water refuges or the cooling inputs of major tributaries, play a key role in the persistence and vulnerability of cold-water fishes (Monk et al. 2013; Ebersole et al. 2020).

4.6. Acknowledgements

We gratefully acknowledge funding from the Gordon and Betty Moore Foundation, which provided the opportunity to conduct research on the remote Babine River, British Columbia. We are grateful for Skeena Watershed Conservation Coalition, Alfred Schaefer, Morag Gibb, Todd James, Ben Pittman, and Ali Howard for safely navigating us down the river by raft or kayak. Thank you to Ciara Sharpe for your many types of support. We are grateful for Babine Norlakes Steelhead camp and Silverhilton Steelhead lodges for assisting in logger placement and retrieval. Kara Pitman was supported by National Science and Engineering Research Council and Association of Canadian Universities for Northern Studies. We are extremely grateful for Gitxsan and Lake Babine Nations for permitting us to conduct research within their traditional terriroties.

Chapter 5.

General Discussion

The diverse research presented in the preceding chapters presents the multiple ways in which climate change and glacier retreat will alter, shift, and impact Pacific salmon futures. While there is a growing understanding of the pathways by which glacier retreat alters aquatic environments (O'Neel et al. 2015; Milner et al. 2017) and a large body of literature on the environmental variables that influence salmon across their life cycle (Quinn 2018), the contents of this thesis aims to help fill the knowledge gaps on the direct linkages between glaciers and salmon. From constructing a conceptual model, to forecasting future salmon habitat gains, then assessing the thermal dynamics within one salmon watershed, this thesis crosses temporal and spatial scales of glacier retreat and Pacific salmon habitat. Glacier retreat is forecasted to continue with some projections showing accelerated melt rates over the next century (Radić et al. 2013) changing downstream salmon habitat.

Glacier retreat is just one of many symptoms of climate change. There have been vast amounts of work assessing how climate change will impact species, including Pacific salmon. However, much of this work focuses on how temperature warming will shift habitats and has given less consideration for how temperature warming will change ecosystems. In this case, climate change will transform ice that may be 1000s of years old into meltwater. Here I examine some of the direct and indirect consequences of this climate-induced transformation and how it will change Pacific salmon's habitat. Perhaps the lessons from this thesis apply broadly to the consideration of climate change in glacierized regions of the world.

5.1. Connections between salmon and glaciers

Pacific salmon evolved over millions of years ago, enduring various climatic conditions including repeated phases of glacier advance and retreat that reworked the landscape of northwestern North America (Stearley 1992; Waples et al. 2008). Over time, various landscape disturbances, such as those associated with glacier dynamics, have shaped the life histories and traits of salmon that we see today (Waples et al. 2008, 2009).

Presently, 85% of major salmon watersheds within the range of Pacific salmon have at least some glacier coverage (Pitman et al. 2020). Thus, the story between salmon and glaciers has long been established, and glaciers continue to play a key role in salmon watersheds.

In chapter 2, I built off previous literature that addresses the pathways of impact glacier retreat has on aquatic environments and the environmental variables that influence salmon across their life cycle to construct a conceptual model of glacier change on salmon habitat over four distinct phases. This conceptual model highlights the many ways in which downstream effects from glacier retreat will impact Pacific salmon and their habitat across their range. For example, in warm rivers, the loss of glacier melt water during summer months could lead to increase stress and higher mortality rates for adult Pacific salmon (Martins et al. 2012). Whereas in cool waters, a reduction of cold water input from glacier fed rivers could increase juvenile salmon growth potential (Fellman et al. 2014). Given the drastic changes projected for the North American glaciers, I hope that the contents of chapter 2, will be used in understanding how salmon futures may shift within glacierized watersheds. Salmon management plans will need to be revisited and revied as salmon productivity shifts within and between watersheds with glacier retreat, and this chapter provides a framework for understanding how salmon may respond to glacier retreat changes over their range.

5.2. Pacific salmon habitat gains

Globally, glaciers are rapidly declining in volume and area, accelerated by recent anthropogenic climate warming (Marzeion et al. 2014, 2020). In western Canada, glaciers are projected to lose up to 80% of their ice volume by 2100 in some regions. This loss in glacier ice will alter salmon watershed drastically over the next century. Thus, in chapter 3, I considered Pacific salmon habitat gains following the transformation of glacier ice to rivers and lakes. I forecasted, throughout the Pacific mountain ranges of North America, the total amount of river kilometer gains over the next century. I projected that by 2100, glacier retreat will create ~6,000 kilometers of new streams that can be colonized by Pacific salmon, of which ~1,900 kilometers have the potential to be used for spawning and rearing, representing a 0 to 27% gain depending on the region. Regions that are currently heavily glacierized, particularly in southcentral Alaska, could lead to emerging fisheries in the future. Meanwhile, southern parts of Pacific salmon's range, particularly in British Columbia, may experience very little to no habitat gain as glaciers have already retreated far upslope. Through identifying salmon future hotspots, I hope the contents of this chapter will inform forward-looking management and conservation. Glacier retreat may not only present opportunities for Pacific salmon, but also for resource extraction such as mining opportunities (Sexton et al. 2020). Our findings in chapter 3 indicates that effective protection of Pacific salmon from watershed development will entail conserving current salmon habitat while also avoiding the degradation of their future habitat.

Pacific salmon habitat gains in chapter 3 only considers the direct association between glacier ice and the expansion of new habitat. I did not consider the indirect, or downstream, effects glacier retreat will have on salmon habitat. Downstream effects will present as gains or losses depending on how landscape features integrate across the changes of stream flow patterns following glacier retreat, as suggested in chapter 2. The analysis in chapter 3 considered the entire range of Pacific salmon habitat within glacierized regions. Thus, projecting downstream impacts at this spatial scale was not possible. However, future research could build off the modelled salmon habitat gains presented in chapter 3 and assess the associated downstream changes following the modelled glacier retreat rates within select watersheds. Additionally, I did not consider the creation of lake habitat. Lakes provide key habitat for salmon spawning and rearing, particularly for sockeye salmon. It was not possible to model future gains in lake area within chapter 3 due to the DEM’s resolution and limitations to the glacier retreat model. However, glacier-created lakes can be key habitat for salmon. Thus, this chapter provides a broad-scale spatial forecast of salmon habitat creation by glacier retreat.

5.3. Downstream thermal dynamics

One of the main pathways of impact glacier retreat has on downstream rivers is via changes to thermal regimes, which plays an important role for migrating Pacific salmon. Glaciers have a cooling effect on summer stream temperature, where water temperatures are reported to decrease ~1°C for every 10% increase in glacier cover (Moore 2006; Fellman et al. 2014). This cold glacier fed water can be beneficial for salmon by cooling downstream rivers during critical upstream migration periods when river temperatures are typically their warmest. Along an important salmon migratory river, the Babine River (Chapter 4), water temperatures along the mainstem were cooled by large glacier fed tributary rivers. Over the Babine River’s 96-kilometer distance, the river cooled by approximately 2°C, with two large tributary rivers beheaded by glaciers providing most of the cooling.

British Columbia glaciers are projected to decline by 70% over the next century (Clarke et al. 2015), and winter snowpack levels are expected to decline 20% by 2050 (Islam et al. 2017). The loss of glacier ice and winter snowpack will alter the rivers thermal regime potentially impacting adult migrating salmon. While limiting the effects of glacier retreat and reduced winter snowpack levels may require a global effort in reducing greenhouse gas emissions (IPCC 2013), there are options for localized management actions to try to mitigate climate impacts. For example, further restriction of forest harvest within important tributaries that cool downstream Babine River sections would likely help maintain the cold water refugia during upstream migration. Thus, as we globally work towards limiting our greenhouse gas emissions to slow or dampen the effects of climate change and glacier retreat, it will be necessary to also implement conservation or management plans that protect important salmon watersheds from climate change effects such as rising water temperatures.

5.4. Salmon in a warming world

While this thesis considers relationships between glacier retreat and salmon habitat, there are many ways climate change and other anthropogenic stressors are presenting challenges for salmon populations. In chapter 3, we model where salmon populations will gain from glacier ice loss. However, the findings from this chapter should be taken with caution, as climate change will present many challenges to salmon futures. Anthropogenic stressors, such as ocean acidification, habitat loss, warming ocean and freshwater temperatures, shifting precipitation regimes, and hatchery influences are threatening salmon populations and their habitat. For example, if the capacity of the ocean to support thriving salmon populations is compromised by climate change, then salmon may be slower or unable to colonize new habitats such as those presented in chapter 3. Additionally, if we are unable to slow the rate of global air temperature rise, glacier ice will vanish, leaving all salmon watersheds in the final phase – watersheds without permanent ice (Chapter 2). In this phase, water temperatures could be too warm negatively affecting salmon by decreasing survival for migratory adult salmon (Eliason et al. 2011; Martins et al. 2012). It is unknown how the multiple processes will interact and affect salmon and their ecosystems, and glacier retreat is only one of the many ongoing stressors. Thus, glacier retreat will present potential opportunities in some locations, but these opportunities will only be available if the other consequences of climate change do not diminish salmon populations.

Beyond salmon, glacier retreat will have many detrimental effects potentially harming humans and other species. Globally, glacier meltwater is crucial for multiple societal needs such as agriculture, hydropower generation, drinking water supplies, and industry, whereby half of the worlds population depends on mountain water downstream (Huss et al. 2017). Glacier retreat is also causing sea level rise, changing downstream river patterns, and increasing geohazards. The changes to the cryosphere are impacting species globally, from penguins in the Antarctic to polar bears in the Arctic. Thus, incorporating the impacts glacier retreat is having on the physical world is integral for understanding the Earth's ecosystems.

5.5. Salmon management and conservation

Glacier loss will pose challenges and opportunities for effective management and conservation of salmon and their habitats. Salmon productivity will likely shift across space and time as landscapes and rivers change following glacier retreat. I present some considerations for the conservation and management of salmon within glacier fed systems:

1) Salmon management plans need to be fluid – revised and revisited – as salmon productively shifts with environmental conditions changes and past relationships are pushed beyond their historical enumerated bounds and other conditions become dominant drivers.

2) In regions where glacier retreat will degrade salmon habitat via reduced stream flow and warming water temperatures fisheries need to be managed more conservatively and cautiously.

3) Glacier retreat is predicted to create new salmon habitat, but is also presenting opportunities for resource extraction, particularly mining. Thus, there is a need for

proactive conservation and decision making that incorporates the potential values and benefits of future salmon habitat.

4) Salmon restoration activities should be designed and undertaken with a forward-looking outlook that considers how landscapes may change because of glacier retreat.
5) There is a need for localized protection and preservation of tributary watersheds, from resource management activities that additively warm water temperatures, that play a key role in regulating thermal regimes of migration corridors for highly valued salmon.
6) Consider integrating socio-ecological systems within salmon management plans.

More broadly, salmon have persisted through multiple drastic changes to their environments (Waples et al. 2009). Due to attributes such as having multiple reproducing populations, metapopulation structure, high genetic diversity, phenotypic plasticity, variable life-history traits, and opportunistic use of habitat (Healey 2009) salmon have remained resilient to these environmental changes. However, in many instances, human stressors (e.g. hatcheries or dams) and management actions (e.g., maximizing yields) have threatened the resilience of salmon. In addition, salmon hold cultural and watershed importance; thus, a loss of salmon resilience will also affect the resilience of humans and ecosystems. There is a need to integrate harvest management and habitat protection into fisheries management to enhance resilience. One such example is through co-management arrangements that involve community and indigenous fisheries so that those who depend on the resource have an input in the management plans.

5.6. In conclusion

The fate of salmon futures lies in the hands of societies ability to curb greenhouse gas emissions stalling the effects of climate change and reducing the number of other stressors such as habitat loss, hatchery influence, and mismanaged fisheries. For example, since the mid-20th century, salmon populations in British Columbia have reduced by 13 to 50% of historic levels with some small populations being lost completely (Slaney et al. 1996; Northcote and Atagi 1997). However, salmon are a highly resilient species. Given reasonable access to good-quality habitat and protection of overfishing and their habitat, they are capable of recovery and productivity. Within this thesis, I present a conceptual model of glacier retreat and Pacific salmon habitat, forecast future salmon habitat gains, and assess the thermal dynamics within one salmon watershed. I hope that the contents of this thesis will be incorporated into the management and conservation of our salmon futures.

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Appendix.

Linking anglers, fish, and management in a catch-and-release steelhead trout fishery[2]

Abstract

Fisheries are complex social-ecological systems with multiple potential linkages between fish and anglers. Understanding these linkages help support effective fisheries management. We examined the social-ecological dynamics of a recreational fishery by assessing relationships between fish, anglers, and a management intervention. We focus on catch-and-release steelhead trout (*Oncorhynchus mykiss*) fisheries on six rivers within the Skeena River Watershed, British Columbia, Canada, the location of a recent management intervention. First, based on analyses of annual steelhead trout abundance and annual angler effort information, years with higher abundance of returning steelhead trout were associated with years of higher catch rates and angler effort. Second, based on analyses of non-resident angler effort, we discovered that a new management intervention provided periods of lower angler effort, but effort was apparently redistributed to other rivers and time periods. Third, responses from angler interviews post-management intervention revealed that anglers were more satisfied if they caught more fish and experienced less crowding and at higher crowding levels, it took higher catch rates to increase satisfaction. Thus, we found that this recreational fishery is influenced by both human dimensions and natural ecological dynamics such as fish population fluctuations.

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[2] Aversion of this chapter appears as Pitman KJ, Wilson SM, Sweeney-Bergen E, Hirshfield P, Beere MC, Moore JW. 2019. Linking anglers, fish, and management in a cath-and-release steelhead trout fishery. Canadian Journal of Fisheries and Aquatic Sciences 76:1060–1072.

Introduction

Fisheries are social-ecological systems with bi-directional connections between fish, anglers, and managers (Arlinghaus et al. 2013; Fenichel et al. 2013; Hunt et al. 2013; Ward et al. 2016). For instance, angler effort – the aggregate of how individual fishing effort is distributed across space and time – can influence fish populations (Fulton et al. 2011; Fenichel et al. 2013; Hunt et al. 2013). Reciprocally, variation in fish abundance can affect the spatial and temporal distribution of angler effort. For example, if fish abundance in a specific site declines, some anglers may become less satisfied with their fishing experience and shift their effort to other sites (Gillis 2003; Abernethy et al. 2007; Wilson et al. 2016). Lack of consideration of angler effort can lead to unexpected consequences of fisheries management and undermine management objectives. For example, creation of marine protected areas (MPA) can displace fishing effort to outside of the protected area and increase fishing pressure and risks of local over-fishing (Halpern et al. 2004; Hilborn et al. 2004; Kellner and Hastings 2009). Similarly, management interventions that limit or reduce fishing seasons can lead to a redistribution of effort at other times, increasing fishing pressure before or after the closure period (Hall and Shelby 2000; Murray et al. 2001). Therefore, understanding the drivers of angler effort and how effort may respond to management interventions is a key component of effective fishery management.

Angler effort in recreational fisheries may be particularly unpredictable because individual angler incentives may be more complicated or dynamic than in other fisheries. It is generally thought that commercial fishers prioritize a single attribute (i.e., net profit) and therefore have a tightly coupled relationship between predator and prey (Hilborn and Walters 1992; Smith 1999; Post et al. 2002). Thus, their utility function, that is preferences for certain options over others, may be focused on profit. However, in recreational fisheries, anglers' choices may be driven by their own personal satisfaction, which can depend on multiple attributes that individual anglers seek to maximize when making their choice of where and how much to fish (i.e., their utility function). Many variables have been reported to contribute to angler satisfaction, some include: catch rate, size of fish, general enjoyment, natural beauty and serenity, or gear type (Holland and Ditton 1992; Miko et al. 1995; Arlinghaus 2006; McCormick and Porter 2014). Anglers may be satisfied with a fishing trip even if there were dissatisfied with their fishing success (Fedler and Ditton 1994; Beardmore et al. 2015). Conversely, anglers may have high fishing success and be dissatisfied with their fishing trip based on the social environment of the trip (Beardmore et al. 2015). For example, crowding has been shown to negatively affect anglers’ choices of fishing sites independent of catch (Hunt 2005). Thus, angler effort in recreational fisheries is likely linked to multiple potential factors that could influence their personal satisfaction with their fishing experience. Understanding the factors that influence angler satisfaction can help illuminate what underpins their decisions about effort allocation and therefore help inform recreational fisheries management.

One important and illustrative recreational fishery is that of steelhead trout (*Oncorhynchus mykiss*) in the rivers of the Skeena River Watershed, British Columbia (BC), Canada. This fishery is well known to both local anglers as well as anglers who travel from around the world to target these migratory fish (Hooton 2011). This fishery is exclusively catch-and-release, which can cause stress and some low level of incidental mortality in the hooked and handled fish (Twardek et al. 2018). However, one of the primary management challenges in this region is that of crowding. Stakeholder engagement processes suggested that increases in fishing effort over the last several decades were leading to crowding concerns and potentially reducing satisfaction of the local anglers (Alan Dolan & Associates 2009; Ministry of Environment 2010). Accordingly, the Skeena Region BC Ministry of Forests, Lands, Resource Operations, and Rural Development Fisheries Section (Skeena Region Fisheries Section) implemented new regulations (hereafter “management intervention”) starting in 2012 that restricted unguided non-resident anglers, any angler who was not Canadian and had not hired a fishing guide, from fishing during certain times and zones (Ministry of Environment 2010; Ministry of Forests Lands and Natural Resource Operations 2013). Therefore, there is an opportunity to examine the degree to which this management intervention altered angler effort and thus crowding within the larger context of other potential controls on angler effort, such as annual variation in steelhead trout abundance. Given angler effort is ultimately a product of individuals’ incentives and perceptions, further insight can be gained through connected social studies of factors that influence angler satisfaction. More generally, given successful management of fisheries hinges on the effective management of people (Hilborn 2007), this important recreational fishery can serve as a broadly-relevant examination of how multiple factors, including management intervention, could influence both catch rate and angler effort.

Here we examined the factors associated with angler effort, catch, and satisfaction in a globally-notable recreational fishery over a period with a management intervention. While there is increasing appreciation that effective fisheries management depends on the consideration of multiple potential feedbacks between social and ecological aspects of fisheries and their management (Carpenter and Brock 2004; Hunt et al. 2011; Ward et al. 2016; Arlinghaus et al. 2017), there still are relatively few studies that bring together data on both the ecological and social dimensions (Arlinghaus et al. 2013). Through combining extensive datasets from both social science approaches and ecological analyses, here we asked three questions. First, how does angler annual catch rate and effort change in response to annual variation in steelhead trout abundance and a management intervention? Second, did unguided non-resident anglers redistribute effort across space and time in response to the management intervention? Third, how do crowding and catch rates influence angler satisfaction post-management intervention? These analyses provide insight into the socio-ecological linkages that underpin the management and dynamics of a catch-and-release fishery.

Materials and methods

Study system

The large Skeena River Watershed in northwestern British Columbia (BC), Canada, drains 54 532 km^2 from the Nechako Plateau and Coast Mountains into the Pacific Ocean (Gottesfeld and Rabnett 2008). The Skeena River and its tributaries are internationally recognized as a world-class fishing destination for steelhead trout. Steelhead trout are anadromous rainbow trout that spend one to six years in freshwater, migrate to the ocean for one to three years, and then return back to freshwater to spawn (Moore et al. 2014). Within the Skeena River Watershed, there are many locally-adapted steelhead trout populations (Beacham et al. 2012) that spawn in the different tributaries (Tautz et al. 1992). This paper focuses on the recreational fisheries for summer-run steelhead trout, the populations that enter the drainage between June and October and spawn from mid-May to late June of the following year (Beacham et al. 2012).

Return migrating adult steelhead trout are highly sought after by recreational anglers. Each year, approximately 3,000 non-resident anglers visit the Skeena River Watershed to fish for steelhead trout, bringing in approximately $16 million to the economy of this watershed (Counterpoint Consulting 2008). Since the mid-2000s in BC, the steelhead trout recreational fishery has been restricted to catch-and-release due to conservation concerns and efforts to maintain the viability of the recreational fishery (Hooton 2011). A small proportion of steelhead trout are caught by First Nation peoples for food, social or ceremonial fisheries and as bycatch in international and local commercial salmon fisheries (Hooton 2011).

This study focuses on the six most popular steelhead trout rivers within the Skeena River Watershed: the Babine, Bulkley, Kispiox, Morice, and Zymoetz rivers as well as the mainstem of the Skeena River (Figure A1). These six rivers are designated as Classified Waters by a BC provincial management framework implemented in 1990 (Ministry of Environment 1998). Anglers fishing rivers or river sections designated as such are required to purchase a “Classified Waters licence”. There are a total of 20 Classified Waters within the Skeena Region, ranging in foot and boat accessibility. Of the six rivers included in our study, the Morice, Bulkley, and Skeena rivers are highly accessible for both foot and boat-based anglers. The Kispiox and Zymoetz rivers have remote road-access points for most of their lengths, however, have limited boat access. The Babine River is relatively inaccessible; therefore, anglers are generally guided by one of the fishing outfitters located on the river.

One of the emerging management challenges for the steelhead trout recreational fishery in the Skeena River Watershed is increasing crowding pressure. In 2010, a stakeholder consultation and engagement process revealed that the quality of angling experience was being compromised in the Skeena Region for some BC anglers due to overcrowding (Ministry of Forests Lands and Natural Resource Operations 2013). The Skeena Region Fisheries Section therefore implemented new regulations to 12 Classified Waters within the region in 2012. The most significant change was mandating Canadian-only fishing times and zones. This regulation restricted angling to all unguided non-residents, on many of the Classified Waters, including all six study rivers (Figure A1). However, the Skeena River mainstem (Skeena IV) had sections that were void of the regulations. Therefore, the Skeena River offers an experimental contrast for understanding the potential influence of the new regulations on angler effort. This management intervention attempted to balance the local economic benefits of visiting non-resident anglers while providing angling opportunities with lower crowding for BC residents, and thus maintaining a high-quality angling experience for all anglers (Ministry of Environment 2010).

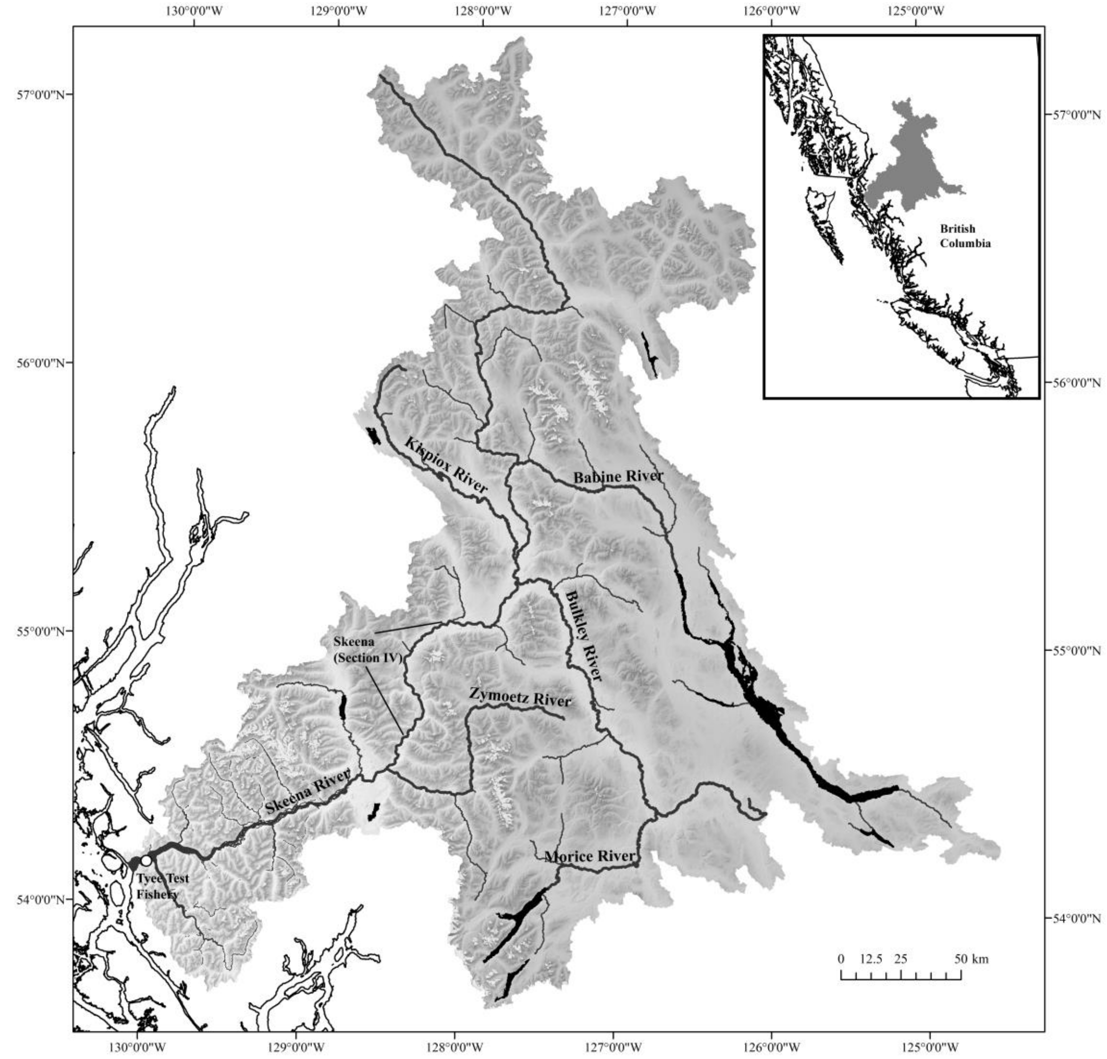


Figure A1 **The Skeena River Watershed and its major tributary rivers overlaid on a digital elevation model in British Columbia, Canada. All of the listed major tributary rivers had a mangement intervention that restricted unguided non-residents from fishing (mainly) during the weekend, while the Skeena (Section IV) had sections void of this management intervention. The map is projected in BC Albers to provide equal area depiction of the region, but labels are expressed in WGS84 latitude and longitude.**

Analysis Overview

This study consisted of three main sets of analyses which are overviewed here and described in more detail below (Table A1):

1. Annual catch rate and angler effort as a function of annual steelhead trout abundance and a management intervention. These analyses examined the relationships between annual angler catch rates or effort and annual steelhead trout abundance as well as years before and after the management intervention. Angler catch rates and effort were obtained from the Steelhead Harvest Analysis (SHA; 1997-2016; De Gisi 1999) and steelhead trout index of abundance data was obtained from the Tyee test fishery (1997-2016). The Skeena River, for which there were mixed regulations imposed, was used as a reference with regards to the management intervention. These analyses examine the interannual patterns of effort and catch for the whole recreational fishery population (Canadians and non-residents).

2. Management intervention and distribution of angler effort. The management intervention restricted unguided non-resident anglers from fishing at certain times and places. Therefore, to understand if unguided non-resident angler effort redistributed across space and time due to the management intervention we examined daily unguided non-resident angler effort information from the Classified Waters e-licensing database in the six focal rivers (2009-2016).

3. Angler satisfaction. To understand the determinates of angler satisfaction, and thus perhaps the factors that influence their effort, we performed and analyzed data from a large survey study (River Guardian Program). This survey occurred post-management intervention (2013-2015). These analyses considered if Canadians and non-residents had different satisfaction levels, if satisfaction varied by river, and how satisfaction was associated with catching fish and crowding.

Table A1 Databases used in this study

Database name	Organization	Location	Year range	Years used in this study	Associated Figure	Angler residency surveyed	Variables used in analysis
Steelhead Harvest Analysis (SHA)	BC provincial government	BC Province wide	1967-present	1997-2016	Figure A2 Figure A3	Canadian and non-residents	*response variables*: 'annual angler catch' and 'annual angler effort' used for angler catch and effort models (Table A2).
Tyee test fishery	Fisheries and Oceans Canada	Skeena River	1955-present	1997-2016	Figure A2 Figure A3	NA	*explanatory variables*: 'annual steelhead trout abundance' used for angler catch and effort models (Table A2).
Classified Waters e-licencing	BC provincial government	BC Province wide	2009-present	2009-2016	Figure A4	unguided non-residents	daily angler effort data showing weekly temporal displacement by non-residents
River Guardian Program	Skeena Region Fisheries Branch	Bulkley, Kispiox, Zymoetz	2013-2015	2013-2015	Figure A5	Canadian and non-residents	*variables*: 'number of anglers seen' and 'number of fish landed' used to predict angler 'satisfaction level' (Table A3)

Annual catch rate and angler effort as a function of annual steelhead trout abundance and a management intervention

To understand if annual catch rate and angler effort reflected annual steelhead trout abundance, and if angler catch or effort changed before or after the management intervention, we used two datasets that spanned the management intervention: the Steelhead Harvest Analysis (SHA) and Tyee test fishery steelhead trout index of abundance datasets (Table A1). Since 1967, the BC government has conducted an annual mail-out survey, known as the SHA, to document catch and effort trends in the steelhead trout recreational fishery throughout the province. This survey provides a means for the provincial fisheries managers to monitor angling activity on more than 400 streams in BC (De Gisi 1999). In March of each angling licence year, approximately 62% of anglers who purchased a steelhead licence receive a questionnaire requesting information on steelhead trout angling activity and catch in the previous year. Over the years, approximately 27% of the surveyed anglers who fished for steelhead trout provided a response to the questionnaire (De Gisi 1999). Although this survey has been conducted since 1967, we only focused on data from 1997-2016 to align with the Tyee test fishery data. From the SHA, we obtained annual angler effort for each river (total number of reported angler days fished during the fishing licence year) and annual catch rate, calculated by dividing the annual total reported fish landed by the annual total angler days reported for each river, providing a mean catch per angler day for each year of the six study rivers. According to the SHA responses, on the six study rivers there was an average of 5380 ± 3564 (this and the following represent mean ± sd) reported angler days fished and annual mean catch rate of 1.1 ± 0.4 steelhead trout landed per angler day between the years 1997 and 2016.

We obtained annual steelhead trout index of abundance data from the Tyee test fishery located on the Skeena River mainstem (Figure A1). In operation annually since 1955, the Tyee test fishery uses gillnet sets in the tidal portion of the Skeena River. Each year, the fishery starts operation on June 10 and ends on August 31 (and more recently into September). Prior to 2002, an undyed, fibrous nylon gillnet was used, subsequently replaced with a 6 strand “Alaska Twist” net being set across a channel measuring two to five km long and 0.8 km wide multiple times per day, providing an index of abundance for returning salmon and steelhead trout to the Skeena River Watershed (Jantz et al. 1990). The annual cumulative index for steelhead trout represents the cumulative sum of the daily catch per hour standardized to June 10, allowing for comparison across years. We obtained the cumulative index of abundance values, thereafter, “steelhead trout abundance”, until August 31 (date at which the Tyee test fishery was consistently operated across all years). While the Tyee test fishery steelhead trout is only an index of abundance, the annual steelhead trout abundance from Tyee has a strong positive linear relationship (r^2=0.67) with the annual estimates of steelhead trout abundance from a tagging program conducted on the Bulkley River, a tributary to the Skeena River that supports the largest steelhead population (analyses not shown, Saimoto and Saimoto 2011). Thus, it is likely that different rivers within the Skeena have steelhead abundances that are positively correlated with each other (Kendall et al. 2017) and that the Tyee test fishery provides a reasonable index of abundance for steelhead trout within the watershed.

In two independent models, we examined the relationship between either reported annual catch rates (mean catch per angler day) or annual effort (total angler days) for each year and potential predictor variables of steelhead trout abundance, river, and the interaction of the management intervention (i.e. before vs. after regulations) and river. Angler effort and catch rates were from the SHA database. We had hypotheses about all covariates considered and consequently compared all possible model combinations of variables using Akaike's Information Criteria corrected for small sample sizes (AICc). For each of the annual catch rate and angler effort models, we compared 10 candidate models using AICc (Burnham and Anderson 2002), and assessed the relative plausibility of each candidate model using Akaike weights (Table A.S1 and A.S2). We centered and standardized the steelhead trout abundance variable so that its mean was 0 and standard deviation was 2 (Grueber et al. 2011). To compare the effect that steelhead trout abundance and the management intervention had on the six study rivers, we considered the Skeena River mainstem as a reference, given that the management intervention was not applied to all sections of the Skeena River mainstem, making the Skeena a "mixed" system. Therefore, all other rivers significance levels are compared to the Skeena River mainstem. To determine if anglers' effort in one year was based on steelhead trout abundance from the previous year, we competed the top candidate model from the AICc results with a model using the same covariates but with a one-year time lag for angler effort. The one-year time lag model received a higher AICc score and was therefore not considered in any further analyses. Model selection results are available in the Supporting Information (Table A.S1 and A.S2). All analyses were performed in R version 3.4.2.

Management intervention and distribution of angler effort

The management intervention restricted unguided non-resident anglers from fishing during certain times and zones. Therefore, to understand if unguided non-resident angler effort redistributed across space and time due to the management intervention we examined effort information from the Classified Waters e-licensing database. In 2009, the BC provincial government created an electronic database that records all licence sales information from anglers who purchased any type of angling licence, including the Classified Waters licence (Table A1). For rivers in the Skeena Region, non-resident anglers are required to purchase a Classified Waters license for the specific river and day that they will be fishing during the steelhead trout season (September through

October). Therefore, the database records a unique angler ID associated with the number of days (organized by date) each non-resident angler fished on any specific river in BC, and whether they were guided or unguided. BC anglers are only required to purchase one annual Classified Waters license, are able to fish any river over the entire licensing year (April 1 to March 31), and are therefore not included in this analysis as day- and river-specific data are not available. On the six study rivers there was an average of 12.5 ± 15.7 (mean ± sd) unguided non-resident angler license sales sold per day between the years 2009 and 2016.

We compared unguided non-resident angler effort (based on Classified Waters license sales) for the three years before and five years after the 2012 management intervention on each of the six study rivers. To determine how the management intervention influenced angler effort by unguided non-residents, we averaged the daily unguided non-resident angler licence sales for each day (Monday – Sunday) for each river (Babine, Bulkley, Kispiox, Morice, Skeena (Section IV), Zymoetz) during the Classified Waters period (September 1 – October 1, while excluding any dates outside this range). We normalized these data by the 2009-2011 mean angler licenses sold for each day of the week and river to facilitate comparison before and after management intervention. We examined post-hoc daily guided non-resident angler effort to determine if non-residents were hiring guides more often since the management intervention, given that guided non-resident anglers are void of the weekend angling restriction.

Angler satisfaction

After the management intervention was implemented, a Skeena River Guardian Program was initiated to gain insight into how the management intervention may have impacted anglers (Table A1). This three-year program from 2013-2015 involved stream-side angler surveys on the Bulkley, Kispiox and Zymoetz rivers during the peak angler season (September through October). Stream-side angler surveys were based on a stratified random sampling design (Zar 1984; Pollock et al. 1994), whereby interviews were scheduled to occur 3 days/week during the weekdays, and 2 days/week during the weekend days. There were three crews of two River Guardians each surveying one of the three rivers during either early (830-1630) or late (1100-1900) shifts to allow for interception of anglers at different times of the day. River Guardians accessed known angling locations by truck or jet boat and surveyed all accessible anglers, that is anglers who could exit the water to conduct an interview. Anglers surveyed were asked a suite of questions pertaining to their basic licence information, quality of angling experience rating (i.e., satisfaction), effort, catch, and compliance (see: Pitman and Hirshfield 2015 for questionnaire). For this study, we only included the survey questions pertaining to crowding, catch, and satisfaction. These questions included, “How many anglers do you remember seeing today?”, “How many steelhead have you landed?”, and “Between 1 and 5, how would you rate your quality angling experience today, 1 being very poor and 5 being excellent” (thereafter “satisfaction level”).

We examined how the number of steelhead trout landed and crowding levels impacted angler satisfaction level based on angler residency and the specific river they were fishing. To identify the best predictors of angler satisfaction level, we fit ordinal logistic regression models using the MASS package in R (Venebles and Ripley 2002). We examined the relationship between angler satisfaction as an ordered categorical factor (very poor < poor < fair < good < excellent) and covariates such as number of steelhead trout landed, number of anglers seen, residency status (Canadian or non-resident), and river (Bulkley, Kispiox, and Zymoetz). We also examined the potential support of including the following interactions: residency status and number of anglers seen, residency status and number of steelhead trout landed, and the number of anglers seen and number of steelhead trout landed. BC residents and Canadian non-BC residents are combined and considered “Canadian” in this analysis due to the small sample size of Canadian non-BC residents. Ordinal logistic regression models are ideal for analyzing ranked categorical response variables, such as satisfaction level, because they preserve the structure of the original ordinal ranks of the categorical response variable. We had hypotheses about all covariates considered and subsequently compared all possible model combinations of variables, including only single interactions. We compared the 28 candidate models using AICc (Burnham and Anderson 2002) and assessed the relatively plausibility of each candidate model using Akaike weights. We centered and standardized our covariates to a mean of 0 and standard deviation of 2 to enable direct comparison of effect sizes among variables (Grueber et al. 2011). Model selection results are available in Supporting Information (Table A.S3).

For all data on steelhead trout anglers, information was aggregated and anonymized prior to analyses. This study was approved by Simon Fraser University’s Office of Human Ethics.

Results

Annual catch rate and angler effort as a function of annual steelhead trout abundance and a management intervention

The most parsimonious model for annual catch rate (mean catch per angler day) included river, management intervention, and annual steelhead trout abundance (Table A.S1). This model accounted for 94% of the Akaike weight and was strongly supported as the top model by ΔAICc (next best model had ΔAICc = 6.7; Table A.S1). Across all rivers, the relationship between annual catch rate and annual steelhead trout abundance was positive, with the overall annual catch rate varying by river (Table A2; Figure A2). As predicted, the catch rate was higher in years when there was greater steelhead trout abundance. Surprisingly, the management intervention had a significant positive effect on annual catch rate, where annual catch rate was slightly higher after the management intervention ($p < 0.001$; Table A2). The model selection results did not support the inclusion of an interaction term between management intervention and river.

Table A2 Parameter estimates obtained from the linear regression model fit to estimate either annual catch rate (mean catch per angler day, model 1) or annual angler effort (total angler days, model 2) in the six study rivers of the Skeena River Watershed, in British Columbia, Canada. Management intervention was a categorical variable of either unregulated (before 2012 management intervention) or regulated (reg; after 2012 management intervention) when unguided non-resident anglers were restricted angling at certain times and zones. Model results are references to unregulated years.

Parameter	***Model 1**: catch rate*		***Model 2**: angler effort*	
	Estimate ± SE	*p*	Estimate ± SE	*p*
(intercept)	0.567 ± 0.041	**<0.001**	6325.7 ± 330.8	**< 0.001**
steelhead trout abundance	0.240 ± 0.034	**<0.001**	603.1 ± 242.6	**0.015**
Babine River	0.968 ± 0.057	**<0.001**	-2938.7 ± 467.5	**< 0.001**
Bulkley River	0.398 ± 0.057	**<0.001**	4603.7 ± 467.5	**< 0.001**
Kispiox River	0.256 ± 0.057	**<0.001**	-3017.9 ± 467.5	**< 0.001**
Morice River	0.603 ± 0.057	**<0.001**	-2882.7 ± 467.5	**< 0.001**
Zymoetz River	0.682 ± 0.057	**<0.001**	-3605.9 ± 467.5	**< 0.001**
reg	0.118 ± 0.040	**0.004**	5159.1 ± 684.0	**<0.001**
Babine River: reg			-5542.3 ± 963.7	**<0.001**
Bulkley River: reg			-2227.2 ± 963.7	**0.023**
Kispiox River: reg			-5162.3 ± 963.7	**<0.001**
Morice River: reg			-4696.1 ± 963.7	**<0.001**
Zymoetz River: reg			-4116.1 ± 963.7	**<0.001**

Note*:* Coefficient (*b)* and standard error (*SE*) are given in standard deviation units, which allow for comparisons of effect sizes among explanatory variables. All river specific levels of significance are based on the model confidence intervals and fit relative to the Skeena River. **Bolded** probability (*p)* values are significant to the 95% confidence level.

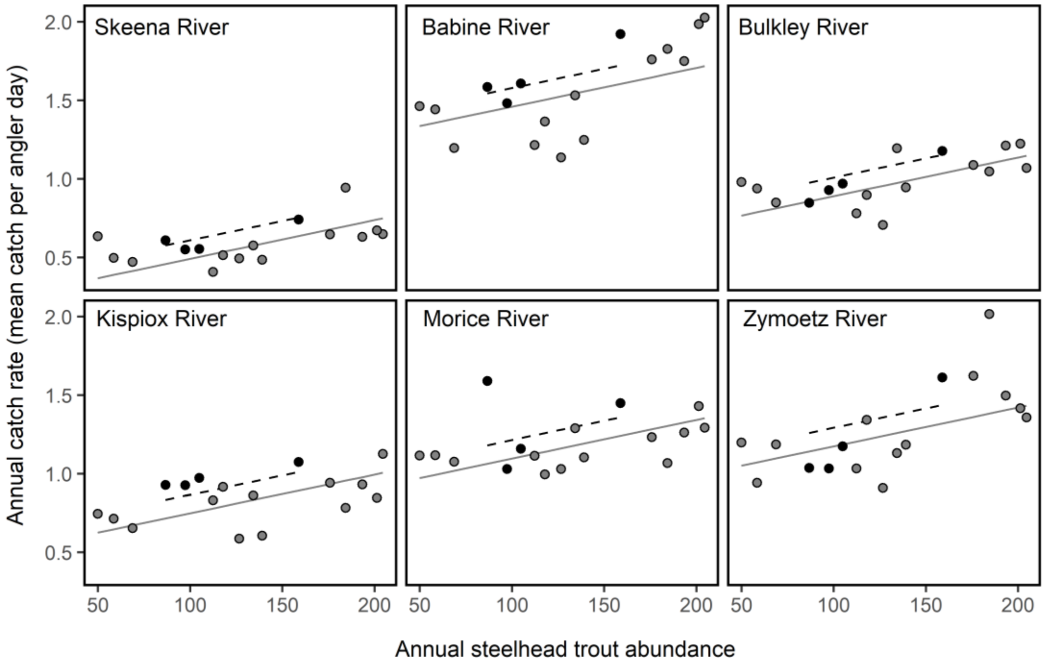


Figure A2 **Relationships between annual steelhead trout abundance and annual catch rate (mean catch per angler day) by recreational anglers in the six study rivers. Shown is a predicted line before and after the management intervention in 2012, grey line indicates before the 2012 management intervention, dashed black line indicates after the 2012 management intervention. Each point is the annual catch rate from 1997-2016, where grey points are years before the management intervention and black points are years after the management intervention.**

The most parsimonious model for annual angler effort (total angler days) included annual steelhead trout abundance, river, management intervention, and interaction between management intervention and river (Table A.S2). This model accounted for 89% of the Akaike weight and the next-best model had a ΔAICc of greater than 4 (Table A.S2), indicating substantial support for the top model. Across all rivers, the relationship between annual angler effort and annual steelhead trout abundance was significantly positive with annual angler effort varying by river (Table A2; Figure A3). There was a significant interaction effect between river and management intervention on annual angler effort, where annual angler effort appeared to increase after the management intervention on all rivers except for the Babine and Kispiox rivers (Table A2; Figure A3). Over time, angler effort has varied by year and river. There has been an increase in annual angler effort on the Bulkley, Morice, Skeena, and Zymoetz rivers, a decrease on the Babine River, and has stayed relatively constant on the Kispiox River (Figure A.S1).

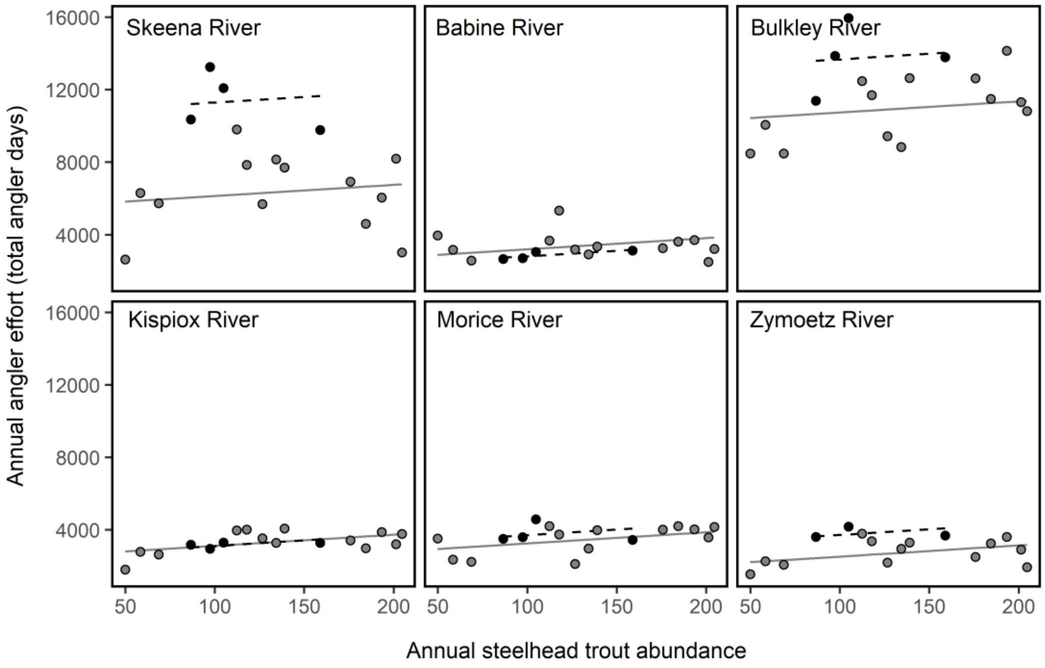


Figure A3 **Relationships between annual steelhead trout abundance and annual angler effort (annual total angler days) by recreational anglers in the six study rivers. Shown is a predicted line before and after the management intervention in 2012, grey line indicates before the 2012 management intervention, dashed black line indicates after the 2012 management intervention. Each point is the annual catch rate from 1997-2016, where grey points are years before the management intervention and black points are years after the management intervention.**

Management intervention and distribution of angler effort

The 2012 management intervention, which was applied to certain rivers at certain times, appeared to redistribute unguided non-resident angler effort temporally and spatially. Before the 2012 management intervention, unguided non-resident angler effort was distributed throughout the week (Monday-Sunday) (Figure A4). However, after the management intervention was implemented on the Bulkley, Kispiox, Morice and Zymoetz rivers, unguided non-resident angler effort decreased during restricted times (primarily weekends) (Figure A4), as expected given the restrictions during these times. For example, prior to the management intervention, there were an average 36.2 ± 19.2 (mean ± sd) unguided non-resident licences sold per day during the weekdays, and 32.0 ± 15.8 licenses sold per day during the weekend day for the Bulkley River. After the management intervention, weekday sales by unguided non-resident anglers increased by 35% on average, while weekend sales decreased by 93%, given that some unguided non-resident anglers either violate the regulation, or accidentally purchase angler days during restricted times. In contrast, sections of the Skeena River were not affected by the management intervention, and angler effort has been generally higher on this river since 2012 regardless of day of the week (Figure A3; Figure A.S1). Angler effort from unguided non-resident anglers appears to be slightly lower on the Babine River after the management intervention (Figure A4). The Kispiox River does not exhibit an increase in during-week fishing by unguided non-residents after the regulations as seen on the Bulkley, Morice and Zymoetz rivers. Non-residents who hire a guide are void of the weekend fishing restriction. Angler effort by guided non-residents since the management intervention has increased (with the exception of the Zymoetz River), however, there has been no particular increase in guided non-resident angler effort during restricted times (primarily weekends) specifically (Figure A.S2). There is no equivalent effort data for BC resident anglers. Regardless, the management intervention appears to be associated with temporal and spatial redistribution of unguided non-resident angler effort in the Skeena River Watershed.

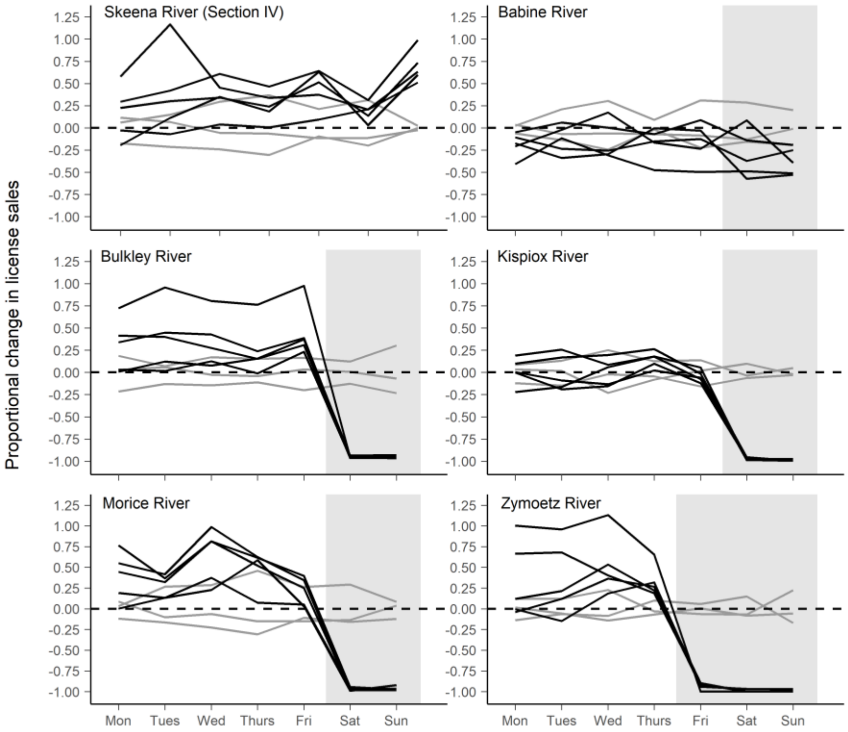


Figure A4 **Proportional change in daily license sales by unguided non-residents from 2009-2016 for the six study rivers in the Skeena River Watershed, British Columbia, Canada. All values are expressed relative to the mean angler licenses sold for each weekday and river from 2009 to 2011, prior to the 2012 management intervention. Positive values therefore represent increased sales since the management intervention. BC residents are not included as they are not required to purchase daily licences. Each line represents one year of licence sales. Light grey lines are sales before the management intervention and black lines are sales after the management intervention. Shaded grey regions are restricted angling days when unguided non-residents are not allowed to fish. Bulkley, Kispiox, Morice, and Babine Rivers are restricted on Saturday and Sunday, the Zymoetz River is restricted on Friday, Saturday and Sunday, and the Skeena IV section has restricted and unrestricted sections. Skeena IV is a management unit of the Skeena River (Figure A1).**

Angler satisfaction

We used interview information post-management intervention on steelhead trout anglers to examine their fishing experience and provide insight into angler satisfaction. A total of 1,972 anglers provided their satisfaction level: 761 rated their experience as ‘excellent’, 578 as ‘good’, 416 as ‘fair’, 142 as ‘poor’, and 75 as ‘very poor’. The median satisfaction level was ‘good’. Of the satisfaction levels reported, 1,274 were Canadian and 698 were non-residents. There were 945 satisfaction levels reported on the Bulkley River, 408 on the Kispiox River, and 619 on the Zymoetz River. Based on these interviews, the average number of anglers seen was 7 (sd=7.5); the average number of steelhead trout landed was 0.5 (sd=1.2).

The most parsimonious model of angler satisfaction included river, angler residency, number of steelhead trout landed, number of anglers seen, and the interaction between number of steelhead trout landed and number of anglers seen (Table S3). This model accounted for 72% of the Akaike weight and the next-best model had a ΔAICc of greater than 4 (Table A.S3), indicating substantial support for the top model. This top model was used to predict the probability that an angler would respond with a satisfaction level (very poor, poor, fair, good or excellent) given different scenarios of number of steelhead trout landed and anglers seen.

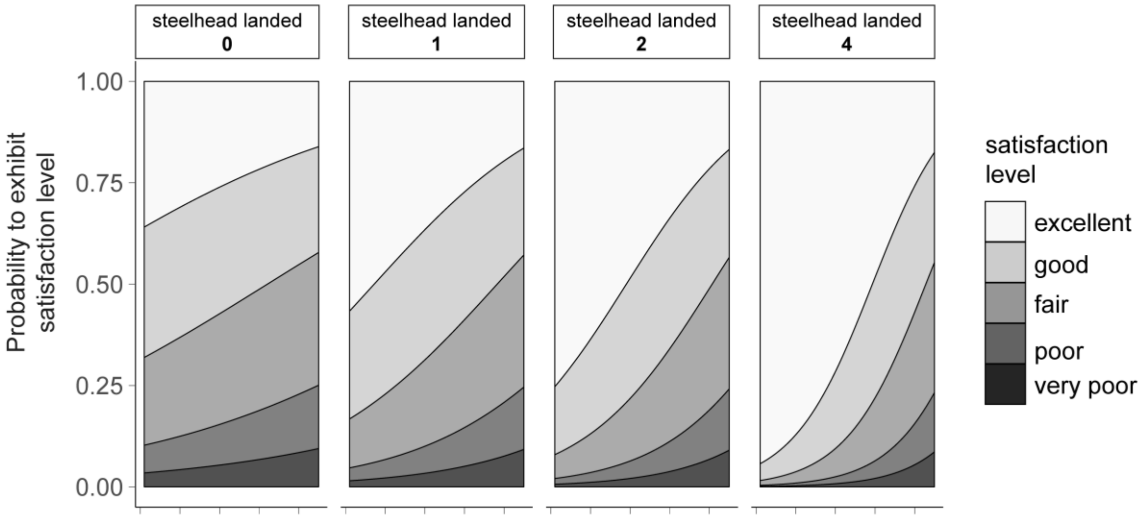
An angler’s satisfaction level increased as a function of the number of steelhead trout they landed and decreased with the number of anglers seen and depended on river and angler residency (Table A3; Figure A.5). For example, for every one additional steelhead trout landed by a Canadian angler fishing the Bulkley River, which is approximately the equivalent of two standard deviations from the mean, an angler was approximately three times as likely to have a higher satisfaction level. In contrast, if that angler encountered 14 other additional anglers on the river (i.e. 2 sd), the odds that the angler responded with a higher satisfaction level (e.g., excellent) instead of a lower satisfaction level (e.g., poor) decreased by approximately 70%. In other words, if more anglers were seen on the river, anglers were more likely to respond with a lower satisfaction level. There was also a significant interaction between the number of steelhead trout landed and number of other anglers seen ($p < 0.001$, Table A3). Specifically, it took more fish landed at higher crowding levels to maintain a high satisfaction level (Figure A.5). In addition, angler satisfaction level depended on angler residency; anglers who were Canadian had a higher probably of reporting a higher satisfaction level than non-resident anglers (Table A3, Figure A5). Last, anglers fishing different rivers had different satisfaction levels (Table A3; Figures A.S3 and A.S4).

Table A3 Parameter estimates obtained from the ordinal logistic regression model explaining angler satisfaction level as a function of angler residency (Canadian or non-resident), river (Bulkley, Kispiox, and Zymoetz river), the number of steelhead trout landed (num steelhead trout landed), and number of other anglers seen (num anglers seen) in the Skeena River Watershed, British Columbia, Canada. Coefficients are interpreted as odds ratios relative to Canadian resident anglers on the Bulkley River.

Parameters	Estimate ± SE	Confidence intervals		*p*
		Lower	Upper	
non-resident angler	0.61 ± 0.09	0.51	0.73	**<0.001**
Kispiox River	1.37 ± 0.12	1.1	1.7	**<0.001**
Zymoetz River	1.01 ± 0.1	0.83	1.23	0.9
num anglers seen	0.60 ± 0.09	0.51	0.71	**<0.001**
num steelhead trout landed	5.77 ± 0.15	4.36	7.74	**<0.001**
num steelhead trout landed * num anglers seen	0.51 ± 0.25	0.32	0.85	**0.007**

Note: Coefficient and standard error (*SE*) are given in standard deviation units, which allow for comparisons of effect sizes among explanatory variables. **Bolded** probability (*p)* values are significant to the 95% confidence level. Parameter levels of significance are based on the model confidence intervals and fit relative to Canadian resident anglers on the Bulkley River.

a) Canadian residents (including BC residents)



b) non-residents

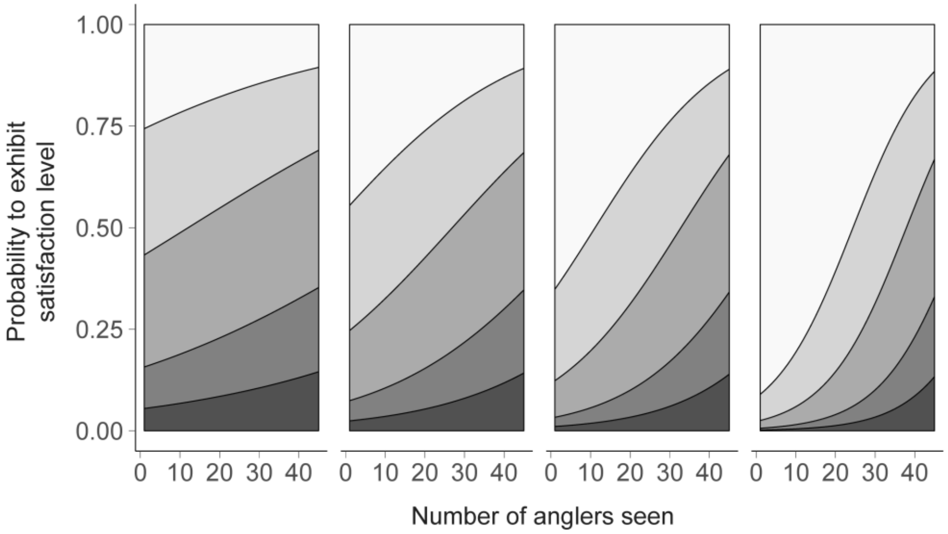


Figure A5 Probability of either a Canadian (including BC residents) or a non-resident angler having a predicted satisfaction level of “excellent”, “fair”, “good”, poor”, or “very poor” given landing either zero, one, two, or four steelhead trout and the number of anglers seen that day (0-50) on the Bulkley River. These ranges capture most of the range in the observed catch and crowding.

Discussion

This study examined extensive datasets utilizing both social science approaches and ecological analyses to examine the linkages that underpin the dynamics of an internationally-recognized catch-and-release steelhead trout fishery over the period of a management intervention. The study had several key findings. First, we found that annual catch rates and effort were higher in years when there were more steelhead trout. In addition, we found that the management intervention did indeed reduce unguided non-resident anglers' effort during the weekend, as intended, but was also apparently associated with the spatial and temporal displacement of effort to other times and places. Last, angler surveys revealed that anglers were more satisfied when they caught more fish and encountered fewer anglers, but that this satisfaction also depended on residency of the angler as well as the river they were fishing. Collectively, this study not only helps evaluate a specific management intervention but also provides a broadly-relevant example of how both ecological and social factors influence recreational fishery dynamics.

In all of our study rivers, anglers caught more fish in years when there was greater steelhead trout abundance. Perhaps not surprisingly, anglers often catch more fish when there are more fish around to catch (Beard et al. 1997; Harley et al. 2001; Wilson et al. 2016). However, this is not always the case. In some fisheries, catch rates plateau as fish abundance increases likely due to saturation of anglers (Peterman 1980). Other studies of recreational fisheries have found that catch rates stay high as fish abundance declines, also called hyperstability (Erisman et al. 2011; Ward et al. 2013). Several processes may cause hyperstability; for example "effort sorting" (Walters and Martell 2004), where fishing skill level varies across individual anglers, and therefore success rate that anglers are willing to tolerate varies – less skilled anglers will typically exit the fishery (or seek other recreational opportunities) before more skilled individuals during periods of fish decline (Ward et al. 2013; Post 2013; van Poorten et al. 2016). In contrast, our analyses indicated that on all study rivers the relationship between annual catch rate and fish abundance appears to be positive and linear in the range of the data we examined. This pattern is analogous to a Type I functional response of predator-prey relationships (Holling 1959), with the major difference that catch-and-release fisheries often do not kill the fish. Accordingly, in this system, higher steelhead trout abundances translate to higher angler catch rates and thus alter their angling experience.

Our study found that there was a significant positive relationship between annual angler effort and annual steelhead trout abundance. These results complement many studies showing strong effort-abundance relationships (Carpenter et al. 1994; Johnson and Carpenter 1994; Cox et al. 2002; Post et al. 2002), similar to a numerical response of predatory-prey relationships, where the density of predators (angler effort) changes as prey numbers (steelhead trout abundance) increase (Holling 1959). We note that the relationship between annual angler effort and steelhead trout abundance was not as strong as the relationship between annual catch rate and steelhead trout abundance (Figures A2 and A3). It is likely challenging for anglers to predict returns of steelhead trout or respond to within-season steelhead trout abundance estimates because of the travel costs and pre-planning required for many anglers to visit the Skeena River Watershed. While we hypothesize that there may also be longer-term feedbacks between steelhead trout abundance, angler satisfaction, and future effort, our analyses did not observe lag effects of steelhead trout abundance on total angler effort in the next year. The observation that years with more steelhead trout are associated with higher angler effort is of importance given that steelhead trout angling has been estimated to bring upwards of $16 million CAD to the local economy (Counterpoint Consulting 2008). More fish should translate into more effort and more money for the local economy.

The management intervention was associated with shifts in both annual catch rates and angler effort. First, for all angler residency types combined there was an intriguing increase in annual catch rates after the regulations, with annual catch rate increasing after management implementation on all six study rivers. This pattern might be because the management intervention was associated with a general increase in relative use of guides by non-resident anglers on all rivers (with the exception of the Zymoetz River) after the management intervention (Figure A.S2). Guided non-resident anglers are exempt from the management intervention that restricts fishing on weekends; thus, the new regulations may have incentivized non-residents to hire guides. Presumably guided anglers have a greater success at landing fish. Therefore, it is possible that the increase in guided activity on these rivers has contributed to the increase in catch rate after the management intervention. However, the increase in catch rate after the management intervention could also be due to other factors, such as developments in gear or fishing techniques or shifts in the experience level of anglers. Second, the management intervention was associated with shifts in total angler effort (Canadians and non-residents), but these shifts manifested differently depending on the river. Total angler effort increased on the Skeena, Bulkley, Morice, and Zymoetz rivers after the management intervention, however, decreased or stayed the same on the Babine and Kispiox. Thus, in terms of total annual angler effort, the management intervention was not associated with a consistent pattern.

Our study found that the management intervention, which focused on reducing angler effort by unguided non-resident anglers, did most likely provide times and places with less fishing pressure, but that this effort was apparently displaced to other times and places. As intended, the management intervention resulted in a shift to virtually no angler effort by unguided non-resident anglers during the weekend days, which likely provided fishing opportunities for BC resident anglers with lower angler crowding on the Bulkley, Kispiox, Morice, and Zymoetz rivers (Figure A4). Thus, the new regulation achieved its primary objective. However, following the management intervention, unguided non-resident angler effort increased during the weekdays on these rivers (with the exception of the Kispiox River) (Figure A4), likely increasing crowding challenges at a different time. This temporal displacement of effort has been previously observed in other systems – temporary closures can lead to an increase in angler effort outside of the closure window (Hall and Shelby 2000; Murray et al. 2001). Furthermore, unguided non-resident angler effort also increased on river sections (Skeena River section IV; Figure A4) where there were areas void of the management intervention during times when other rivers were restricted. This spatial displacement is analogous to the movement of fishing effort to the edges of MPAs following designation (Halpern et al. 2004; Hilborn et al. 2004). Thus, our study indicates that Skeena Region fisheries managers did achieve the goal of reducing crowding for local anglers on some rivers during the weekends, yet there was an apparent temporal and spatial displacement of unguided non-resident angler effort to other times and places, which exacerbates crowding challenges at different times. Therefore, our study contributes to building understanding of how the spatial and temporal displacement of angler effort can complicate fisheries management (Hall and Shelby 2000; Murray et al. 2001; Halpern et al. 2004)

Our study found that landing a fish and seeing few other anglers were determinants of angler satisfaction in this recreational steelhead trout fishery, and that satisfaction varied by angler residency and river. Importantly, there was an interaction between the number of fish landed and crowding – as anglers experience higher levels of crowding, higher catch rates are needed to maintain a high level of angler satisfaction (Figure A5). Our work adds to the understanding of how both ecological (fish abundance) and social (angler effort and crowding) processes define angler satisfaction. Previous studies have shown that both catch-related attributes, such as the number of fish landed and fish size, as well as non-catch-related factors, such as crowding, accessibility, and fishing regulations can be important to anglers, however, some factors are more important than others (Holland and Ditton 1992; Fisher 1997; Aas et al. 2000; Hunt 2005; Askey et al. 2006; Dorow et al. 2010; Mee et al. 2016; Wilson et al. 2016). In some recreational fisheries, angler satisfaction can be determined primarily by catch rates or size of fish landed (Graefe and Fedler 1986; Arlinghaus 2006; Hutt and Neal 2010; McCormick and Porter 2014; Beardmore et al. 2015), while in others, non-catch-related factors, such as crowding, take precedence (Martinson and Shelby 1992; Hunt 2005). These different angler satisfaction levels are likely determined by the diversity of fisheries and anglers (Beardmore et al. 2011; 2015). Indeed, we found that different types of anglers (Canadian vs. non-residents) had slightly different levels of satisfaction. Regardless, this portion of the study reveals that both catching fish and crowding influence the satisfaction of both Canadian and non-resident anglers in this fishery.

Our study suggests that the multiple factors that control steelhead trout abundance in the Skeena River Watershed can translate into angler satisfaction and angler effort. Because catching fish was important to anglers (Figure A5), and catch rates were linked to steelhead trout abundance, higher abundances of steelhead trout should lead to higher levels of angler satisfaction (Figure A6). On the other hand, angler effort was also positively associated with steelhead trout abundance, which could lead to crowding and lower levels of angler satisfaction. There are many factors that contribute to the population dynamics of steelhead trout in the Skeena River Watershed and beyond (Kendall et al. 2017). The commercial mixed-stock salmon fishery in the Skeena River directed at sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*) intercepts a variable number of summer-run steelhead trout (ranging from and estimated 1000-17,000 fish caught, depending on the year) as bycatch because they overlap in their migration timing (J.O. Thomas and Associates Ltd. 2010; Beacham et al. 2012), with recent continued attempts to implement alternative practices to decrease steelhead trout bycatch (Walters et al. 2008). Catch-and-release fishing for steelhead trout can kill some individuals and has negative physiological consequences (Bartholomew and Bohnsack 2005; Cooke and Schramm 2007; Pollock and Pine 2007; Twardek et al. 2018), with unknown population-level consequences (Policansky 2002; Arlinghaus et al. 2007). Multiple other factors can influence steelhead trout abundance, such as changes in freshwater habitat (Gustafson et al. 2007; Kendall et al. 2017) and ocean conditions, which have been unfavourable for many populations of steelhead trout over the last several decades (Moore et al. 2015; Kendall et al. 2017). Regardless of the multiple mechanisms governing variation in steelhead trout abundance, our analyses make the important linkage that processes that impact steelhead trout abundance will alter angler catch rate, satisfaction, and effort.

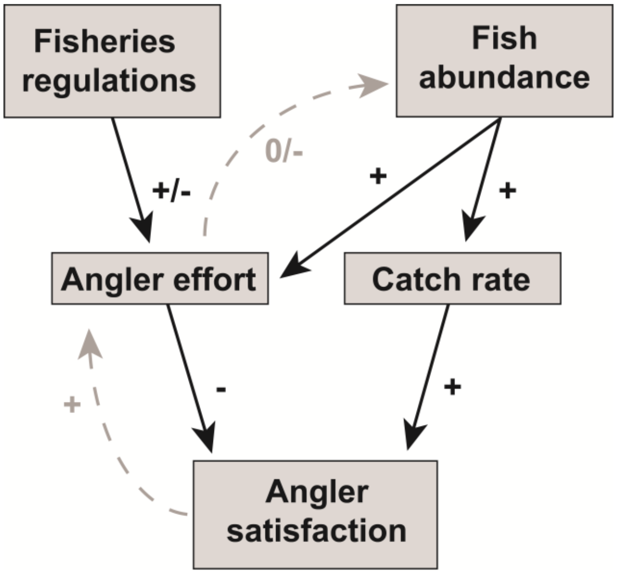


Figure A6 **Conceptual model of social-ecological linkages in Skeena River steelhead trout fisheries. Black arrows indicate pathways of connections quantified in this paper. Positive relationships are indicated by a plus symbol, negative relationships are indicated with a minus symbol, and zero or negative relationships are indicated by a 0/- symbol. For example, Figure A5 demonstrates the positive relationship between annual catch rate and angler satisfaction. Grey arrows indicate hypothesized connections.**

Our study integrated multiple data sources that have limitations and caveats. Annual catch rates were based on SHA self-reported catch numbers. We believe that these self-reported catch rates are likely biased high. Indeed, the median self-reported catch estimate was approximately twice as high as the median catch rates quantified by the River Guardians angler survey. It is likely that the self-reported catch rates were exaggerated due to prestige or recall bias. Prestige bias occurs when angler catch reporting is biased high due to a subconscious or conscious urge for anglers to demonstrate their angling prowess (Pollock et al. 1994; Sullivan 2003). Recall bias occurs when anglers can’t recall fishing failure due to the time span between when the angler was fishing and when they received the survey, leading to an overestimation of catch (Sullivan 2003). Unless prestige or recall bias shifted unevenly across years, we believe the qualitative patterns we observed are robust to this bias. It is also possible that anglers completing mail-in surveys may have been vague in identifying where they were fishing. For example, anglers might have reported that they fished the “Skeena River”, when they may have actually fished one of its tributaries (e.g., the Bulkley, Babine, and Kispiox rivers). Another potential bias in the SHA is non-response error, a potentially serious shortcoming of mail-in surveys, where non-respondents are typically less active or more successful participants in the fishery, resulting in an over represented sample of less success or more successful anglers (Brown 1991; Pollock et al. 1994). These types of errors and biases are typical for mail-in surveys, and still provide benefit for understanding the social science of the fishery (Pollock et al. 1994). Furthermore, actual numbers of returning steelhead trout to the different focal study rivers are generally unknown; analyses relied on the Skeena River mainstem indices of abundance that integrate multiple river systems. However, population dynamics of nearby steelhead trout populations are generally positively correlated (Kendall et al. 2017), lending support to our use of these data sources. We also highlight that there is not within-season effort information for BC residents as they are not required to purchase day-specific Classified Waters licences. Collectively these factors undoubtedly contributed unexplained variation to the dynamics that we describe in our analyses.

Our study illuminates the direct and indirect linkages between anglers, management, and fish abundance in this recreational catch-and-release fishery (Figure A6). Angler satisfaction is directly influenced by catch rate and crowding, which are in turn influenced by management intervention and fish abundance. Higher steelhead trout abundance was not only associated with higher catch rates but also higher effort, which could be interpreted as having opposing effects on angler satisfaction given that higher angler effort would lead to more crowding. It also seems likely that there will be a longer-term feedback between angler satisfaction and the popularity of the fishery (gray arrow between angler effort and angler satisfaction in Figure A6). The resultant future higher effort could erode angler satisfaction due to crowding. In addition, there is likely some level of mortality imposed on steelhead trout from catch-and-release angling – even if mortality rates are low (<10%) – (Bartholomew and Bohnsack 2005; Taylor and Barnhart 2010), the tens of thousands of angler days each year and catch rates of approximately one fish per angler per day could lead to lower numbers of steelhead trout, and therefore dissatisfied anglers (grey arrow between angler effort and fish abundance in Figure A6). Thus, this fishery is influenced by a complicated combination of socio-cultural (e.g., management intervention), socio-economic (e.g., by-catch in commercial fisheries) and ecological processes (e.g., ocean survival, habitat integrity). Our study adds to the growing appreciation of the importance of social-ecological linkages into fisheries management (Ward et al. 2016; Arlinghaus et al. 2017).

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Supplementary Material

Table A.S1 Comparison of linear regression models that estimate annual catch rate (mean catch per angler day) for the six study rivers in the Skeena River Watershed, British Columbia, Canada. Number of parameters (*k*), Akaike's information criteria corrected for small sample sizes (AICc), change in AICc score (ΔAICc), and AICc weight (Weight) were used to select the top model from all possible combinations of candidate models. Variables considered in the models included management intervention (reg), river, and annual steelhead trout abundance.

Models	*k*	AICc	ΔAICc	Weight
reg + river + steelhead abundance	9	-64.488	0.000	0.940
river + steelhead trout abundance	8	-57.759	6.729	0.033
reg + river + steelhead trout abundance + reg * river	14	-57.421	7.067	0.027
river	7	-24.006	40.483	0.000
reg + river	8	-23.265	41.223	0.000
reg + river + reg * river	13	-14.423	50.065	0.000
steelhead abundance	3	83.511	148.000	0.000
reg + steelhead trout abundance	4	83.701	148.190	0.000
null	2	90.661	155.150	0.000
reg	3	92.316	156.805	0.000

Table A.S2 Comparison of linear regression models that estimate annual angler effort (total angler days) for the six study rivers in the Skeena River Watershed, British Columbia, Canada. Number of parameters (*k*), Akaike's information criteria corrected for small sample sizes (AICc), change in AICc score (ΔAICc), and AICc weight (Weight) were used to select the top model from all possible combinations of candidate models. Variables considered in the models included management intervention (reg), river, and annual steelhead trout abundance.

Models	*k*	AICc	ΔAICc	Weight
reg + river + steelhead trout abundance+ reg * river	14	1753.358	0.000	0.889
reg + river + reg * river	13	1757.516	4.159	0.111
reg + river + steelhead trout abundance	9	1784.858	31.501	0.000
reg + river	8	1786.936	33.578	0.000
river	7	1800.852	47.495	0.000
river + steelhead trout abundance	8	1802.039	48.681	0.000
reg	3	1960.325	206.967	0.000
null	2	1961.046	207.689	0.000
reg + steelhead trout abundance	4	1961.772	208.414	0.000
steelhead trout abundance	3	1962.953	209.595	0.000

Table A.S3 Comparison of ordinal logistic regression models that estimate satisfaction levels of anglers (1=very poor: 5= excellent) on the Bulkley, Kispiox, and Zymoetz rivers in the Skeena River Watershed, British Columbia, Canada. Number of parameters (*k*), Akaike's information criteria corrected for small sample sizes (AICc), change in AICc score (ΔAICc), and AICc weight (Weight) were used to select the top model from all possible combinations of candidate models. Variables considered in the models included residency, river, number of anglers seen, and number of steelhead trout landed.

Models	*k*	AICc	ΔAICc	Weight
residency+ river + num anglers seen + num steelhead landed + num anglers seen * num steelhead landed	10	5151.5	0.0	0.721
residency + num anglers seen + num steelhead landed + num anglers seen * num steelhead landed	8	5155.8	4.3	0.083
residency + river + num anglers seen + num steelhead landed	9	5156.2	4.7	0.068
residency + river + num anglers seen + num steelhead landed + residency * num steelhead landed	10	5156.5	5.0	0.059
residency + river + num anglers seen + num steelhead landed + residency * num anglers seen	10	5156.9	5.5	0.047
residency + num anglers seen + num steelhead landed + residency * num steelhead landed	8	5160.3	8.8	0.009
residency + num anglers seen + num steelhead landed	7	5160.5	9.0	0.008
residency + num anglers seen + num steelhead landed + residency * num anglers seen	8	5161.7	10.2	0.005
num anglers seen + num steelhead landed + num anglers seen * num steelhead landed	7	5177.0	25.6	0.000
river + num anglers seen + num steelhead landed + num anglers seen * num steelhead landed	9	5178.2	26.7	0.000
num anglers seen + num steelhead landed	6	5181.2	29.7	0.000
river + num anglers seen + num steelhead landed	8	5182.4	30.9	0.000
residency + river + num steelhead landed + residency * num steelhead landed	9	5184.9	33.4	0.000
residency + river + num steelhead landed	8	5184.9	33.5	0.000
residency + num steelhead landed + residency * num steelhead landed	7	5195.1	43.6	0.000
residency + num steelhead landed	6	5195.6	44.1	0.000
river + num steelhead landed	7	5212.6	61.1	0.000
num steelhead landed	5	5216.1	64.6	0.000
residency + river + num anglers seen	8	5360.3	208.8	0.000
residency + river + num anglers seen + residency * num anglers seen	9	5360.8	209.3	0.000
residency + num anglers seen	6	5371.2	219.7	0.000
residency + num anglers seen + residency * num anglers seen	7	5372.1	220.6	0.000
river + num anglers seen	7	5375.6	224.1	0.000
residency + river	7	5377.9	226.5	0.000

num anglers seen	5	5381.4	229.9	0.000
river	6	5394.5	243.0	0.000
residency	5	5397.8	246.3	0.000
null	4	5408.2	256.7	0.000

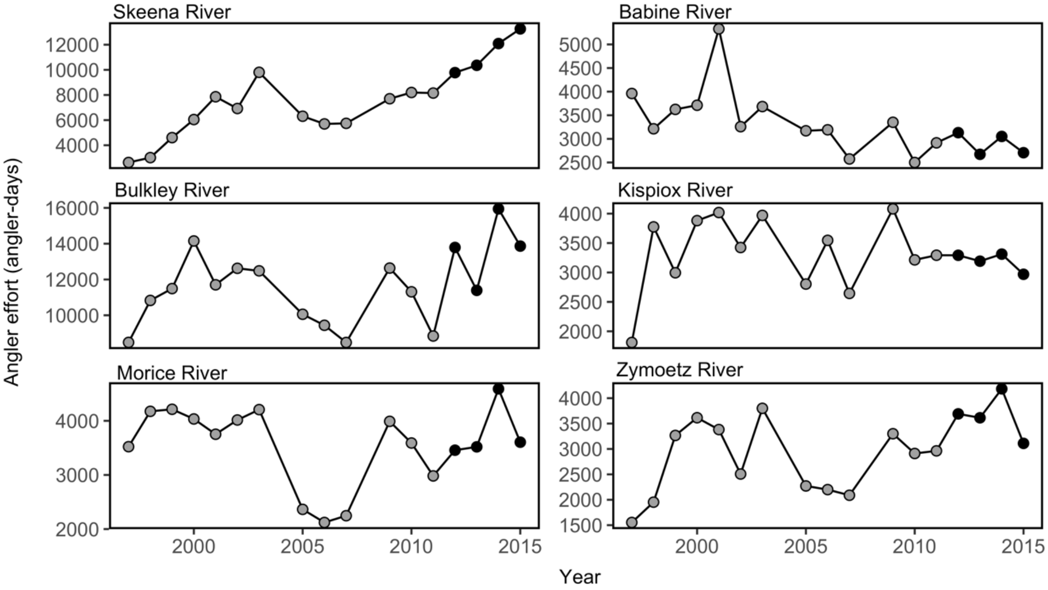


Figure A.S1 **Annual angler effort across time for the six study rivers in the Skeena River Watershed. Black points are years after the management intervention, grey points are years before the management intervention. Note that the y-axes vary.**

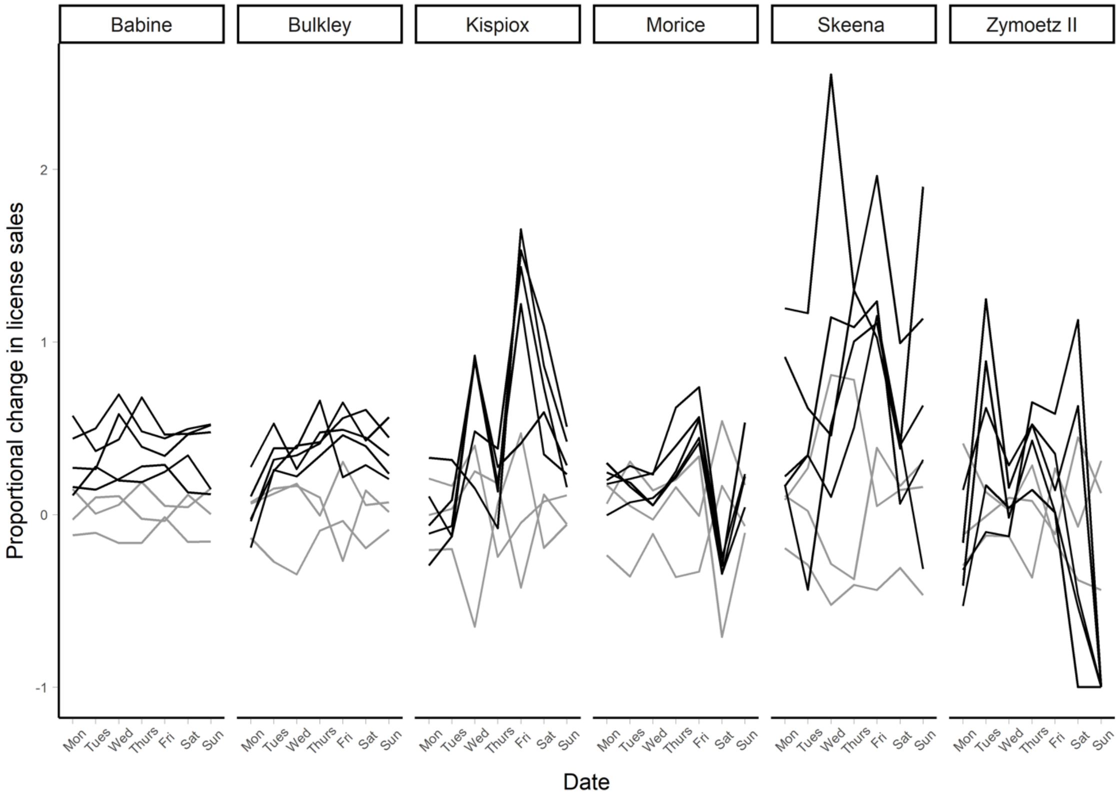
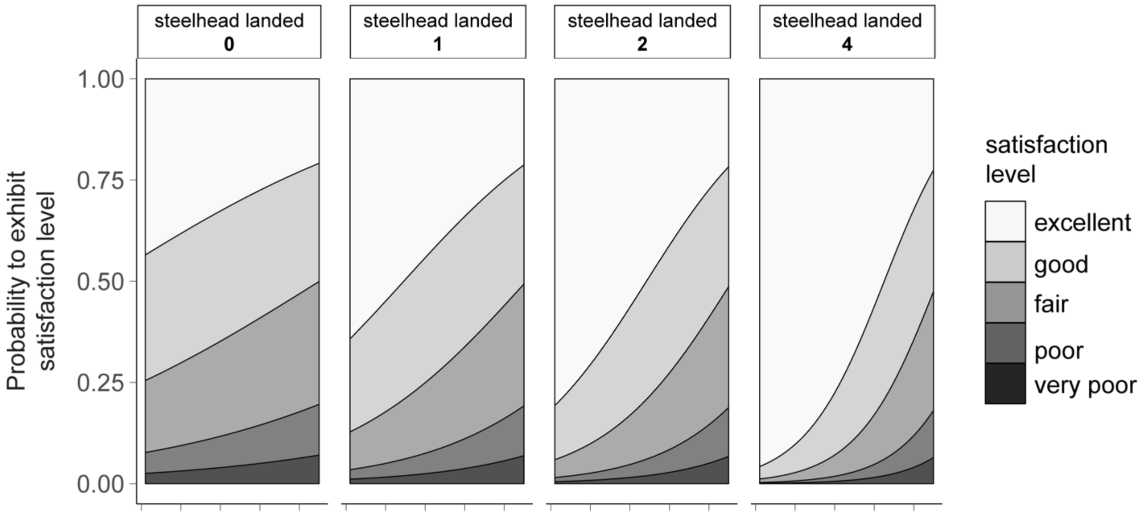


Figure A.S2 **Proportional change in license sales by guided non-residents from 2009-2016 for the six study rivers in the Skeena River Watershed, British Columbia, Canada. All values are expressed relative to the mean angler licenses sold for each weekday and river from 2009 to 2011, prior to the 2012 management intervention. Positive values therefore represent increased sales since the management intervention. BC residents are not included as they are not required to purchase daily licenses. Each line represents one year of license sales. Light grey lines are sales before the management intervention and black lines are sales after the management intervention.**

a) Canadian residents (including BC residents)



b) non-residents

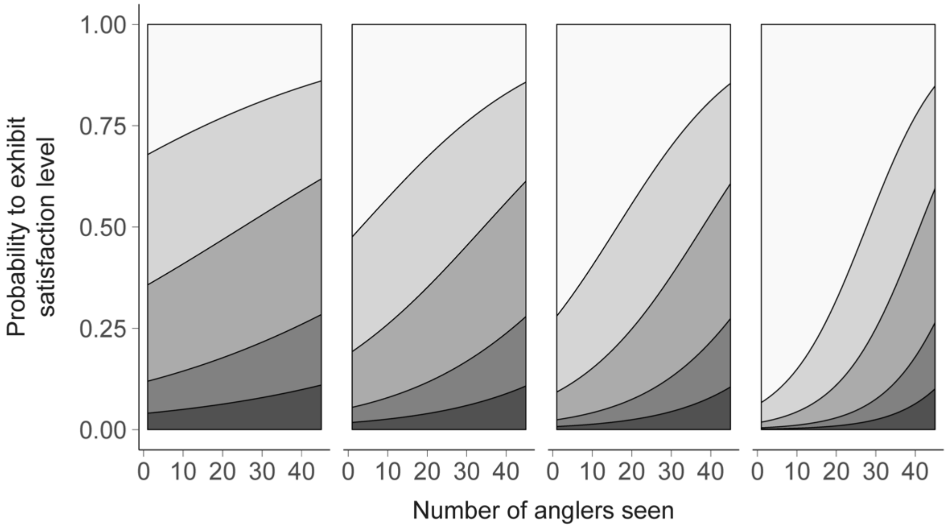
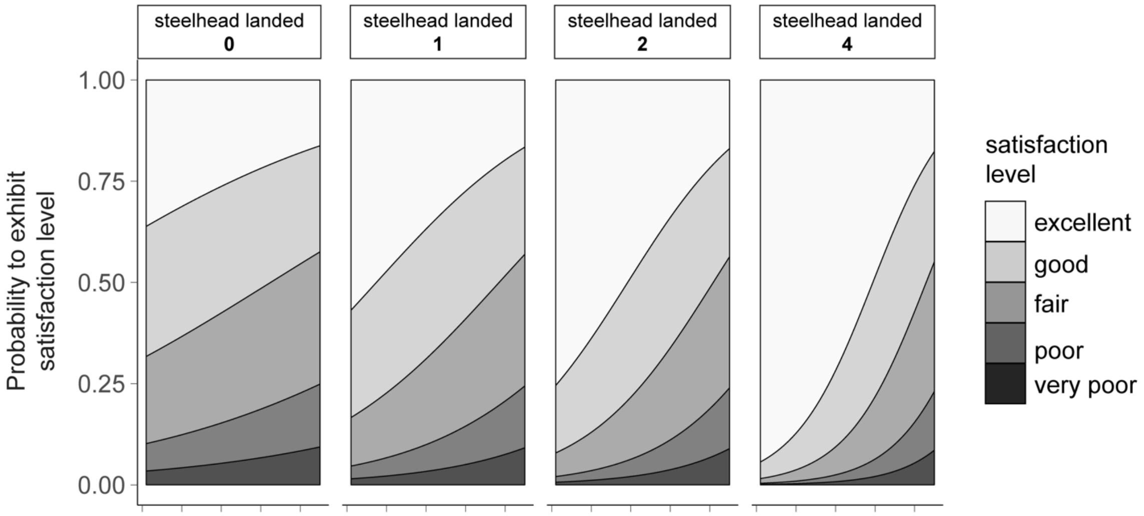


Figure A.S3 Probability of either a Canadian (including BC residents) or a non-Canadian resident angler having a predicted satisfaction level of “excellent”, “fair”, “good”, “poor”, or “very poor” given landing either zero, one, two, or four steelhead trout and the number of anglers seen that day (0-50) on the Kispiox River. These ranges capture most of the range in the observed catch and crowding.

a) Canadian residents (including BC residents)



b) non-residents

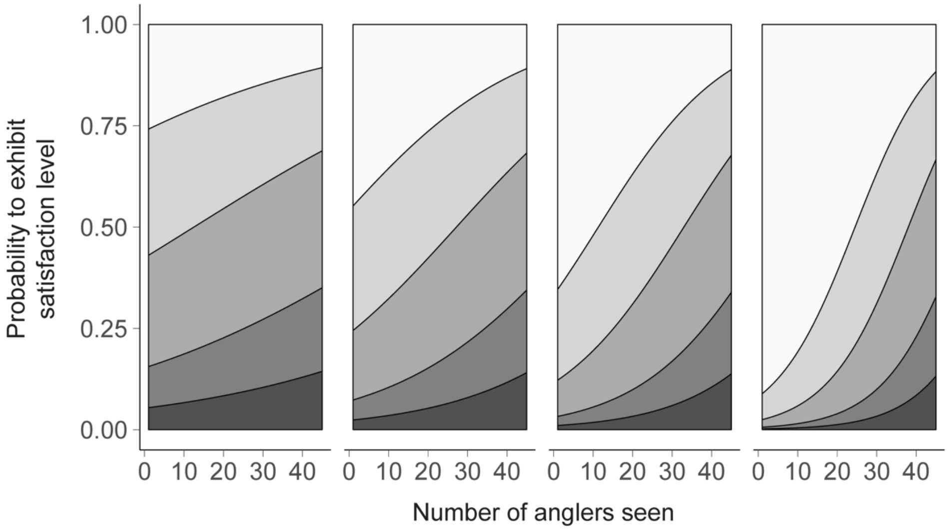


Figure A.S4 **Probability of either a Canadian (including BC residents) or a non-Canadian resident angler having a predicted satisfaction level of “excellent”, “fair”, “good”, “poor”, or “very poor” given landing either zero, one, two, or four steelhead trout and the number of anglers seen that day (0-50) on the Zymoetz River. These ranges capture most of the range in the observed catch and crowding.**

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