THERMAL ECOLOGY OF BULL TROUT (*SALVELINUS CONFLUENTUS*) AND POTENTIAL CONSEQUENCES OF CLIMATE WARMING IN MONTANE WATERSHEDS

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Abstract

The biodiversity of freshwater fishes has declined rapidly across North America over the past 50 years. At higher latitudes (>60°N) knowledge of freshwater fish biodiversity is incomplete, hampering our abilities to understand how species may respond as climate changes. Bull trout (*Salvelinus confluentus*) is a societally important salmonid that is considered a sentinel species for monitoring impacts of climate change due to its requirement for cold water. In this thesis, I describe the thermal ecology and assess potential effects of climate warming on north-temperate montane bull trout populations. In Chapter 2, I used juvenile distributional data to evaluate design considerations for detecting watershed-scale population trends. Detectability of juveniles was not uniform, and imperfect detection affected accuracy of assessments most in fringe habitats near distributional boundaries. Detecting a 30% change in watershed-level occupancy ≥78% of the time is possible, but requires three repeat surveys (i.e., temporal replicates) and increased sampling intensity of fringe habitats. Additional sampling effort in fringe sites could be offset by sampling fewer sites in core habitats, while still minimizing risk of non-detection. In Chapter 3, I use full-year stream temperature records to describe thermal regimes that populations experience across a broad latitudinal gradient. All streams showed high thermal stability and similar insensitivity to the warming effects of air temperature. However, fish distribution at higher latitudes was constrained by cold-limiting streams in both the summer and winter (i.e., do not freeze); which is opposite to lower latitudes, where distributional patterns are governed by warm-limiting streams. In Chapter 4, I examined how climatic and geomorphic factors influence the distribution of juveniles in a northern watershed and forecast effects of climate warming on the distribution of suitable habitat. Juvenile distribution is driven by cold-limiting streams, prevalence of perennial groundwater, and stream size. Suitable habitat, based on both climatic and geomorphic factors, is projected to decline across all warming scenarios. Conversely, availability of thermally suitable habitat, which does not consider other habitat factors, is projected to increase. The dichotomy in these projections illustrates the importance of considering broader dimensions of the ecological niche for climate change vulnerability assessments of northern stream fishes.

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Table of Contents

Page

List of Tables

List of Figures

Chapter 1: Introduction

Knowledge of global freshwater biodiversity is still very incomplete, especially in watersheds at northern latitudes (>60°N) (Dudgeon et al. 2006; Reist et al. 2006a; Strayer and Dudgeon 2010). Despite such uncertainty, biodiversity declines have occurred across aquatic ecosystems and with globally pervasive and persistent stressors, such as climate change, these declines are likely to continue (Comte et al. 2013). To further compound this issue, over 65% of rivers across the world are under threat from cumulative stressors, which include rising water temperatures, reductions in flow, alterations in groundwater prevalence, and impacts to water quality (Vörösmarty et al. 2010; Isaak et al. 2012; Taylor et al. 2013). Mitigating declines in freshwater biodiversity requires a holistic approach that focuses on four key principles. First, long-term data analyses of species distributions and population demographics using reliable data collected using robust sampling designs. Second, methodological improvements in assessments to more efficiently collect densely populated data sets that provide a more accurate understanding of species distributions and enable more precise projections of ecological responses to habitat alteration. Third, assessment of non-climatic and climatic stressors across species distributional ranges and higher levels of organization (e.g., community assemblages). Last, systematic assessment of observed versus predicted effects of stressors across broad spatial scales (i.e., local to global) and multiple levels of biological organization, which include assemblages, species, and populations (Dudgeon et al. 2006; Comte et al. 2013; Hannah et al. 2014).

Effectively documenting species distributions is a fundamental element of conserving freshwater biodiversity, as an accurate understanding of species assemblages across the landscape serves as a baseline for assessing population trends and the status of taxa (Comte et al. 2013). Documenting how the geographical ranges of freshwater fishes change (e.g., expand, shift, contract) in response to ecosystem alterations represents a natural experiment providing insight into the resilience and resistance of species to habitat alteration. A recent example is the response of terrestrial and aquatic taxa to changing climate, resulting in poleward distributional shifts and altered phenology across both these ecosystems (Parmesan and Yohe 2003; Perry et al. 2005; Chen et al. 2011). But in the context of ecosystem functioning, it is also important to recognize that not all species are created equal. For example, keystone species have disproportionately larger effects on ecosystem structure and function, relative to their abundance, than redundant species occupying lower trophic levels (Post et al. 1999; Giller and O'Donovan 2002). Therefore, any alteration to a keystone species (e.g., population decline, behavioral shift, extirpation), typically results in regime shifts signifying that an ecological threshold may have been crossed (Post et al. 1999; Walther et al. 2002; Tunney et al. 2014). Here, I define an ecological threshold as the point at which a small change in environmental conditions result in a major shift to ecosystem structure and function (Groffman et al. 2006). Mitigating further declines in freshwater biodiversity requires a deeper understanding of both community and species-level responses to ecosystem alterations (Comte and Olden 2017b, 2017a).

The contemporary distribution of North American freshwater fishes is a result of historical processes, environmental conditions, and local adaptation (Wiens and Donoghue 2004; Sexton et al. 2009; Griffiths 2010). The broader distributional pattern of most North American freshwater fish was shaped primarily by the Late Wisconsinan glaciation, which culminated 23 000 -18 000 years ago (McPhail and Lindsey 1970; Hocutt and Wiley 1986; Rempel and Smith 1998). Residence in unglaciated areas or post-glacial dispersal and recolonization events resulted in lower species richness across latitudinal gradients. Migratory species show lower species diversity related to latitudinal gradients than residents and this pattern is a reflection of dispersal abilities and connectivity of suitable habitat within and across watersheds (Griffiths 2010). Post-glaciation, the distribution of species within and across watersheds evolved based on environmental heterogeneity and species biological traits. On an ecological time scale, some species have evolved to become specialists that can survive in a narrow range of favorable but stable environments; whereas, generalists are often found in areas with less predictable and often more stressful conditions (Somero 2005; Sexton et al. 2009). The ability of fish species to disperse, adjust, or adapt has further shaped contemporary freshwater fish distributions. All are related to phenotypic plasticity and evolutionary processes, but for most species that recolonized glaciated areas, genetic adaptation to local habitats is a less likely mechanism as these species have had less time to evolve than those from unglaciated areas (Sexton et al. 2009; Griffiths 2010). Many species that recolonized glaciated watersheds were able to adjust their phenotype to different conditions and the breadth of a species' phenotypic plasticity and dispersal abilities combine to shape distributional boundaries within and across watersheds (Sexton et al. 2009).

Ecological niche and species range limits

When the ecological niche that a species occupies is portrayed across geographic space it represents that species' range limit (Sexton et al. 2009; Peterson 2011). Here I define the ecological niche as a set of non-consumed abiotic variables that affect an organism physiologically and characterize the environment in which a species can persist in the presence of competitors (Soberón 2007; Peterson 2011). By examining a species' ecological niche, one can gain a better understanding of the ecological patterns and processes that influence fitness and survival. A key challenge is to identify environments near the edge of range limits where population fitness declines (Pörtner and Peck 2010), as the characteristics of these areas theoretically represent ecological thresholds (Thorpe 1994; Pulliam 2000; Sexton et al. 2009).

Although identifying these areas may seem simple, it is often very difficult to disentangle different ecological and evolutionary processes (e.g., competition, local extinction/colonization, habitat selection) that influence population fitness (Sexton et al. 2009). These processes can obscure our understanding of the patterns we see on the land, especially at range margins (Elith and Leathwick 2009; Sexton et al. 2009). An alternative approach is to examine populations across the range and describe abiotic and biotic factors that may influence their distribution based on abundance or habitat occupancy. Once ecological niches are defined, experiments can be done to test the capacity of populations to survive in conditions outside of their niches (e.g., comparing fundamental versus realized niche; Allen-Ankins and Stoffels 2017). The latter, when combined with molecular tests, provides insight into mechanisms of adaptive potential (i.e., phenotypic plasticity, evolution) for a species (Hoffmann and Sgro 2011; Narum et al. 2013).

Thermal ecology

Changes in the thermal properties of streams affect the aquatic ectotherms that inhabit them because these organisms rely on ambient temperature from the environment for thermoregulation (Angilletta 2009). This makes ectotherms more sensitive to temperature changes, especially taxa such as cold-water stenotherms that occupy a narrow range of temperatures and have longer generation times (e.g., Arctic char, *Salvelinus alpinus*; Reist et al. 2006b; Pörtner and Farrell 2008). It is well understood that functional constraints associated with temperature extremes vary across life stages in fishes (Dahlke et al. 2020). Consequently, spawning adults, eggs, and early juvenile life stages occupy the narrowest thermal niches and are most susceptible to temperature changes (Pörtner and Farrell 2008; Dahlke et al. 2020). Further thermal constraints exist for cold-water stream salmonids by virtue of the dendritic structure of stream networks these fish occupy, which limits their ability to track thermal environments through limited connectivity at both local and regional scales (Fagan 2002). In many areas where these species occur, the stream temperature regime has been altered, and for some fishes this has resulted in either range contraction or extirpation of local populations (Wenger et al. 2011; Isaak et al. 2012; Eby et al. 2014).

Thermal niche

Temperature is one of the key factors that shapes species' distributions, as the thermal conditions that organisms experience strongly affect their fitness, distribution, and abundance (Kingsolver 2009; Somero 2010). Given the importance of stream temperature for survival of cold-water stenotherms and threats posed by climate warming, ecologists have sought to define their thermal niche to inform conservation actions (Wenger et al. 2011; Parkinson et al. 2016; Isaak et al. 2017). The thermal niche represents a dimension of the ecological niche defined by an organism's physiological tolerance to temperature (Angilletta 2009). Broad correlative studies (e.g., Isaak et al. 2017) allow biologists to define a species' thermal niche and identify thermal thresholds. These studies can be extended to directly test thermal thresholds. For example, Eliason et al. (2011) demonstrated that genetically distinct sockeye salmon (*Oncorhynchus nerka*) populations exhibit different thermal tolerances based on physiological performance across a range of ecologically relevant temperatures.

Precisely defining the realized thermal niche for stream fishes can be done by combining point distribution data and high-resolution stream temperature data across a stream network(s). Gathering temperature data has been facilitated recently by the advent of relatively inexpensive temperature sensors and a class of spatial statistical stream network models that can be used to predict stream temperatures with good precision (Isaak et al. 2013; Isaak et al. 2014). However, for rare species, gathering accurate distributional data across streams has been more challenging due to imperfect detection (Dextrase et al. 2014; Rodtka et al. 2015; Reid and Haxton 2017). Occupancy-based sampling designs, which use temporal or spatial replicates to quantify imperfect detection, can be used to mitigate the effects of false-absences (MacKenzie et al. 2002; MacKenzie et al. 2018). Occupancy and detection models can then be used to improve inferences of species distribution models and resulting response curves associated with important elements of the ecological niche (Lahoz-Monfort et al. 2014; MacKenzie et al. 2018).

Study organism: Bull trout

Bull trout (*Salvelinus confluentus*) is a cold-water stenotherm that is patchily distributed across montane streams networks in western North America (Rieman and McIntyre 1995; Rodtka et al. 2015). The biogeographical pattern of bull trout is largely a result of recolonization of Wisconsinan-glaciated North America via the Columbia and Chehalis refugia, with further separation of populations occurring to the west and east of the continental divide. In the north-central part of the range, populations are believed to have recolonized glaciated areas via the Bering and (or) Nahanni refugia, but this is less certain (Haas and McPhail 2001). The broad ecological patterns of bull trout are thought to be a result of three historical processes. First, populations originating from areas that were not Wisconsinan-glaciated are suspected to be primarily non-anadromous, whereas populations that arose from Wisconsinan-glaciated regions form western and eastern-northern groups. These two groups correspond to an in increase in anadromy across the western unit and none of the eastern group exhibit anadromy but many possess strong migratory abilities, just not via the ocean (Haas and McPhail 2001). It is now known that non-anadromous groups exhibit further life history diversity corresponding to resident and migratory ecotypes (Homel et al. 2008; Warnock et al. 2011; Warnock and Rasmussen 2014) that reflects strong phenotypic plasticity common in chars (Klemetsen 2010).

The broader distribution of bull trout is a reflection of post-glacial dispersal and recolonization events, which appear to have been driven largely by the importance and extent of anadromy and migration, shaping the general life history patterns of contemporary populations (Fig. 1.1; Haas and McPhail 2001).

The thermal ecology of bull trout in the southern range extent is well understood and shows that populations occupy one of the coldest thermal niches within the cold-water stream fish guild (Isaak et al. 2017). In the northwestern United States, bull trout are most commonly found in streams with mean August stream temperatures < 11 °C at mid-to high elevations (Rieman et al. 2007; Isaak et al. 2015). Adults use smaller headwater tributaries for spawning and, once juveniles emerge, they remain in these natal streams for 3-5 years (Paul and Post 2001; Rieman et al. 2007; Al-Chokhachy et al. 2010). The requirement for cold water and projected climate warming scenarios for streams (0.22 °C/decade until the 21st century) present an interesting paradox for bull trout. Climate change scenarios suggest that in many watersheds across the northern-western United States, suitable thermal habitat for bull trout could decline by as much as 40% (Isaak et al. 2015) and, in one watershed, increasing stream temperatures has been attributed to range contraction (Eby et al. 2014; LeMoine et al. 2020). Such range contractions are a reflection of southern bull trout populations occupying habitat near the warm-edge boundary of the species' thermal niche. Therefore, as streams warm, southern populations will be forced to occupy cold-water refugia found at higher elevations (Isaak et al. 2015; Isaak et al. 2016). Conversely, at the northern geographical range boundary one would expect populations to occupy a colder thermal niche, and perhaps be at the cold-edge boundary of the species' thermal niche. This notion is supported, to some degree, by results showing that related chars occupy a much colder niche than southern bull trout populations (Dolly Varden, *Salvelinus malma malma*, Dunmall et al. 2016; Arctic char, Sinnatamby et al. 2015; Reist et al. 2006b), but requires further validation. Although the outlook for bull trout in the southern range extent may seem grim given climate warming scenarios, recent work suggests that streams these populations occupy may not be as sensitive to warming as previously postulated. Many of the habitats that support core bull trout populations in the southern range extent exhibit high resilience to the seasonal warming effects of air temperature (Isaak et al. 2016), which could ameliorate the long-term effects of climate warming. Although this appears to be a promising avenue of research, it cannot move forward at mid- to high-latitudes until more high-resolution stream temperature data are available in these regions.

Climate warming and threats

Although the ecological niche that a species occupies is shaped by historic processes, environmental conditions, and physiological capabilities, changes to the characteristics of their niche via stressors also influence distributions. Climate warming is an example of a pervasive global stressor that has, and continues to affect all organisms to some degree (Parmesan 1996; Walther et al. 2002; Sunday et al. 2012). Global surface temperatures warmed by an average of 0.85 °C between 1880 and 2012 and, although projections show this trend could slow over the next 80 years, surface temperatures are still expected to increase (Allen et al. 2014). By the end of the 21st century, global mean surface temperatures are predicted to increase by 0.3-1.7 °C under the lowest greenhouse gas emission scenario (RCP2.6) and as much as 2.6-4.8 °C under the highest scenario (RCP8.5) (Allen et al. 2014). Moreover, the projected magnitude of warming across the world will not be uniform. For example, surface temperatures in temperate (23.6 – 66.5 N latitude) and Arctic (> 66.5 N latitude) regions of North America have experienced a 2.5 fold increase relative to the global average (Allen et al. 2014). From an ecological perspective this is important because species occurring across broad latitudinal gradients will encounter differences in the rate and magnitude of surface temperature warming. These differences are a result of spatial heterogeneity in topography across ecosystems that influences the rate of climate warming (Loarie et al. 2009), which is relevant because populations will respond in manners unique to their location based on an interaction between local warming patterns and relative niche position (Walther et al. 2002). For example, ectotherms at higher latitudes and elevations in montane landscapes typically occupy their cold-edge niche boundary; therefore, as climate warms local populations may benefit from improvements in the quality and extent of thermal habitat (Chamaillé-Jammes et al. 2006; Clarke and Zani 2012). Conversely, populations occupying warm-edge niche boundaries, where physiological thermal safety margins are smaller, are likely to experience negative consequences (extirpation, range contraction) as climate warms if they cannot behaviorally thermoregulate (Deutsch et al. 2008; Sunday et al. 2014; LeMoine et al. 2020).

Stream temperatures across temperate and Arctic regions have increased on average by 0.27 °C/decade (Isaak et al. 2012; Michel et al. 2020) and 0.16 °C/decade (Park et al. 2017), respectively, over the past 30 years. Although these trends represent a broadly coherent response to climate warming, individual streams respond differently to changes in air temperature (Luce et al. 2014; Lisi et al. 2015) based on their hydrological and geomorphic characteristics (Kelleher et al. 2012; Piccolroaz et al. 2016). Streams that are resilient to the effects of air temperature have flatter air temperature/water temperature response cycles than those that are more reactive (Piccolroaz et al. 2016). The slope of the relationship between weekly air temperature and water temperature measurements represents a stream’s thermal sensitivity. Streams with lower slopes are less sensitive to the warming effect of air temperature and streams with higher slopes are more sensitive to the influence of air temperature and have stream temperature profiles that track air temperatures more closely (Kelleher et al. 2012; Piccolroaz et al. 2016). The thermal sensitivity of a stream is influenced by local topography, riparian shading, perennial groundwater, origin of surface water input (i.e., precipitation, snowmelt, upstream lakes), and stream size (Kelleher et al. 2012; Lisi et al. 2015; Piccolroaz et al. 2016).

Thesis Outline

The overall goal of this thesis was to broaden understanding of the thermal ecology of bull trout across the range and assess potential effects of climate warming on this species. Study sites from similar montane watersheds in the south, central, and northern part of the range were used for analyses. This thesis is broken up into three elements: methods development (Chapter 2), describing thermal regimes and defining the thermal niche (Chapter 3), and climate modelling (Chapter 4). Chapter 2 focuses on understanding how to most efficiently and effectively sample bull trout at sites across watersheds. I used distributional data (presence-absence) collected from 275 sites across the northern study site over a two-year period. Temporal replicates within years were taken and an occupancy-detection model was used to quantify the prevalence of false-absences, identify sites where detectability was lowest across environmental gradients, and provide recommendations on optimal sampling design. In Chapter 3, I used stream temperature data from southern, central, and northern montane watersheds to describe the thermal regimes in bull trout spawning and rearing streams. Hourly stream temperature data collected from 15 sites across each watershed over a three-year period were used to describe four temperature metrics: August mean, winter mean, thermal sensitivity, and accumulated thermal units. These temperature metrics were then analyzed to determine if they differed across south, central, and northern sites. In Chapter 4, distributional data was combined with climatic and geomorphic data from 415 sites in a watershed near the northern geographical range boundary, to define the thermal niche occupied by bull trout, understand how thermal sensitivity of streams influence their distribution, and forecast how suitable habitat may be affected by climate warming. Lastly, in the General Discussion (Chapter 5), I provide a synthesis of Chapters 2-4 and comment on how this work advances understanding of the thermal ecology of bull trout across the range and broadens understanding of potential vulnerability of bull trout habitat to effects of climate warming.

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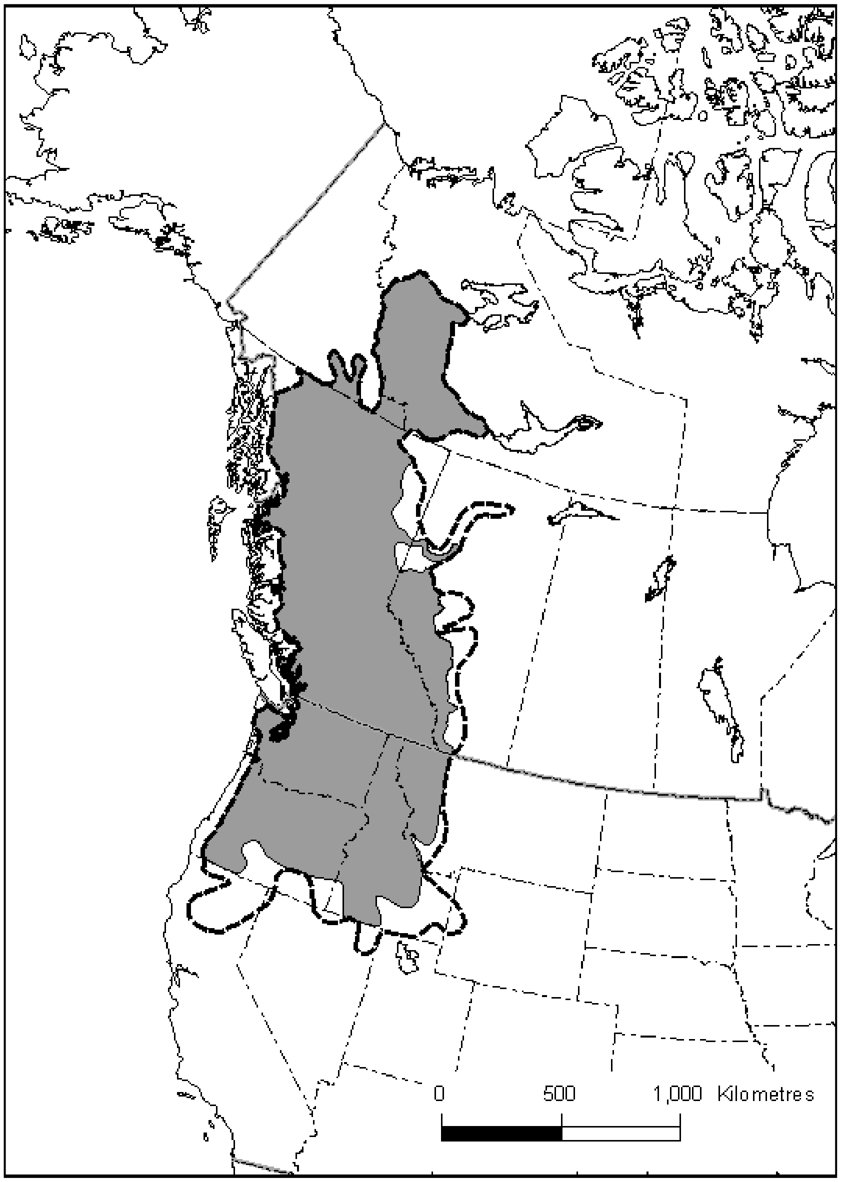

Figure 1.1. Bull trout distribution in North America (COSEWIC 2012). The dark shaded area is the current known approximate distribution and the hatched line represents the historic distribution. Reused with permission from COSEWIC.

Chapter 2: Fringe effects: detecting bull trout (*Salvelinus confluentus*) at distributional boundaries in a montane watershed

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Abstract

Robust assessment and monitoring programs are critical for effective conservation, yet for many taxa we fail to understand how trade-offs in sampling design affect power to detect population trends and describe spatial patterns. We tested an occupancy-based sampling approach to evaluate design considerations for detecting watershed-scale population trends associated with juvenile bull trout (*Salvelinus confluentus*) distributions. Electrofishing surveys were conducted across 275 stream sites from the Prairie Creek watershed, Northwest Territories. Site-level detectability of juvenile bull trout was not uniform, and imperfect detection affected modelled occupancy probabilities most in fringe habitats near distributional boundaries in steep reaches and large streams. We show that detecting a 30% change in watershed-level occupancy ≥78% of the time as conservation guidelines suggest, may require three repeat surveys (i.e., temporal replicates) and increased sampling intensity of fringe habitats. Additional sampling effort in fringe sites could be offset by sampling fewer sites in core habitats to optimize designs for detecting demographic shifts in bull trout, while still minimizing risk of non-detection for this cryptic species.

Keywords: bull trout, detectability, occupancy modelling, distributional boundaries

Introduction

The biodiversity of freshwater fishes has declined rapidly across North America over the past 50 years due to habitat perturbation and fragmentation, interactions with non-native species, and overharvest (Dudgeon et al. 2006). Given that threats to biodiversity across rivers are predicted to increase, conservationists must act quickly to prevent further declines in biodiversity (Strayer and Dudgeon 2010; Vörösmarty et al. 2010). However, implementing effective conservation actions to reverse demographic trends requires a precise understanding of the status of populations and effective methods to monitor trends over time (Strayer and Dudgeon 2010).

Historically, assessment methods have focused on abundance estimates using either mark-recapture or census methods at a small number of sites (Thurow et al. 2006; Dunham et al. 2009); however, both are time consuming, potentially costly, and may not represent population status, or broader scale trends, due to local demographic stochasticity (Maxwell and Jennings 2005), spatial heterogeneity, or non-representative sample allocation (MacKenzie and Nichols 2004; Jones 2011). Consequently, species occurrence data are increasingly collected, as they can be obtained more rapidly and inexpensively at many sites. Moreover, there is often a positive relationship between occupancy probability and abundance for many taxa (Gaston et al. 2000; Zuckerberg et al. 2009; Linden et al. 2017). Regardless of how well occupancy and abundance metrics are correlated, occupancy has been shown to be a state variable well-suited for monitoring the status of populations across broad spatial-temporal scales (Muths et al. 2005; Miller and Grant 2015; MacKenzie et al. 2018).

Although occupancy-based survey designs are commonly used for terrestrial taxa, similar approaches are less often applied to stream fishes (Elith and Leathwick 2009; Comte and Grenouillet 2013; Eby et al. 2014). Occurrence data for fish can be gathered from wadeable streams using various sampling techniques, such as electrofishing, snorkeling, seining, and, more recently, environmental DNA (eDNA) (McKelvey et al. 2016). The detectability of stream fishes, and therefore the ability to determine habitat occupancy status, varies by sampling method (Pregler et al. 2015; Baker et al. 2017), environmental heterogeneity, phenotypic variability among taxa (e.g., behaviour, swimming physiology, and life history) and ontogenetic differences within taxa (Dextrase et al. 2014; Rodtka et al. 2015; Baker et al. 2017). Imperfect detection that results in high rates of "false-absences" can confound true absence with non-detection, which can have detrimental effects on initial assessments and monitoring results, or on inference from models developed with these data (Tyre et al. 2003). To alleviate this potential sampling bias, an occupancy modelling framework has been developed using detection histories from spatial or temporal replicates (MacKenzie et al. 2002; Bailey et al. 2004; Gu and Swihart 2004).

Occupancy-based surveys typically provide more accurate estimates of species' presence than conventional distributional assessments, when the species is imperfectly detected by the field methods (MacKenzie et al. 2018). When spatial habitat heterogeneity exists and explains variation in detectability, habitat covariates can be used in models to account for imperfect detection and improve accuracy of occupancy estimates in species distribution models (MacKenzie et al. 2002; Kuehne and Olden 2016; Baker et al. 2017). This is a key benefit of occupancy-detection models since detectability is rarely uniform across a species distributional range. In fact, detectability is often highest in the core (centre) of regional distributions and declines towards the edges, due to differences in local abundance related to habitat suitability (Sexton et al. 2009; Peterson 2011; MacKenzie et al. 2018). Although detecting species effectively in fringe habitat may be difficult, it is an integral step for accurately documenting species distributional limits and a key element of effective distributional monitoring (Noon et al. 2012; Comte et al. 2013). Furthermore, when a species declines, sites near distributional boundaries are often lost first (Comte et al. 2013; Eby et al. 2014). However, for many taxa, we fail to understand how trade-offs between additional effort allocated to sampling more sites across larger geographic areas versus temporal replicates at fewer sites will affect the accuracy of distributional assessments, precision of parameter estimates from species distribution models (SDMs), and the power to detect trends in occupancy over time (Noon et al. 2012; Barata et al. 2017). Surprisingly, few studies have used empirical data to evaluate survey effort required to detect changes in fish populations across stream networks (Reid and Haxton 2017) or explore how imperfect detection affects precision and accuracy of habitat-occupancy relationships derived from SDMs (Peterson and Dunham 2003; Comte and Grenouillet 2013; Mollenhauer et al. 2017).

In this study, we used bull trout (*Salvelinus confluentus*) to test the utility of an occupancy-based sampling approach to assess its distribution in a northern montane watershed and evaluate sampling design considerations for detecting spatial patterns and temporal population trends. Bull trout is a cold-water char species found across western North America that has declined in the southern and central part of its range due to land use, invasive species, and recent climatic trends (USFWS 2008; COSEWIC 2012). Within its range, bull trout occurs at relatively low densities and is patchily distributed among headwater streams within river networks (Rieman and McIntyre 1995; Dunham et al. 2003; Rieman et al. 2007). Effective conservation of bull trout requires assessment and monitoring approaches that are logistically feasible, cost-effective, and capable of detecting spatial and temporal trends. Such data are lacking for populations at the northern range extent (Mochnacz et al. 2013) and, although a general protocol to assess bull trout distributions at stream scales is available (Rodtka et al. 2015), evaluating trade-offs between power to detect trends in occupancy and different sampling designs — i.e., number of sites versus number of replicates — has not been attempted. Given that occupancy at larger habitat patch scales (e.g., streams) using spatial replicates is relatively well understood for bull trout (Peterson and Dunham 2003; Isaak et al. 2015; Rodtka et al. 2015), we focus on site-level occupancy (i.e., sites across streams) estimation and temporal replication within sampling seasons. A better understanding of occupancy dynamics at the site scale may translate to more sensitive monitoring schemes (e.g., Tingley and Beissinger 2009; Eby et al. 2014) and spatial status assessments and species distribution models, which often discount detectability (Elith and Leathwick 2009).

Our aim was to design an assessment and monitoring protocol that improves precision and accuracy of initial distributional surveys and is capable of detecting population trends over time. To explore these issues, juvenile bull trout were sampled at sites across the Prairie Creek watershed in the Northwest Territories, Canada, and occupancy and detection modelling was used to: (1) examine the effect of detectability on the accuracy of site occupancy estimates across environmental gradients; (2) consider the influence of detectability in the use of occupancy models to describe relationships with stream-landscape covariates by comparing results derived from occupancy-detection, constant-detection, and generalized linear models; and (3) examine how detectability influences power to detect temporal trends in occupancy to inform optimal survey design.

Methods

Study area

Surveys were conducted during the summers of 2014 and 2015 in the Prairie Creek basin (61°37' N, 124°48' W) which drains approximately 870 km^2 and is within the South Nahanni River watershed, in the Northwest Territories (NWT). Peak precipitation in Prairie Creek occurs from June to August with approximately 508 mm/year of precipitation, of which 300 mm/year falls as rain. Flow rates peak in May-June during the spring freshet and in July-August during high precipitation events (Environment Canada 1991). The climate of the region is characterized by cool summers (mean temperature is 9^{o}C) and cold winters (mean temperature is -19.5^{o}C; (Halliwell and Catto 2003). The lower half of Prairie Creek bisects dolostone and limestone strata creating high elevation plateaus and steep canyons (Halliwell and Catto 2003). The lower half of the creek is turbulent and fast flowing, characterized by deep plunge pools or pools created by stabilized rock fall, and swift run and riffle sequences. Flood cycles in this reach have removed much of the finer clasts, leaving cobble and mid to large size boulders. Tributaries to Prairie Creek in the lower half are few, short, and almost entirely ephemeral. The upper half of Prairie Creek changes dramatically to rolling hills dominated by shale, calcareous shale, and minor sandstone (Halliwell and Catto 2003). Stream bed characteristics of the mainstem of Prairie Creek also change to deep alluvium of small boulders, cobbles and pebbles, occasionally punctuated with bedrock outcrops. Large aufeis fields, created by perennial groundwater sources, dominate expansive areas of third order streams in the upper quarter of the watershed. Mixed geological formations of limestone, dolomite, shale mantled by till and sandy fluvioglacial drift support groundwater resources across the basin (Halliwell and Catto 2003). Bull trout, slimy sculpin (*Cottus cognatus*), mountain whitefish (*Prosopium williamsoni*), and in the lower reaches, Arctic grayling (*Thymallus arcticus*), are present in Prairie Creek (Babaluk et al. 2015).

Sampling design

The basin was stratified into patches of potentially suitable habitat for juvenile bull trout based on Strahler stream order (Strahler 1952), stream gradient, and catchment area. We defined habitat patches as all first-to-third order reaches that had <15% gradient and a contributing area >70 hectares. A geographic information system (GIS) was used to generate a stream network and delineate patches using a 1:50 000 Canadian digital elevation model (DEM). Our broad definition of suitable patches was based on habitat associations of juvenile bull trout from other areas (Isaak et al. 2009; Al-Chokhachy et al. 2010; Rodtka et al. 2015). Of the 60 suitable patches, 20 were randomly selected and 15 sites (100 m long) within these patches were surveyed. Sites were randomly assigned across patches in a spatially balanced fashion using a generalized random-tessellation stratified (GRTS) design (Fig. 2.1; Stevens and Olsen 2004). Fewer sites were sampled in some patches (e.g., 12-13) due to logistical constraints, barriers, or insufficient water. The GRTS process was completed in R (R Development Core Team 2018), and sites were georeferenced and transposed onto the stream network using a GIS. Fourth order or higher streams were not sampled because they were too deep to sample effectively with backpack electrofishing gear. Any potential patches with suitable stream lengths <3000 m were excluded from consideration because local populations of bull trout rarely occur in areas this small (Isaak et al. 2015).

Each summer, sites within a subset of the 20 patches were surveyed to document the occurrence of juvenile bull trout, defined as bull trout with fork lengths <150 mm (Fig. S2.1). In total, 275 unique sites were surveyed over two years (2014, *n* = 134; 2015, *n* = 141) because all sites could not be surveyed in one field season. Sampling occurred between July 16 and July 26 and sites were fished by a two-person crew from downstream to upstream using a single pass with a Smith-Root LR-24 backpack electrofisher (pulsed DC, voltage 400 V, frequency 30 Hz, duty cycle 8). In larger streams, crews moved systematically in a zig-zag direction. All fish were collected, identified to species, counted, measured, and returned to the stream. Block nets were not used because sampling during a pilot study showed no appreciable difference in occupancy and relative abundance with or without block nets. This is consistent with what others have found when conducting surveys of small streams to determine species occupancy (Samarasin et al. 2017). The electrofishing experience of crews varied, so crews were rotated during stream inventories to alleviate potential biases related to crew experience. The settings on the electrofisher were held relatively constant (i.e., voltage increased or decreased by ≤10 V) across sampling sites to standardize fishing catchability. Sampling occurred when streams were at base flow because this is when capture efficiency with electrofishing gear is relatively high (Kuehne and Olden 2016; Baker et al. 2017).

An equal number of stream patches were randomly selected and sampled each year. At each site, 2-5 temporal replicates (surveys) were taken and occurred at 2-5 day intervals so that fish distributions could readjust between surveys. First and second order streams were surveyed twice and third order streams were surveyed three times. A pilot study in 2012 showed that detectability was highest in second order streams, followed by third and first order streams. Detection estimates were derived from these data and used to determine the number of surveys required to achieve similar false absence rates across stream orders using the RPresence package (https://www.mbr-pwrc.usgs.gov/software/presence.html). Even though most first order streams were fishless, we wanted unequivocal evidence that this result was not an artifact of imperfect detection, so we conducted five surveys at a subset of sites (*n* = 14) across three first order streams in 2014 and 2015. Field sampling was conducted in accordance with Parks Canada Agency research and collection permits NAH-2013-14385 and NAH-2015-19118.

Occupancy-detection modelling

A single-season occupancy-detection model (MacKenzie et al. 2002) was used to estimate site-level occupancy and detectability across the basin and examine the effects of landscape covariates on these two parameters. In order to use the full data set (*n* = 275; Fig. 2.1) for this analysis, we included year as a covariate (see below) because we did not sample any of these sites in both years. Detection histories of bull trout at stream sites (e.g., 101; detection, non-detection, detection) were formed from the outcomes of the repeated site surveys within each year. The single-season model has four key assumptions: (1) there are no false detections and failure to detect individuals at a site is a function of the species being truly absent or missed due to imperfect detection; (2) detection of individuals at a sampling unit are independent of detections at all other units; (3) probability of occupancy is equal across all sampling units; and (4) the occupancy status of the species does not change within the sampling period (i.e., closure). To avoid violating the closure assumption, within and across years, we focused on the early juvenile life stage because: (1) juveniles make limited movements in natal streams during mid-summer (Downs et al. 2006); (2) juveniles typically remain in natal streams for 3-4 years (Downs et al. 2006; Homel and Budy 2008); and, (3) although annual recruitment of young juveniles (age-1, 2, 3; < 150 mm) varies, complete absence of individuals from all three cohorts at a site across multiple years is rare (Paul et al. 2000; Johnston et al. 2007). Additionally, sites were sampled randomly across both time and space to prevent systematic bias in occupancy; sampling within seasons occurred within a short time period (7-10 days); and sampling year

(2014 or 2015) was included as a covariate in models to account for potential inter-annual variation in occupancy and detection (MacKenzie et al. 2018).

Occupancy estimation and detection efficiency may be affected by environmental conditions, so a single-season model was generalized to accommodate landscape covariates to explore those effects. A GIS platform was used to derive elevation (m), stream gradient (%), and contributing area (ha) covariates for each site that was surveyed (Table 2.1). These covariates were selected because they have either been shown to influence the distribution of bull trout elsewhere (elevation/contributing area: see Paul and Post 2001; Isaak et al. 2015), or represent surrogates of stream habitat attributes that we predicted may influence juvenile bull trout occurrence or detectability (stream size and velocity: see Rich et al. 2003; Al-Chokhachy et al. 2010). More specifically, we predicted that detectability would decrease as stream size and water velocity increased. Contributing area and stream gradient were selected as covariates for detection because they are indirect measures of stream size and water velocity, respectively (Gordon et al. 2004). Elevation, contributing area, and stream slope (gradient) were selected as covariates for occupancy because we predicted that juveniles would occupy a subset of habitats across these environmental gradients (Paul and Post 2001; Dunham et al. 2003; Isaak et al. 2015). Correlation analysis was performed on continuous covariates to assess multicollinearity and showed only low-moderate correlation, so all were retained for modelling (elevation:gradient = 0.22; gradient-contributing area = - 0.50; contributing area-elevation = -0.45).

We used a three-step modelling process. In the first step, we compared different detection efficiency models to determine the importance of detection covariates while holding the full set of occupancy covariates constant (elevation, contributing area, stream gradient, year). A total of 20 candidate models were specified based on the global model:

$$logit\,(p_i) = p(\text{survey} + \text{CA} + \text{CA}^2 + \text{grad} + \text{grad}^2 + \text{year}) \qquad (1)$$

where grad is stream gradient, CA is contributing area, survey is the temporal replicate, year is the year that sampling was conducted, and *p* is detection. Quadratic terms for continuous covariates were included. In step two, we examined relationships between both occupancy and detection and these covariates, to better understand systematic trends and the degree to which basin-scale estimates of occupancy might be refined by the incorporation of detection covariates. Results of the detection modelling in step one revealed there was clearly no top model, based on differences in Akaike's information criteria (AIC) values from the top ranked model and model weights (1st: CA + CA^2 + grad + year, weight = 0.52; 2nd: CA + CA^2 + grad + grad^2 + year, ΔAIC = 1.03, weight = 0.31; 3rd: CA + CA^2 + year, ΔAIC = 2.86, weight = 0.12; Table 2.2). Therefore, different combinations of occupancy covariates were specified against each of these three detection covariate combinations for the full occupancy candidate model set. A constant-detection model was included, as this model assumes occupancy is not affected by imperfect detection and, therefore holds detection constant across surveys and sites. A total of 105 candidate models were specified based on the global model:

$$logit\,(\Psi i) = \Psi(\text{elev} + \text{elev}^2 + \text{CA} + \text{CA}^2 + \text{grad} + \text{grad}^2 + \text{year}),\ p(\text{CA} + \text{CA}^2 + \text{grad} + \text{grad}^2 + \text{year}) \qquad (2)$$

where elev is stream elevation (m) and Ψ is occupancy.

In step three, a generalized linear model was fit to the same data set using only data from the first survey. This was done to simulate a study design without temporal replicates. Only a global modal was defined for this step:

$$logit\,(\Psi i) = \Psi(\text{elev} + \text{elev}^2 + \text{CA} + \text{CA}^2 + \text{grad} + \text{grad}^2 + \text{year}) \qquad (3)$$

Parameter estimates and standard errors from the generalized linear model were then compared to the top ranked occupancy-detection and constant-detection models. For the detection and occupancy models (steps 1 and 2), a global model was initially specified and subsequent combinations of covariates were fit to the data with no interaction terms. For all models, covariate effects were represented by the GIS attributes described previously, and both linear and quadratic terms were assessed for each covariate based on knowledge of occupancy-habitat relationships from other studies (Paul and Post 2001; Al-Chokhachy et al. 2010; Isaak et al. 2015). The logit-link function was used to model response variables as a function of covariates in all models. The top ranked occupancy-detection model and the generalized linear model were then used to predict occupancy probabilities at three spatial scales: sampling sites (*n* = 275), points at 1-km intervals across the watershed, and all stream segments. These outputs were then used to develop distribution maps of stream segment probabilities and corresponding standard errors, as well as absolute differences in point probabilities derived from the two models. Prior to analysis, covariates were standardized to a mean of zero and a standard deviation of one. A square-root standardization was used for contributing area to reduce the potential influence of a few, relatively large values on the effect size of this covariate (MacKenzie et al. 2018).

Maximum likelihood methods were used to estimate detection and occupancy parameters and occupancy models/outputs were run using the programs RPresence and PRESENCE, version 11.6 (Hines 2006). For each candidate model set, AIC was used for model selection (Burnham and Anderson 2002). 95% confidence intervals were calculated using the Wald method on the logit-scale, then limits were transformed to the probability scale. If no top model was selected from the candidate set, model-averaging was done using ΔAIC (< ~ 2.0) and cumulative model weights (≥ 0.96) to derive probability estimates for occupancy and detection (MacKenzie et al.

2018). Model fit was assessed using Pearson's χ^2 goodness-of-fit (GOF) and variance inflation factor (ĉ) (MacKenzie and Bailey 2004) and graphical diagnostics were performed with Dunn-Smyth residuals (Warton et al. 2017). Since the variation inflation factor from our global occupancy-detection model was less than one (ĉ = 0.04), no adjustment of standard errors was necessary.

Optimal survey design and trend detection

Power analyses were used to explore the effectiveness of detecting watershed-level trends in occupancy over time across different occupancy and detection scenarios using results from the single-season model. We specified our effect size (R) as the proportional difference between occupancy from time 1 to time 2. The effect size was then used to calculate $\Psi_{1,}\ \Psi_2$ as the underlying occupancy probabilities for the two samples, where $\Psi_2 = \Psi_1 (1 - R)$ (Guillera-Arroita and Lahoz-Monfort 2012). Our effect size varied across a range of values (0.20 to 0.50) to encompass ecological thresholds relevant to conservation and management. Endangered status designations are often assessed as a 30% reduction in a relevant population metric (e.g., area of occupancy) across generational time frames (Dudgeon et al. 2006; COSEWIC 2012; Lemieux Lefebvre et al. 2018). Therefore, an absolute decline between 0.3 and 0.5 (30-50% reduction) should motivate management action.

Results from the top five single-season occupancy models indicated strong quadratic effects of stream gradient and elevation on occupancy, and contributing area on detectability. This suggested that both occupancy and detectability were not homogenous across our data frame. Using these relationships, we subset our data set into core and fringe habitats. The former encompassed sites where occupancy and detection probability was high and relatively stable; whereas, the latter included sites where probabilities started to decrease and then decline to zero.

Core habitat was defined as sites with contributing area >250 and <2500 ha and stream gradient >3.0 and <7.5 % (*n* = 195), whereas fringe habitat were sites with contributing area <251 and >2501 ha, stream gradient <2.9 and >7.6 % (*n* = 80). Since the top five single-season models resulted in site-specific occupancy and detectability estimates, mean values of occupancy and detection probability were calculated for each respective area. Mean estimates from both core and fringe areas were then used in simulations to examine how trade-offs in survey design affected power to detect changes in occupancy using tools described in Guillera-Arroita and Lahoz-Monfort (2012). The Type I error rate (α; probability of incorrectly rejecting null hypothesis of no change in occupancy) was set at 0.1 as this best reflected priorities for monitoring at-risk populations (Isaak et al. 2009; COSEWIC 2012; Rodtka et al. 2015).

We first examined the number of temporal surveys (k) required to determine if the species was present at an occupied site for a given proportion. The probability of detecting the species at least once from k surveys at a site when present is:

$$p^* = 1 - (1 - p)^k \tag{4}$$

where p is the detection probability for a single survey. Using this expression, the number of surveys required to achieve p^* of 0.80, 0.90, and 0.95 was derived as:

$$k = \frac{\log(1 - p^*)}{\log(1 - p)} \tag{5}$$

We then examined how the number of surveys (k) affected power (G) to detect differences in occupancy using:

$$G = 1 - \beta = \left\{1 - \Phi\left(\frac{z_{\alpha/2}\sqrt{\sigma_1^2+\sigma_2^2} - (\Psi_1 - \Psi_2)}{\sqrt{\sigma_1^2+\sigma_2^2}}\right)\right\} + \Phi\left(\frac{-z_{\alpha/2}\sqrt{\sigma_1^2+\sigma_2^2} - (\Psi_1 - \Psi_2)}{\sqrt{\sigma_1^2+\sigma_2^2}}\right) \qquad (6)$$

where $\Phi(x)$ is the cumulative distribution function for the standard normal distribution, σ_i^2 is the asymptotic variance of the occupancy estimator, $z_{\alpha/2}$ is the upper 100 $\alpha/2$-percentage point for the standard normal distribution, and $\Psi_{1,}\ \Psi_2$ are the underlying occupancy probabilities for the two samples (Guillera-Arroita and Lahoz-Monfort 2012). For these analyses, the sample size (i.e., density of sampling sites) and initial occupancy and detectability estimates were set at values corresponding to core and fringe sites (as described above).

In the final analysis, we used simulations to assess how sample size (spatial replicates) influenced the power to detect changes in occupancy and included our current sampling design based on fringe (*n* = 80) and core (*n* = 195) habitats. Two-tailed power curves were generated using the closed-form equation above (6) while keeping occupancy, detectability, and number of surveys (temporal replicates) constant (Guillera-Arroita and Lahoz-Monfort 2012).

Results

Juvenile bull trout were captured from 13 of the 20 stream patches that were surveyed in Prairie Creek between 2014 and 2015, and from 75 of the 275 sites (Fig. 2.1). The relative density per 100-m site ranged from 0 to 30 fish, and mean (± SD) catch was 1.28 (± 2.30) fish per site.

Detectability

In the single-season detection candidate model set (*n* = 20), there was little support for the constant detection model (ΔAIC = 16.9, weight = 0.0002), as detection probability differed across sites but not surveys (Table 2.2). Both contributing area and stream gradient had an influence on detectability, however, the influence of contributing area was greater. Detection probability was lowest in very small streams (< 250 ha), peaked in medium-sized streams (500 – 2500 ha), and then declined across large streams. Detection probability was moderate in low-gradient streams, increased to an intermediate position along this axis, and then was consistently high across mid to high gradient sites (Fig. 2.2). In core habitats, fish could be detected >80% of the time with two or fewer surveys, whereas in fringe habitats three or more surveys were required (Table S2.1). Five surveys were completed at 14 sites to examine presence-absence near hypothesized upstream distributional boundaries and juvenile bull trout were never detected at 12 of the 14 sites surveyed (Table S2.2). The logit-scale year coefficient (±SE) was 0.45 (0.48), and indicates a moderate difference in detectability between 2014 and 2015.

Occupancy

Naïve site-level occupancy was 0.30, which is lower than the modelled site-level occupancy (± SE) of 0.36 ± 0.03 derived from the single-season model. Of the 104 candidate models specified, there was clearly no preferred model based on AIC values and model weights. Despite model selection uncertainty, elevation, contributing area, stream gradient, and their quadratic terms were included in the occupancy component of the top five models (ΔAIC < 2.9, cumulative weight = 0.96). Quadratic terms for contributing area were only included in two of the top five models for occupancy (Table 2.3). Site occupancy was estimated to be slightly lower in 2015 than in 2014 (logit-scale coefficient = -2.17 ± 0.40). Model-averaged site occupancy estimates from the top five single-season models show that occupancy probability was highest in streams ranging in elevation from 1000 to 1275 m and gradients between 3% and 7%. Occupancy estimates were lowest in small streams (< 250 ha) but high across intermediate to large-sized streams (Fig. 2.3a). Few differences were observed between the top occupancy-detection model and the constant-detection model, but the constant-detection model did have larger confidence intervals for modelled estimates at higher stream elevation and in large streams with contributing areas greater than 4000 ha (Fig. 2.3). Conversely, occupancy estimates derived from the generalized linear model showed different relationships with elevation and contributing area than both the occupancy-detection and constant-detection models (Fig. 2.3; Table 2.3). The magnitude and precision of coefficients differed among models and differences were most notable between the generalized linear model and occupancy-detection model (Table 2.4). Distribution maps of occupancy probabilities derived from the occupancy-detection model and the generalized linear model showed that the largest differences in point predictions (occupancy-detection probability – generalized linear model probability) occurred near upstream and downstream distributional limits and in these areas most of the occupancy model probabilities were larger than the generalized linear model (Fig. 2.4c). In several stream segments the standard error of occupancy estimates from the occupancy-detection model were higher than the ones generated using the generalized linear model (Fig. 2.4b); however, detectability was low in most of these segments. Goodness-of-fit and residual diagnostics suggested that the top five occupancy-detection models and the generalized linear model fit these data reasonably well, whereas the constant-detection model was a poor fit.

Optimal survey design and trend detection

Results of power curves generated using mean occupancy and detection estimates from core ($\Psi = 0.40$, $p = 0.78$; $n = 195$) and fringe habitats ($\Psi = 0.29$, $p = 0.48$; $n = 80$) are shown in Figure 2.5. In core areas, two surveys were sufficient to detect 30-50% changes in occupancy ≥77% of the time and the increase in power by using more than two surveys was minimal (Fig. 2.5a). Conversely, in fringe habitats the power to detect similar changes in occupancy was much lower overall, increased with three or more surveys, and plateaued at five surveys regardless of effect size (Fig. 2.5b).

Results of two-tailed power curves generated using mean occupancy and detection estimates from core ($\Psi = 0.40$, $p = 0.78$; $n = 195$) and fringe sites ($\Psi = 0.29$, $p = 0.48$; $n = 80$) are shown in Figure 2.6. Simulations show that in core areas using the sample size from this study ($n = 195$), a 30% change in occupancy can be detected 77% of the time (Fig. 2.6a). Conversely, in fringe sites using the sample size from this study ($n = 80$), a 30% change in occupancy can be detected 29% of the time but if sample size is quadrupled ($n = 320$) then power to detect a similar change increases to 70% (Fig. 2.6b). The last simulation shows that as sampling density (i.e., sampling sites) in fringe habitats increases so does the power to detect a change in occupancy. Detecting changes in occupancy with equal probability in fringe sites as core sites requires three temporal surveys at each site and a five-fold increase in the sampling density ($n = 400$) across this area (Fig. 2.6c).

Discussion

Site-level detectability of juvenile bull trout is not uniform across environmental gradients in the Prairie Creek watershed and is lowest in fringe habitats near distributional boundaries. Consequently, failing to account for imperfect detection in these habitats makes it difficult to accurately delineate distributional limits and affects model inferences. For example, modelled occupancy estimates derived from a generalized linear model in downstream sites were much lower than estimates from the occupancy-detection model. This reflects the inability of the generalized linear model to impose an upward adjustment of occupancy estimates at sites where there is imperfect detection, and similar effects of detectability on occupancy estimates have been reported for stream fishes (Comte and Grenouillet 2013; Baker et al. 2017). Ignoring the effect of detectability on site-level surveys could negatively affect trend detection because it is impossible to disentangle the reason for observed distributional changes – i.e., site extirpation or false-absence. This presents a conservation risk, because as shown by others, downstream distributional boundaries are most likely to be abandoned by bull trout as they move upstream from marginal habitats to presumably better habitat at higher elevations (Eby et al. 2014; LeMoine et al. 2020). However, one can mitigate the risk of failing to detect juvenile bull trout in downstream fringe habitats by implementing three temporal replicates and imposing a five-fold increase in the density of spatial replicates. Implementing these changes in study design improves accuracy of assessments by allowing one to relax assumptions of constant detection. Further, we show how a modified watershed-scale sampling approach, tailored to both core and fringe areas, can detect 30% changes in juvenile occupancy >78% of the time. This approach capitalizes on detectability results by allocating more sampling effort near distributional boundaries and less effort (fewer sampling sites and temporal replicates) in core areas where occupancy and detectability are high. In fact, our results suggest that in core areas a single survey may be as effective as two for detecting juveniles because occupancy and detection are high in these habitats. Although this could be a more cost-effective sampling strategy, the risk (i.e., increasing the probability of false-absence) should be balanced against conservation objectives — e.g., single assessments versus monitoring watershed-level population trends.

Detectability

The difference between our naïve and modelled site occupancy (0.30 vs. 0.36, respectively) is similar to what others have found (Rodtka et al. 2015). Although this difference is well below the threshold shown by Tyre et al. (2003) to significantly degrade estimation of model parameters, we highlight how ignoring detectability affects parameters in our model. Overall, the generalized linear model and the constant-detection models predict juveniles occupy different environmental gradients than the occupancy-detection model, although the difference between the latter two models is quite small. Given that false-absences occurred disproportionately across sites, it is not surprising that the constant-detection model ranked far lower than our top occupancy-detection model and reinforces that imperfect detection is important to consider in this watershed. The constant-detection model is more similar to the generalized linear model as both models assume constant detection; however, the generalized linear model does not account for false-absences. Differences in modelled occupancy probabilities between the occupancy-detection model and the generalized linear model are primarily driven by low detectability in small (80-250 ha) and large streams (> 2500 ha), which we define as fringe habitats.

Within fringe habitats, the influence of imperfect detection on modelled probabilities was greatest in the downstream extent of our sampling frame and emphasizes the importance of using temporal replicates in larger streams. Similar detectability patterns with discharge have been reported for other stream fish (Mollenhaur et al. 2017), and given discharge is positively related to contributing area (Gordon et al. 2004) our results are consistent with what others have observed. The generalized linear model predicts juvenile occupancy follows a logistic relationship with elevation, which is not supported by our data nor what others have found (Rich et al. 2003; Rieman et al. 2007) but could also simply be an artefact of the logit-link. The latter pattern may also be partially driven by high detectability in areas with intermediate to high stream gradients (5-7%) that typically coincide in higher elevation areas. The detection probability confidence intervals at the upper boundary of the stream gradient sampling dimension (8-10%) were large and is a result of low occupancy and small sample size near upstream distributional boundaries. Consequently, none of the models did particularly well predicting occupancy in these areas. Similar effects of detectability on modelled occupancy estimates have been observed in other stream fishes (Comte and Grenouillet 2013) and across other taxa (e.g., small mammals, Gu and Swihart 2004; pronghorn antelope, MacKenzie et al. 2018).

Optimal survey design and trend detection

When we extend our detectability analyses to a monitoring application, we show that two surveys are sufficient to detect moderate to large changes in occupancy (0.3-0.5) in core habitats where detectability is high with reasonable precision (≥78%). Conversely, in fringe habitats where occupancy and detection are lower, detecting changes in occupancy with similar precision is not possible with two surveys. However, in fringe sites power does increase if additional surveys (i.e., temporal replicates) are done but plateaus at five suggesting that additional surveys would provide little additional benefit. Rodtka et al. (2015) reported a similar range of site-level detection (20 - 80%) in streams for this species. We are aware of one other study on riverine fish that reports sampling requirements to detect changes in occupancy (Reid and Haxton 2017), but this study was also different than ours as it examined how the amount of time spent electro-fishing influenced detectability and power to detect changes in occupancy. Although results from Reid and Haxton (2017) are not directly comparable with ours, they also illustrate that when detection is low the only way to increase power is by allocating more sampling effort in these areas.

In fringe habitats we show that one can realize improvements in power to detect trends in watershed-scale occupancy by not only increasing the number of surveys (temporal replicates) but also the density of sampling sites (i.e., spatial replicates). In similar studies, investigators have done simulations to generate power curves using mean occupancy and detection probability estimates derived from their entire sampling frame (Steenweg et al. 2016; Barata et al. 2017). This approach is reasonable if estimates are uniform across sites; however, in Prairie Creek this is not the case. Therefore, detecting changes in juvenile occupancy across the watershed with similar precision requires different sampling strategies for fringe and core habitats. In fringe habitat, simulations showed that by increasing the number of surveys to three and increasing the density of sampling sites from 80 to 400, a 30% change in occupancy can be detected >78 % of the time. Trade-offs in sampling effort versus trend detection could be achieved by adjusting sampling design to increase effort (i.e., number of surveys and sampling density) in fringe areas and reduce sampling effort in core areas where occupancy and detectability are higher. We simulated a scenario showing how detecting 30-50% changes in watershed-level occupancy can be achieved with reasonable confidence (≥ 0.78%) by surveying 195 sites twice in core habitats and 400 sites three times in fringe habitats. This is similar to other studies that demonstrate when initial occupancy and detectability levels are low the ability to detect changes in occupancy in subsequent time periods can be improved by increasing the number of surveys, number of sampling sites, or a combination of both (Steenweg et al. 2016; Barata et al. 2017; Reid and Haxton 2017). Further reductions in total sampling effort could be realized by reducing effort in core areas to offset additional effort requirements in fringe habitats but this should be balanced against the risk of failing to detect fish in core areas. Our simulations offer insight into this but a more comprehensive understanding of the risks of these actions requires testing predictions through field validation.

For initial assessments where detectability is unknown, power curves could serve as a guideline to identify how many temporal surveys and sampling sites are needed to minimize false-absences. This will increase the chance of detecting juveniles, when present, but also provide greater assurance of “true absence”. Once detectability estimates are known for a watershed, users can balance trade-offs in sampling efficiency versus power to detect changes in occupancy by adjusting the number of temporal surveys and sampling sites to achieve desired power for assessing populations trends. The latter will be especially important in situations where monitoring population trends is a key conservation objective. Overall, designing and implementing standardized sampling protocols will be critical for effectively monitoring sentinel species, like bull trout, and detecting effects of climate change on northern freshwater ecosystems (Heino et al. 2020). Furthermore, documenting range contraction, expansion, or shifts from climate change in stream fishes requires effective monitoring at distributional boundaries (i.e., fringe habitat) within watersheds, rather than core areas where populations are most abundant (Gibson-Reinemer et al. 2017).

Watershed-level occupancy

Juvenile bull trout are patchily distributed in streams across the Prairie Creek watershed, and although only a small proportion of the streams surveyed (30%) appear to represent strongholds for core populations, occupancy within these streams is relatively high (0.40). This distributional pattern and occupancy estimate is similar to what others have observed in montane watersheds further south (Rodtka et al. 2015; Isaak et al. 2015). However, we have further refined our understanding of site occupancy estimates to include estimates for fringe habitats. Given that this bull trout population occurs in a minimally-perturbed watershed, our juvenile occupancy estimates represent those from an otherwise healthy population and could serve as a benchmark for monitoring the status of this population. Also, our detectability and occupancy estimates suggest juveniles exhibit two distributional patterns at downstream and upstream boundaries. First, in upstream areas our modelled occupancy and detection probabilities and detection data suggest a relatively abrupt transition from high to low occupancy. This is similar to what others have seen related to upstream boundaries associated with elevation (Paul and Post 2001; Rieman et al. 2007). Conversely, the transition from high to low occupancy in downstream areas appears to encompass a much broader spatial dimension. The broader downstream transitional zone from high to low occupancy is a result of low detectability and occupancy, which reflects differences in abiotic (e.g., stream size) and, presumably biotic characteristics between downstream and upstream areas. We highlight that contributing area is an important abiotic factor to consider but the influence of biotic parameters on detectability of juvenile bull trout requires further investigation.

Ecological relationships

Occupancy-landscape covariate relationships derived from the single-season occupancy model offer two additional benefits beyond informing development of more effective sampling programs. First, site-level occupancy predictions could be validated in similar watersheds as a further test of model performance and to assess transferability of these relationships to other regions — an important step often skipped in the iterative modelling process (Araújo and Peterson 2012; MacKenzie et al. 2018). Second, these occupancy-covariate relationships provide ecological insight into habitat associations of juvenile bull trout from a northern watershed. The stream elevation where we started to see juvenile occupancy decline (~1350 m) is lower than what others have reported in Alberta and Idaho (Paul and Post 2001; Dunham et al. 2003) and probably reflects differences in local climatic conditions from latitudinal variation. Although elevation, contributing area, and stream gradient are in all the top ranked models, stream gradient had the greatest influence on juvenile occupancy. The presence of juveniles across a narrow range of stream gradients may be a function of physiological limitations associated with swimming capability and habitat suitability. This seems plausible given that juveniles often seek low velocity refugia in streams with moderate gradient and larger substrate (Al-Chokhachy et al. 2010), exhibit high fidelity to natal spawning/emergence sites (Homel and Budy 2008), and may seek refuge from predators in these types of habitat (Banish et al. 2008; Al-Chokhachy et al. 2010).

Conclusion

We show that presence-absence data collected during distributional assessments for juvenile bull trout in Prairie Creek is very reliable in core areas where occupancy and detectability is high. Despite this, we show why it is important to recognize that detectability of juveniles is context-dependent and how it can affect the accuracy of distributional assessments. In Prairie Creek, detectability of juveniles was lower in habitats near distributional boundaries compared to core areas, and models that accounted for imperfect detection in these areas yielded higher occupancy estimates than those that did not. The influence of detectability on survey accuracy has two potential conservation consequences. First, not accounting for imperfect detection during initial and follow-on assessments could result in failure to detect a change in occupancy. Failing to detect a declining trend in an imperilled population could prevent management intervention (e.g., fishing restriction) and ultimately hinder recovery efforts. Second, because stream habitat protection is usually based on habitat quality, modelled occupancy probabilities can help guide this classification (see Isaak et al. 2015). If models that ignore detectability are used to assign occupancy probabilities to fringe habitats, these habitats may be misclassified as low quality habitat or may be grossly underestimated and fail to receive suitable protection. A better understanding of where and when to implement temporal replication and increase sampling density will help biologists design more sensitive site-scale monitoring schemes (e.g., Tingley and Beissinger 2009; Eby et al. 2014) and improve chances of detecting changes in bull trout occupancy across montane watersheds. Given that few local streams support juvenile bull trout populations in Prairie Creek, effective monitoring should be a critical element of the overall conservation plan for this population.

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Tables

Table 2.1. Covariates describing the 275 stream sampling sites with replicated surveys from the Prairie Creek watershed.

	Mean	Standard deviation	Range
Elevation (m)	1107.0	123.0	795-1399
Stream gradient (%)	4.4	2.5	0.7-13.8
Contributing area (ha)	1219.0	1235.0	73-5060

Table 2.2. Model ranking and summary statistics for the top 10 single-season detection models fit to the data (n = 275). The full set of covariates (Elev + Elev^2 + CA + CA^2 + Grad + Grad^2 + Year) was held constant for the occupancy component of all candidate models.

Model	Rank	AIC	ΔAIC	AIC w	Cumulative w	K	-2Log(L)
p (CA + CA^2 + Grad + Year)	1	489.76	0.00	0.52	0.52	13	450.60
p (CA + CA^2 + Grad + Grad^2 + Year)	2	490.80	1.03	0.31	0.83	14	453.16
p (CA + CA^2 + Year)	3	492.62	2.86	0.13	0.96	12	449.28
p (survey + CA + CA^2 + Grad + Year)	4	497.02	7.26	0.01	0.97	17	458.10
p (survey + CA + CA^2 + Grad + Grad^2 + Year)	5	498.04	8.28	0.01	0.98	18	455.05
p (Grad + Year)	6	498.88	9.12	0.01	0.99	11	457.13
p (survey + CA + CA^2 + Year)	7	499.12	9.35	0.00	0.99	16	460.23
p (Grad + Grad^2 + Year)	8	499.68	9.92	0.00	0.99	12	458.25
p (CA + Grad + Year)	9	500.74	10.98	0.00	0.99	12	449.18
p (Grad + Grad^2 + Year)	10	501.64	11.88	0.00	1.00	13	447.98

Note: AIC is Akaike information criterion; ΔAIC is the change in AIC values between the lowest AIC (i.e., highest ranking model) and the given model; AIC w is AIC weight; cumulative w is the cumulative AIC weight; k is the number of parameters; and -2Log(L) is the model multinomial log-likelihood value multiplied by negative two. Abbreviations: Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); squared transformations of continuous covariates (CA^2, grad^2) were included to assess quadratic effects; p, is detection; and survey, is survey-specific detection (i.e., detection varies across surveys). A total of 20 models were fit to these data.

Table 2.3. Model ranking and summary statistics for the top 10 single-season occupancy-detection models fit to the data (*n* = 275).

Model	Rank	AIC	ΔAIC	AIC *w*	Cumulative *w*	*K*	-2Log(L)
Ψ(Elev + Elev^{2} + CA + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Grad + Year)	1	488.05	0.00	0.38	0.38	12	464.05
Ψ(Elev + Elev^{2} + CA + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Grad + Grad$^{2 +}$ Year)	2	489.05	1.00	0.23	0.61	13	463.05
Ψ(Elev + Elev^{2} + CA + CA^{2} + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Grad + Year)	3	489.76	1.71	0.16	0.77	13	463.76
Ψ(Elev + Elev^{2} + CA + CA^{2} + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Grad + Grad^{2} + Year)	4	490.80	2.74	0.10	0.87	14	462.80
Ψ(Elev + Elev^{2} + CA + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Year)	5	490.97	2.92	0.09	0.96	11	468.97
Ψ(Elev + Elev^{2} + CA + CA^{2}+ Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Year)	6	492.62	4.56	0.04	0.99	12	468.62
Ψ(Elev + Elev^{2} + CA + Grad + Year), *p* (CA + CA^{2} + Grad + Grad$^{2 +}$ Year)	7	499.24	11.19	0.00	0.99	12	475.24
Ψ(Elev + Elev^{2} + CA + Grad + Year), *p* (CA + CA^{2} + Grad + Year)	8	502.20	14.14	0.00	0.99	11	480.20
Ψ(Elev + Elev^{2} + CA + CA^{2} + Grad + Grad^{2} + Year), *p* (.)	9	506.62	18.56	0.00	0.99	9	488.62
Ψ(Elev + CA + CA^{2} + Grad + Grad^{2} + Year), *p* (CA + CA^{2} + Grad + Year)	10	507.63	19.58	0.00	0.99	12	483.63

Note: AIC is Akaike information criterion; ΔAIC is the change in AIC values between the lowest AIC (i.e., highest ranking model) and the given model; AIC w is AIC weight; cumulative w is the cumulative AIC weight; *k* is the number of parameters; and -2Log(L) is the model multinomial log-likelihood value multiplied by negative two. Abbreviations: Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); p, is detection; Ψ, is occupancy; squared transformations of continuous covariates (elev^{2}, CA^{2}, grad^{2}) were included to assess quadratic effects; survey, survey-specific detection; and (.) is where parameters are constant. A total of 105 models were fit to these data.

Table 2.4. Comparison of single-season occupancy-detection model to constant-detection and generalized linear models. Only coefficients for covariates of occupancy are shown for the occupancy-detection model and the constant-detection model after adjustment of detection. The coefficient and standard error values reported for the occupancy-detection model are model-averaged estimates based on the top five models shown and coefficients for all models are expressed on the logit-scale.

Model	Predictor	*b*	SE	AIC
Occupancy-detection^A				
Ψ(Elev + Elev^2 + CA + Grad + Grad^2 + Year), *p* (CA + CA^2 + Grad + Year)	Intercept	2.49	0.47	488.05
Ψ(Elev + Elev^2 + CA + Grad + Grad^2 + Year), *p* (CA + CA^2 + Grad + Grad^2 $^+$ Year)	Elev	0.38	0.30	
Ψ(Elev + Elev^2 + CA + CA^2 + Grad + Grad^2 + Year), *p* (CA + CA^2 + Grad + Year)	Elev^2	-0.96	0.23	
Ψ(Elev + Elev^2 + CA + CA^2 + Grad + Grad^2 + Year), *p* (CA + CA^2 + Grad + Grad^2 + Year)	CA	1.56	0.35	
Ψ(Elev + Elev^2 + CA + Grad + Grad^2 + Year), *p* (CA + CA^2 + Year)	CA^2	-0.08	0.15	
	Grad	1.04	0.46	
	Grad^2	-1.73	0.57	
	Year	-2.17	0.40	
Constant detection model				
Ψ(Elev + Elev^2 + CA + CA^2 + Grad + Grad^2 $^+$ Year), *p* (.)	Intercept	2.23	0.44	506.62
	Elev	0.52	0.30	
	Elev^2	-0.65	0.21	
	CA	1.49	0.35	
	CA^2	-0.39	0.09	
	Grad	1.32	0.47	
	Grad^2	-1.50	0.47	
	Year	-1.62	0.36	
GLM				
(Elev + Elev^2 + CA + CA^2 + Grad + Grad^2)	Intercept	1.49	0.38	
	Elev	0.50	0.28	
	Elev^2	-0.50	0.21	
	CA	1.29	0.33	
	CA^2	-1.02	0.33	
	Grad	1.36	0.44	
	Grad^2	-1.63	0.48	
	Year	-1.31	0.34	

A. Model-averaged values from top five models specified below. *b* is the beta parameter value; AIC is Akaike information criterion; and SE is standard error. Abbreviations: Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); *p*, is detection; Ψ, is occupancy; squared transformations of continuous covariates (elev^2, CA^2, grad^2) were included to assess quadratic effects; (.) is a model where detection is constant across all sites and surveys. The constant-detection model coefficients for occupancy were adjusted based on a constant detection coefficient across sites and surveys.

Figures

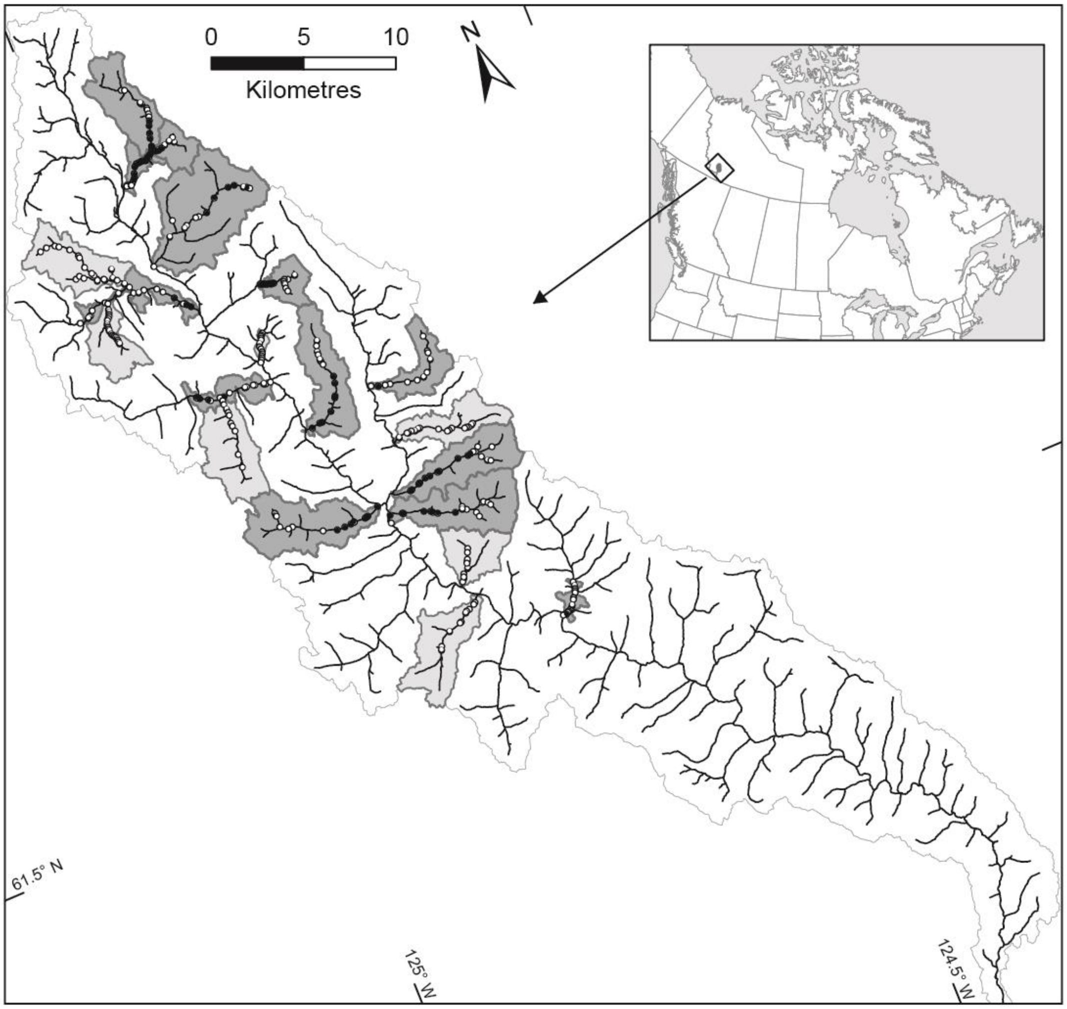


Figure 2.1. Location of the 20 stream patches and 275 sampling sites in the Prairie Creek watershed, Northwest Territories, Canada. White and black circles are unoccupied and occupied sites, respectively. Dark shaded patches are occupied and lighter ones are unoccupied.

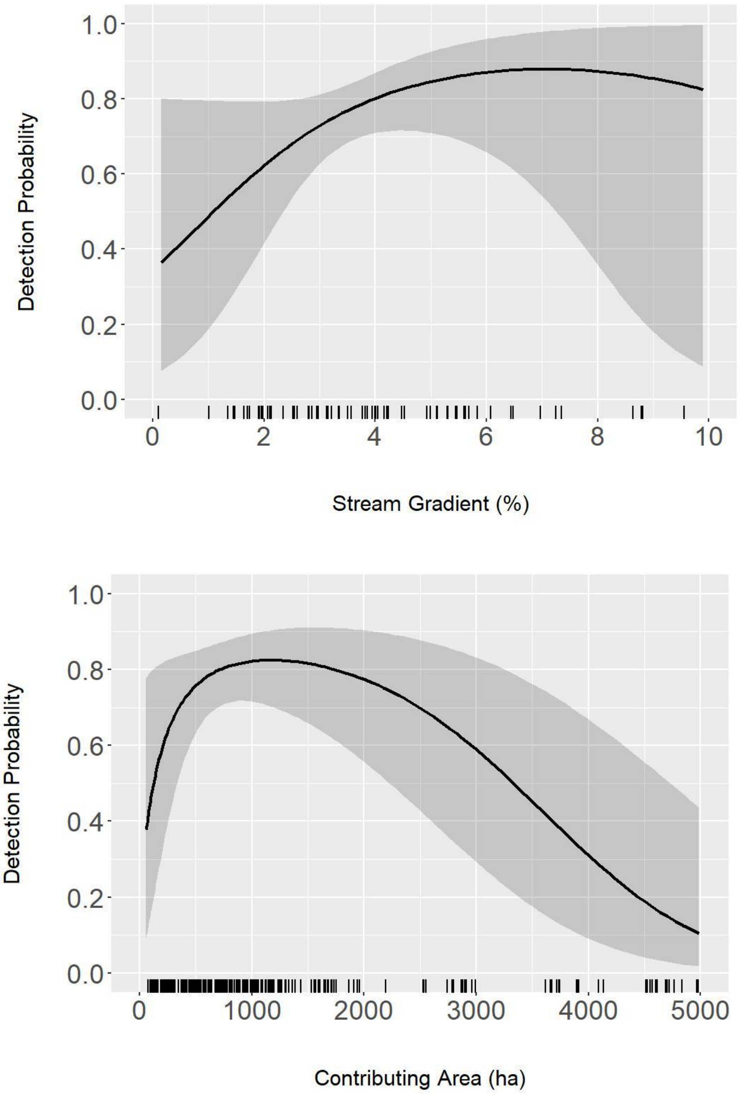


Figure 2.2. Relationship between detection probability and stream gradient (top) and contributing area (bottom) using model-averaged detection estimates derived from the top five ranked single-season occupancy-detection models shown in Table 2.3. Detection probability was predicted for each covariate while holding the other covariate on detection constant. Dark vertical lines on the x-axis show points where data were taken during the sampling campaign.

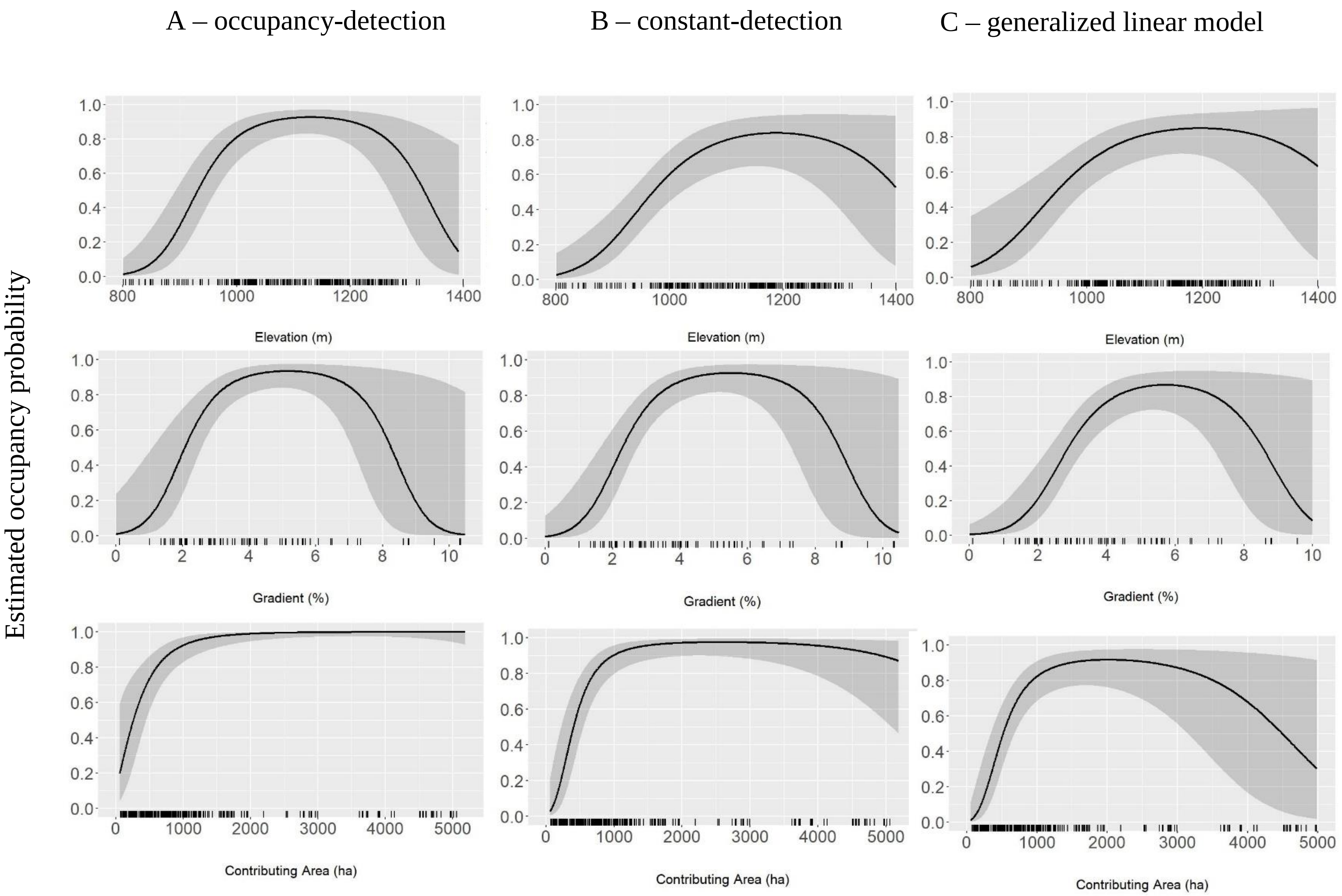


Figure 2.3. Relationship between occupancy and covariates using estimates from occupancy-detection (A), constant-detection (B), and generalized linear (C) models. Estimates are the black lines and 95% confidence intervals are shown by the dark shaded areas. Model-averaged estimates of the occupancy-detection model were derived from the top five models shown in Table 2.3. Occupancy probability was predicted for each covariate after accounting for detection probability and holding all other covariates constant. Dark vertical lines on the x-axis show points where data were taken during the sampling campaign.

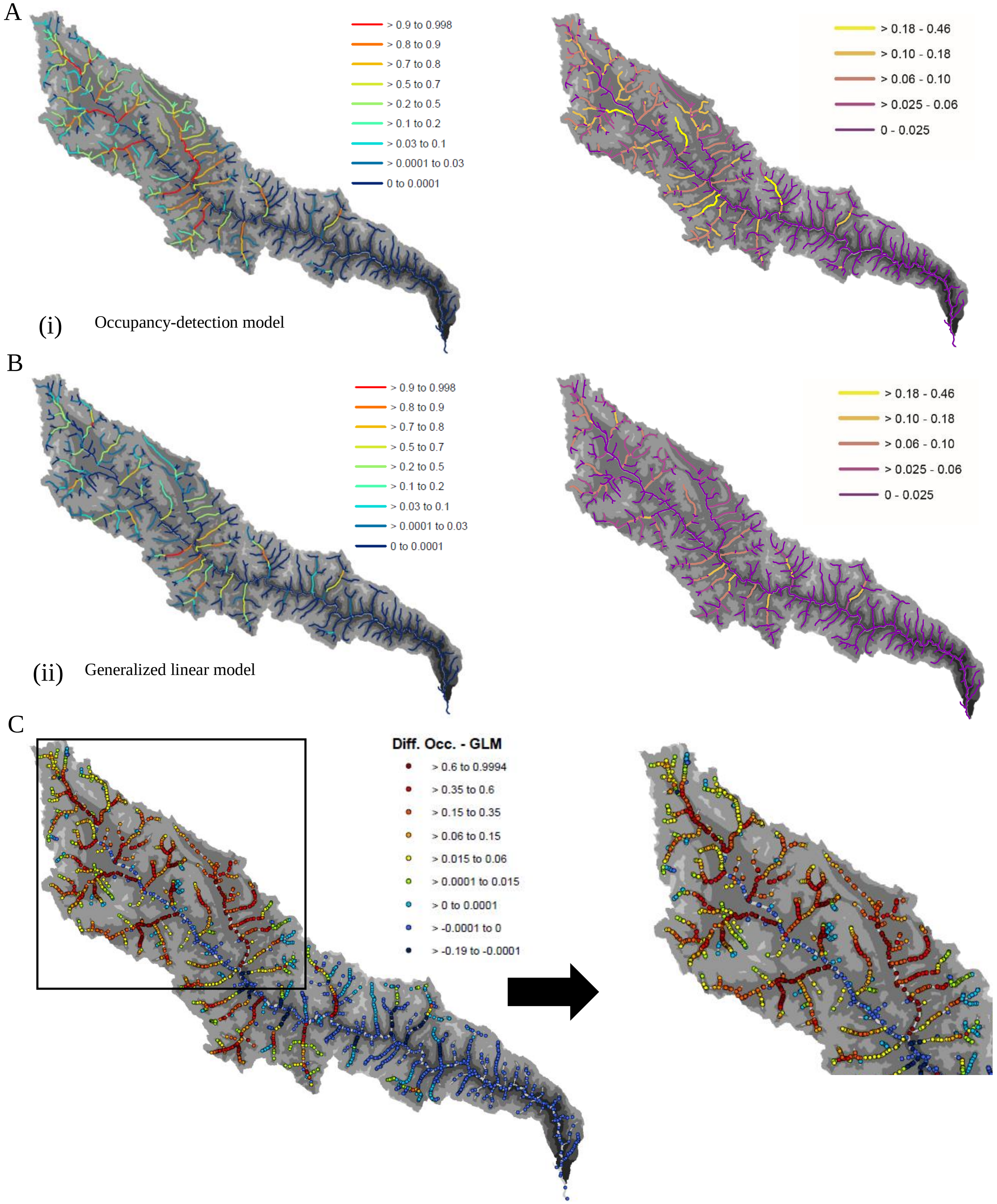
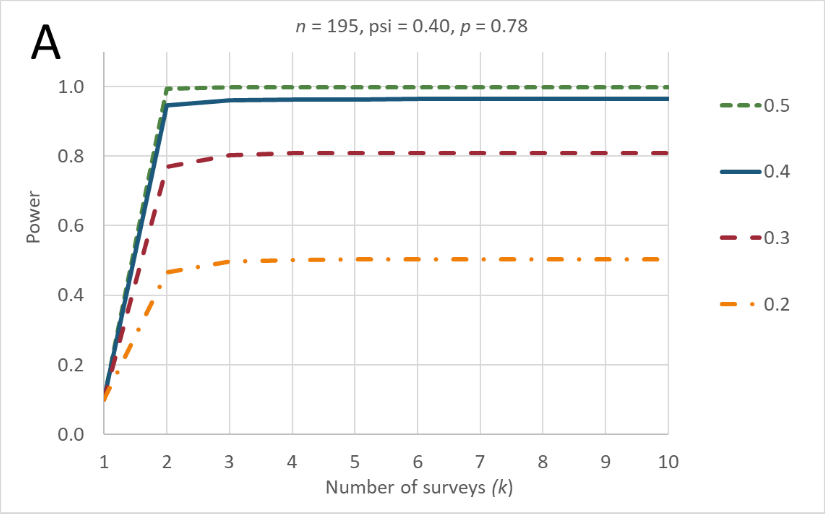


Figure 2.4. Juvenile bull trout distribution maps for Prairie Creek derived from (A) the occupancy-detection model and (B) generalized linear model. Distribution is expressed as the probability of juvenile bull trout being present in a 1 km stream segment. Corresponding standard error estimates for each model are shown in panels to the right of A and B. Absolute differences between point probability estimates derived from the occupancy-detection model and the generalized linear model (occupancy-detection – generalized linear model) are shown in panel (C).



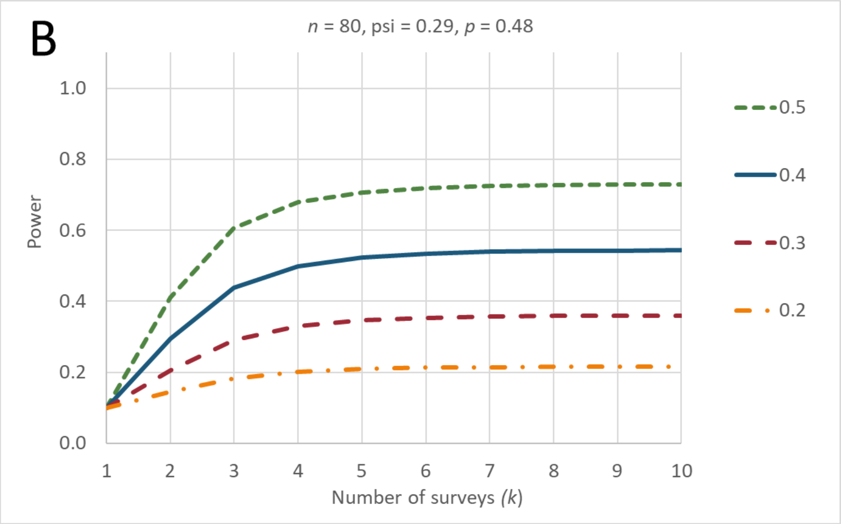


Figure 2.5. Power to detect absolute changes in occupancy based on simulations using mean occupancy (psi) and detection (*p*) estimates for varying levels of survey effort (*k*) and different effect sizes (0.2-0.5). Two scenarios are presented using mean model-averaged occupancy and detection estimates derived from the top five occupancy-detection models corresponding to core (A) and fringe (B) habitats. The following were held constant for each scenario (A: $\Psi = 0.40$, $p = 0.78$, $n = 195$; B: $\Psi = 0.29$, $p = 0.48$, $n = 80$). Power was assessed at an alpha level = 0.10.

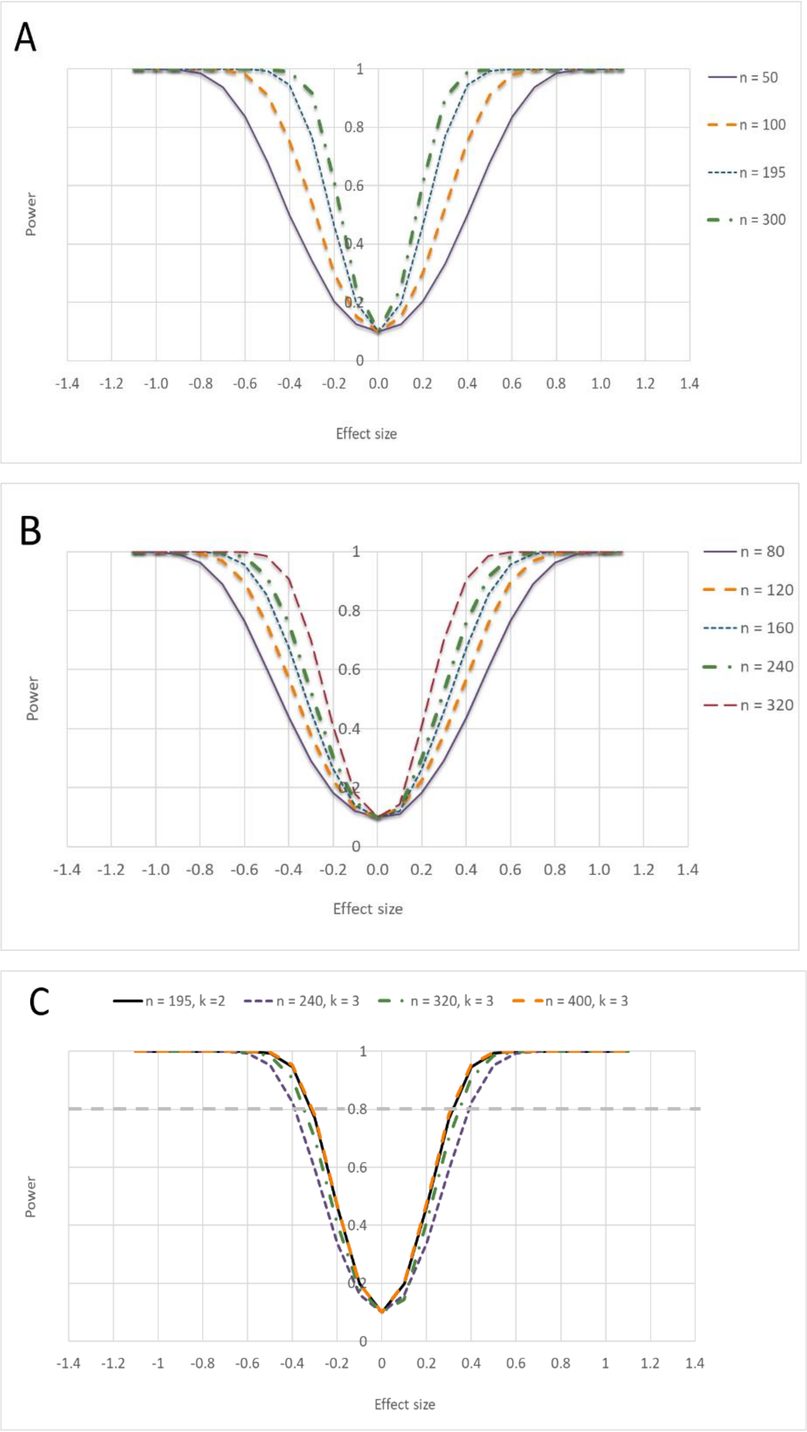


Figure 2.6. Power to detect absolute changes in occupancy (effect size) for core (A), fringe (B), and both core and fringe sites (C) based on number of sampling sites (*n*). The third simulation provides potential outcomes of a hybrid sampling approach where we compared power to detect changes in occupancy for core sites using the sampling design from this study ($n = 195$, $k = 2$) and different sampling densities for fringe sites ($n = 240, 320, 400$) while holding temporal replicates constant ($k = 3$). The following parameters were held constant for each scenario (A: $\Psi = 0.40$, $p = 0.78$, $n = 195$, $k = 2$; B: $\Psi = 0.29$, $p = 0.48$, $n = 80$, $k = 3$) and power was calculated at an alpha level of 0.10. The hatched grey line depicts an 80% power level.

Supplemental information

Sample size

We determined how many sites to survey within a patch using the following equation:

$$f_{patch} = (1 - \Psi(1 - (1 - p)^{k}))^{n} \quad (1)$$

where f_{patch} is the patch-level false absence probability, Ψ is patch-level occupancy, p is patch-level detectability, k is the number of surveys/site, and n is the number of sites/patch. Although patch-scale occupancy and detection estimates have been published (Isaak et al. 2015, Rodtka et al. 2015), we were not sure if our estimates would be similar, so we took a conservative approach and specified two surveys per site and used 0.40 and 0.30 as patch-level occupancy and detection estimates, respectively, when assessing f_{patch} for different designs (Fig. S2.2)

Table S2.1. Number of surveys required to detect the species at least once 80%, 90% and 95% of the time if detection per survey = *p*. Ψ = estimated occupancy, *p* = estimated detectability, and n = sample size. Ψ and *p* estimates are based on mean detection probability derived from the single-season model for core and fringe sites with corresponding sample size from each respective area.

Habitat	*n*	Ψ	*p*	Number of surveys needed		
				80%	90%	95%
Core	195	0.4	0.78	**1.1**	1.5	2
Fringe	80	0.29	0.48	2.5	3.5	**4.5**

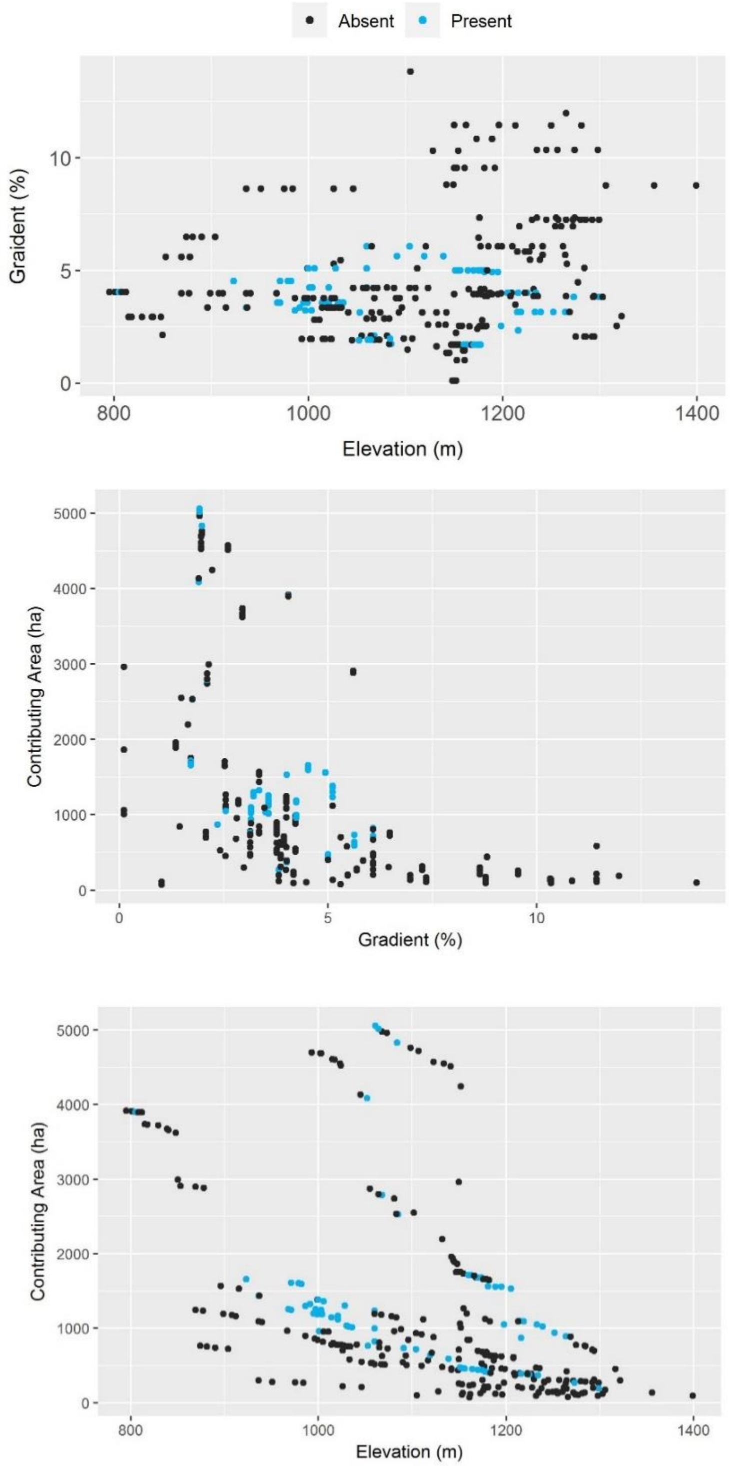


Figure S2.1. Scatterplots of predictor variables associated with the 275 sites used to develop single-season occupancy models.

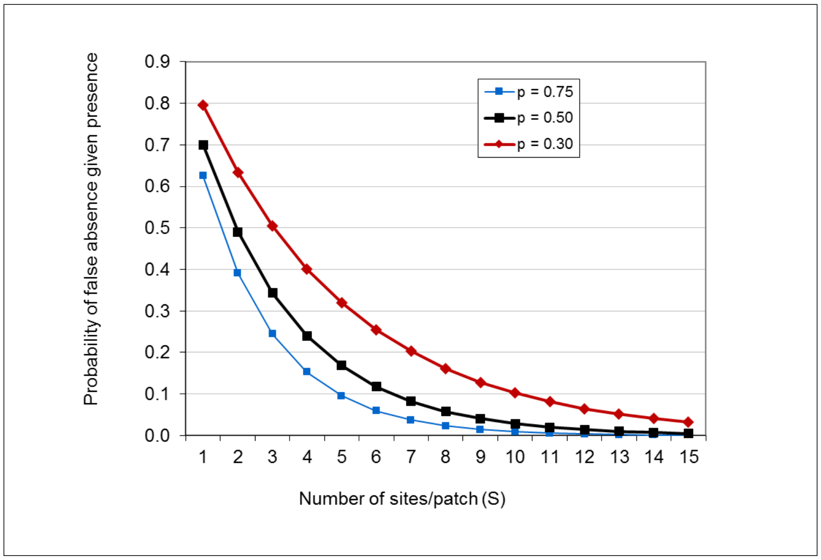


Figure S2.2. Relationship between the probability of false absence of juvenile bull trout where present in an occupied patch and number of sites surveyed in a patch. Occupancy was specified as 0.40 for all three curves and *p* is detectability.

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
10-3-03	0	0	0	-	-	2014	3
10-3-04	0	0	0	-	-	2014	3
10-3-05	0	0	0	-	-	2014	3
10-3-07	0	0	0	-	-	2014	3
10-3-09	1	1	0	-	-	2014	3
10-3-11	0	0	1	-	-	2014	3
10-3-13	0	0	1	-	-	2014	3
10-3-17	0	0	0	-	-	2014	3
10-3-19	0	1	1	-	-	2014	3
10-3-21	1	1	1	-	-	2014	3
10-3-22	1	0	0	-	-	2014	3
10-3-23	1	1	1	-	-	2014	3
10-3-25	1	1	0	-	-	2014	3
10-3-27	1	1	1	-	-	2014	3
10-3-29	1	1	1	-	-	2014	3
10-3-30	1	1	1	-	-	2014	3
122-1-03	0	0	0	-	-	2015	2
122-1-07	1	0	1	-	-	2015	2
122-1-11	0	0	0	-	-	2015	2
122-1-14	0	0	0	-	-	2015	2
122-1-24	0	0	0	-	-	2015	2
122-1-30	0	0	0	-	-	2015	2
122-1-34	0	0	0	-	-	2015	2
122-1-37	0	0	0	-	-	2015	2
122-1-45	0	0	0	-	-	2015	1
122-1-49	0	0	0	-	-	2015	1
122-1-50	0	0	-	-	-	2015	1
122-1-59	0	0	-	-	-	2015	1
2-3-02	0	0	0	-	-	2015	3
2-3-03	0	0	0	-	-	2015	3
2-3-04	1	0	0	-	-	2015	3
2-3-06	0	0	-	-	-	2015	3
2-3-07	0	0	0	-	-	2015	3
2-3-08	0	0	0	-	-	2015	3
2-3-10	0	0	-	-	-	2015	3
2-3-13	0	0	-	-	-	2015	3
2-3-14	0	0	-	-	-	2015	3
2-3-17	0	0	0	-	-	2015	3

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
2-3-18	0	0	0	-	-	2015	3
2-3-19	0	0	0	-	-	2015	3
2-3-21	0	0	0	-	-	2015	3
2-3-23	0	0	0	-	-	2015	3
32-2-05	0	0	-	-	-	2014	2
32-2-07	0	0	-	-	-	2014	2
32-2-17	0	0	-	-	-	2014	2
32-2-25	0	0	-	-	-	2014	2
32-2-26	0	0	-	-	-	2014	2
32-2-32	0	0	-	-	-	2014	2
32-2-33	0	0	-	-	-	2014	2
32-2-35	0	0	-	-	-	2014	2
32-2-39	0	0	-	-	-	2014	2
32-2-40	0	0	-	-	-	2014	2
38-13	0	0	-	-	-	2014	2
38-14	0	0	-	-	-	2014	2
38-15	0	0	-	-	-	2014	2
38-16	0	0	-	-	-	2014	2
38-17	0	0	-	-	-	2014	2
38-18	0	-	-	-	-	2014	2
38-19	0	0	-	-	-	2014	2
38-20	0	0	-	-	-	2014	2
38-21	0	0	-	-	-	2014	2
38-22	0	0	-	-	-	2014	2
40-1-03	0	0	0	0	0	2014	1
40-1-06	0	0	0	0	0	2014	1
40-1-21	0	0	0	0	0	2014	1
40-1-34	0	0	0	0	0	2014	1
40-1-38	0	0	0	0	0	2014	1
40-2-12	-	-	-	-	-	2014	2
40-2-13	1	1	-	-	-	2014	2
40-2-18	1	1	-	-	-	2014	2
40-2-19	1	1	-	-	-	2014	2
40-2-23	1	1	-	-	-	2014	2
40-2-26	1	1	-	-	-	2014	2
40-2-31	1	1	-	-	-	2014	2
40-2-32	1	1	-	-	-	2014	2
40-2-45	1	1	-	-	-	2014	2

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
40-2-51	1	1	-	-	-	2014	2
40-2-53	1	1	-	-	-	2014	2
41-1-13	1	1	-	-	-	2015	1
41-1-14	0	0	0	-	-	2015	1
41-1-15	0	0	0	-	-	2015	1
41-1-17	0	0	-	-	-	2015	1
41-1-18	0	0	0	-	-	2015	1
41-2-06	0	0	-	-	-	2015	2
41-2-11	0	0	-	-	-	2015	2
41-2-12	0	0	-	-	-	2015	2
41-2-14	0	0	-	-	-	2015	2
41-2-16	0	0	-	-	-	2015	2
41-2-18	0	0	-	-	-	2015	2
41-2-19	0	0	-	-	-	2015	2
41-2-30	0	0	-	-	-	2015	2
41-2-35	0	0	-	-	-	2015	2
41-2-36	0	0	-	-	-	2015	2
41-2-38	0	0	-	-	-	2015	2
44-1-09	0	0	-	-	-	2015	1
44-1-15	0	-	-	-	-	2015	1
44-1-16	0	0	0	-	-	2015	1
44-1-17	0	-	-	-	-	2015	1
44-1-43	0	-	-	-	-	2015	2
44-2-12	0	0	-	-	-	2015	2
44-2-15	0	0	-	-	-	2015	2
44-2-33	0	0	-	-	-	2015	2
44-2-41	0	0	-	-	-	2015	2
44-2-46	0	1	-	-	-	2015	2
44-2-50	1	1	-	-	-	2015	2
44-2-52	1	1	-	-	-	2015	2
44-2-59	1	-	-	-	-	2015	2
44-2-60	1	1	-	-	-	2015	2
44-2-61	1	1	-	-	-	2015	2
44-2-69	1	1	-	-	-	2015	2
45-1-24	0	0	0	0	0	2014	1
45-1-26	0	0	0	0	0	2014	1
45-1-32	0	0	0	0	-	2014	1
45-1-901	0	0	0	0	0	2014	1

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
45-1-902	0	0	0	0	0	2014	1
45-2-05	1	0	0	-	-	2014	2
45-2-10	1	1	1	-	-	2014	2
45-2-12	1	1	1	-	-	2014	2
45-2-20	1	0	1	-	-	2014	2
45-2-28	1	0	0	-	-	2014	1
45-2-29	1	1	1	-	-	2014	1
45-2-36	1	1	0	-	-	2014	1
45-2-40	0	0	0	-	-	2014	1
45-2-49	0	0	0	-	-	2014	1
45-2-51	0	0	0	-	-	2014	1
46-2-28	0	0	-	-	-	2015	2
46-2-31	0	0	-	-	-	2015	2
46-2-33	0	0	-	-	-	2015	2
46-2-37	0	0	-	-	-	2015	2
46-2-39	0	0	-	-	-	2015	2
46-2-41	0	0	-	-	-	2015	2
46-2-44	0	0	-	-	-	2015	2
46-2-46	0	0	-	-	-	2015	2
48-01	0	-	-	-	-	2014	1
48-03	0	-	-	-	-	2014	1
48-08	0	-	-	-	-	2014	1
48-12	0	1	-	-	-	2014	2
48-13	0	0	-	-	-	2014	2
48-14	0	0	-	-	-	2014	2
48-15	1	1	-	-	-	2014	2
48-16	0	1	-	-	-	2014	2
48-17	0	-	-	-	-	2014	2
48-18	0	0	-	-	-	2014	2
48-19	1	1	-	-	-	2014	2
48-20	1	0	-	-	-	2014	2
48-22	0	1	-	-	-	2014	2
48-23	0	1	-	-	-	2014	2
48-901	0	-	-	-	-	2014	1
52-1-02	0	0	-	-	-	2015	1
52-1-04	0	0	-	-	-	2015	1
52-1-06	0	0	-	-	-	2015	1
52-1-07	0	0	-	-	-	2015	1

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
52-1-08	0	0	-	-	-	2015	1
52-1-10	0	-	-	-	-	2014	2
52-1-12	0	-	-	-	-	2014	2
52-1-17	0	0	-	-	-	2015	1
52-2-02	1	1	-	-	-	2014	2
52-2-03	1	1	-	-	-	2014	2
52-2-04	1	1	-	-	-	2014	2
52-2-05	0	1	-	-	-	2014	2
52-2-06	1	1	-	-	-	2014	2
52-2-07	1	1	-	-	-	2014	2
52-2-08	1	1	-	-	-	2014	2
52-2-09	1	0	-	-	-	2014	2
52-2-10	0	1	-	-	-	2014	2
55-2-02	0	-	-	-	-	2015	2
55-2-04	0	0	-	-	-	2015	2
55-2-05	0	0	-	-	-	2015	2
55-2-06	0	-	-	-	-	2015	2
55-2-07	0	0	-	-	-	2015	2
55-2-08	0	0	-	-	-	2015	2
55-2-09	0	0	-	-	-	2015	2
55-2-11	0	0	-	-	-	2015	2
55-2-12	0	0	-	-	-	2015	2
55-2-13	0	0	-	-	-	2015	2
55-2-14	0	0	-	-	-	2015	2
55-2-15	0	0	-	-	-	2015	2
55-2-18	0	0	-	-	-	2015	2
55-2-19	0	0	-	-	-	2015	2
55-2-20	0	0	-	-	-	2015	2
55-2-21	0	0	-	-	-	2015	2
58-1-113	0	0	0	0	0	2014	1
58-1-66	1	1	1	1	1	2014	1
58-1-70	1	0	0	0	0	2014	1
58-1-77	0	0	0	0	0	2014	1
58-2-02	0	0	-	-	-	2015	2
58-2-23	0	0	-	-	-	2015	2
58-2-34	0	0	-	-	-	2015	2
58-2-36	0	0	-	-	-	2015	2
58-2-43	0	0	-	-	-	2015	2

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
58-2-45	0	0	-	-	-	2015	2
58-2-50	1	1	-	-	-	2015	2
58-2-60	1	0	-	-	-	2015	2
6-3-06	0	1	0	-	-	2014	3
6-3-07	0	0	1	-	-	2014	3
6-3-08	1	0	0	-	-	2014	3
6-3-13	0	0	1	-	-	2014	3
6-3-14	0	0	0	-	-	2014	3
6-3-20	0	0	0	-	-	2014	3
6-3-23	0	0	0	-	-	2014	3
6-3-27	0	0	0	-	-	2014	3
6-3-37	0	0	0	-	-	2014	3
6-3-38	0	0	0	-	-	2014	3
6-3-42	0	0	0	-	-	2014	3
6-3-43	0	0	0	-	-	2014	3
6-3-48	0	0	0	-	-	2014	3
6-3-49	0	0	0	-	-	2014	3
6-3-52	0	0	0	-	-	2014	3
61-2-03	1	1	1	-	-	2014	2
61-2-04	1	1	1	-	-	2014	2
61-2-08	1	1	1	-	-	2014	2
61-2-11	1	1	1	-	-	2014	2
61-2-15	1	1	1	-	-	2014	2
61-2-18	0	1	0	-	-	2014	2
61-2-20	0	0	0	-	-	2014	2
61-2-22	0	0	0	-	-	2014	2
61-2-24	0	0	0	-	-	2014	2
61-2-25	0	0	0	-	-	2014	2
61-2-29	0	0	0	-	-	2014	2
61-2-30	0	0	0	-	-	2014	2
61-2-42	0	0	0	-	-	2014	2
61-2-44	0	0	0	-	-	2014	2
66-03	0	0	-	-	-	2014	1
66-06	0	0	-	-	-	2014	1
66-13	0	0	-	-	-	2014	2
66-15	1	1	-	-	-	2014	2
66-18	1	0	-	-	-	2014	2
66-20	1	1	-	-	-	2014	2

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
66-21	1	1	-	-	-	2014	2
66-23	0	0	-	-	-	2014	2
68-01	0	0	-	-	-	2015	1
68-03	0	-	-	-	-	2015	1
68-05	0	0	-	-	-	2015	1
68-06	0	-	-	-	-	2015	1
68-07	0	0	-	-	-	2015	1
68-08	0	0	-	-	-	2015	1
68-10	0	-	-	-	-	2015	1
68-14	0	-	-	-	-	2015	2
68-15	0	0	-	-	-	2015	2
68-16	0	0	-	-	-	2015	2
68-17	0	0	-	-	-	2015	2
68-19	0	0	-	-	-	2015	2
68-20	0	0	0	-	-	2015	2
68-21	0	0	-	-	-	2015	2
68-22	0	0	-	-	-	2015	2
7-3-01	0	-	-	-	-	2015	3
7-3-02	0	-	-	-	-	2015	3
7-3-03	0	-	-	-	-	2015	3
7-3-04	0	-	-	-	-	2015	3
7-3-05	0	-	-	-	-	2015	3
7-3-06	0	-	-	-	-	2015	3
7-3-07	0	-	-	-	-	2015	3
7-3-09	0	-	-	-	-	2015	3
7-3-10	0	-	-	-	-	2015	3
7-3-12	0	-	-	-	-	2015	3
7-3-14	0	-	-	-	-	2015	3
7-3-15	0	-	-	-	-	2015	3
7-3-16	0	-	-	-	-	2015	3
7-3-17	0	-	-	-	-	2015	3
7-3-18	0	-	-	-	-	2015	3
9-3-05	0	0	0			2015	3
9-3-06	0	0	0			2015	3
9-3-07	0	0	0			2015	3
9-3-10	0	0	0			2015	3
9-3-19	0	0	0			2015	3
9-3-27	0	0	0			2015	3

Table S2.2. Juvenile bull trout occurrence data from sites that were surveyed in Prairie Creek, NWT in 2014 and 2015.

Site	S1_1	S1_2	S1_3	S1_4	S1_5	Year	SO
9-3-39	0	0	0			2015	3
9-3-45	0	0	0			2015	3
9-3-53	0	0	0			2015	3
9-3-57	0	0	0			2015	3
9-3-64	0	1	1			2015	3
9-3-70	0	0	0			2015	3
9-3-71	0	0	0			2015	3
9-3-72	0	1	0			2015	3
9-3-75	0	1	1			2015	3

Note: S, is survey and number corresponds to the year followed by survey number (S1_1 = survey one, year 1); SO, is stream order.

Chapter 3: Stream thermal regimes and ecological niche of juvenile bull trout (*Salvelinus confluentus*) in montane watersheds across a latitudinal gradient

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Contributions of Authors: Under the oversight of D. Isaak, I developed and implemented a stream temperature monitoring network in Prairie Creek, Northwest Territories. M. Docker provided direction on organization and content of the manuscript. M. Taylor gathered and provided stream temperature data from a monitoring network in the central study location. I analyzed the data and wrote the initial and final drafts of the manuscript. All co-authors commented on earlier drafts of the manuscript.

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Abstract

Maintaining natural thermal regimes in montane stream networks is critical for sustaining ecosystem structure and function, but as climate warms, thermal regimes will undoubtedly change. Mitigating impacts of changing thermal regimes on aquatic biodiversity requires knowledge of which elements of the thermal regime act as limiting factors for aquatic biota. Full-year stream temperature records, spanning a broad latitudinal gradient, were used to describe the diversity of the thermal landscape that bull trout (*Salvelinus confluentus*) occupy and identify potential divergences from thermal regimes already classified in watersheds where this species occurs. Populations occupied narrow and cold summer thermal niches that differed across a south to north latitudinal gradient (Location: $F_{2,233} = 203.1$, $p < 0.0001$; mean ±SE, south: 9.6 ± 0.11; central: 7.5 ± 0.18; north: 6.2 ± 0.10). All streams exhibited low to moderate thermal sensitivity, but winter thermal regimes in central and northern streams were colder and more stable than the south, reflecting slightly lower thermal sensitivities and greater contributions of perennial groundwater to baseflow. In the south, some streams are near the upper thermal limit for bull trout, whereas in the north, many streams appear to be at the cold-edge boundary of thermally suitable habitat. Results suggest that the distribution of juveniles at higher latitudes is driven by cold-limiting streams in both the summer and winter (i.e., do not freeze). This result is opposite to what others report for bull trout at the southern range extent, where distributional patterns and population demographics are governed by warm-limiting streams during the open water season.

Keywords: bull trout, stream temperature regimes, mean August temperature, accumulated thermal units, thermal sensitivity

Introduction

The ecological niche that freshwater fishes occupy is a reflection of historic processes and biotic and abiotic factors (Griffiths 2010; Peterson 2011a). In stream ecosystems, both biotic and abiotic factors are important determinants defining the geographic distributions of North American fishes due to limitations imposed by the hierarchical, dendritic structure of stream networks (Fagan 2002). Because stream-dwelling fish are confined to linear stream segments, which vary in size across spatial-temporal scales, they must adjust to occupy ecological niches within a narrower range of habitat dimensions than terrestrial organisms (Rieman and McIntyre 1995; Fagan 2002). If the characteristics of the ecological niche a species occupies changes beyond acceptable limits, then individuals must disperse to suitable habitat, adjust, or adapt; and if they are not capable of doing this then they may perish (Holt 2009). However, all organisms possess the phenotypic plasticity to adjust to a range of abiotic conditions, but the extent to which they can adjust beyond acceptable known physiological limits varies across taxa and serves to shape geographic range boundaries (Pulliam 2000; Sexton et al. 2009; Seebacher et al. 2015). For species occupying a narrow range of habitats, only minor changes to their ecological niche will necessitate adjustments or potential adaptation to novel niches (Holt 2009). Since post-glacial dispersal, freshwater stream fishes have undergone selection to occupy ecological niches that promote long-term survival (Sexton et al. 2009; Griffiths 2010). In many taxa, genes linked to key physiological processes (e.g., thermoregulation) are conserved across their geographic range and portrayed as a common ecological niche – i.e., niche conservatism (Wiens and Graham 2005; Holt 2009). As stream fishes are ectotherms, temperature is an important abiotic factor that influences their distribution; therefore, any changes to stream thermal regimes could have profound consequences (e.g., extirpation) on stenothermal species with limited adaptive capacity (Somero 2010; Sunday et al. 2014).

Over the past three decades, research has demonstrated that maintaining natural environmental regimes in rivers and streams is a critical element for sustaining ecosystem structure and function (Poff 2009; Poff and Zimmerman 2010). Although the natural flow regime has been at the forefront of this research, there has been a recent paradigm shift to include metrics of water quality, including water temperature (Olden and Naiman 2009), primarily because the latter has a strong influence on both physiochemical (Gordon et al. 2004) and biological processes (Angilletta 2009; Kingsolver 2009). Recent studies have refined understanding of how natural thermal regimes affect both the ecology and biology of stream fishes (Benjamin et al. 2016; Austin et al. 2019). In addition, a broader suite of studies show how thermal habitat availability differs across latitudinal and altitudinal gradients (Steel et al. 2016; Isaak et al. 2017b; Michel et al. 2020) and is influenced by local climatic and hydrological factors (Mayer 2012; MacDonald et al. 2014; Bolduc and Lamoureux 2018).

The recent advent of inexpensive temperature loggers has led to a better understanding of thermal habitat availability and thermal regimes across systems, but has also shown that the thermal properties of streams in these systems has changed due to climate warming (Isaak et al. 2012; Michel et al. 2020). Because the sensitivity of streams to climate warming differs over spatial-temporal scales (Luce et al. 2014; Isaak et al. 2016; Bolduc and Lamoureux 2018), increasing air temperatures will have disproportional effects on thermal regimes, both within watersheds and across regions, leading to potentially different consequences for biota. The consequences of increasing stream temperatures (e.g., range contraction or shift) could be more severe for organisms occupying warm-limiting and cold-limiting thermal habitats at distributional range boundaries, whose acute thermal limits lie near thermal thresholds (Somero 2010; Sunday et al. 2012; Sunday et al. 2014). At warm-edge boundaries, populations may experience range contraction near downstream distributional limits where streams warm beyond thermal thresholds (Comte et al. 2013; Eby et al. 2014; LeMoine et al. 2020). Conversely, at cold-edge boundaries, where species may have greater thermal safety margins, increasing temperatures could provide new opportunities for distributional expansion and population growth (e.g., Pacific salmon; Babaluk et al. 2000; Dunmall et al. 2016; Farley Jr et al. 2020).

Since annual temperature patterns are not uniform across streams (Maheu et al. 2016), documenting natural thermal regimes in streams is important for understanding their susceptibility to climate warming and assessing trends over time. In larger streams and rivers, thermal regimes are well described; however, similar understanding is lacking in small montane streams due to data inadequacies as these areas are difficult to sample (Isaak et al. 2013; Park et al. 2017). At higher latitudes, sampling difficulty is compounded because many streams completely freeze to the bottom during winter (Yang and Peterson 2017; Bolduc and Lamoureux 2018). In montane watersheds where thermal regimes have been characterized, results show that a subset of habitats within these ecosystems possess distinct thermal characteristics and are ecological hot spots for sustaining biota and maintaining biological diversity (Dunmall et al. 2016; Isaak et al. 2016). Describing thermal regimes across additional montane watersheds will help determine if the distinct thermal characteristics that others report are prevalent across local, regional, or global spatial scales.

Different elements of stream thermal regimes have been linked to the biology (Neuheimer and Taggart 2007; French et al. 2017), distribution (Wenger et al. 2011; Comte et al. 2013; Isaak et al. 2017a) and physiology (Eliason et al. 2011; Raby et al. 2016) of stream fishes. These studies have refined our understanding of thermally mediated ecological processes at discrete times of the year and thermal tolerance associated with physiological capacity. However, focusing on discrete elements of the annual stream thermal regime (e.g., summer temperature) limits adequate understanding of how other aspects of the annual thermal regime may further influence species persistence and survival across spatial-temporal scales. Although thermal regimes may differ across latitudes, fish still must occupy habitat within an acceptable thermal range (i.e., the species' thermal niche) to survive. Within watersheds, some streams will be either too cold or too hot for fish to survive (Harig and Fausch 2002; Coleman and Fausch 2007a) and this results in the heterogeneous distribution of stream fishes (Wenger et al. 2011; Isaak et al. 2017a). However, we do expect to see some level of intraspecific variability in the thermal regimes (and niche) that species experience across their distributional range, and this variation results in differences in phenology and growth trajectories that reflect adjustments, or adaptations to local climatic conditions (Shuter and Post 1990; Shuter et al. 2012).

Recent work in the northwestern United States has characterized different elements of annual thermal regimes in montane watersheds (Benjamin et al. 2016; Steel et al. 2016; Isaak et al. 2018). Here, I use full-year temperature data compiled from three montane watersheds in the southern, central, and northern regions of the bull trout (*Salvelinus confluentus*) distributional range to describe annual thermal regimes for this societally important salmonid. My aim was to gain a broader understanding of thermal regimes that bull trout experience across their distributional range and which elements might act as limiting factors. The watersheds selected for this study span a broad latitudinal gradient (45° - 61° N) and the southern and northern watersheds are at the respective range boundaries of this species. Bull trout is a cold-water stenotherm that is patchily distributed across montane watersheds and uses headwater streams for spawning and rearing (Rieman and McIntyre 1995; Isaak et al. 2017a). The distributional patterns and demographics of bull trout populations have been shown to be driven largely by cold summer stream temperatures (Isaak et al. 2015; Kovach et al. 2016) related to low thermal tolerances described in laboratory experiments (Selong et al. 2001). However, these relationships and patterns are based on August stream temperature, which is only one component of the annual thermal regime, and it is well documented that annual thermal regimes are diverse across river networks (Steel et al. 2016; Isaak et al. 2018). One element that has not been examined is whether streams at higher latitudes, near the northern geographic range extent, are cold-limiting for bull trout. Studies have shown two ways in which cold stream temperatures act to limit fish survival. First, some streams do not provide enough thermal units throughout the growing season for juveniles to attain sufficient size and lipid stores to survive throughout the winter (Finstad et al. 2004b; Coleman and Fausch 2007b; Berg et al. 2009). Conversely, streams that do not freeze completely during winter provide viable year-round fish habitat, but survival can be low in streams that exhibit high environmental variability during winter (Cunjak et al. 1998). Despite thermal tolerance limitations, stream-dwelling salmonids have evolved to capitalize on the diversity of thermal landscapes to maximize growth and survival based on biological traits and physiological capabilities (Coleman and Fausch 2007b; Sparks et al. 2017; Campbell et al. 2019). Therefore, by understanding annual thermal regimes, one can identify when and where thermal thresholds may be crossed and translate to important population-level responses. The annual thermal regime in watersheds that bull trout occupy have only been described in the southern and central range and, in most instances, focus on summer thermal regimes. This limits our ability to adequately understand the diversity of the thermal landscape that bull trout occupy both within and across watersheds and identify potential divergences from thermal regimes already classified in watersheds where this species occurs (Isaak et al. 2018).

The thermal sensitivity of streams to changes in air temperature varies across spatial-temporal scales and is driven by the contribution of perennial groundwater, seasonal precipitation, and snowpack (Luce et al. 2014; Lisi et al. 2015; Bolduc and Lamoureux 2018). The former is emerging as an important mechanism for maintaining stable water temperatures (Bolduc and Lamoureux 2018) and provides spawning, incubation, and rearing habitat for temperate and northern stream fishes (Isaak et al. 2015; Dunmall et al. 2016; Mochnacz et al. 2020). I developed and tested three hypotheses. My first hypothesis was that bull trout would occupy a narrow range of stable, cold-water thermal habitats that are most energetically profitable, and I predicted that the thermal sensitivity of streams that bull trout occupy would be similar across latitude. Niche conservatism is a relevant concept for cold-water stenotherms, such as bull trout, as it implies that species conserve inherited biological traits over broad temporal and spatial scales (Wiens and Graham 2005). Given that bull trout occupy very cold streams within and across regions (Kovach et al. 2016; Parkinson et al. 2016; Isaak et al. 2017a), my second hypothesis was that this cold-water adapted trait would be conserved across the distributional range, and I predicted that mean summer and winter stream temperatures would not differ across latitude. Although I expected that summer thermal regimes would be similar across the bull trout range, I did not expect this pattern to hold during other seasons. At higher latitudes, the winter season is longer and the growing season is shorter, and fish have adapted their phenology to optimize growth during these respective periods (Shuter et al. 2012). Therefore, my third hypothesis was that regional climatic differences associated with latitude would drive phenology, and I predicted that hatch timing and magnitude of accumulated thermal units during developmental periods would differ among regions.

Methods

Study areas

The study area encompasses three montane watersheds situated in the southern (45° N, 124° W), central (55° N, 124° W), and northern (61° N, 124° W) regions of the bull trout distributional range, spanning a distance of approximately 2000 km (Fig. 3.1). All three watersheds have topographically complex terrain but experience different climatic conditions. The southern watershed (Idaho, United States) has cold, wet winters, and dry hot summers, whereas the central (Alberta, Canada) and northern (Northwest Territories, Canada) watersheds experience colder and longer winters, and shorter, hot, dry summers (Holland and Coen 1983; Halliwell and Catto 2003; Isaak et al. 2018). Vegetation in all three watersheds is dominated by mixed coniferous forests in higher elevation areas and shrubs, grasses, and willows in lower elevation areas, but the overall density of vegetation is far less in the northern watershed than the two others. The geology in the south consists of resistant granites and volcanics (Isaak et al. 2018), whereas the central and northern locations are composed of limestone, dolomite, shale mantled by till, and sandy fluvioglacial drift (Holland and Coen 1983; Halliwell and Catto 2003). Unpaved roads/trails are present in all three areas but are least extensive in the north. The southern watershed has the most diverse fish assemblage with twelve species (Isaak et al. 2017b), followed by the central with five species (M. Taylor per. comm.), and the northern with four species (Babaluk et al. 2015).

River networks and temperature data set

Streams within the study area were delineated using 1:100 000-scale National Hydrography Datasets from both Canada (NHN: https://open.canada.ca/data/en/dataset/a4b190fe-e090-4e6d-881e-b87956c07977, last access: 15 January 2020) and the United States (Isaak et al. 2018) to portray synthetic stream layers across each respective watershed using a GIS platform. In each watershed, stream networks were filtered to exclude reaches with channel slopes > 15%, stream orders greater than four, and contributing areas < 70 ha, because these smaller streams are typically ephemeral. Self-sustaining bull trout populations occupy all of the watersheds, and all life stages (i.e., eggs, juveniles, adults) are present in streams where temperature records were selected for the analysis. Environmental characteristics of the three watersheds across the study region are summarized in Table 3.1. Hourly temperature data were collected across all three watersheds using Tidbit temperature sensors (Onset Computer Corporation, Pocasset, Massachusetts, USA), which had measurement accuracies of 0.21 °C and resolutions of 0.02 °C.

The data set for analysis was obtained by filtering records from each area based on similar stream size and stream gradient (Table 3.1). Since many of these rivers freeze during winter, I only used records with monthly mean daily water temperatures that were not colder than -1.2 °C. This threshold was based on both experimental and field data, which show that supercooling temperatures in rivers range between -0.07 and -1.0 °C (Devik 1949; Nafziger et al. 2013) and, since the accuracy of our temperature sensors was ± 0.21 °C, I assumed that any values < -1.2 °C were not from flowing waters. Sites from the northern watershed were selected first, as this was the temperature network with the fewest full-year monitoring sites because most first, second, and third order streams freeze completely during winter (N. Mochnacz unpublished data). The stream temperature data set consisted of fifteen unique records taken from each region for a total of 45 sites (Fig. 3.1) and were from a subset of larger temperature data sets (Idaho, $n = 226$; Alberta, $n = 225$; Northwest Territories, $n = 35$). Records from northern (NT) and southern (ID) watersheds covered the period of August 1, 2013 to August 31, 2016 and the central (AB) watershed was from July 1, 2016 to July 26, 2019. Missing daily stream temperature values were imputed using the MDA package (Missing Values with Multivariate Data Analysis; Josse and Husson 2012) in R (R Development Core Team 2018). The minimum threshold for record completeness was 60% but average completeness of most records ($n \geq 12$) was ≥ 80%. Similar to what others have shown (Isaak et al. 2018), I found that the quality of imputed data based on temporal covariation from nearby stream sites was good, as all of the correlations between daily observed records and predictions from the imputation were high ($r \geq 0.99$). After imputation, the complete data set consisted of 1127 mean daily temperature records across three years for each watershed. The data set from the northern watershed included six records with only one year of full data (30%) but, in order to maximize sample size, I decided to retain these sites and only use observed values, not imputed values. Mean daily air temperature data were downloaded from local monitoring stations within 100 km of sites in each watershed (Idaho: Cooperative Observer Network, https://www.ncdc.noaa.gov/data-access, last access, 01 July 2020; Canada: Environment Canada, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html, last access, 01 July 2020).

Bull trout thermal requirements

Bull trout is a cold-water stenotherm that occupies lakes and streams across western North America (Haas and McPhail 1991). Adults spawn in late summer to early fall in streams with cobble to boulder substrate, eggs incubate throughout the winter, and juveniles emerge in the spring. Juveniles remain in their natal stream for 3-5 years and then move downstream into either larger rivers or lakes (Al-Chokhachy et al. 2010). The phenology of life history events varies across the range because both climate and the length of development and growing seasons differ across latitude – i.e., winter begins earlier and is longer in the north than it is in the south (Reist et al. 2006; Shuter et al. 2012). Consequently, bull trout populations at higher latitudes spawn earlier in the season (mid-late August; 15-30 days earlier) than those found in central and southern areas (N.J. Mochnacz, unpublished data). Both laboratory and field studies show that adults require stream temperatures ranging from 5 to 10 °C for spawning, and eggs incubate across a narrow thermal niche approaching minimum thresholds (Gould 1987; Selong et al. 2001; Benjamin et al. 2016; Fig. 3.2). Juveniles and adults in the southern and central regions of the range prefer to occupy streams with mean summer stream temperatures < 11 °C and, although adults can survive in warmer water (> 16 °C), growth is typically poor at these temperatures (Selong et al. 2001; Isaak et al. 2015; Parkinson et al. 2016). It is important to note that this definition of the bull trout thermal niche does not include populations found north of 60° latitude where their thermal ecology has not been well-described (Stewart et al. 2007; Mochnacz et al. 2013).

Temperature is an important determinant of hatching and emergence phenology, and growth in stream-dwelling salmonids, reflecting either local adjustments, or adaptations, to unique thermal regimes that act to maximize individual fitness (Sparks et al. 2017; Austin et al. 2019; Campbell et al. 2019). Once eggs are deposited in the gravel, the rate and magnitude of thermal units that accumulate throughout the incubation and initial growth period determine when hatching occurs and juveniles emerge — i.e., where the yolk sac is absorbed and juveniles can swim on their own (Neuheimer and Taggart 2007; Fuiman and Werner 2009). Accumulated thermal units (ATU) are often used to quantify how temperature influences developmental rates, and is quantified by calculating cumulative thermal units over time, where 1°C for 24 hr = 1 thermal unit (Neuheimer and Taggart 2007). If juvenile salmonids do not experience sufficient ATU between hatching and the onset of winter, fish may not attain sufficient size and lipid stores to survive the winter (Coleman and Fausch 2007a, 2007b; Berg et al. 2009). Laboratory studies on a southern bull trout population show that eggs require 500 ATU to hatch and juveniles require 800 ATU to emerge (Gould 1987). Bebak et al. (2000) show that juvenile survival of Arctic char (*Salvelinus alpinus*) is highest when fish experience an additional 800 ATU after emergence. Together, these data suggest that bull trout require 1600 ATU from egg deposition to the onset of winter to increase their chance of survival during this season.

Metrics and timing windows

Mean daily stream temperatures were calculated from hourly temperature records at each site across all time periods. Four temperature metrics were then calculated to describe the thermal regimes of streams from each region based on magnitude, variability, and timing (Table 3.2). We chose to select a subset of thermal regime metrics used by others (Chu et al. 2010; Arismendi et al. 2013; Isaak et al. 2018) so that we could focus on those related to key elements of bull trout biology and thermal thresholds of key life stages (Fig. 3.2).

Thermal sensitivity, which is a method for quantifying a stream’s response to air temperature, is an important thermal metric for understanding how streams will respond to climate warming (Isaak et al. 2016; Bolduc and Lamoureux 2018). Streams with low thermal sensitivity have more stable stream temperatures throughout the year and are affected minimally by changes in air temperature (Kelleher et al. 2012). Additionally, the contribution of perennial groundwater is an underlying mechanism driving low thermal sensitivity in streams, and habitat associated with perennial groundwater is considered high quality spawning and rearing habitat for bull trout

(Baxter and McPhail 1999; Baxter and Hauer 2000). To identify variations in water temperature relative to changes in air temperature, we calculated the thermal sensitivity of all sites across years in each watershed. The thermal sensitivity at a site was the slope of the linear regression relationship between weekly water temperature (T_w) and weekly air temperature (T_w) using records across a given year. I used weekly time steps because they typically provide more precise thermal sensitivity relationships than daily time steps (Kelleher et al. 2012). Negative air temperatures were not included in this calculation, since linear relationships below this threshold poorly predict stream temperatures (Morrill et al. 2005).

Given that many stream temperature metrics associated with magnitude are correlated (Isaak et al. 2018), August mean and winter mean temperature were used as magnitude metrics. The former has been used to define the thermal niche that bull trout occupy in southern latitudes (Dunham et al. 2003; Isaak et al. 2015; Isaak et al. 2017a) but has not been well reported at mid- and high-latitudes across the range. Accounts of winter stream thermal regimes that bull trout experience are sparse, but the winter season is considered by many as a survival bottleneck for freshwater salmonids as it influences development and growth of eggs, timing of hatching and juvenile emergence (i.e., free swimming fish), and survival of adults and juveniles (Cunjak et al. 1998; Shuter et al. 2012). During winter, early life stages of salmonids often experience high mortality due to exhaustion of energy reserves (Finstad et al. 2004b).

Lastly, I looked at ATU, as this metric has been attributed to differences in growth of fish across latitudinal gradients, hatching and juvenile emergence phenology, and growth throughout the summer-early fall (Coleman and Fausch 2007a; Neuheimer and Taggart 2007; Neuheimer and MacKenzie 2014). The latter can be particularly important for successful recruitment of salmonids in cold-edge boundary habitats (Coleman and Fausch 2007b). ATU were analyzed across annual, incubation, and growing periods (Table 3.1), as all are biologically relevant periods for growth across life stages (Fig. 3.2). The rate that ATU increase during the incubation period is particularly important for development and survival of embryos and emergence phenology of juveniles (Finstad et al. 2004b; Shellberg et al. 2010; Shuter et al. 2012). The incubation period began at the mid-point of the spawning season and extended until 50% of eggs had hatched. Calculations for analyses during this period started on different dates (NT: August 15; AB: September 01; ID: September 15) to reflect latitudinal differences in the median spawning date across these watersheds. These dates were selected based on known spawning dates published in the literature and unpublished data for central and northern sites (N. Mochnacz and M. Taylor, unpublished data; Baxter and McPhail 1999; Guzevich and Thurow 2017). Because egg hatching dates were not known for these populations, I used a reciprocal hatch timing model developed by Sparks et al. (2019) for *Oncorhynchus* spp. in Alaska. This model is a modification of the existing model developed by Beacham and Murray (1990) and is known as the Effective Value model and expressed as:

$$E_i = \frac{1}{\exp[log_e\, a - log_e\, (T_i - b)]} \tag{1}$$

where *E* is an effective value (range of 0–1) describing the relative daily contribution to development; $log_e\, a = 6.727$and *b* = - 2.394 are model coefficients based on thermal relationships and hatch timing for Pacific salmon, *Oncorhynchus* spp. (Beacham and Murray 1990; Austin et al. 2019); and *T* is the daily mean water temperature on each day of incubation. Pacific salmon coefficients were used because this model fit our data better than the only existing bull trout model (Austin et al. 2019). The Pacific salmon model was validated in a northern Alaskan watershed (Sparks et al. 2017) where thermal regimes were more similar to streams from this study. This explains why this model fit our data better than the current bull trout model, which was developed using data from populations in southern British Columbia where thermal regimes were warmer throughout the incubation and hatch period (Austin et al. 2019). Since fish eggs accumulate E over the course of the incubation period, the model predicts that 50% will hatch when the sum of $E = 1$. The model developed by Beacham and Murray (1990) requires an estimate of mean water temperature during incubation but, when this is unknown, the Sparks et al. (2019) model allows one to predict hatch timing by using daily mean temperature and each day's respective contribution towards development. The growing period went from the estimated egg hatch date for each respective watershed through to the fall period when stream temperatures were ≤ 1.5°C for 7 consecutive days. The latter criterion was used to define the onset of winter: November 01 in the south and October 15 in the central and northern watersheds. These timing windows were not chosen to predict exactly when timing of key events happen, but rather to compare differences in the estimated hatch dates and magnitude of thermal units across developmental periods and among regions.

Data analyses

Since presence-absence data for juvenile bull trout (< 150 mm fork length) were available from all three areas, we combined these data with modelled mean August stream temperatures to compare and describe the thermal niche occupied by bull trout across all three regions. In each watershed, sampling sites were assigned across streams using a random-stratified sampling design and encompassed a broad environmental gradient. This design was implemented to refine understanding of how landscape and abiotic (e.g., temperature) factors influence juvenile distribution in each respective watershed. Sites were electrofished in an upstream fashion using temporal or spatial (3-pass removal) replication and the presence of juvenile bull trout was documented at each site.

Temperature sensors were deployed in all three watersheds and used to model mean August stream temperatures using a spatial statistical stream network model (Ver Hoef and Peterson 2010). Temperatures previously derived using this model for the southern site were used for this analysis (Isaak et al. 2017b). In each model, site and year were specified as random effects to account for repeated measures within and across years, mean August air temperature and stream elevation were specified as fixed effects, and an autocorrelation structure accounting for spatial dependency among sites was also specified as a random effect. The latter included exponential Euclidean (EUC) and exponential tail-down (TD) covariance functions, as well as an exponential tail-up (TU) function with a spatial weighting scheme based on watershed area (Ver Hoef and Peterson 2010). Different combinations of these spatial-autocorrelation structures (TU, TD, EUC) were used to select the best fitting model from each area. In instances where stream temperatures were collected across years, the average of the mean August air temperatures were used for models. Models were specified this way to integrate both temporal and spatial variation in air temperature across years and regions, respectively. A more complex set of fixed effects were used for the model from the south (e.g., discharge, riparian canopy, base flow index) as these covariates improved model fit (Isaak et al. 2017b), but these data were not readily available for the central and northern sites. Despite this, the root mean squared predictive error (RMSE) was similar for all models (ID = 1.0°C, AB = 1.1°C, NT = 1.1°C). Models from the three regions were built using stream temperature data spanning different but overlapping periods (ID: 1993-2016; AB: 2015-2017; NT: 2012-2016). To account for potential differences in model results caused by spatial-temporal variation in air temperatures, the average August mean air temperature was calculated for each respective period when data was used to build models. These values were then included as a covariate in the model comparing mean August stream temperature across regions (see details below).

A combination of generalized linear (binomial) and linear mixed models were used to test for differences in thermal regime metrics among regions. These models can handle unbalanced data, which allowed for inclusion of all sites from the north, as this data set had six fewer sites with full year data than the other regions. Additionally, because data were not collected across the same period in the central region (2016-2019) as the southern/northern regions (2013-2016), I included year as a fixed effect in all models to account for potential differences across years. For models examining winter stream temperature, thermal sensitivity, egg hatch date, and accumulated thermal units, site was specified as a random intercept to account for repeated measures across years. The assumptions of models were tested following the methods of Zuur and Leno (2016). Tukey pairwise post-hoc multiple comparisons tests were used for among-region comparisons when location was found to be an influential fixed effect. For linear mixed models, marginal (R^2m) and conditional (R^2c) coefficients of determinations were used to determine the proportion of variance explained by only fixed factors and fixed and random factors, respectively. All analyses and figures were completed in R (R Development Core Team 2018) and significance was assessed at the 0.05 level. Analyses were performed using the following R packages: Tukey tests with *lsmeans* (Lenth 2016), LMM with *nlme* (Pinheiro et al. 2016), and R^2m and R^2c with *MuMIn* (MuMIn 2016).

Juvenile distributional data collected across all three watersheds (ID, n = 180; AB, n = 185; NT, n = 415) was combined with modelled mean August stream temperature data to portray the availability of thermal habitat in each respective area and the thermal niche occupied by juveniles using presence-absence data. These data were analysed as a two-step process. First, among-region differences in mean August stream temperature (dependent variable), at sites occupied by bull trout, were examined using a linear model with location (as factor), elevation, and mean August air temperature included as fixed effects, and site as a random effect. Second, a generalized linear model was used to define the realized thermal niche that juvenile bull trout occupy in each region. For this model, juvenile presence-absence data (dependent variable) was regressed against mean August stream temperature. This model was fit with both linear and quadratic terms for mean August stream temperature because both of these relationships have been shown to explain variation in occupancy of stream-dwelling salmonids elsewhere (Isaak et al. 2017a). Thermal response curves were plotted as the probability of occupancy versus mean August stream temperatures across the range of values from the data set. Modelled thermal response curves for each region were plotted together to visualize the degree of similarity in the realized thermal niche among populations. Because prevalence differed across each region and resulted in differences in peak probability of thermal response curves (i.e., height of response curves), probabilities were rescaled to the maximum value observed (0.80) for comparison. Since most streams freeze completely to the bottom during the winter in the northern watershed, full year water temperature records are sparse. Consequently, small sample sizes for other metrics (e.g., winter, ATU) precluded integration with distributional data and modelling, as described above in step two (generalized linear model).

Winter mean temperature, thermal sensitivity index, estimated egg hatch date, and ATU were quantified using linear mixed models with location (i.e., region – as factor), elevation, their interaction (location * elevation) and year (factor) included as fixed effects. Seasonal differences in ATU were compared among regions across incubation, growing, and annual periods. Model selection for both generalized and linear mixed models were performed using backwards stepwise regression with marginal *F* tests. No data transformations were performed for linear mixed model analyses but, for the generalized linear model, continuous variables were standardized to a mean of zero and a standard deviation of one.

Results

Variability

A comparison of daily mean air temperatures to daily mean water temperatures showed that streams from all three regions exhibited low thermal reactivity to variation in air temperatures (Fig. 3.3). This is especially apparent during the summer months where hysteresis cycles were flatter, resulting in inhibited reactivity and a dampened response of stream temperature to extreme air temperature fluctuations – i.e., lower thermal sensitivity (Fig. 3.3). Results of our linear mixed model showed that the mean (±SD) thermal sensitivity index was low for all three areas (ID: 0.43 ± 0.06; AB: 0.35 ± 0.09; NT: 0.35 ± 0.12) but differed between southern and central-northern regions (Location: $F_{2,42} = 4.03$, $p = 0.02$; Tukey test: ID-AB, $Z = 0.08$, $p < 0.0001$; Tukey test: ID-NT, $Z = 0.09$, $p < 0.0001$; Tukey test: AB-NT, $Z = 0.005$, $p = 0.955$; Fig. 3.4) and varied across years (Year: $F_{6,129} = 8.03$, $p < 0.0001$). An interaction between location and elevation was removed from the model because it was not significant ($F_{2,39} = 1.10$, $p = 0.34$). The fixed effects accounted for 20% of the variation in thermal sensitivity, whereas the random effect of site accounted for 65%.

Magnitude

The breadth of the available August stream temperature niche differed across locations and was widest in the north (1.2 – 10.6°C) and narrower in both the central (3.5 – 11.6°C) and south

(7.9 – 14.1°C). The available August thermal niche was much warmer in the south than both the central and north (Fig. 3.5A). As expected, the thermal niche that bull trout occupied transitioned from warmest to coldest following a south to north latitudinal gradient (Fig. 3.5A). Consequently, August stream temperatures in streams occupied by bull trout (mean ±SE) differed among regions with the southern being the warmest (9.6 ± 0.11) followed by central (7.5 ± 0.18), and northern (6.2 ± 0.10) watersheds (Location: $F_{2,233} = 203.1$, $p < 0.0001$; Tukey test: ID_AB, $Z = 2.54$, $p <0.0001$; Tukey test: ID-NT, $Z = 3.39$, $p <0.0001$; Tukey test: AB-NT, $Z = 0.85$, $p <0.0001$; Fig. 3.5A). Both elevation and year had a significant effect on August stream temperature (Elevation: $F_{1,233} = 9.08$, $p = 0.002$; Year: $F_{3,233} = 13.0$, $p = 0.0003$). The fixed effects in the model accounted for 65% of the variation in mean August stream temperature and the random effect of site accounted for 25%. Variation in juvenile occupancy was best described by a quadratic relationship with mean August temperature across northern and central regions and a negative linear relationship in the southern region (Table 3.4). The linear effect observed in the southern watershed is likely due to sampling bias, where management organizations focus more on sampling streams that are closer to this species upper thermal threshold (11.0°C) (Isaak et al. 2017a). Both the linear and quadratic curves for the southern region were presented in order to consistently compare response curves across regions. Results show that the realized thermal niches of these populations overlap, but the northern population occupies a colder and narrower thermal niche than both the central and southern populations (Figs. 3.5B,C).

Mean winter stream temperature (mean ±SE) differed among regions with temperatures in the south (0.71 ± 0.10) being warmer than both the central (0.20 ± 0.14) and north (0.07 ± 0.19) (Location: $F_{2,41} = 16.8$, $p < 0.0001$), although the magnitude of differences were relatively small (Tukey test: ID_AB, $Z = 0.52$, $p <0.001$; Tukey test: NT-ID, $Z = - 0.64$, $p <0.001$; Fig. 3.6). A somewhat unexpected result was that there was no difference in mean winter stream temperature between the central and northern sites (Tukey test: $Z = -0.12$, $p = 0.24$). Elevation did not influence mean winter stream temperatures, but there was a significant year effect (Elevation: $F_{1,41} = 0.69$, $p = 0.41$; Year: $F_{6,97} = 4.24$, $p = 0.0008$). The fixed effects in the model accounted for 41% of the variation in mean winter stream temperatures and the random effect of site accounted for 47%.

Timing and magnitude

Estimated number of days to hatch (mean ±SD) differed among regions with days to hatch in the south (189 ±15.9) being fewer than the north (243 ±1.2) and central (262 ±7.4) watersheds (Location: $F_{2,41} = 41.8$, $p = 0.0003$; Table 3.5). Interestingly, the length of time to hatch was longest in the central region and did not differ from the northern region (Tukey test: NT-AB, $Z = -0.19$, $p = 0.01$; NT-ID, $Z = 53.6$, $p = 0.13$; ID-AB, $Z = -73.0$, $p = 0.0002$). However, this was not an unexpected result because the winter thermal regime was coldest in the central location, and the Sparks et al. (2019) model uses daily thermal degree units to predict hatch dates (Fig. 3.7).

ATU differed among regions across all developmental periods (Table 3.5). In the south, ATU were at least double that of the central location and 1.5 to 1.8 times greater than the northern location. However, differences in mean ATU between central and northern locations were much smaller (Table 3.5). Time series plots of ATU are illustrated in Figure 3.7 for southern, central, and northern regions. These data show that in all years, ATU from all sites show an immediate increase during the initial part of the incubation period just after spawning, followed by a plateau during the winter months, an increase during the early spring, and then a more pronounced increase throughout the growing period. During the growing period, the northern and central locations showed a slower rate of increase in ATU than the southern location.

Results of linear mixed models for the incubation, growing, and annual development periods support the patterns shown in Figure 3.7, as ATU differed between southern and central-northern locations during all periods (incubation: Location: $F_{2,41} = 24.5$, $p < 0.001$; growing: Location: $F_{2,41} = 120.0$, $p < 0.0001$; annual: Location: $F_{2,41} = 120.0$, $p < 0.0001$), but intercepts did not differ between the central and northern locations (incubation: Tukey: $T_{41} = -0.12$, $p = 0.97$; growing: Tukey, NT-AB: $T_{41} = 53$, $p = 0.44$; annual: Tukey, NT-AB: $T_{41} = 99.8$, $p = 0.12$). Year had a significant influence on ATU across all three periods, but the effect of elevation was significant only during the growing and annual periods (incubation: Elevation: $F_{1,41} = 1.8$, $p = 0.19$, Year: $F_{4,86} = 15.1$, $p < 0.0001$; growing: Elevation: $F_{1,41} = 6.89$, $p = 0.01$, Year: $F_{3,72} = 45.3$, $p < 0.0001$; annual: Elevation: $F_{1,41} = 7.21$, $p = 0.01$, Year: $F_{3,72} = 46.0$, $p < 0.0001$). The interaction between location and elevation was removed from all models as it was not significant in any. The random effect of repeated measures across sites accounted for 37%, 10%, and 11% of the variation in ATU during the incubation, growing, and annual periods, respectively, while the fixed effects accounted for 50%, 82%, and 83%, respectively.

Discussion

As predicted, all the streams across these watersheds respond similarly to fluctuations in air temperature due to their low thermal sensitivity. This is a key abiotic feature of these streams, and similar to what others report (Luce et al. 2014; Isaak et al. 2016). However, in the north, only streams with moderate thermal sensitivity do not completely freeze to the bottom during the winter, and represents a divergence from thermal regimes described in the south (Isaak et al. 2018). Results also provide evidence of niche similarity across a broad latitudinal gradient for both the summer and winter thermal niches. Despite this similarity, in the south, some streams are near the upper non-lethal thermal limit for bull trout (Selong et al. 2001; Isaak et al. 2017a), whereas in the north many streams appear to be at the cold-edge boundary of thermally suitable habitat. Together, my findings demonstrate that the distribution of juveniles at higher latitudes is driven by cold-limiting streams in both the summer and winter (i.e., do not freeze). This result is opposite to what others report for bull trout at the southern range extent, where distributional patterns and population demographics are governed by warm-limiting streams during the open water season (Isaak et al. 2015; Benjamin et al. 2016; Kovach et al. 2016). The assertion that some high latitude streams are too cold to sustain juvenile bull trout populations is supported by what others report for cold-water salmonids. For example, Coleman and Fausch (2007b) found that survival and recruitment of juvenile cutthroat trout *Oncorhynchus clarkii* was low in streams accumulating <700 thermal units (°C) throughout the growing season (Coleman and Fausch 2007b). My results show that all streams in the south accumulate enough thermal units to surpass this threshold, but some streams in the central and northern watersheds do not, and I propose two plausible mechanisms. First, populations at higher latitudes have adapted to maximize growth and fitness at temperatures which they experience most often in their local native environment (i.e., thermal adaptation hypothesis; Lonsdale and Levington 1985; Kaspari et al. 2015). This implies that individuals from high latitudes possess reaction norms for optimal growth at lower temperatures than those from more southerly latitudes. Alternatively, populations at higher latitudes possess a compensatory growth mechanism where individuals grow more efficiently during shorter growing seasons than those at lower latitudes. The second proposed mechanism is suggestive of countergradient variation (Conover and Schultz 1995), and has been reported in chars occurring at higher latitudes (e.g., Arctic char; Chavarie et al. 2010; Sinnatamby et al. 2015). Although thermal resilience will buffer the effects of climate warming across all these streams, some populations at southern range limits will succumb to the reality of dwindling cold-water habitat and, as shown by Eby et al. (2014), either disperse or be extirpated. Conversely, as streams warm in the north, the availability of thermally suitable habitat may increase and provide more productive habitat for these populations.

Thermal Sensitivity

Thermal sensitivity differed across watersheds, but the magnitude of these differences were small (0.08) in the context of air-water temperature hysteresis cycles (Piccolroaz et al. 2016). Although this was contrary to my prediction, on average, thermal sensitivity of these streams was low (<0.40) and all are classified as thermally resilient, meaning that air temperature has minimal influence on stream temperatures and all these streams will warm at approximately the same rate (Kelleher et al. 2012; Piccolroaz et al. 2016). This is an important element of stability in the thermal regime for cold-water stenotherms, such as bull trout, because streams with these properties are projected to buffer effects of climate warming (Lisi et al. 2015). Slightly higher mean thermal sensitivity values for streams in the southern watershed versus mid- to high-latitude watersheds could be related to the characteristics of these streams (i.e., elevation, sun angle, riparian canopy) and the prominent mechanism responsible for mediating effects of air temperature. Very stable water temperatures observed throughout the winter in the central and northern watersheds produce flatter air-water temperature hysteresis cycles that are consistent with systems where perennial groundwater is the prevalent underlying mechanism (Kelleher et al. 2012). Conversely, the streams in the south exhibit slightly broader and higher air-water temperature hysteresis cycles that are reflective of systems where thermal sensitivity is driven by snow-melt contribution (Kelleher et al. 2012; Lisi et al. 2015). Although it is not possible to precisely define the mechanisms responsible for the patterns I report, a first order understanding of the most likely mechanisms will be useful for predicting how climate change may affect these systems differently. For example, Lisi et al. (2015) show that as climate warms, the heterogeneity pattern of thermal sensitivity in high elevation snow-melt stream systems may be lost, resulting in more uniform warming across all streams. Overall, my results are consistent with thermal sensitivity characteristics for montane streams that bull trout occupy across the northwestern United States (Isaak et al. 2016) and perennial groundwater streams in northern Canada (Bolduc and Lamoureux 2018).

Mean August and winter stream temperatures

Results show that the summer thermal niche juvenile bull trout occupy across a broad latitudinal gradient is narrow and clearly reflective of a cold-water stenotherm. Although there were statistical differences in mean August stream temperatures following a south to north gradient, the magnitude of differences between watersheds across southern-northern range boundaries are relatively small (difference = 3.4°C). The degree of overlap in the thermal niches that these populations occupy, across such a wide a latitudinal gradient, provides preliminary support of niche similarity (Warren et al. 2008). Subsequent tests of niche conservatism would benefit from broader and more comprehensive data sets, preferably with replication across multiple watersheds from each region (Peterson 2011b), and common garden experiments to examine physiological responses to temperature across these three populations (e.g., *Eucalyptus* spp.; Drake et al. 2017). Despite this, results expand the current definition of summer thermal limits for juvenile bull trout corresponding to northern and southern range boundaries. The upper limit of the August thermal niche that juveniles occupy in the south is 11.5°C and is consistent with what others have reported in both laboratory and field studies (Selong et al. 2001; Benjamin et al. 2016; Isaak et al. 2017a). This finding further reinforces that populations in watersheds near the southern distributional range extent occupy streams near their upper thermal limits and are at the species' warm-edge range boundary. For these populations, if streams warm beyond acceptable thermal limits, individuals will need to disperse upstream to colder, higher elevation streams or adapt to warmer thermal regimes. In the Bitteroot Basin in Montana, both Eby et al. (2014) and LeMoine et al. (2020) report range contraction of bull trout through abandonment of previously occupied sites, suggesting either dispersal or extirpation as possible mechanisms. In most instances, fish will probably move from warmer downstream habitat upstream to colder habitats at higher elevations; however, in some systems, these habitats may be at their carrying capacity or occupied by competitors (e.g., brook trout *Salvelinus fontinalis*). On the other end of the August thermal niche spectrum, juveniles in the north occupy the cold-edge boundary where fish are found in streams as cold as 4.3°C during August, despite having access to much warmer streams. The population in the central watershed occupies a slightly warmer August thermal niche but are still found in some very cold streams (i.e., 4.9°C). At the northern range extent, the fact that juveniles occupy a subset of warmer streams within the available summer thermal niche suggest that some streams may be too cold to sustain populations.

In the winter, thermal regimes were similar at mid- to high-latitudes but slightly warmer in the south. Since streams from central and northern regions exhibit similar thermal sensitivity and experience similar local climatic conditions during the winter, it is not surprising that these two areas exhibit similar stream temperature regimes during the winter. Conversely, air temperature profiles show that streams in the south experience warmer air temperatures throughout the winter and likely explain why streams in this area are warmer than mid- to high-latitude streams. The differences observed in mean winter temperatures between southern and northern watersheds were relatively small (0.64°C), but streams from all three regions showed high thermal stability during this period. This is an important feature of the thermal regimes of these streams, as winter is considered a survival bottleneck for stream-dwelling salmonids (Cunjak 1988, Finstad et al. 2004b; Coleman and Fausch 2007a), and instability of environmental regimes during winter has been shown to negatively affect their survival (Cunjak et al. 1988). Despite differences in mean winter temperatures, juvenile bull trout do successfully overwinter in these streams and perhaps, as seen in related species (Finstad et al. 2004a), central and northern populations have adapted to grow more efficiently at lower winter temperatures. A more detailed understanding of whether this mechanism exists in bull trout will aid in understanding how populations may respond to changes in winter thermal regimes as local climatic conditions change.

Hatch phenology

As predicted, results show differences in estimated hatch dates associated with latitude. The mean time for eggs to hatch was much earlier in the south (March 22) than it was in the northern (April 14) or central (May 20) watersheds. Although I compared hatch dates across latitude, temperature can also influence the length of time to hatch. A closer look at the mean thermal regime during the incubation period shows that ATU in the central watershed were consistently the lowest of all three areas and indicates that the winter thermal regime is coldest in this area. Variability in hatch timing across streams with different thermal regimes was also reported by Austin et al. (2019) for bull trout in Washington State and Sparks et al. (2019) for sockeye salmon (*Oncorhynchus nerka*) in Alaska. However, my results are contrary to those of Campbell et al. (2019), who reported high synchrony in hatch dates for coho salmon (*O. kisutch*) across streams with vastly different thermal regimes. This discrepancy could be related to an indirect interaction (i.e., not statistical) between latitude and winter thermal regime that are present in my results, but not considered by Campbell et al. (2019). Asynchronous hatch dates for these populations could represent different strategies that reflect local adaptations to these watersheds and their respective winter thermal regimes (Shuter et al. 2012). Validation of hatch date estimates using otoliths would refine our understanding of hatch phenology for populations from these watersheds (Fuiman and Werner 2009; Campbell et al. 2019).

Accumulated thermal units

As predicted, I did observe differences in ATU across latitude, highlighting possible differences in growth potential among these populations. During the growing period, both the rate and magnitude of ATU was greater in the southern watershed than the central-northern watersheds. These differences are a result of variation in thermal regimes across these respective watersheds, where the thermal regime in the south is warmer than the thermal regimes in the central and northern locations. Differences appear to be driven by local climatic conditions, as air temperatures remain above freezing from September through to November in the south but start to approach, or fall slightly below, 0°C in late September to early-October in the central and northern watersheds. This difference translates into fewer thermal units being available for fish in the central and northern locations before the onset of winter and highlights a potential recruitment bottleneck associated with cold-limiting streams for central and northern populations. For example, Coleman and Fausch (2007b) show that cutthroat trout will not grow large enough to survive the winter unless they occupy streams with at least 800 thermal units from egg deposition to the onset of winter. If I apply a similar threshold to the populations from my study, it is clear that all streams in the southern watershed will exceed this threshold but not all from the central and northern systems. Although this is somewhat speculative, due to potential differences in juvenile growth rates between the populations examined by Coleman and Fausch (2007a) and bull trout from our study, it does present an interesting hypothesis. This logic suggests that the distribution of juvenile bull trout at the northern range extent, or in watersheds with very cold thermal regimes (e.g., central site), may be limited by streams that are too cold. Follow-on analyses examining survival and condition of juvenile bull trout across streams with varying thermal regimes in the north would shed light on this hypothesis.

An alternate hypothesis to explain how fish cope with differences in thermal units across latitude is that juveniles from mid- to high-latitude watersheds have a compensatory mechanism to grow more efficiently during short growing seasons (i.e., countergradient variation; Conover and Schultz 1995). All of the streams in the northern watershed where I describe thermal regimes have abundant, self-sustaining juvenile bull trout populations (Chapter 2), yet several of these streams accumulate very few thermal units throughout the growing season (i.e., ≤ 800). However, I would not expect juveniles to occupy these streams if they could not survive under these growing conditions; therefore, these populations have probably adjusted to successfully occupy these colder streams. It follows that differences in ATU between southern and central-northern watersheds may reflect local adaptations, which allow central and northern populations to perform more efficiently at lower temperatures. Such adaptations to colder winter thermal regimes have been observed in other salmonids (Finstad et al. 2004a). Furthermore, the acclimation time to readjust efficiency of physiological energy pathways is reduced as a species' fundamental thermal niche gets closer to ambient temperature (Pörtner 2006). Similar compensatory growth has been reported in Arctic char (Chavarie et al. 2010; Sinnatamby et al. 2015) and warrants further investigation in bull trout.

Conclusion

A broader examination of full-year thermal regimes has revealed three key findings. First, all streams that bull trout occupy across these three regions have very similar thermal sensitivity, making them resilient to effects of fluctuating air temperatures. Second, there was evidence of niche similarity based on substantial overlap in the summer thermal niche that populations occupy across a wide latitudinal gradient. Third, at higher latitudes, thermal sensitivity moderates the effect of cold-limiting streams during both the open water and winter season, and is an important element of the thermal regime in these areas. These are important findings for bull trout conservation, as it is clear that this species occupies a very cold, and narrow thermal niche but, divergent elements appear to limit populations at southern and northern range extents (i.e., warm vs cold-limiting streams). However, as air temperatures continue to rise, managers will need to monitor and maintain the properties (e.g., groundwater, riparian zones) of these cold-water refugia to ensure long-term survival of core populations (Isaak et al. 2016). Future work on populations found at higher latitudes should examine adaptive mechanisms (i.e., phenotypic plasticity, adaptive potential) that allow these populations to be successful in colder streams. Better knowledge of the adaptive potential of these populations will improve understanding of how populations may respond to altered thermal regimes as climate warms (Somero 2010). This study is an initial step in broadening understanding of thermal regimes that bull trout populations experience across a wide latitudinal gradient. I hope my results will motivate others to expand stream temperature monitoring networks and build on what I have done across additional watersheds in the central and northern regions. Doing so will determine if the patterns I report are a local watershed effect in central and northern regions or are reflective of a broader classification of thermal regimes for montane watersheds across the bull trout range.

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Tables

Table 3.1. Descriptive statistics of site characteristics for the stream temperature records taken from watersheds in the southern, central, and northern regions. Fifteen unique records were taken from each respective area.

Northwest Territories, CAN (north)	Mean	Median	Standard deviation	Range
61° N, 124° W				
Elevation (m)	1094.0	1087.0	101.0	935-1273
Stream gradient (%)	0.04	0.04	0.01	0.02 - 0.06
Contributing area (ha)	1066.9	1083.7	655.6	375 - 4181
Air temperature (°C)	-1.1	2.1	15.7	-39.1 - 23.8
Alberta, CAN (central)	Mean	Median	Standard deviation	Range
55° N, 124° W				
Elevation (m)	2063.0	2070.0	84.3	1904 - 2241
Stream gradient (m/m)	0.04	0.03	0.01	0.02 - 0.06
Contributing area (ha)	1455.0	1139.0	983.0	328 - 4109
Air temperature (°C)	2.5	3.2	10.6	-28.4 - 21.8
Idaho, USA (south)	Mean	Median	Standard deviation	Range
45° N, 124° W				
Elevation (m)	1817.0	1863.0	300.0	1291-2305
Stream gradient (m/m)	0.06	0.06	0.03	0.02 - 0.11
Contributing area (ha)	1327.0	1066.0	991.6	411 - 3973
Air temperature (°C)	9.2	9.5	9.5	-16.9 - 29.3

Table 3.2. Metrics used to compare different elements of thermal regimes across montane river networks in Idaho, Alberta, and the Northwest Territories.

Category	Metric	Definition
Magnitude	Mean winter temperature	Average of mean daily temperatures during the months of December, January, and February
	Mean August temperature	Average of mean daily temperatures during the month of August
	Annual thermal units	Cumulative total of thermal units during the course of a year (1°C for 24 hours = 1 thermal unit)
Variability	Thermal sensitivity	Slope from mean weekly water temperatures (T_w) divided by mean weekly air temperatures (T_a) across a calender year.
Timing	Incubation season thermal units[A]	Cumulative total of thermal units from spawning until the estimated date when 50% of eggs hatch
	Growing season thermal units[B]	Cumulative total of thermal units from the estimated egg hatching date to the onset of winter in each respective watershed.

A. Cumulative thermal unit calculations started and ended on different dates to coincide with spawning timing windows (September 14, September 01, August 15) and estimated egg hatching dates (March 22, May 20, April 14) associated with southern, central, and northern watersheds, respectively.

B. The start of the growing period coincided with the estimated egg hatching date (March 22, May 20, April 14) and the end of the growing season was defined by the date when water temperatures were ≤ 2°C on two consecutive days (November 01, October 15). These dates correspond to southern, central, and northern watersheds, respectively. Note that the end date was the same for the central and northern watersheds.

Table 3.3. Timing windows considered in this study. Spawning windows were estimated based on those reported in the literature. The incubation window was designated as the midpoint of the spawning window reported in the literature until approximately May 31 of the next calendar year. The end date of the incubation period was based on the best approximation of when sufficient thermal units would be accumulated using estimates reported in Gould et al (1987) and emergence time from the literature.

Category	Time window	Date range
Seasonal	Full-year	Septebmer 15 - September 15
	Summer	July 01 - August 31
	Winter	December 01 - February 28
Biological	Spawning	August 15 - October 15
	Growing season[A]	June 01 - November 01
	Incubation[B]	September 15 - May 31

[A] These are general start-end dates for the growing period. For calculations, the start of the growing period coincided with the estimated egg hatching date (March 22, May 20, April 14) and the end of the growing season was defined by the date when water temperatures were ≤ 2°C on seven consecutive days (November 01, October 15). These dates correspond to southern, central, and northern watersheds, respectively. Note that the end date was the same for the central and northern watersheds.

[B] Calculations for analyses during this period started and ended on different dates to coincide with spawning timing windows (September 14, September 01, August 15) and estimated egg hatching dates (March 22, May 20, April 14) associated with southern, central, and northern watersheds, respectively.

Table 3.4. Parameter estimates (± SE) and *p*-values of the top models fit to the data and used to model thermal response curves for each region across the study area.

Parameter	b_x	SE	*p*-value
Northwest Territories (NT)			
Intercept	-0.70	0.16	< 0.0001
Aug_Temp	-1.38	0.44	0.002
Aug_Temp^2	-2.31	0.49	< 0.0001
Alberta (AB)			
Intercept	0.64	0.23	< 0.0001
Aug_Temp	1.49	0.30	< 0.0001
Aug_Temp^2	-1.44	0.30	< 0.0001
Idaho (ID) - Model 1: linear			
Intercept	2.54	0.50	< 0.0001
Aug_Temp	-2.08	0.37	< 0.0001
Idaho (ID) - Model 2: quadratic			
Intercept	1.13	1.09	0.301
Aug_Temp	0.46	1.86	0.804
Aug_Temp^2	-1.00	0.75	0.179

Abbreviations: Aug_Temp, August mean temperatrure (°C); b_x, is the parameter estimate; Elev, elevation (m). Quadratic terms are displayed with "2" as superscript.

Table 3.5. Descriptive statistics for accumulated thermal units (ATU) across different growing seasons used to compare thermal variability among watersheds in Idaho (ID), Alberta (AB), and the Northwest Territories (NT). Accumulated thermal unit statistics were calculated for the period of 2013 -2016 for the Northwest Territories and Idaho and 2016-2019 for Alberta. The mean of median hatch dates across years are shown for reference and to define the end of the incubation season in each respective area.

	Accumulated thermal units					No. days to hatch		
	Mean (°C)	Median (°C)	SD (°C)	Minimum (°C)	Maximum (°C)	Mean (°C)	SD (°C)	Date (M-D)
Annual ATU								
NT	918	950	186	547	1341	-	-	
AB	819	805	142	547	1139	-	-	
ID	1611	1603	272	1162	2330	-	-	
Incubation season ATU								
NT	268	259	69.6	144	449	243	1.2	4-14
AB	206	188	76.9	86.2	353	262	7.4	5-20
ID	381	389	96.7	143	585	189	15.9	3-22
Growing season ATU								
NT	651	640	152	378	936	-	-	
AB	597	592	112	321	787	-	-	
ID	1230	1256	242	807	1745	-	-	

Figures

Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org. This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap^{TM} are the intellectual property of Esri and are used herein under licence. Copyright © Esri. All rights reserved.

Figure 3.1. Locations of the three watersheds from Idaho (ID - red), Alberta (AB-orange), and Northwest Territories (NT-blue) where stream temperature records (*n* =15/site) were used for this study. The black line depicts the approximate bull trout distribution.

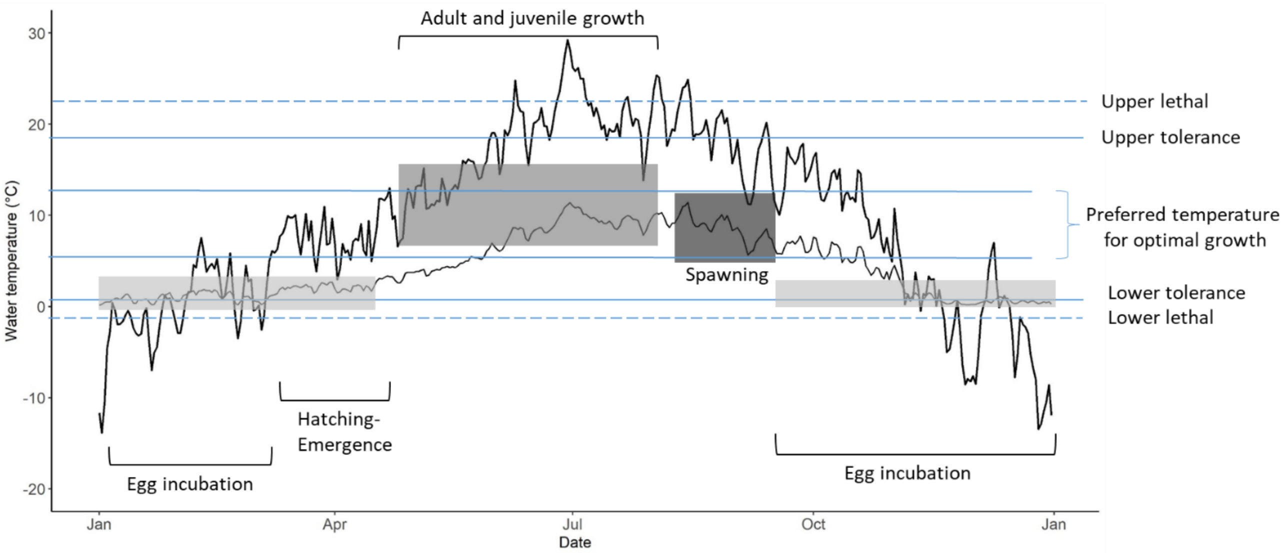

Figure 3.2. Thermal tolerance corresponding to the time of year for different life stages of bull trout. These are approximate temperature ranges based on values reported in the literature (Selong et al. 2001; Isaak et al. 2015; Austin et al. 2019).

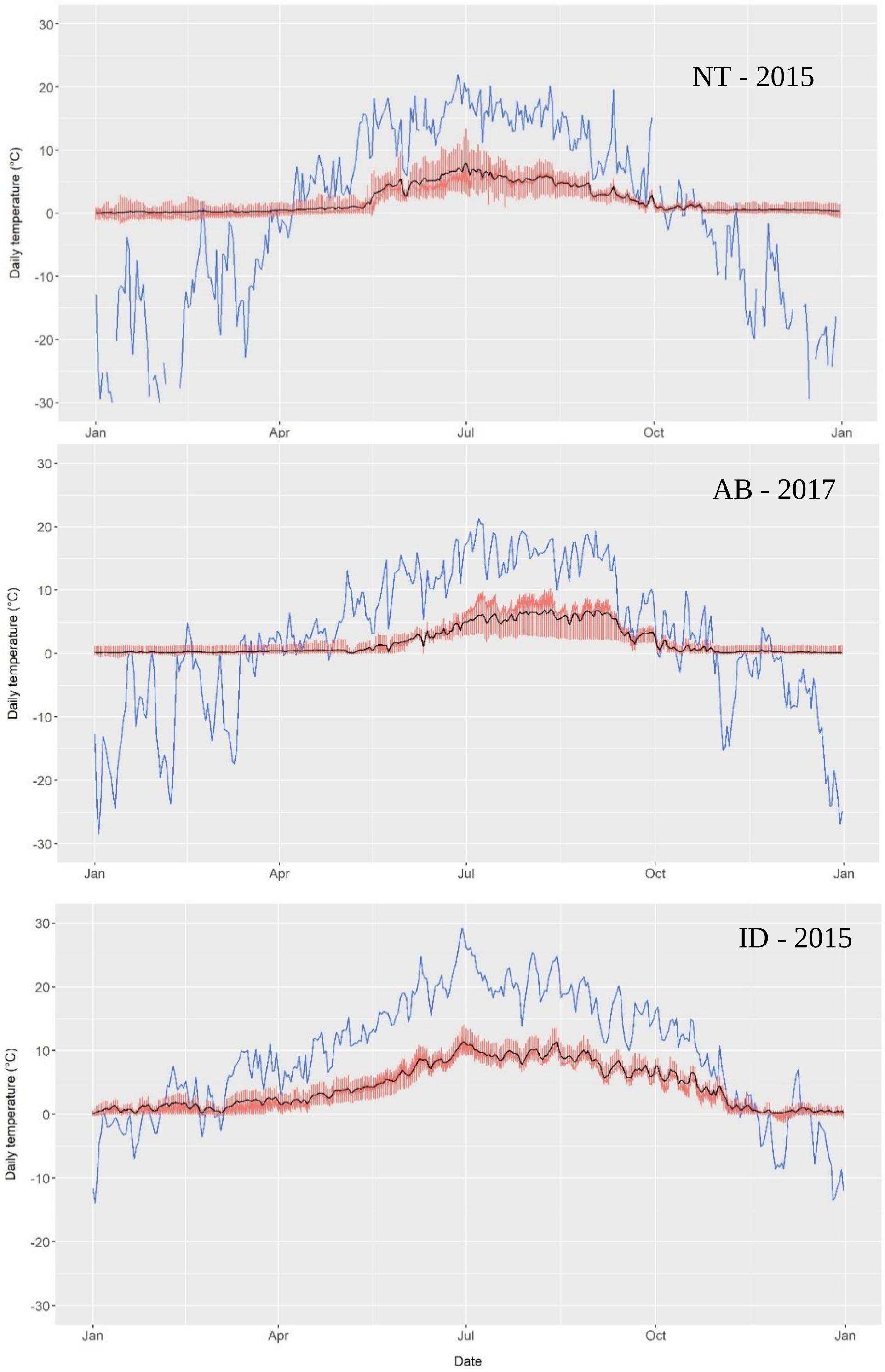

Figure 3.3. Time series of mean daily air (blue line) and stream (pink line) temperatures from Idaho (ID), Alberta (AB), and the Northwest Territories (NT). The water temperature values are from all sites in each respective area for a given year and the thick black line is the daily mean of all sites.

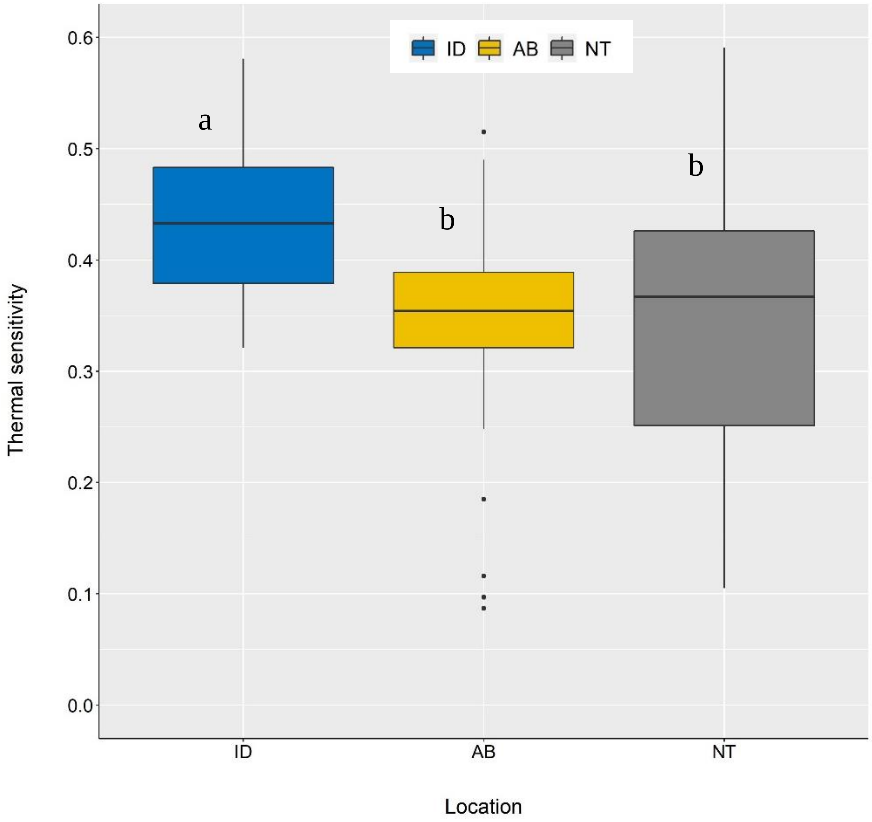

Figure 3.4. Comparison of the thermal sensitivity index across sites in Idaho (ID), Alberta (AB), and the Northwest Territories (NT). For each boxplot, the thick horizontal line represents the median and values within the box represent the interquartile range. Whiskers below and above the boxes represent the 10th and 90th percentiles and observations falling outside these percentiles are shown as points.

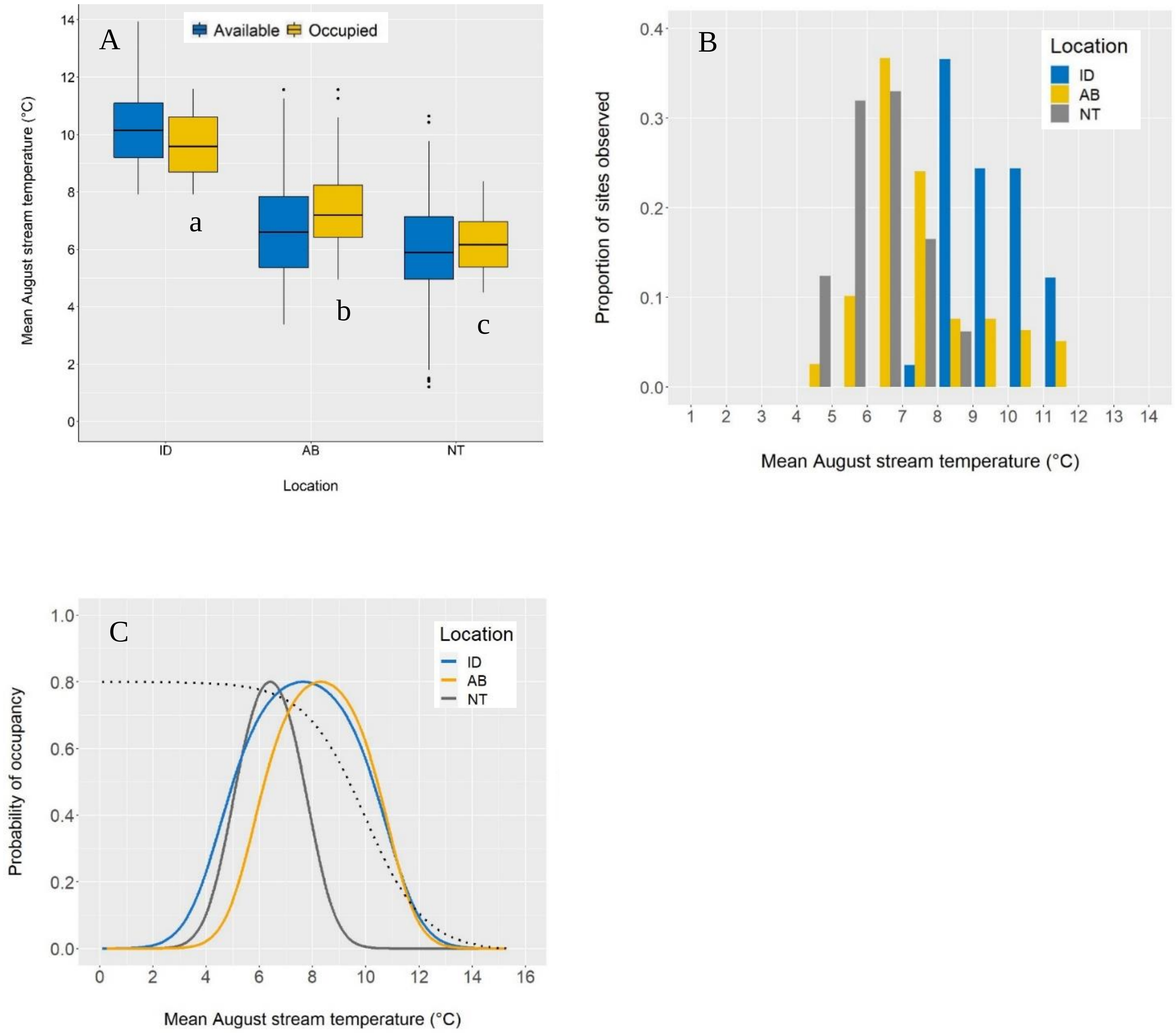

Figure 3.5. Comparison of mean August stream temperature at occupied and unoccupied sites (A), observed across occupied sites (B), and modelled thermal response curves (C) in Idaho (ID), Alberta (AB), and the Northwest Territories (NT). Available mean August stream temperatures are from all sites surveyed and occupied temperatures are only from sites where juvenile bull trout were captured. For each boxplot, the thick horizontal line represents the median and values within the box represent the interquartile range. Whiskers below and above the boxes represent the 10th and 90th percentiles and observations falling outside these percentiles are shown as points. Lower case letters denote significant differences in each metric across locations. The black dotted line in figure C is the linear thermal response curve for Idaho. Variation in juvenile occupancy was best described by a quadratic relationship with mean August stream temperature across northern and central regions and a negative linear relationship in the southern region (ID). Therefore, both linear and quadratic curves are shown for Idaho to consistently compare response curves across regions.

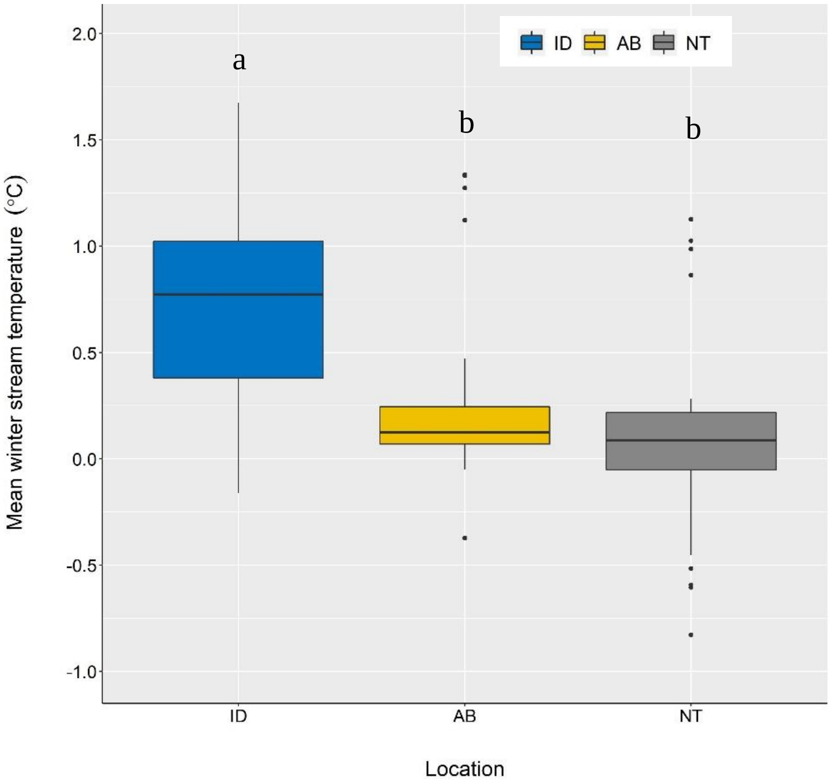

Figure 3.6. Comparison of mean winter stream temperature in Idaho (ID), Alberta (AB), and the Northwest Territories (NT). Temperatures are from sites where juvenile bull occur during the winter in each respective area. For each boxplot, the thick horizontal line represents the median and values within the box represent the interquartile range. Whiskers below and above the boxes represent the 10th and 90th percentiles and observations falling outside these percentiles are shown as points. Lower case letters denote significant differences in each metric across locations.

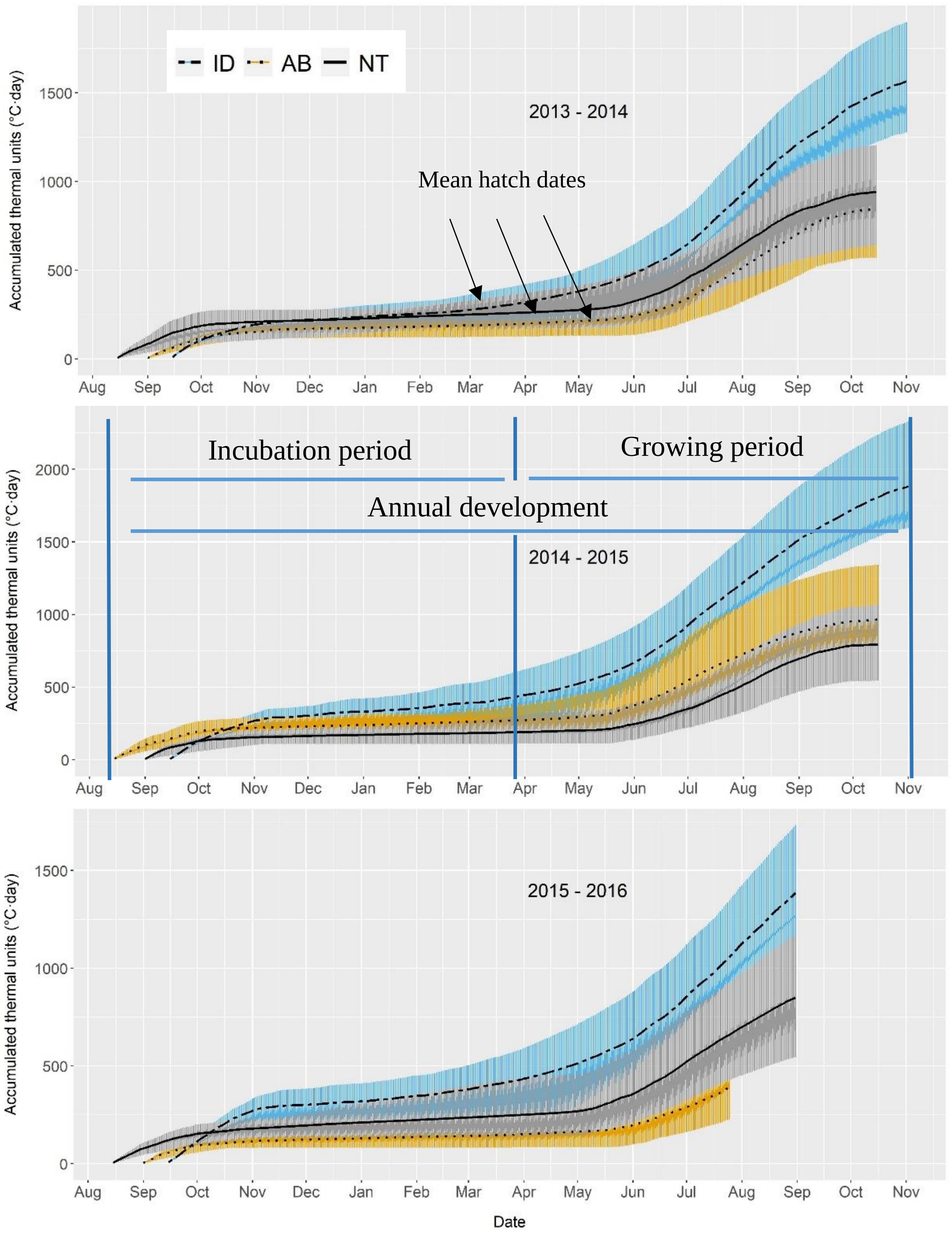

Figure 3.7. Annual time series of accumulated thermal units (°C·day) for all stream temperature records from Idaho (ID - blue), Alberta (AB - yellow), and the Northwest Territories (NT - grey). The range of thermal units for all sites are shown as vertical lines and dark lines represent means. Data for ID and NT are from the years indicated on the plots. Alberta data are from 2016-2017, 2017-2018, and 2018-2019, respectively, and were superimposed on these plots for a visual comparison. Mean hatch dates for each region are shown on the top plot and periods coinciding with incubation and growing seasons are indicated on the middle plot. Data spanning the entire growing season were not available in 2015-2016 and 2018-2019 for each respective area.

Chapter 4: Climate warming effects on a cold-water stenothermal fish occurring near a northern geographical range boundary

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Contributions of Authors: Under the oversight of D. Isaak, I developed and implemented a sampling program in Prairie Creek, Northwest Territories to set up a stream temperature monitoring network and collect distributional information on bull trout. M. Docker provided direction on study design and content of the manuscript. I analyzed the data and wrote the initial and final drafts of the manuscript. All co-authors commented on earlier drafts of the manuscript.

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Abstract

Broad-scale studies examining effects of climate warming on cold-water salmonids have focused mainly on taxa occurring in stream networks at their warmer, southern geographical range extent, and largely ignored northern populations. However, the north is warming twice as fast as the global average and distributional boundary extensions could occur to partially offset range contractions in warmer areas. Here, I use a spatially dense occurrence data set to examine how climatic and geomorphic factors influence the distribution of juvenile bull trout in the Prairie Creek watershed, Northwest Territories, Canada (61° N, 124° W). Downscaled climate projections were coupled with a species distribution model, to forecast the effects of stream temperature warming on the distribution of suitable habitat for contemporary, 2040s, and 2080s periods, based on RCP 4.5 and RCP 8.5 emissions scenarios. Juvenile bull trout are sparse across this watershed and their patchy distribution is driven by the availability of warm-water refugia in the winter, cold-limiting habitat in the summer, and stream size. Juveniles occupy streams within a narrow summer thermal niche (4.7°C – 7.5°C) that are thermally resilient enough to prevent freezing during the winter. Although the thermal properties of these streams will mediate effects of climate warming, suitable habitat, based on both climatic and geomorphic habitat associations, is projected to decline across all warming scenarios. Conversely, availability of thermally suitable habitat (i.e., does not consider other habitat factors) is projected to increase between now and the 2040s, and is consistent with broad-scale predictions suggesting poleward expansion of distributional boundaries as climate warms. The dichotomy in these projections illustrates the importance of considering other dimensions of the ecological niche (e.g., groundwater) when forecasting climate warming vulnerability of northern stream fishes.

Keywords: bull trout, stream temperature, thermal sensitivity, climate warming

Introduction

Anthropogenic climate change is a globally pervasive stressor that has exerted, and continues to exert, selective pressures on taxa worldwide (Sunday et al. 2012). However, the rate and magnitude of climate warming varies across latitudinal gradients, and over the next 50-80 years, temperate and Arctic areas are projected to warm 2.5 times faster than the global average (Allen et al. 2014; Zhang et al. 2019). Such latitudinal variation in warming rates could result in different outcomes for taxa based on the rate of climate velocity and climate sensitivity (Williams et al. 2008). As ecological conditions change across a species' range, populations in affected areas will either disperse to track their realized ecological niche or adapt to occupy novel niches (Sexton et al. 2009). Niche tracking results in either range contraction or range shift, depending upon the magnitude and direction of ecological change (Sunday et al. 2012), whereas niche evolution results in range expansion or shift (Parmesan et al. 1999; Thomas et al. 2001). Taxa most vulnerable to climate warming will be those that occupy the narrowest thermal niches, have the lowest thermal tolerances, and have dispersal limitations. These taxa may be unable to keep pace with climate velocity to track suitable thermal habitat and will either have to adapt to novel thermal environments or face potential extirpation (Schloss et al. 2012; Sunday et al. 2012). Populations occupying thermal niches at, or near, upper thermal thresholds will be most susceptible to negative consequences of climate warming (Sunday et al. 2014; Whitney et al. 2016).

Climate warming poses a significant threat to biodiversity of freshwater ecosystems, but outcomes will differ based on organism and life stage climate sensitivity (Williams et al. 2008; Sunday et al. 2012; Dahlke et al. 2020). Stream-dwelling salmonids at their southern distributional range boundaries are particularly sensitive to climate warming because many populations occupy relatively warm thermal landscapes where temperatures are near upper physiological tolerance thresholds (Wenger et al. 2011b; Isaak et al. 2017). Salmonid populations at warm-edge range boundaries face the challenge of finding and occupying suitably cold thermal habitat, even as these cold-water habitats shrink over time. Moreover, the challenge of finding and occupying suitably cold thermal habitats is compounded by the dendritic structure of stream networks that can constrain dispersal opportunities for these fish (Fagan 2002; Gibson-Reinemer et al. 2017). Conversely, salmonids occupying streams in high-latitude or altitude watersheds face a different challenge, as some streams may be too cold and unproductive to sustain populations. For example, Coleman and Fausch (2007) show that some high elevation streams are too cold for cutthroat trout (*Oncorhynchus clarkii*), as they do not provide enough thermal units during the open water season to support sufficient juvenile growth to sustain individuals throughout the winter.

In montane stream networks at higher latitudes (>60°N), there is a narrow range of thermal regimes that support populations based on a balance between streams being too cold or too warm during the summer (see Chapter 3). Streams that are very cold in the summer typically have high perennial groundwater input to baseflow (Utting et al. 2013; Dunmall et al. 2016; Bolduc et al. 2018) and exhibit low thermal sensitivity, meaning they are very resilient to the warming influence of summer air temperatures (Kelleher et al. 2012; Piccolroaz et al. 2016; Bolduc and Lamoureux 2018). These streams do not completely freeze to the bottom during the winter and are viable year-round habitat; however, they are not very productive during the open water season because they are so cold. Conversely, streams that are warm during the summer are more productive but do not have sufficient groundwater to prevent freezing completely to the bottom during winter. This presents an interesting paradox for cold-water stenothermal fishes living at northern geographical range boundaries, whereby individuals must inhabit streams that are productive enough to sustain populations but do not freeze completely during the winter (e.g., Dolly Varden, *Salvelinus malma malma*; Dunmall et al. 2016). These streams typically have summer thermal regimes that lie somewhere in the middle of the thermal niche of cold-water stenotherms and exhibit moderate thermal resiliency to warming effects of air temperature (Dunmall et al. 2016; Bolduc and Lamoureux 2018; Chapter 3).

Although stream temperature is an important determinant of the distribution of stream-dwelling salmonids (Wenger et al. 2011a; Wenger et al. 2011b; Isaak et al. 2015), the characteristics of the thermal niche these cold-water fishes occupy also encompasses other dimensions of their broader ecological niche (e.g., geomorphology, presence of competitors) and should not be overlooked (Wenger et al. 2011b; Isaak et al. 2017; Troia et al. 2019). For example, bull trout (*Salvelinus confluentus*) occupy a very narrow and cold thermal niche (see Chapter 3, Fig. 3.5) but, in watersheds across the northwestern United States, studies show that the ecological niche populations occupy is driven by a combination of climatic, geomorphic, and biotic factors (Wenger et al. 2011a; Isaak et al. 2015). Similarly, Troia et al. (2019) show that in the southern Appalachian Mountains of the United States, although some stream habitat is thermally suitable for many species, other habitat conditions preclude successful establishment of these areas. These studies show that, when using species distribution models (SDMs) to define the ecological niche a species occupies across the landscape, it is important to select model covariates spanning multiple environmental dimensions, based on sound ecological relevance (Araújo and Peterson 2012). These models can also be used to predict how the distribution of thermally suitable habitat may change by integrating downscaled climate warming effects. However, large, dense sampling networks are necessary to provide sufficient local precision to make results of these models useful for conservation planning (Hannah et al. 2014; Isaak et al. 2017). Appropriate use of these models will provide more precise estimates of the ecological niche that species occupy, improve the chance of highlighting important ecological patterns and processes, and provide more precise climate risk assessments (Elith and Leathwick 2009; Araújo and Peterson 2012; Hannah et al. 2014).

Bull trout is a societally and ecologically important salmonid that occupies one of the coldest and narrowest thermal niches of all North American stream-dwelling salmonids (Benjamin et al. 2016; Isaak et al. 2017). A comparison of the summer thermal niche that populations occupy across a broad latitudinal gradient shows that this species inhabits streams between 6.2°C and 9.6°C, with an upper thermal limit of 11.5°C in the south and lower limit of 4.3°C in the north (Chapter 3, Fig. 3.5A). In the southern geographical range extent, where many populations are at warm-edge range boundaries, projections suggest that the availability of thermally suitable habitat may decline by as much as 60% by 2080 as climate warms (Isaak et al. 2015). The predicted overall decline of thermally suitable habitat will likely be tempered because many of these cold-water streams are insensitive to warming effects of air temperature (Luce et al. 2014; Isaak et al. 2016); however, despite this, some populations have already experienced range contraction (Eby et al. 2014; LeMoine et al. 2020). Similar climate vulnerability assessments are lacking for populations at the northern range extent. In addition, although the relative importance of landscape-level factors (e.g., contributing area, elevation, stream slope) on distribution has been assessed in a northern population (Chapter 2, Prairie Creek), a more thorough assessment of how both temperature and other factors influence the distribution of this population has not been done. A better understanding of the latter will provide broader comprehension of the habitat associations that influence the ecological niche this species occupies in the north and may translate into more precise outputs from species distribution models (Elith and Leathwick 2009).

In this study, I assessed the relative effects of climate, stream geomorphology, and riparian vegetation in structuring the distribution of bull trout across a northern montane watershed. I then used water-air temperature sensitivities and downscaled temperature projections to forecast how thermally suitable habitat for this species may change in the future. As stated earlier, the thermal properties of streams is a key determinant of bull trout distribution and population dynamics across the southern geographical range extent (Isaak et al. 2015; Benjamin et al. 2016; Kovach et al. 2016). However, groundwater has also been shown to be an important element of the ecological niche that bull trout occupy (Baxter and McPhail 1999; Baxter and Hauer 2000; MacDonald et al. 2014) but has received less attention with respect to how it may influence distributional patterns. In addition, as latitude increases perennial groundwater becomes an important mechanism for maintaining year-round habitat for stream fishes (Prowse et al. 2006a; Utting et al. 2013). Given that winters at higher latitudes (>60°N) are long and cold, it follows that prevalence of perennial groundwater could be an important determinant of viable habitat for stream fishes in this region. I developed and tested two hypotheses based on this theory. My first hypothesis was that juvenile bull trout distribution would be influenced by habitat heterogeneity based on a stream's thermal properties, and I predicted that summer stream temperature would be an important factor explaining variation in juvenile occupancy. My second hypothesis was based on the finding that Dolly Varden, which is closely related to bull trout, occupy streams in high latitude (> 65°N) montane watersheds where baseflow is primarily from perennial groundwater (Loewen et al. 2015). Therefore, I hypothesized that juvenile bull trout would seek streams with high thermal stability because these habitats provide warm thermal refugia during winter, and I predicted that juveniles would occupy streams that exhibit low-to-moderate thermal sensitivity. Further, I predicted that the magnitude of projected climate warming effects on these streams would be lower than those reported elsewhere due to their thermal properties.

Methods

Study area

The study area is situated in the Prairie Creek basin, Northwest Territories (61° N, 124° W), which is within the Nahanni River watershed and near the northern extent of the bull trout distributional range (Fig. 4.1). This basin is within the sub-Arctic boreal ecoregion and is characterized by cold, long winters, and short, hot, dry summers (Halliwell and Catto 2003). Vegetation is dominated by mixed coniferous forests in higher elevation areas and shrubs, grasses, and willows in lower elevation areas. The overall density of vegetation is far less in the northeastern part of the watershed. The geology consists of limestone, dolomite, and shale mantled by till, and sandy fluvioglacial drift (Halliwell and Catto 2003). Unpaved roads/trails are present in limited areas across the central basin. Arctic grayling (*Thymallus arcticus*), bull trout, mountain whitefish (*Prosopium williamsoni*), and slimy sculpin (*Cottus cognatus*) occur in this watershed, but only the latter two species live in sympatry with bull trout in tributaries to Prairie Creek. Mountain whitefish are rare in this watershed, whereas slimy sculpin are abundant in first-to third-order streams (Babaluk et al. 2015).

Regional differences in climatic conditions are apparent at southern and northern distributional range extents across the bull trout range. Broadly, when comparing seasonal climates between southern and northern latitudes, summers are longer, drier, and hotter than in the north (Chapter 3, Methods). This translates into potentially different seasonal mechanisms governing distributional patterns of northern fish. To date, studies show that perennial groundwater is an important element of the year-round hydrological regime of small northern streams, as those with high groundwater contributions do not freeze during the winter and provide viable fish habitat (Utting et al. 2013; Bolduc and Lamoureux 2018; Bolduc et al. 2018).

Stream geospatial and geomorphic data

A Geographic Information System (GIS) was used to generate a stream network and delineate potentially suitable habitat patches using a 1:50 000 Canadian digital elevation model (DEM). The basin was stratified into 60 patches of potentially suitable habitat for juvenile bull trout based on Strahler stream order (1-3) (Strahler 1952), stream gradient (<15%), and catchment area (>70 ha). This definition of potentially suitable habitat patches was based on habitat associations of juvenile bull trout from the literature (Al-Chokhachy et al. 2010; Isaak et al. 2015). Application of the geomorphic filters to define suitable patches reduced the original extent of available stream habitat in the watershed from 710 km to 491 km, and the latter was used to represent the baseline. At each stream segment along the network, stream gradient (%), elevation (m), extent of stream vegetation (%), and contributing area (ha) were derived using the GIS. The CanVec wooded area dataset was downloaded from Natural Resources Canada (https://open.canada.ca) and used to calculate percent vegetated area next to the stream. CanVec wooded areas are covered by trees or shrubs having a minimum height of 2 metres. A 50.8 m radius circle centered over each fish sampling site was used to determine percent vegetated area using 30 m resolution, and was similar to the method described by Kelleher et al. (2012). These geomorphic attributes were linked with fish collection sites for modelling and then used to predict occurrence probability of juveniles across the watershed (see below for details).

Biological Sampling

Of the 60 suitable patches, 26 were randomly selected and 15 sites (100 m long) within these patches were electrofished to document occurrence of juvenile bull trout (< 150 mm in length). Between 2012 and 2016, fish surveys were done across 411 unique sites during the summer and two or more temporal or spatial replicates were done at most sites. Sites were randomly assigned across patches in a spatially balanced fashion using a generalized random-tessellation stratified (GRTS) design in R (Stevens Jr and Olsen 2004; R Development Core Team 2018). This method is designed to prevent spatial clustering and spread the samples throughout the study area. The user specifies a minimal distance for separating sampling sites and, if this condition is violated, the process randomly allocates sites across the sampling frame iteratively until conditions are met. I specified that sites be at least 1 km apart and final inspection of the sampling data frame revealed that most sites were, on average, 1.5 km apart from one another. Fourth order or higher streams were not sampled because they were too deep to sample effectively with a backpack electrofisher. Any potential patches with suitable stream lengths <3000 m were excluded from consideration because local populations of bull trout rarely occur in areas this small (Isaak et al. 2015).

Water temperature monitoring network

To complement the geomorphic descriptors of the network, a water temperature monitoring network consisting of 178 stream temperature sensors was established across the Prairie Creek watershed between 2012 and 2016. Of these 178 sensors, 46 were deployed for two or more years and the remaining 132 were set out for one season encompassing part of July and all of August. The multi-year sensors provided understanding of temporal variation in stream temperature within and across years and the seasonal sensors provided data points for the summer season. Temperature loggers (HOBO Tidbit Water Temperature loggers, Onset) were deployed across a wide environmental gradient to capture as much heterogeneity in stream temperatures as possible (Table 4.1). Loggers were deployed using standard field protocols (Isaak and Horan 2011) and recorded stream temperature at one-hour intervals.

Stream temperature and thermal sensitivity modelling

Mean August stream temperature was used as a surrogate for summer stream temperature, which is reasonable given most stream temperature metrics are highly correlated (Isaak et al. 2018). August stream temperature was modelled using a spatial statistical stream network (SSN) model (Ver Hoef et al. 2006; Isaak et al. 2014) applied to 178 summers of measurement across 132 unique sites recording temperature between 2012 and 2016. The final model included a linear sill tail-up, and Gaussian Euclidean covariance structure to integrate spatial dependency present in the sampling data frame; stream elevation and air temperature were included as fixed effects, and site and year were specified as random effects. Further details on this model can be found in Chapter 3 (Methods). The precision of the modelled mean August stream temperatures was similar to what others have reported using this model ($r^2 = 0.70$; RMSE = 1.1°C). Stream temperatures were predicted across all fish collection sites and at 1 km intervals across the entire stream network to use as a covariate for species distribution modelling and for climate change projections. Predicting temperature at this resolution addresses a commonly cited issue whereby course scale resolution hinders precision of climate vulnerability assessments (Potter et al. 2013; Hannah et al. 2014).

To complement the spatial map of August stream temperature, I developed a thermal sensitivity covariate to provide a measure of how a stream responds to short-term variability in air temperatures. An additional motivating factor for including this covariate was that it is a surrogate for prevalence of perennial groundwater in high-latitude stream systems (Bolduc and Lamoureux 2018; Bolduc et al. 2018). In the absence of directly measuring groundwater contribution to baseflow, there is a negative relationship between groundwater prevalence and a stream's response to changes in air temperature (i.e., thermal sensitivity; Kelleher et al. 2012; Bolduc and Lamoureux 2018). Therefore, as thermal sensitivity values decline the relative contribution of groundwater increases. Extending this concept, streams with large perennial groundwater inputs are cold in the summer but provide relatively warm (i.e., above freezing) and stable thermal habitat during the winter (Utting et al. 2013; Bolduc and Lamoureux 2018; Chapter 3). Thermal sensitivity was quantified by regressing the mean weekly temperature of a stream against mean weekly air temperatures from the nearest (~100 km) environment Canada weather station (Nahanni Butte; https://climate.weather.gc.ca). The resulting slope of this relationship represents the thermal sensitivity of a stream. Streams with lower slopes are characterized as thermally resilient and are minimally affected by fluctuations in air temperature, and streams with larger slopes are thermally sensitivity and have stream temperature profiles that track air temperatures more closely (Piccolroaz et al. 2016). Given that cold-water stenotherms, like bull trout, occupy narrow thermal niches, streams with lower thermal sensitivity are likely to provide suitable thermal conditions for improved spawning, egg incubation, and year-round residence by juveniles (Baxter and McPhail 1999; Baxter and Hauer 2000). Thermal sensitivity was calculated across the entire year for 28 unique stream temperature monitoring sites spanning 60 full years of data. The thermal sensitivity slopes, derived using weekly water-air temperature time steps, provided similarly precise estimates to what others report (min $r^2 \geq 0.70$, mean $r^2 = 0.82$; Kelleher et al. 2012). These thermal sensitivity values were then integrated into an SSN model with site specified as a random effect due to repeated measures across years; percent vegetation, stream order, contributing area, and elevation as fixed factors; and a linear sill tail-up, and Gaussian Euclidean covariance structure to account for spatial dependency. Model selection of fixed effects was done using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002) while holding covariance structures constant with the final model including percent vegetation and elevation as fixed factors. Because sample size was relatively low, I chose to select a simple covariance structure that has been shown to perform well with similar data from this watershed (linear sill tail-up, Gaussian Euclidean; Chapter 3, Methods). Thermal sensitivity was predicted across all fish collection sites and at 1 km intervals across the entire watershed to use as a covariate for species distribution modelling and for climate change projections.

Hypothesized relationships

I developed six hypotheses based on expected relationships between climatic, geomorphic, and biotic covariates and juvenile occupancy in the Prairie Creek watershed (Table 4.1). Two hypotheses were developed for climatic covariates. First, because mean August stream temperature has been shown to be an important predictor of juvenile distribution in the northwestern United States (Isaak et al. 2017), I hypothesized that juveniles would occupy habitat within their preferred summer thermal niche and this would follow a quadratic relationship with mean August stream temperature. Second, I hypothesized that because bull trout is a cold-water stenotherm, juveniles would seek stable, cold-water habitat with low-to-moderate thermal sensitivity following either a quadratic or negative relationship. This hypothesis was based on work demonstrating the importance of groundwater for bull trout persistence and similarly for a closely related northern char, Dolly Varden (Baxter and McPhail 1999; Baxter and Hauer 2000; Dunmall et al. 2016).

Previous work in this watershed shows that contributing area, elevation, and stream gradient are important geomorphic variables that help explain juvenile distributional patterns across this watershed (Chapter 2). However, as shown by others, I suspected that the strength and form of these relationships could change using a broader suite of covariates in this modelling approach (Isaak et al. 2017). Since contributing area is a surrogate for stream size (Gordon et al. 2004), I hypothesized that juvenile occupancy would be low in small headwater streams, peak in intermediate-sized streams, and decline in larger downstream areas following a quadratic relationship. Stream elevation has been shown to be a good indicator of both upstream and downstream distributional limits elsewhere (Paul and Post 2001; Rich et al. 2003; Rieman et al. 2007); therefore, I hypothesized that juvenile occupancy would increase linearly with elevation. Stream gradient is related to stream velocity (Gordon et al. 2004) and juveniles prefer to occupy low-to-moderate velocity habitat, plus low gradient areas have an abundance of gravels that is well suited for constructing redds and juveniles often reside near these areas (Baxter and Hauer 2000; Al-Chokhachy et al. 2010). Therefore, I hypothesized that juvenile occupancy would decline linearly as stream gradient increased.

Riparian vegetation is important for maintaining cooler stream temperatures in the summer through shading (Cross et al. 2013) and also provides an indirect source of terrestrial food subsidies for juvenile and resident salmonids (Wipfli 1997; Kawaguchi et al. 2003; Baxter et al. 2005; Wallace et al. 2015). Given productivity is lower at higher latitudes due to shorter growing seasons and longer winters (Prowse et al. 2006a), I hypothesized that the proportion of stream-side vegetation would be an important food subsidy for juveniles, and predicted juvenile occupancy would increase linearly with increasing vegetation coverage.

Species distribution model

Occurrence data from 411 sites were integrated into a generalized linear model (GLM) to examine the relative importance of climatic, geomorphic, and biotic factors on juvenile bull trout distribution across the watershed, based on a priori hypotheses (Table 4.1). Since occurrence records were gathered between 2012 and 2016, I view this as the contemporary known distribution of juvenile bull trout in this watershed. Previous work in this watershed suggests that detectability is high (>0.70) in core areas where healthy juvenile populations occur, and detectability is low in fringe habitat near the edge of distributional limits (Chapter 2). However, imperfect detection in fringe habitats did not have a large effect on the relationships between landscape-level covariates and juvenile occupancy (Chapter 2). Furthermore, a combination of temporal and spatial replicates was used to document bull trout presence-absence across sites, and the sum of these detection histories (e.g., 010 = 1; non-detection, detection, non-detection) were used for modelling. For these reasons, I was confident that false-absence rates were low across most fish collection sites and had minimal influence on this data set. Since a combination of spatial and temporal replicates was used during sampling, a single-season occupancy-detection model could not be used for analysing these data, as spatial replicates must be modelled using a variation of the single-season model. The juvenile life stage was selected for these analyses because juveniles reside in natal streams for 3-5 years; therefore, streams with high juvenile occupancy and abundance suggest successful spawning has occurred. Additionally, emergent juvenile life stages occupy narrower thermal niches than adults (Chapter 3, Fig. 3.2). Although these biological attributes require juveniles to occupy a narrower ecological niche and geographic distribution than that of adults, residency in these habitats over multiple generations means they are important for population persistence (Paul et al. 2000; Al-Chokhachy et al. 2010;

Isaak et al. 2015). Characterizing the properties of these habitats is important in order to understand how these habitats may change as climate warms.

I selected six variables across climatic, geomorphic, and biological categories to use as candidate predictors of juvenile bull trout occurrence (Table 4.1). A Pearson correlation matrix was computed for all covariates in the model and pairwise correlations were low-to-moderate (r = 0.16 - 0.57; AugTemp: CA = 0.57; Table 4.2), so none of the covariates were removed from the analysis. Prior to analysis, covariates were standardized to a mean of zero and a standard deviation of one. A square-root standardization was used for contributing area to reduce the potential influence of a few, relatively large values on the effect size of this covariate.

Modelling was done as a two-step process. In the first step, the relative importance of both linear and quadratic effects of continuous covariates on juvenile occupancy was tested with a GLM. The resulting set of linear and quadratic covariates was then integrated into the broader candidate set of climatic, geomorphic, and biological predictor variables. In the second step, candidate predictor variables were assigned to test models based on a priori hypotheses. AIC was used to compare models in each step, where models with lower scores are viewed to be better than those with higher scores and a change in value of two or more is viewed as substantial model difference (Burnham and Anderson 2002). Within sample predictive performance of the top model was assessed using the area under the curve (AUC) of the receiver operator characteristic plot and internal classification accuracy (ACC). The data set was split into training and testing data sets that comprised 80% and 20% of the original data set, respectively, and repeated (*n* =5) five-fold cross validation was conducted. Each of the training data sets were used to establish a presence-absence threshold based on prevalence (Liu et al. 2005). Similarly, a threshold for modelling probability of occupancy across the entire watershed for contemporary and climate change scenarios was based on prevalence from the entire training data that yielded the most accurate probability estimates, set at 0.23. The top model, selected based on AIC, AIC weight, and performance metrics, was used to develop response curves to describe the relationship between covariates and juvenile occurrence probability. Some of the complex model combinations did not converge because of high correlation (>0.80) among quadratic and/or linear combinations of covariates, so these were not included in the final candidate model set. I also integrated these data into a generalized linear mixed effects model (GLMM), where habitat patch was included as a random intercept, to account for potential spatial dependency in juvenile occupancy within habitat patches, which is common for this species (Isaak et al. 2017; Wilcox et al. 2018), and can bias parameter estimates (Zuur et al. 2009). However, results showed that the top GLMM did not perform as well as the top GLM, which lacked a random intercept for patch, (GLM, ACC/AUC = 0.82/0.80; GLMM, ACC/AUC = 0.75/0.74), so I decided to use the simpler approach. Further details regarding the GLMM can be found in supplemental information (see alternative modelling approach).

Climate projections

Since stream temperature was likely to occur in the final model due to its well documented effects on bull trout, the potential effect of future climate warming was assessed. I did not include other climatic factors (e.g., precipitation, snowpack, stream discharge) in my climate warming assessment because, unlike stream temperature, I lacked sufficient data at the appropriate spatial resolution (e.g., basin-level precipitation, stream level/flow) to directly link these factors to the biology of bull trout in this system. The top model (Table 4.3) was used to predict occurrence probabilities at sites across the Prairie Creek stream network under contemporary conditions (2012 – 2016) and climate projections for 2040s (2030-2059) and

2080s (2070-2099) using the Representative Concentration Pathways (RCP) 4.5 and 8.5 emissions scenarios. Site-level occurrence probability predictions from this model were based on both climatic and geomorphic covariates from the top model. The RCP 4.5 represents a mid-level emissions reduction scenario, whereas the RCP 8.5 is one where minimal reduction in greenhouse gas emissions would occur. The RCP 4.5 scenario was also chosen because it is relatively consistent with the AIB scenario used to predict climate warming effects on bull trout at the southern range extent (Isaak et al. 2015). An ensemble of 10 global climate models that best represented historical air temperature trends in Canada was used to project regional changes in air temperature during these periods, as this approach helps account for uncertainty across models (Araujo and New 2006). The change in mean summer air temperatures was bracketed by projected increases of 2.0°C and 4.5°C, based on the lowest (RCP 4.5, 2040s) and highest (RCP 8.5, 2080s) emissions scenarios, respectively (Zhang et al. 2019).

Since long-term temperature records were not available to calculate stream temperature warming rates (°C·decade^{-1}), thermal sensitivity was used to estimate the rate of intra-annual warming for streams in the Prairie Creek basin, based on local water-air heat exchange dynamics (Piccolroaz et al. 2016). Although this method does not account for broader spatial-temporal atmospheric warming effects on stream temperature, the data used to calculate thermal sensitivity spanned multiple years (1-4 yr; mean = 2.5 yr), and therefore, did integrate some level of inter-annual variation into downscaled stream temperature projections. Projected increases in air temperature were downscaled to mean August stream temperatures using thermal sensitivity estimates. To do so, the mean projected change in air temperature, based on RCP scenarios relative to the baseline air temperature (i.e., 1948-2018), was multiplied by thermal sensitivity estimates and then added to mean August stream temperatures. The top model response curves were used with network reach covariates and projected changes in stream temperature to map the availability of suitable habitat across the watershed under contemporary, 2040s, and 2080s emissions scenarios. The availability of suitable thermal habitat was defined by the August temperature-occurrence response curve from the top species distribution model. I used two transition temperatures to bracket the lower and upper limits of the thermal niche that juvenile bull trout occupied and all habitat that fell within this temperature range was classified as available thermally suitable habitat. This range of temperatures was then used to calculate and map habitat availability.

Two additional scenarios were also presented based on niche tracking and niche evolution theory. In the first scenario, I assumed that juvenile bull trout in the Prairie Creek watershed currently occupy their entire realized thermal niche and as stream temperatures change will disperse and redistribute themselves in streams that fall within the same thermal niche. In the second scenario, I assumed that juvenile bull trout are capable of occupying a warmer thermal niche with maximum summer stream temperatures ≤ 10.0°C, based on a broader understanding of upper thermal limits for populations across the range (Isaak et al. 2015, Isaak et al. 2017). I chose to use 10.0°C as the upper limit because it seemed plausible for these fish to adjust to occupy streams that are 2.5°C warmer but still below the known upper limit for the species, it is well within thermal acclimation or acclimatization potentials for ecologically similar species (Eliason et al. 2011; Kelly et al. 2014), and this increase acknowledges that adjustments associated with upper thermal thresholds are less flexible in freshwater fishes (Sandblom et al. 2016; Morrison et al. 2020). The two scenarios were compared to determine how availability of thermally suitable habitat would be affected by climate warming relative to the baseline contemporary conditions. In both of these scenarios, the effects of other geomorphic and abiotic covariates (e.g., elevation, stream size, thermal sensitivity) were not taken into account when calculating and mapping thermally suitable habitat.

Results

Occupancy and species distribution modelling

Juvenile bull trout were captured in 9 of 26 patches and occurred in 98 of 411 sites corresponding to mean patch and site scale prevalence of 0.35 and 0.24, respectively. The distribution of juveniles across the watershed was very sparse at both the site and patch scales, and within occupied patches fish distributions were highly aggregated (Fig. 4.1a). Juvenile occupancy was highest in third and second order streams with mean August stream temperatures between approximately 4°C and 8°C, thermal sensitivity between 0.25 and 0.58, stream gradients between 2% and 6%, and contributing areas between 100 ha and 3000 ha with a few fish occupying larger streams. Juveniles occupied a subset of available thermal habitat but favored sites that were warmer and near the upper limit of available stream temperatures. Vegetation did not influence the distribution of juveniles or affect stream temperature (Fig. S4.1). The Prairie Creek stream temperature map illustrates that, although thermal heterogeneity exists across the watershed, most streams are relatively cold in the summer (1.7-12.1°C; Fig. 4.1b). The August stream temperature response curve defines the thermal niche that juveniles occupy, and identifies peak occurrence (6.1°C), cold-transition (4.7°C), and warm-transition (7.5°C) temperatures (Fig. 4.2). Mean thermal sensitivity (± SD) across 1 km sites in first-to-third order streams was 0.43 (0.12) and ranged between 0.15 and 0.68. Of the 492 km of potentially suitable stream habitat across the watershed, 309 km fell within the thermal niche that juvenile bull trout occupy.

The best model based on AIC ranking, model weight, and predictive performance included mean August stream temperature, thermal sensitivity, contributing area, and elevation (Table 4.3). Since both of the top two models (ΔAIC < 2.0) had the same predictors and both models performed similarly (Model 1: ACC = 82%, Model 2: ACC = 81%) I chose to use the simpler model to predict juvenile occupancy probabilities. Contrary to my predictions, stream gradient and vegetation were not in the top model. However, as predicted, variation in juvenile occupancy was explained by quadratic relationships with August stream temperature and contributing area, and both positive and linear relationships with stream elevation and thermal sensitivity, respectively (Fig. 4.2). Model performance was good for the best supported models, and the top model had mean classification accuracy of 82% (AUC =0.80), across 411 sites, based on a 0.23 prevalence threshold (Table 4.4).

Climate predictions

The predicted changes in mean stream temperature ranged between 0.85°C and 1.93°C (Table S4.1). Multiple regression model predictions show that bull trout occupy 120 km of the 309 km of available thermally suitable habitat in Prairie Creek (Table 4.5). This reflects that not all thermally suitable habitat will be occupied by juveniles as other climatic and geomorphic factors such as contributing area, elevation, and thermal sensitivity also influence juvenile distribution (Table 4.3, Fig. 4.2). Occupancy probabilities from the top multiple regression model show that the amount of suitable habitat will decline by 23% and 28% between now and 2040s and 2080s, respectively, based on the RCP 4.5 scenario (Table 4.5). More substantial declines in suitable habitat are predicted to occur during the same time periods (2040s, 33%; 2080s, 42%) under the RCP 8.5 scenario (Table 4.5; Fig. 4.3). Under the niche tracking scenario, where I assume bull trout will disperse to track the thermal niche they currently occupy, results show an initial increase in available habitat from baseline to the 2040s, followed by a decline into the 2080s. Under scenarios where I assume bull trout has adjusted to occupy a broader and warmer thermal niche, results show that the amount of available thermal habitat would actually increase by at least 24% across all scenarios and then remain stable into the 2080s (Table 4.5, Fig. 4.4b,d).

Discussion

The patchy distribution of juvenile bull trout in the Prairie Creek watershed is primarily a reflection of the thermal properties of the streams these fish occupy. Juveniles require streams that are within a narrow cold-water summer thermal niche (4.7°C – 7.5°C), yet must have sufficient perennial groundwater contribution to prevent streams from completely freezing during the winter. Year-round residency is only possible in streams that exhibit low-to-moderate thermal sensitivity – a signature seen in all streams where juvenile occurrence was high. Although low thermal sensitivity can be driven primarily by snowpack/snowmelt mechanisms, this is not the case in the Prairie Creek watershed. Stream-air temperature response cycles of thermally resilient streams in this watershed are consistent with a class of small headwater streams where perennial groundwater is the primary contribution to baseflow (Kelleher et al. 2012; Lisi et al. 2015; Fig. 3.3). Others have shown a similar dependence by bull trout on streams with low thermal sensitivity at the southern range extent; however, thermal sensitivity appears to be more important in mediating the effects of stream warming during summer so that populations can persist in habitat below warm-edge boundaries associated with upper thermal limits (Mayer 2012; Luce et al. 2014; Isaak et al. 2016). Although the streams juveniles occupy in this watershed are cold and highly resilient to effects of air temperature warming, multiple regression model results show that the amount of suitable habitat is likely to decline under both RCP 4.5 and 8.5 scenarios between now and 2040s and 2080s. However, this decline is contrary to what others predict for northern cold-water fishes, where populations are expected to benefit from climate warming by expanding their ranges poleward (Parmesan 2006; Reist et al. 2006). I also present alternate projections showing that if this population is not constrained by stream geomorphology and thermal sensitivity, and is capable of adjusting to occupy a warmer thermal niche, then the availability of thermally suitable habitat will expand and could provide better opportunities for individuals to exploit warmer, higher productivity habitat. As reported by others, the dichotomy in the projections I present illustrates the importance of considering other dimensions of the ecological niche (e.g., groundwater) when forecasting climate warming vulnerability of north-temperate stream fishes (Snyder et al. 2015; Troia et al. 2019). The adaptive potential of this population via phenotypic plasticity or adaptation may determine whether or not it will be a winner or loser as climate warms (Somero 2010).

Climatic and non-climatic descriptors of juvenile distribution

Juvenile bull trout in Prairie Creek are found in very few streams (Table S4.3) and, as predicted, this patchy distribution is driven primarily by the availability of thermal refugia during winter, followed by summer stream temperature, and to a lesser extent, stream size. Similar to other areas, juvenile bull trout in Prairie Creek occupy a narrow thermal niche, but in this watershed, the upper thermal limit of that niche is much colder than areas at the southern range extent. For example, Isaak et al (2015) report that bull trout across much of the northwestern United States occupy streams with mean August temperatures as high as 11°C, whereas the upper limit for the Prairie Creek population is 8.0°C with a warm-transition temperature where occurrence probability declines at 7.5°C. In addition, it looks like there are some streams in the this watershed that are too cold for juveniles, even though they appear to have acceptable thermal sensitivity and are large enough to support fish. These streams bracket the cold-transition temperature for juveniles at 4.7°C and I propose two possible mechanisms explaining why fish do not occupy these streams. First, as seen in other salmonids (e.g., Atlantic salmon *Salmo salar*, Finstad et al. 2004; cutthroat trout, Coleman and Fausch 2007; Chinook salmon *Oncorhynchus tshawytscha*, Falke et al. 2019), these streams may be too unproductive to support sufficient growth of juveniles during the summer to ensure that they can survive the winter. Second, this population may not possess the physiological capability of tolerating such low temperatures to carry out key life processes (Whitney et al. 2016), and the cold-transition temperature I identify may indeed represent a lower functional thermal tolerance. Although some propose that many species may more readily possess phenotypic plasticity to make downward adjustments to lower thermal tolerance limits (Sandblom et al. 2016), it seems unlikely that this population would do this given that productivity is probably low in this system due to cold temperatures during short summers and long winters (Chapter 3).

As predicted, thermal sensitivity is also an important factor influencing juvenile distribution in the Prairie Creek watershed. Although it is not possible to definitively conclude that perennial groundwater is the only factor influencing thermal sensitivity in these streams, winter thermal regimes (see Chapter 3) suggest that it is a strong driver of the spatial thermal sensitivity patterns I report here (Kelleher et al. 2012; Piccolroaz et al. 2016; Crites et al. 2020). As shown in other northern systems, streams with low-to-moderate thermal sensitivity have high contributions of perennial groundwater to baseflow (Bolduc and Lamoureux 2018). In the Prairie Creek watershed, juvenile bull trout were found in very few habitat patches that were surveyed (35%). This reflects spatial variation in thermal sensitivity across this watershed, and suggests that the distribution of perennial groundwater is patchy. Similar heterogeneity in thermally suitable habitat associated with prevalence of groundwater has been reported in other systems (Snyder et al. 2015). The correlation between juvenile occupancy and prevalence of groundwater in Prairie Creek is not particularly surprising since winters are long and cold, and large contributions of groundwater are required to prevent first-to-third order streams from freezing (Utting et al. 2013; Bolduc et al. 2018). Contrary to populations in the south that seek cold-water refugia in the summer (Isaak et al. 2015; Benjamin et al. 2016; Isaak et al. 2016), bull trout at the northern range extent seek warm-water refugia in the winter for successful juvenile residency. This pattern is also consistent with what others have reported for closely related chars, such as Dolly Varden and brook trout *Salvelinus fontinalis,* that occupy streams with high groundwater inputs (Loewen et al. 2015; Snyder et al. 2015; Dunmall et al. 2016).

Climate warming projections

As predicted, low thermal sensitivity is an important property of bull trout streams in the Prairie Creek watershed and, as climate warms thermally resilient streams are likely to mediate warming effects imposed by increasing air temperatures (Snyder et al. 2015; Bolduc and Lamoureux 2018). In this basin, less than half (38%) of the available thermal habitat is suitable for juvenile bull trout, and even though these habitats are thermally insensitive to warming, they are still predicted to decline by 23% between now and 2040s under reasonably optimistic emissions scenarios (RCP 4.5). My projections, based on multiple regression model predictions, suggest that northern bull trout populations will experience about half as much loss of thermally suitable habitat than southern populations between now and 2040s (Isaak et al. 2015), which seems reasonable since southern populations are living at warm-edge range boundaries. However, habitat declines could be problematic for sustaining juvenile bull trout in the Prairie Creek watershed, if thermally suitable habitats become spatially limiting and individuals are forced to disperse and occupy lower quality habitat due to limits on stream carrying capacity. As seen in other salmonids, occupying poor quality thermal habitat can compromise growth and overall condition (Finstad et al. 2004; Al-Chokhachy et al. 2013; French et al. 2017). The projected decline in thermally suitable bull trout habitat was a somewhat counterintuitive result, as this population occupies a cold thermal niche, and many predict that, as our climate warms, the extent and condition (i.e., productivity) of suitable habitat will increase (Prowse et al. 2006b; Reist et al. 2006). However, even in a worst-case scenario (RCP 8.5 2080s), where suitable habitat is predicted to dwindle to an alarmingly small proportion (decline 58%, 70 km), five of the nine core habitat patches that juveniles currently occupy will remain intact. Maintenance of these thermal refugia is directly attributable to thermal properties of these stream, and as reported elsewhere, could be a key factor ameliorating the effects of climate warming on this cold-water stenotherm (Snyder et al. 2015; Isaak et al. 2016).

I also provide projections showing that the amount of available thermally suitable habitat will increase across all scenarios into the 2040s, and then either decline or plateau. The calculations of suitable habitat for these projections are based solely on the defined summer thermal niche that bull trout currently occupy (4.7°C – 7.5°C) and an expanded thermal niche (4.7°C – 10.0°C), based on the assumption that this population is capable of adjusting or adapting to occupy a broader thermal niche. The latter is based on the niche evolution strategy and warrants consideration. Because the Prairie Creek population occupies a colder thermal niche within the species' thermal niche, it seems plausible that this population possesses the phenotypic plasticity to occupy warmer streams (i.e., > 8.0°C but < 11.0°C). This notion is not outlandish, as other studies have documented that northern salmonids are capable of adjusting to survive in novel thermal niches (Sparks et al. 2017). The niche evolution scenario I present shows if juveniles were capable of occupying streams across a warmer thermal niche, then the amount of available thermal habitat in this basin would increase by 28% between now and the 2040s. It follows that the proportion of suitable thermal habitat juveniles occupy would likely increase in downstream habitats. A niche evolution scenario fits well with predictions suggesting that the effects of climate warming may increase the extent and productivity of habitat for northern fishes (Prowse et al. 2006b; Reist et al. 2006). However, this scenario begs the question: if laboratory and field studies show that bull trout are capable of occupying warmer thermal niches (Selong et al. 2001; Isaak et al. 2017), then why do juveniles in Prairie Creek not reside in warmer streams? I propose two explanations. First, warmer streams in Prairie Creek (>8.0°C, August mean) exhibit higher thermal sensitivity, and suggests that these streams probably freeze to the bottom during winter. Closer inspection of winter stream temperature data confirms this is true for most of these streams (N.J. Mochnacz, unpublished data), so full-year residency is not possible, nor would these streams provide viable incubation habitat. Second, but related, is the possibility that bull trout in Prairie Creek have adapted their physiology to occupy this cold thermal niche and possess the ability to grow more efficiently in these conditions. More efficient growth at higher latitudes has been shown to occur in other northern chars (Chavarie et al. 2010; Sinnatamby et al. 2015) and this phenomenon warrants further investigation in the Prairie Creek bull trout population.

My projections also assume that only stream temperature will change, but that does not represent a holistic approach as other climatic factors, such precipitation, the duration of winter and summer seasons, and stream hydrology are also likely to change as climate warms (Prowse et al. 2006b; Reist et al. 2006). For example, if winter becomes shorter and warmer, streams that currently freeze to the bottom may become viable winter habitat in the future. The climate projections I present could be refined by integrating a broader set of climatic and hydrologic dimensions into prediction scenarios. Measuring the extent and characteristics of perennial groundwater sources in high-latitude montane watersheds will be important for understanding how climate warming may affect this essential habitat feature for northern stream fishes.

Modelling and climate change projections

Although the predictive accuracy of my species distribution model was high, it is important to recognize, as others have, that forecasting future fish distributions is inherently uncertain (Wenger et al. 2011b; Isaak et al. 2015; Troia et al. 2019). Consequently, the value of this model and predictions lies in understanding the direction of the trajectory of changes to suitable thermal habitat under future climate warming scenarios and the sensitivity of these habitats. I do not recommend focusing on the minutiae of site-specific predictions and the absolute amount of habitat lost under climate warming. However, I do encourage others to develop and implement robust field sampling designs to validate predictions made here (see design considerations, Chapter 2). I provide predictions using a similar approach as Isaak et al. (2015), which provides context for my results but some subtle differences in methods warrant comment. First, Isaak et al. (2015) applied an average basin-level thermal sensitivity value when calculating the magnitude of stream temperature warming, whereas I used thermal sensitivity at 1 km points within streams to capture finer scale heterogeneity in this variable. Although average values across Prairie Creek (0.43) were similar to those reported in most basins by Isaak et al. (2015), the more detailed resolution I provide likely yielded more precise stream-scale warming estimates. Second, the RCP 4.5 and A1B scenarios are similar but not exactly the same, so the magnitude of projected air temperature warming in each respective area will be slightly different. Despite these inconsistencies, I am confident that my predictions are precise enough to forecast broader habitat trajectory patterns that are biologically meaningful and useful when placed in the context of other similar studies.

Thermal sensitivity estimates were used to estimate inter-annual stream temperature warming rates because stream temperature records only spanned a short time frame (2012-2016), which is not typically long enough to reflect coherent warming rates associated with climate change (Isaak et al. 2012). This approach introduces potential uncertainty into stream temperature warming estimates due to differences in the physical processes driving inter-annual variation in water temperature and air temperature versus those driving intra-annual variation (Luce et al. 2014). However, I justify using thermal sensitivity as a method to estimate stream temperature warming in three ways. First, studies in the north have shown that streams where primary contributions to baseflow are driven by high snowpack, perennial groundwater, or both, are less sensitive to warming from inter-annual atmospheric effects (Lisi et al. 2015; Bolduc and Lamoureux 2018). Since many of the streams in the Prairie Creek watershed exhibit a similar range of thermal sensitivity characteristics (see Chapter 3), it is reasonable to assume that these streams will respond similarly to atmospheric warming effects. Second, because most sites (>80%) used to model thermal sensitivity had multiple years of data (mean = 2.5 yr), temporal variation in air temperature associated with atmospheric mechanisms was integrated into downscaled stream temperature projections. Although this did not span a particularly long period, it likely accounted for some temporal variation associated with climate warming during this period. Third, because a multi-model ensemble approach was used to predict increases in mean summer air temperatures (Araujo and New 2006), uncertainty was captured in the estimated stream temperature warming rates by both extension of this modelling approach and scenarios that spanned fairly broad temperature ranges. Consequently, I am confident that the distribution of these stream temperature warming rates encompasses the range of potential warming trajectories for this watershed.

Conclusion

The patchy distribution of juvenile bull trout in the Prairie Creek watershed is driven primarily by cold-limiting habitat, the prevalence of perennial groundwater, and stream geomorphology. Streams with suitable thermal properties exhibit low-to-moderate thermal sensitivity, and are therefore, thermally stable throughout the year. Similarly, during their freshwater residency, Dolly Varden also occupy streams that display high thermal stability as a result of perennial groundwater contributions (Loewen et al. 2015; Dunmall et al. 2016). Additionally, Crites et al. (2020) show that the density of perennial groundwater springs is highest across montane areas in northwestern Canada, and displays substantial overlap with both bull trout and Dolly Varden distributions in this region (Mochnacz et al. 2013). Together, these results provide mounting evidence that perennial groundwater is a key determinant of riverine char distribution and persistence across montane watersheds at the northern geographic range extent. Despite the fact that the thermal properties of streams bull trout occupy in the Prairie Creek watershed are likely to mediate effects of climate warming (Isaak et al. 2015; Lisi et al. 2015; Bolduc and Lamoureux 2018), my multiple regression model still projects declines in suitable habitat across all scenarios. This finding is contrary to broader climate change predictions that suggest taxa will shift poleward as climate warms (Parmesan and Yohe 2003; Parmesan 2006; Sunday et al. 2012). However, if the Prairie Creek bull trout population possess greater thermal safety margins then what my results suggest (Sunday et al. 2014), then the projected trajectory of habitat loss for this population could be reversed, even under the most extreme climate warming scenarios. A broader understanding of both the phenotypic and genetic adaptive potential of northern bull trout populations will be an important element for refining the climate vulnerability assessment from this study.

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Tables

Table 4.1. Covariates describing the 411 stream sampling sites from the Prairie Creek watershed used to model the distribution of juvenile bull trout and hypothesized responses to these candidate predictor variables.

Category	Variable	Abbreviation	Description	Mean	Standard deviation	Range	Hypothesized response
Geomorphic	Elevation (m)	Elev	Stream elevatoin in metres	1119.0	117.3	795 - 1400	+
	Stream gradient (%)	Grad	Slope/gradient of the stream segment	4.5	2.4	0.7-13.8	-
	Contributing area (ha)	CA	Upstream contributing area	1105.0	1149.0	70-5060	+/-
Climatic	August mean stream temperature (°C)	Aug_Temp	Mean August stream temperature at collection sites	5.9	1.4	1.3 - 9.11	+/-
	Thermal sensitivity (TS)	TS_VE	Slope of annual weekly stream temperature vs. annual weekly air temperature at collection sites	0.42	0.09	0.18 - 0.65	+/- or -
Biological	Vegetation cover (%)	Veg	Amount of vegetation adjacent to stream segment	0.6	0.4	0.0 - 1.0	+

Note: A " + " and " - " denote positive and negative relationships, respectively; and "+/-" represents a quadratic relationship.

Table 4.2. Pearson correlations among continuous predictor variables used to model the distribution of juvenile bull trout in the Prairie Creek watershed.

	Aug_Temp	TS	CA	Elev	Grad
TS	0.48				
CA	0.57	0.49			
Elev	-0.40	-0.28	-0.50		
Grad	-0.52	-0.35	-0.52	0.17	
Veg	-0.34	0.16	-0.31	0.19	0.19

Abbreviations: Aug_Temp, mean August stream temperatrure (°C); Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); Veg, is percent vegetation (%); TS, is thermal sensitivity.

Table 4.3. Best supported models from the candidate model set based on Akaike's information criterion (AIC), model weight, and predictive performance metrics. Predictive performance was evaluated using five-fold (leave-one-out) cross validation accuracy (ACC) and area under the curve (AUC) of the receiver-operator characteristic plot. The most supported model is shown in bold.

Model	ΔAIC	AIC *w*	ACC	AUC
Aug_Temp + Aug_Temp^2 + TS + Elev + CA + CA^2	0.00	0.72	0.82	0.80
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + CA + CA^2	1.90	0.28	0.81	0.81
Aug_Temp + Aug_Temp^2 + TS + Elev + CA + CA^2 + Grad + Veg	10.77	0.00	0.79	0.78
Aug_Temp + Aug_Temp^2 + CA + CA^2	21.03	0.00	0.78	0.76
Aug_Temp + Aug_Temp^2 + TS + Elev + Grad + Grad2	37.88	0.00	0.75	0.78
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + Grad + Grad^2	39.14	0.00	0.75	0.78
Aug_Temp + Aug_Temp2 + TS + TS2 + Grad + Grad2 + Veg	40.49	0.00	0.72	0.78
Aug_Temp + Aug_Temp^2 + Grad + Grad^2	44.57	0.00	0.77	0.77
TS + TS^2 + CA + CA^2	67.87	0.00	0.71	0.68
Aug_Temp + Aug_Temp^2 + TS + TS^2	72.79	0.00	0.72	0.70
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Veg	74.03	0.00	0.72	0.71
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + Veg	74.21	0.00	0.72	0.70
Aug_Temp + Aug_Temp^2 + Veg	75.27	0.00	0.72	0.71
Aug_Temp + Aug_Temp^2	76.99	0.00	0.73	0.68
CA + CA^2	77.14	0.00	0.71	0.62
Aug_Temp + Aug_Temp^2 + Elev	78.24	0.00	0.72	0.68
TS + TS^2 + Grad + Grad^2	80.32	0.00	0.72	0.69
Grad + Grad^2	85.50	0.00	0.75	0.73
Aug_Temp + CA	109.42	0.00	0.68	0.71
Aug_Temp + Grad	111.34	0.00	0.67	0.60
Aug_Temp + TS	114.75	0.00	0.65	0.59
Aug_Temp + TS + Veg	115.58	0.00	0.64	0.60
Veg	119.14	0.00	0.73	0.62
TS + TS^2 + Elev	119.23	0.00	0.72	0.47
TS + TS^2 + Veg	120.58	0.00	0.71	0.56
Elev	121.74	0.00	0.72	0.50
TS + TS^2	125.19	0.00	0.76	0.57

Note: AIC is Akaike's information criterion; ΔAIC is the change in AIC values between the lowest AIC (i.e., highest ranking model) and the given model; AIC *w* is AIC weight. Abbreviations: Aug_Temp, August mean temperatrure (°C); Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); Veg, is percent vegetation (%); TS, is thermal sensitivity.

Table 4.4. Parameter estimates (± SE) and performance statistics of the top model fit to the data (*n* = 411) and used to predict juvenile occupancy across the study area.

Parameter	b_x	SE	ACC	AUC
Intercept	0.46	0.26	0.82	0.80
Aug_Temp	0.56	0.27		
Aug_Temp^2	-1.88	0.32		
TS	-0.66	0.20		
Elev	0.61	0.20		
CA	1.46	0.20		
CA^2	-0.26	0.07		

Abbreviations: ACC, is actual classification accuracy of five-fold (leave-one-out) cross-validation; AUC, is area under of the curve of the receive operator characteristic plot; Aug_Temp, August mean temperatrure (°C); b_x, is the parameter estimate; Elev, elevation (m); CA, is contributing area (ha); TS, is thermal sensitivity. Quadratic terms are displayed with "2" as superscript.

Table 4.5. Amount of available and occupied thermally suitable juvenile bull trout habitat in kilometers (% in parentheses) across the Prairie Creek watershed, Northwest Territories, Canada. Positive values in parentheses represent an increase in available habitat and those with no sign represent the proportion of habitat relative to the 1980s baseline for each respective category. The total amount of available suitable habitat across the watershed for the 1980s baseline is 492 km. The calculations do not include streams with a gradient > 15% or stream order > 3.

	Available thermal habitat - niche tracking			Occupied thermal niche - niche tracking			Available thermal habitat - niche shift		
	Stream km (>4.7°C < 7.5°C)			Occupancy probability > 0.23			Stream km (>4.7°C < 10.0°C)		
Climate scenario	1980s	2040s	2080s	1980s	2040s	2080s	1980s	2040s	2080s
RCP 4.5	309	341 (+10)	319 (+3)	120	92 (77)	86 (72)	357	457 (+28)	459 (+29)
RCP 8.5	309	310 (0)	215 (70)	120	80 (67)	70 (58)	357	458 (+29)	443 (+24)

Figures

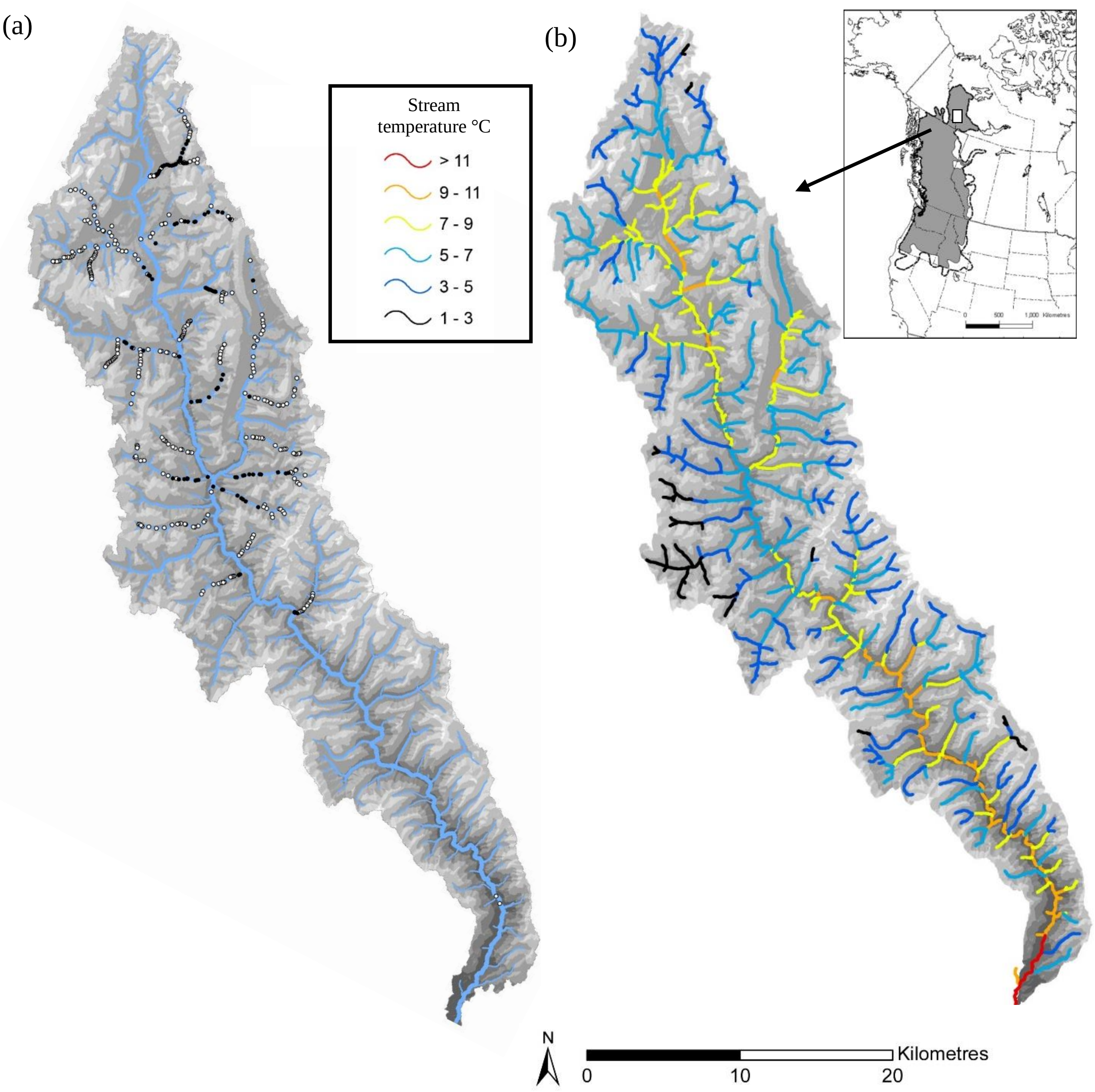


Figure 4.1. Juvenile bull trout distribution (a) and summer stream temperature map (b) for Prairie Creek, Northwest Territories, Canada. The temperatures are based on modelled mean August stream temperature records from 178 summers of data and 132 unique sites. Streams with the lighter and darker blue colors fall within the optimal thermal niche of juvenile bull trout. The white open circles and dark circles correspond to unoccupied and occupied sites, respectively. The dark shaded area on the map in the upper right represents the approximate contemporary distribution of bull trout and the dashed outline is the historic distribution.

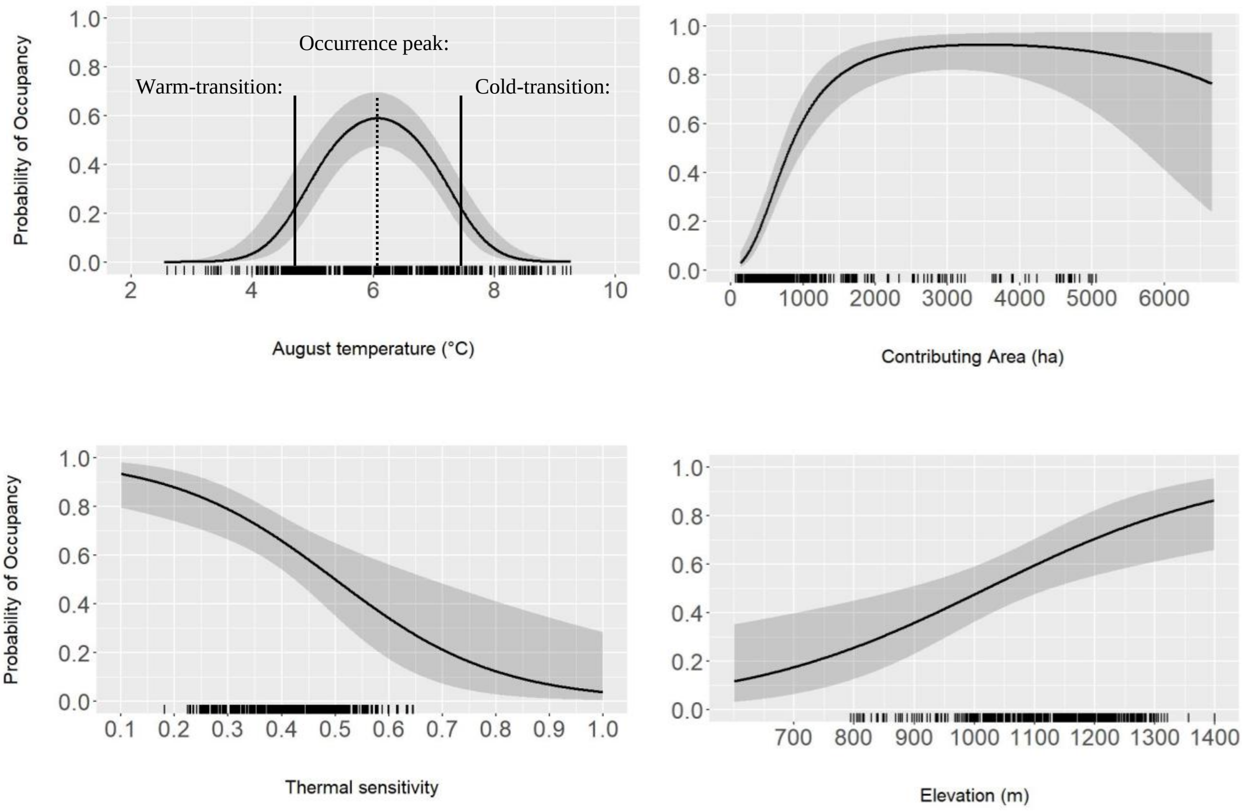
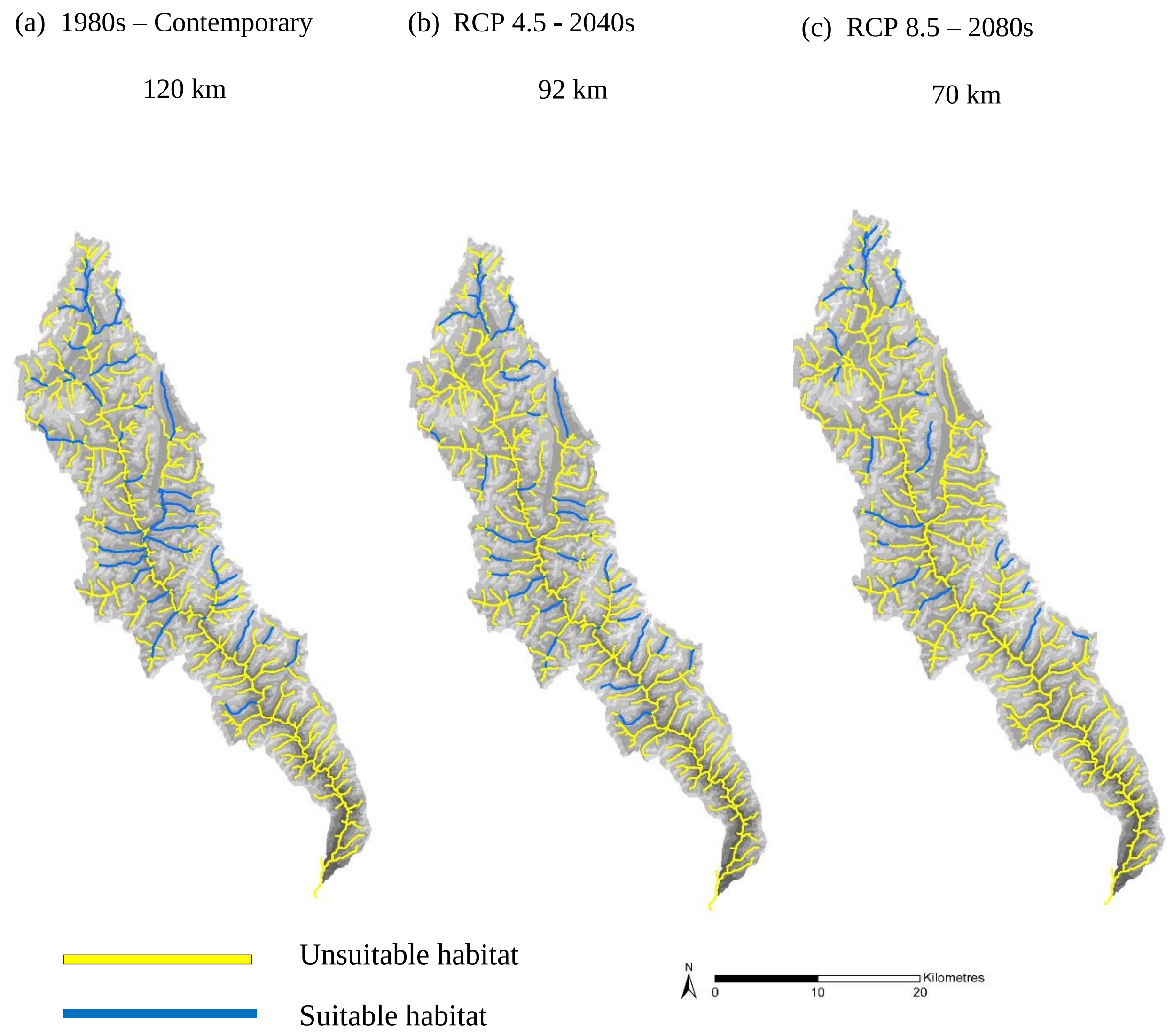


Figure 4.2 Modelled occupancy-response curves for climatic and geomorphic covariates for juvenile bull trout in the Prairie Creek watershed, Northwest Territories. Note that occurrence peak, cold-transition, and warm-transition temperatures are shown on the August stream temperature curve. For each response curve, other covariates from the model were held constant using the mean of each covariate. The solid line represents the mean modelled occupancy probabilities across all sites from the top model and the grey shaded areas are 95% confidence intervals. Dark vertical lines on the x-axis show points where data were taken during the sampling campaign. The range of the contributing area, thermal sensitivity, and elevation occupancy-response curves extend beyond the sampling data frame for illustrative purposes.


(a) 1980s – Contemporary

120 km

(b) RCP 4.5 - 2040s

92 km

(c) RCP 8.5 – 2080s

70 km

Figure 4.3 Comparison of suitable habitat predicted to be occupied by juvenile bull trout in Prairie Creek, Northwest Territories, based on modelled occurrence probabilities for (a) contemporary; (b) RCP 4.5, 2040s; and RCP 4.5, 2080s climate scenarios. Suitable-unsuitable habitats correspond to a prevalence threshold (> 0.23) derived from modelled probabilities using the top model. The total length of suitable habitat for each scenario is expressed as linear stream kilometers.

(a) 1980s – niche tracking

(b) 1980s – niche evolution

(c) RCP 4.5 2040s – niche tracking

(d) RCP 4.5 2040s – niche evolution

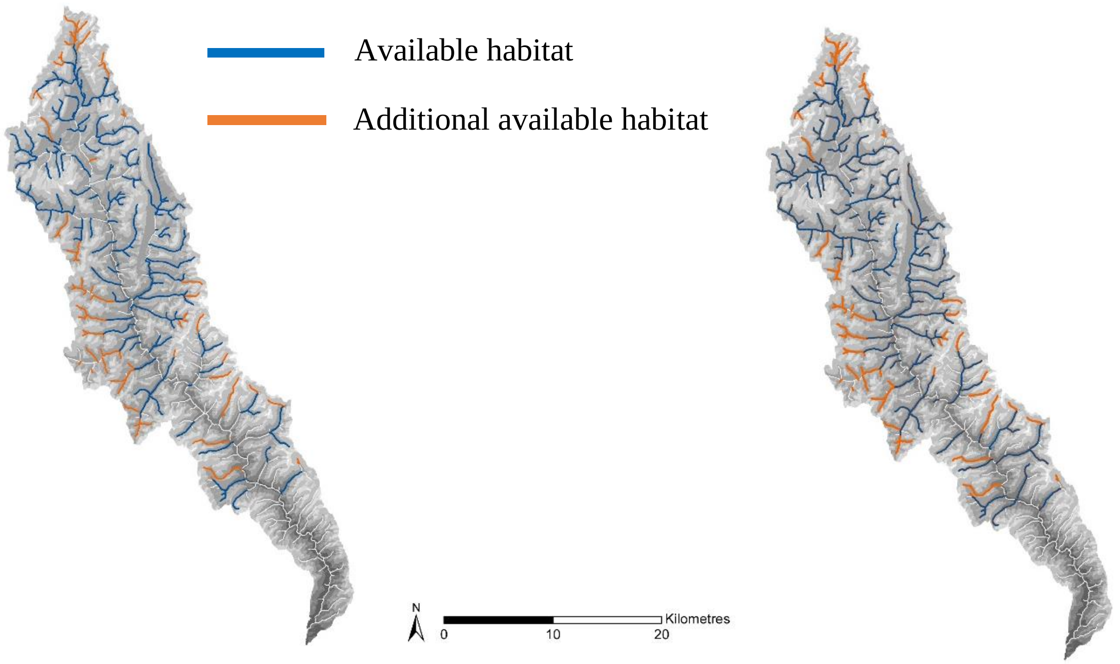


Figure 4.4. Availability of suitable summer thermal habitat for juvenile bull trout across the Prairie Creek watershed corresponding to the current thermal niche this population occupies (4.7°C – 7.5°C; a, c), and a broader hypothetical thermal niche (4.7°C – 10.0°C; b, d). These two scenarios correspond to niche tracking and niche evolution hypotheses. The range of stream temperatures used for the niche evolution scenario was based on the broader definition of the species' thermal niche and assumes this population has the ability to occupy a warmer thermal niche.

Supplemental information

Climate projections

Table S4.1. Projected changes in mean August air temperatures and stream temperatures across the Prairie Creek watershed. Projections are based on RCP 4.5 and 8.5 emissions scenarios and changes in stream temperatures account for differential stream sensitivity at 1 km prediction points across the watershed. Changes in mean stream temperatures are expressed relative to the 1980s (1948 - 2018) baseline climate period.

	2040s (2030-2059)		2080s (2070-2099)	
Climate scenario	Air temperature Δ (°C)	Stream temperature Δ (°C)	Air temperature Δ (°C)	Stream temperature Δ (°C)
RCP 4.5	2.00	0.85	2.60	1.21
RCP 8.5	2.80	1.12	4.50	1.93

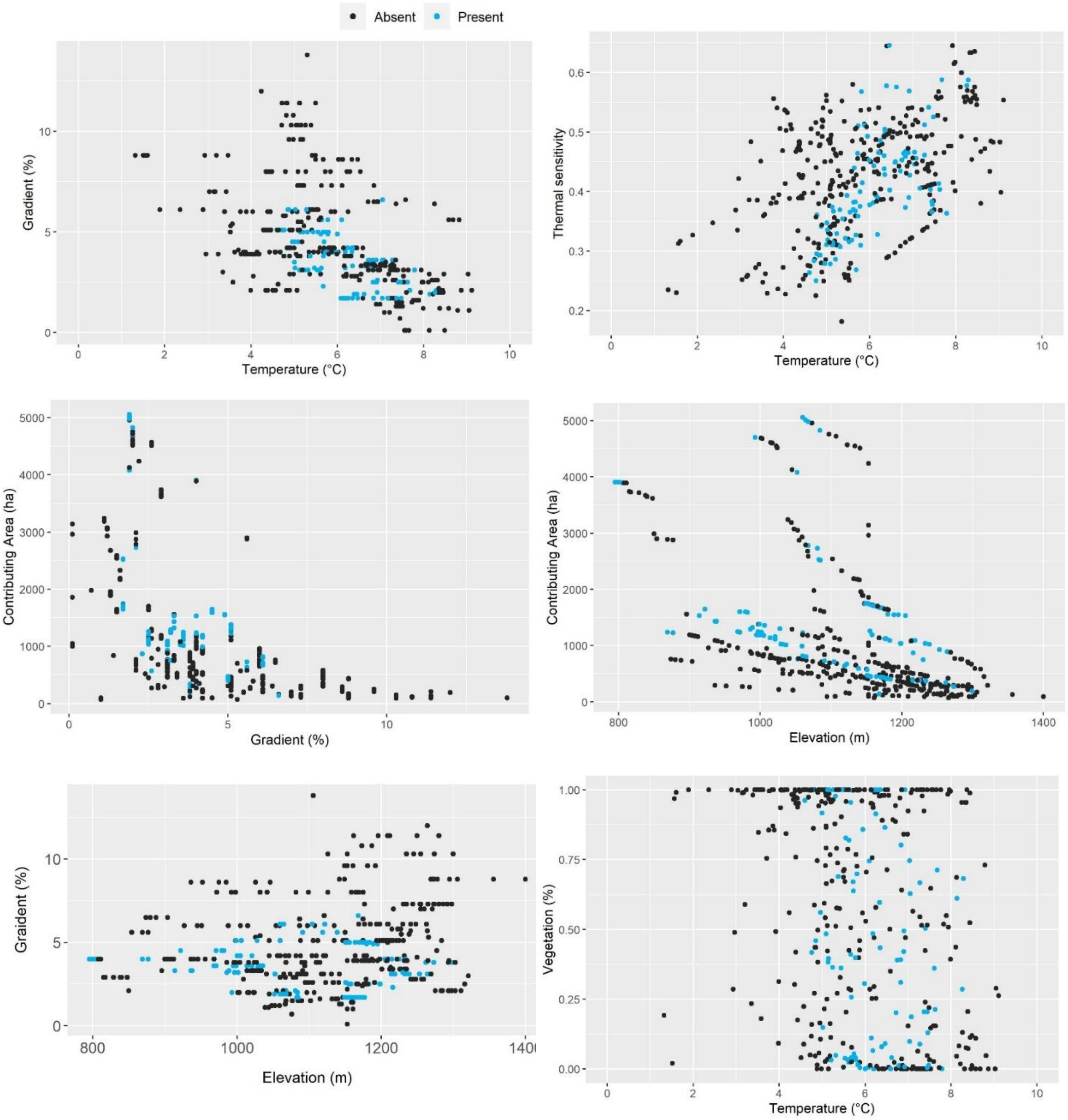


Figure S4.1. Scatter plots of covariates from the 411 fish collection sites used to develop generalized linear models in the Prairie Creek watershed.

Alternative modelling approach

Since I suspected spatial dependency related to habitat patches could influence parameter estimates (Fig. S4.2), a generalized linear mixed effects model (referred to as Model 1), with patch as a random intercept, was also used to examine the relative importance of climatic, geomorphic, and biotic factors on juvenile bull trout distribution using the lme4 package in R (Bates et al. 2018). Results show that the fixed effects and random effect of patch accounted for 78% and 21% of the variation in juvenile occupancy, respectively. Despite this, predictive performance of the best supported GLMM was low compared to the top supported GLM (GLM, Table 4.3; GLMM, Table S4.2). Since patch had an effect on occupancy but model performance was lower than expected, I used the influence.ME (Nieuwenhuis et al. 2012) package to test for highly influential habitat patches that could be affecting parameter estimates. Influential patches were identified through an iterative process whereby each patch was sequentially removed and then parameter estimates were checked to estimate patch influence using Cook's distance (Cook 1977). After nine influential patches were removed from the data set, none of the remaining patches had a large influence on the model parameters (Fig. S4.3). Therefore, a second GLMM (referred to as Model 2) was run on the candidate model set based on a modification of the intercept and the addition of dummy variables for the patches that were most influential (Nieuwenhuis et al. 2012). Predictive performance of Model 2 was low (ACC/AUC = 0.65, 0.60), relative to both the GLMM and GLM that used the full data set. Although two of the GLMMs specified using the full data set (Model 1) had similar predictive performance as the top GLM (M7, ACC = 0.81; M25, ACC = 0.79), the confusion matrix from the cross-validation results showed that the proportion of time that true positives were correctly identified in these models (M7 =0.27, M25 = 0.27), was much lower than the top GLM (0.78). For these reasons, I chose to use the GLM for predicting occupancy probabilities across the watershed.

Table S4.2. Best supported models from the candidate model set based on Akaike's information criterion (AIC), model weight, and predictive performance metrics. Predictive performance was evaluated using five-fold (leave-one-out) cross validation accuracy (ACC) and area under the curve (AUC) of the receiver-operator characteristic plot. The most supported model is shown in bold.

Model	Model No.	ΔAIC	AIC *w*	ACC	AUC
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + Grad + Grad^2	2	0.00	0.90	0.75	0.74
Aug_Temp + Aug_Temp^2 + TS + Elev + Grad + Grad^2	23	4.46	0.10	0.74	0.74
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Grad + Grad^2 + Veg	1	11.10	0.00	0.73	0.72
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + CA + CA^2	3	13.24	0.00	0.74	0.65
Aug_Temp + Aug_Temp^2 + TS + Elev + CA + CA^2	24	15.43	0.00	0.74	0.64
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Elev + Veg	4	20.68	0.00	0.72	0.61
Aug_Temp + Aug_Temp^2 + Grad + Grad^2	6	23.0	0.00	0.72	0.78
Aug_Temp + Aug_Temp^{2+} CA + CA^2	7	24.0	0.00	0.81	0.78
Aug_Temp + Aug_Temp^2 + TS + TS^2 + CA + CA^2 + Veg	25	24.8	0.00	0.79	0.76
Aug_Temp + Aug_Temp^2 + Elev	5	25.5	0.00	0.71	0.66
Aug_Temp + Aug_Temp^2 + TS + TS^2 + Veg	15	47.2	0.00	0.70	0.65
Aug_Temp + TS	13	53.0	0.00	0.70	0.68
Aug_Temp + Aug_Temp^2	18	63.13	0.00	0.69	0.74
Aug_Temp + Aug_Temp^2 + Veg	8	65.06	0.00	0.69	0.74
TS + TS^2 + Grad + Grad^2	10	74.69	0.00	0.60	0.64
Grad + Grad^2	21	83.73	0.00	0.60	0.66
TS + TS^2 + Elev	9	95.74	0.00	0.67	0.56
Elev	20	100.11	0.00	0.68	0.52
CA + CA^2	19	103.08	0.00	0.67	0.61
TS + TS^2 + CA + CA^2	11	103.31	0.00	0.70	0.68
Aug_Temp + CA	27	118.90	0.00	0.67	0.47
Aug_Temp + Grad	26	127.99	0.00	0.59	0.58
TS + TS^2 + Veg	12	131.72	0.00	0.60	0.45
Aug_Temp + TS + Veg	16	135.47	0.00	0.61	0.54
TS + TS^2	17	135.70	0.00	0.45	0.68
Aug_Temp + TS	14	148.66	0.00	0.57	0.55
Veg	22	153.25	0.00	0.57	0.62
	28				

Note: AIC is Akaike's information criterion; ΔAIC is the change in AIC values between the lowest AIC (i.e., highest ranking model) and the given model; AIC *w* is AIC weight. Abbreviations: Aug_Temp, August mean temperatrure (°C); Elev, elevation (m); CA, contributing area (ha); Grad, stream gradient (%); Veg, is percent vegetation (%); TS, is thermal sensitivity.

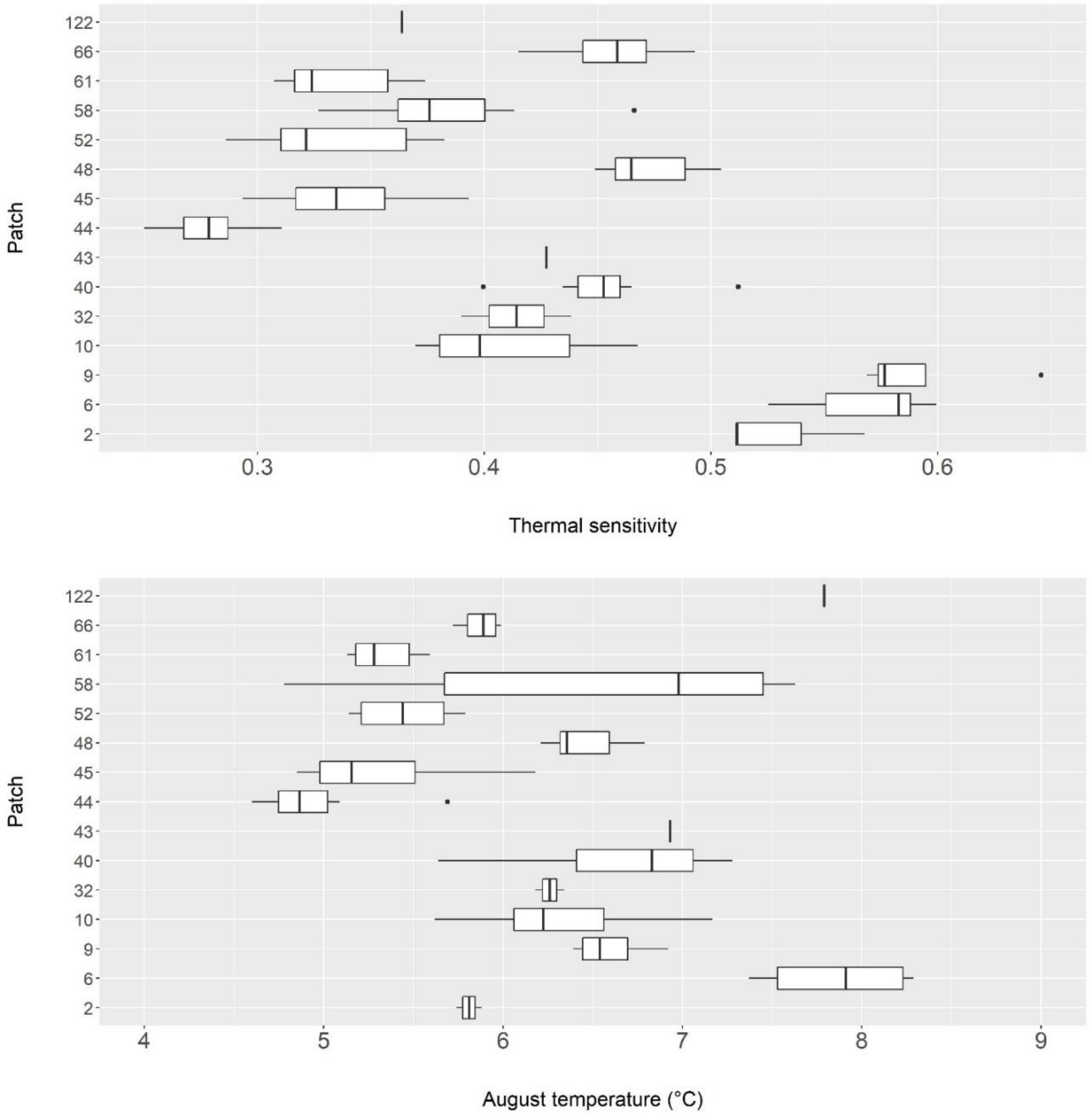


Figure S4.2. Boxplots of mean August stream temperature and thermal sensitivity at sites where juvenile bull trout are present across patches.

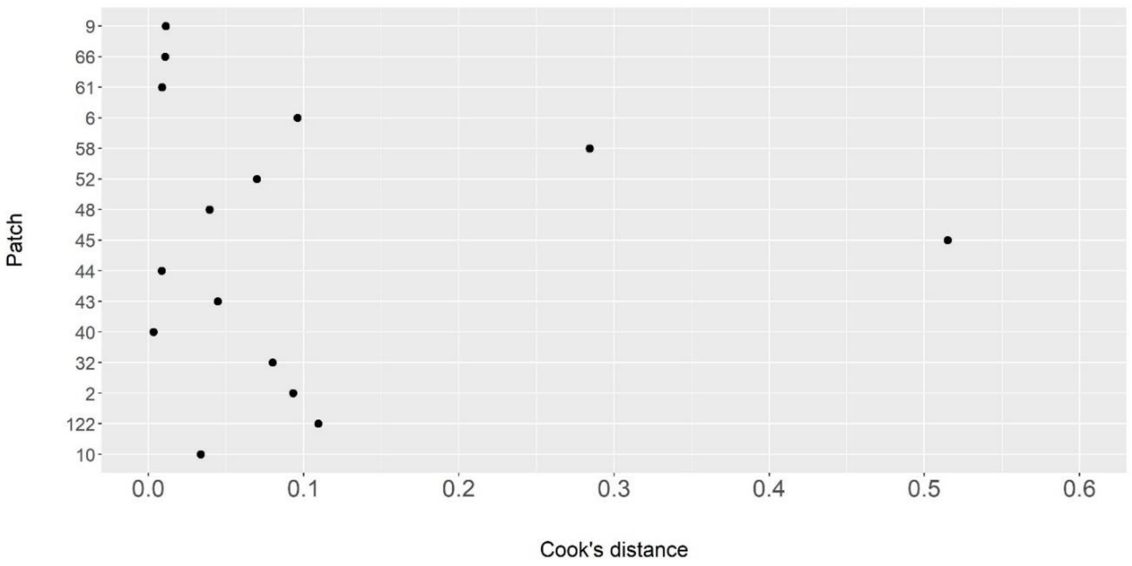


Figure S4.3. Cook’s distance values calculated by patch after the influential patches were removed.

Occurrence data

Table S4.3. Occurrence of bull trout from 2012 to 2016 in the Prairie Creek watershed, NT. Abbreviations: S, is survey and number corresponds to the survey number (S1 = survey one) and presence (1) or absence (0) of bull trout with fork lengths ≤150 mm; SO, is stream order; ≤150mm, presence-absence of bull trout at a site based on data from all surveys; ≥175mm, presence/absence of bull trout at a site with fork lengths greater than or equal to 175 mm; DD, decimal degrees; SiteID, is the sampling site identification number.

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
10-3-03	0	0	0	-	-	3	0	0	124.94789	61.79619
10-3-04	0	0	0	-	-	3	0	0	124.94620	61.79658
10-3-05	0	0	0	-	-	3	0	0	124.94426	61.79625
10-3-06	0	0	0	-	-	3	0	1	124.94279	61.79654
10-3-07	0	0	0	-	-	3	0	0	124.94109	61.79674
10-3-08	0	-	-	-		3	0	1	124.93968	61.79745
10-3-09	1	1	0	-	-	3	1	0	124.93870	61.79785
10-3-11	0	0	1	-	-	3	1	1	124.93686	61.79878
10-3-13	0	0	1	-	-	3	1	0	124.93563	61.80041
10-3-15	0	-	-	-		3	0	1	124.93326	61.80188
10-3-17	0	1	0	-	-	3	1	0	124.93222	61.80342
10-3-19	0	1	1	-	-	3	1	0	124.92962	61.80435
10-3-21	1	1	1	-	-	3	1	0	124.92641	61.80467
10-3-22	1	1	0	-	-	3	1	0	124.92452	61.80470
10-3-23	1	1	1	-	-	3	1	0	124.92289	61.80454
10-3-25	1	1	0	-	-	3	1	0	124.91953	61.80424
10-3-27	1	1	1	-	-	3	1	1	124.91694	61.80489
10-3-29	1	1	1	-	-	3	1	1	124.91487	61.80528
10-3-30	1	1	1	-	-	3	1	1	124.91357	61.80575
111-1-12	0	0	0	-		1	0	0	124.90806	61.62812
111-1-14	0	0	0	-		1	0	0	124.90554	61.62689

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
111-1-15	0	0	0	-		1	0	0	124.90416	61.62636
111-1-16	0	0	0	-		1	0	0	124.90263	61.62586
111-1-19	0	0	0	-		1	0	0	124.89838	61.62412
111-1-23	0	0	0	-		1	0	0	124.89188	61.62259
111-1-25	0	0	0	-		1	0	0	124.88860	61.62192
111-1-29	0	0	0	-		1	0	0	124.88141	61.62130
111-1-30	0	0	0	-		1	0	0	124.87953	61.62124
111-1-35	0	0	0	-		1	0	0	124.87134	61.61991
111-1-36	0	0	0	-		1	0	0	124.86952	61.61976
111-1-38	0	0	0	-		1	0	0	124.86576	61.61963
122-1-03	0	0	0	-	-	2	0	0	124.79914	61.66021
122-1-07	1	0	1	-	-	2	1	0	124.79267	61.65877
122-1-11	0	0	0	-	-	2	0	0	124.78552	61.65788
122-1-14	0	0	0	-	-	2	0	0	124.78042	61.65749
122-1-19	0	0	0	-		2	0	1	124.77198	61.65662
122-1-21	0	0	0	-		2	0	0	124.76853	61.65603
122-1-24	0	0	0	-	-	2	0	0	124.76337	61.65502
122-1-25	0	0	0	-		2	0	0	124.76166	61.65477
122-1-30	0	0	0	-	-	2	0	0	124.75322	61.65398
122-1-31	0	0	0	-		2	0	0	124.75133	61.65392
122-1-34	0	0	0	-	-	2	0	0	124.74614	61.65416
122-1-37	0	0	0	-	-	2	0	0	124.74111	61.65530
122-1-45	0	0	0	-	-	1	0	0	124.73272	61.66071
122-1-49	0	0	0	-	-	1	0	0	124.73196	61.66413
122-1-50	0	0	-	-	-	1	0	0	124.73183	61.66512
122-1-59	0	0	-	-	-	1	0	0	124.72997	61.67229
1-901	0	-	-	-		4	0	1	124.41670	61.34578
1-902	0	-	-	-		4	0	1	124.41144	61.34108
2-3-01	0	-	-	-		3	0	0	124.71215	61.52098

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
2-3-02	0	1	0	-	-	3	1	0	124.71196	61.52098
2-3-03	1	0	0	-	-	3	1	0	124.71009	61.52110
2-3-04	1	0	0	-	-	3	1	1	124.70857	61.52094
2-3-05	0	-	-	-	-	3	0	0	124.70690	61.52123
2-3-06	0	0	-	-	-	3	0	0	124.70541	61.52160
2-3-07	0	0	0	-	-	3	0	0	124.70358	61.52190
2-3-08	0	0	0	-	-	3	0	0	124.70207	61.52238
2-3-10	0	0	-	-	-	3	0	0	124.69966	61.52376
2-3-13	0	0	-	-	-	3	0	0	124.69634	61.52589
2-3-14	0	0	-	-	-	3	0	0	124.69554	61.52672
2-3-17	0	0	0	-	-	3	0	0	124.69209	61.52868
2-3-18	0	0	0	-	-	3	0	0	124.69122	61.52950
2-3-19	0	0	0	-	-	3	0	0	124.69047	61.53029
2-3-21	0	0	0	-	-	3	0	0	124.68962	61.53201
2-3-23	0	0	0	-	-	3	0	0	124.68967	61.53376
32-2-05	0	0	-	-	-	2	0	0	124.84016	61.52889
32-2-07	0	0	-	-	-	2	0	0	124.83831	61.53044
32-2-17	0	0	-	-	-	2	0	1	124.82491	61.53567
32-2-25	0	0	-	-	-	2	0	0	124.81179	61.53729
32-2-26	0	0	-	-	-	2	0	0	124.81014	61.53758
32-2-32	0	0	-	-	-	2	0	0	124.80223	61.54083
32-2-33	0	0	-	-	-	2	0	0	124.80075	61.54130
32-2-34	0	0	0	-		2	0	0	124.79927	61.54159
32-2-35	0	0	-	-	-	2	0	0	124.79746	61.54170
32-2-39	0	1	-	-	-	2	1	0	124.79126	61.54304
32-2-40	1	0	-	-	-	2	1	0	124.78959	61.54351
32-2-901	0	-	-	-		2	0	1	124.81796	61.53622
32-2-902	0	-	-	-		2	0	1	124.81349	61.53700
37-1-06	0	0	0	-		1	0	0	124.92672	61.57002

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
37-1-07	0	0	0	-		1	0	0	124.92822	61.57052
37-1-08	0	0	0	-		1	0	0	124.92967	61.57106
37-1-09	0	0	0	-		1	0	0	124.93151	61.57130
37-2-06	0	0	0	-		2	0	0	124.91749	61.56997
37-2-12	0	0	0	-		2	0	0	124.90727	61.56922
37-2-18	0	0	0	-		2	0	0	124.89683	61.56999
37-2-25	0	0	0	-		2	0	0	124.88598	61.57212
37-2-29	0	0	0	-		2	0	0	124.87887	61.57293
37-2-30	0	0	0	-		2	0	0	124.87757	61.57322
37-2-32	0	0	0	-		2	0	0	124.87437	61.57336
37-2-35	0	0	0	-		2	0	0	124.86909	61.57325
37-2-36	0	0	0	-		2	0	0	124.86757	61.57291
37-2-42	0	0	0	-		2	0	0	124.85719	61.57173
37-2-43	0	0	0	-		2	0	1	124.85539	61.57164
37-2-46	0	0	0	-		2	0	0	124.85058	61.57270
37-2-51	0	0	0	-		2	0	0	124.84322	61.57531
37-2-52	0	0	0	-		2	0	0	124.84216	61.57603
37-2-57	0	0	0	-		2	0	0	124.83858	61.57996
38-13	0	0	-	-	-	2	0	0	124.79049	61.55636
38-14	0	0	-	-	-	2	0	0	124.77450	61.56917
38-15	0	0	-	-	-	2	0	0	124.78234	61.56056
38-16	0	0	-	-	-	2	0	0	124.78851	61.55837
38-17	0	0	-	-	-	2	0	0	124.77639	61.56734
38-18	0	-	-	-	-	2	0	0	124.79250	61.55525
38-19	0	0	-	-	-	2	0	0	124.78981	61.55701
38-20	0	0	-	-	-	2	0	0	124.78003	61.56374
38-21	0	0	-	-	-	2	0	0	124.77936	61.56418
38-22	0	0	-	-	-	2	0	0	124.78110	61.56275
40-1-03	0	0	0	0	0	1	0	0	124.72774	61.61085

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
40-1-06	0	0	0	0	0	1	0	0	124.72377	61.61253
40-1-07	0	-	-	-		1	0	0	124.72272	61.61324
40-1-21	0	0	0	0	0	1	0	0	124.71046	61.60990
40-1-34	0	0	0	0	0	1	0	0	124.72447	61.60731
40-1-38	0	0	0	0	0	1	0	0	124.71997	61.60466
40-1-40	0	-	-	-	-	1	0	0	124.71694	61.60389
40-2-12	1	1	1	-	-	2	1	0	124.80465	61.60608
40-2-13	1	1	1	-	-	2	1	0	124.80282	61.60611
40-2-18	1	1	1	-	-	2	1	0	124.79422	61.60730
40-2-19	1	1	1	-	-	2	1	0	124.79277	61.60766
40-2-23	1	1	1	-	-	2	1	0	124.78586	61.60855
40-2-26	1	1	1	-	-	2	1	0	124.78072	61.60873
40-2-31	1	1	1	-	-	2	1	0	124.77177	61.60903
40-2-32	1	1	1	-	-	2	1	0	124.76989	61.60896
40-2-45	1	1	1	-	-	2	1	1	124.74719	61.61105
40-2-51	1	1	1	-	-	2	1	0	124.73644	61.61065
40-2-53	1	1	1	-	-	2	1	1	124.73298	61.61105
40-2-901	0	-	-	-	-	1	0	1	124.72995	61.61118
41-1-13	1	1	0	-	-	1	1	0	124.72818	61.62341
41-1-14	0	0	0	-	-	1	0	0	124.72622	61.62317
41-1-15	0	0	0	-	-	1	0	0	124.72434	61.62313
41-1-17	0	0	-	-	-	1	0	0	124.72083	61.62349
41-1-18	0	0	0	-	-	1	0	0	124.71915	61.62380
41-2-06	0	0	-	-	-	2	0	0	124.79356	61.63182
41-2-11	0	0	-	-	-	2	0	0	124.78449	61.63230
41-2-12	0	0	-	-	-	2	0	0	124.78306	61.63221
41-2-14	0	0	-	-	-	2	0	0	124.77962	61.63218
41-2-16	0	0	-	-	-	2	0	0	124.77620	61.63187
41-2-18	0	0	-	-	-	2	0	0	124.77241	61.63210

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
41-2-19	0	0	-	-	-	2	0	0	124.77079	61.63188
41-2-30	0	0	-	-	-	2	0	0	124.75334	61.62794
41-2-35	0	0	-	-	-	2	0	0	124.74578	61.62543
41-2-36	0	0	-	-	-	2	0	0	124.74389	61.62546
41-2-38	0	0	-	-	-	2	0	0	124.74044	61.62586
41-2-39	0	0	0	-		2	0	0	124.73857	61.62597
43-1-119	0	-	-	-		1	0	0	124.77981	61.70455
43-1-125	0	0	0	-		1	0	0	124.78135	61.70822
43-1-147	0	0	0	-		1	0	1	124.79451	61.72636
43-1-170	0	0	0	-		1	0	0	124.80367	61.74620
43-1-80	0	-	-	-		1	0	0	124.79071	61.69669
43-1-901	1	-	-	-		1	1	0	124.79835	61.73376
43-1-902	0	-	-	-		1	0	1	124.78268	61.71161
43-1-903	0	-	-	-		1	0	0	124.78103	61.70597
43-2-02	0	0	0	-		3	0	0	124.79204	61.67127
43-2-06	0	0	0	-		3	0	0	124.78903	61.67434
43-2-09	0	0	0	-		3	0	0	124.79048	61.67640
43-2-12	0	0	0	-		3	0	1	124.79100	61.67890
43-2-18	0	0	0	-		3	0	0	124.79074	61.68421
43-2-25	0	0	0	-		3	0	1	124.79129	61.69040
43-2-26	0	0	0	-		3	0	1	124.79032	61.69116
43-2-31	0	0	0	-		2	0	0	124.78720	61.69485
43-2-32	0	0	0	-		2	0	0	124.78669	61.69581
43-2-37	0	0	0	-		2	0	0	124.78254	61.69931
43-2-40	0	0	0	-		2	0	0	124.78002	61.70159
44-1-09	0	0	-	-	-	1	0	0	124.94155	61.61498
44-1-15	0	-	-	-	-	1	0	0	124.94059	61.62026
44-1-16	0	0	0	-	-	1	0	0	124.94046	61.62113
44-1-17	0	-	-	-	-	1	0	0	124.94074	61.62202

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
44-1-43	0	0	-	-	-	2	0	0	124.86978	61.60278
44-2-08	0	0	0	-		2	0	0	124.94098	61.61373
44-2-12	0	0	-	-	-	2	0	0	124.93443	61.61221
44-2-15	0	0	-	-	-	2	0	0	124.92992	61.61245
44-2-33	0	0	-	-	-	2	0	0	124.90273	61.60484
44-2-37	0	0	0	-		2	0	0	124.89584	61.60377
44-2-41	0	1	-	-	-	2	1	0	124.88907	61.60252
44-2-44	0	0	0	-		2	0	0	124.88439	61.60213
44-2-46	0	1	-	-	-	2	1	0	124.88091	61.60218
44-2-50	1	1	-	-	-	2	1	0	124.87393	61.60246
44-2-52	1	1	-	-	-	2	1	1	124.87032	61.60295
44-2-59	1	1	-	-	-	2	1	0	124.85821	61.60231
44-2-60	1	1	-	-	-	2	1	1	124.85668	61.60251
44-2-61	1	1	-	-	-	2	1	0	124.85484	61.60272
44-2-69	1	1	-	-	-	2	1	0	124.84179	61.60514
44-2-901	0	-	-	-		2	0	1	124.94285	61.61416
45-1-24	0	0	0	0	0	1	0	0	124.83611	61.68427
45-1-26	0	0	0	0	0	1	0	0	124.83565	61.68603
45-1-32	0	0	0	0	0	1	0	0	124.83140	61.69093
45-1-901	0	0	0	0	0	1	0	0	124.83616	61.68199
45-1-902	0	0	0	0	0	1	0	0	124.83456	61.68857
45-2-05	1	1	1	-	-	2	1	0	124.87116	61.65278
45-2-10	1	1	1	-	-	2	1	1	124.86261	61.65335
45-2-12	1	1	1	-	-	2	1	0	124.85922	61.65366
45-2-20	1	1	1	-	-	2	1	0	124.84712	61.65661
45-2-28	1	1	0	-	-	1	1	0	124.83762	61.66213
45-2-29	1	1	1	-	-	1	1	1	124.83675	61.66293
45-2-36	1	1	0	-	-	1	1	0	124.83214	61.66836
45-2-40	0	1	0	-	-	1	1	0	124.83026	61.67174

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
45-2-49	0	0	0	-	-	1	0	0	124.83561	61.67897
45-2-51	0	0	0	-	-	1	0	0	124.83646	61.68064
45-2-52	0	0	0	-	-	1	0	0	124.83632	61.68145
46-2-06	0	-	-	-	-	2	0	0	124.95285	61.64854
46-2-14	0	-	-	-	-	2	0	0	124.95146	61.65506
46-2-28	0	0	-	-	-	2	0	0	124.94499	61.66626
46-2-31	0	0	-	-	-	2	0	1	124.94535	61.66891
46-2-33	0	0	-	-	-	2	0	1	124.94546	61.67071
46-2-37	0	0	-	-	-	2	0	1	124.94417	61.67421
46-2-39	0	0	-	-	-	2	0	1	124.94371	61.67592
46-2-41	0	0	-	-	-	2	0	1	124.94401	61.67772
46-2-44	0	0	-	-	-	2	0	1	124.94455	61.68036
46-2-46	0	0	-	-	-	2	0	0	124.94447	61.68204
46-2-902	0	0	0	-		2	0	0	124.94520	61.66656
47-2-05	0	0	0	-		2	0	0	124.99104	61.67147
47-2-06	0	0	0	-		2	0	0	124.99013	61.67221
47-2-07	0	0	0	-		2	0	0	124.98907	61.67303
47-2-08	0	0	0	-		2	0	0	124.98798	61.67367
47-2-09	0	0	0	-		2	0	0	124.98650	61.67432
47-2-10	0	0	0	-		2	0	0	124.98521	61.67488
47-2-11	0	0	0	-		2	0	0	124.98355	61.67544
47-2-12	0	0	0	-		2	0	0	124.98227	61.67609
47-2-13	0	0	0	-		2	0	0	124.98097	61.67666
47-2-14	0	0	0	-		2	0	0	124.97967	61.67731
47-2-15	0	0	0	-		2	0	0	124.97848	61.67800
47-2-18	0	-	-	-		2	0	0	124.97593	61.68038
47-2-21	0	0	0	-		2	0	0	124.97629	61.68303
47-2-22	0	0	0	-		2	0	0	124.97616	61.68390
47-2-23	0	0	0	-		2	0	0	124.97621	61.68478

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
47-2-25	0	0	0	-		2	0	0	124.97633	61.68657
47-2-28	0	0	0	-		2	0	0	124.97669	61.68924
48-01	0	-	-	-	-	1	0	0	124.76244	61.58899
48-03	0	-	-	-	-	1	0	0	124.75176	61.58342
48-08	0	-	-	-	-	1	0	0	124.75044	61.58117
48-12	1	1	-	-	-	2	1	0	124.82138	61.59733
48-13	0	0	-	-	-	2	0	0	124.83573	61.59509
48-14	0	0	-	-	-	2	0	0	124.75951	61.58675
48-15	1	1	-	-	-	2	1	1	124.79229	61.59201
48-16	0	1	-	-	-	2	1	0	124.82001	61.59735
48-17	0	-	-	-	-	2	0	0	124.74216	61.58687
48-18	0	0	0	-	-	2	0	0	124.76359	61.58776
48-19	1	1	-	-	-	2	1	0	124.78818	61.59068
48-20	1	0	-	-	-	2	1	0	124.83348	61.59907
48-21	0	-	-	-	-	2	0	0	124.74052	61.58696
48-22	1	1	-	-	-	2	1	1	124.77108	61.58775
48-23	1	1	-	-	-	2	1	1	124.80024	61.59428
48-901	0	-	-	-	-	1	0	0	124.73700	61.58559
48-902	0	-	-	-	-	1	0	0	124.73504	61.58427
48-903	1	-	-	-	-	2	1	0	124.79413	61.59275
52-1-02	0	0	-	-	-	1	0	0	124.83871	61.71845
52-1-04	0	0	-	-	-	1	0	0	124.83938	61.72021
52-1-06	0	0	-	-	-	1	0	0	124.83873	61.72196
52-1-07	0	0	-	-	-	1	0	0	124.83840	61.72282
52-1-08	0	0	-	-	-	1	0	0	124.83846	61.72371
52-1-10	0	0	-	-	-	2	0	0	124.83736	61.72436
52-1-12	0	0	-	-	-	2	0	0	124.83410	61.72368
52-1-17	0	0	-	-	-	1	0	0	124.82560	61.72450
52-2-02	1	1	-	-	-	2	1	1	124.86193	61.72690

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
52-2-03	1	1	-	-	-	2	1	1	124.86017	61.72655
52-2-04	1	1	-	-	-	2	1	1	124.85849	61.72641
52-2-05	1	1	-	-	-	2	1	1	124.85676	61.72598
52-2-06	1	1	-	-	-	2	1	1	124.85484	61.72583
52-2-07	1	1	-	-	-	2	1	1	124.85313	61.72558
52-2-08	1	1	-	-	-	2	1	1	124.85144	61.72515
52-2-09	1	0	-	-	-	2	1	1	124.84968	61.72499
52-2-10	0	1	-	-	-	2	1	1	124.84818	61.72484
55-2-02	0	-	-	-	-	2	0	0	125.01800	61.72753
55-2-03	0	-	-	-	-	2	0	0	125.01836	61.72841
55-2-04	0	0	-	-	-	2	0	0	125.01845	61.72931
55-2-05	0	0	-	-	-	2	0	0	125.01854	61.73020
55-2-06	0	-	-	-	-	2	0	0	125.01941	61.73100
55-2-07	0	0	-	-	-	2	0	0	125.02029	61.73179
55-2-08	0	0	-	-	-	2	0	0	125.02111	61.73260
55-2-09	0	0	-	-	-	2	0	0	125.02184	61.73343
55-2-11	0	0	-	-	-	2	0	0	125.02258	61.73513
55-2-12	0	0	-	-	-	2	0	0	125.02250	61.73601
55-2-13	0	0	-	-	-	2	0	0	125.02250	61.73691
55-2-14	0	0	-	-	-	2	0	0	125.02263	61.73779
55-2-15	0	0	-	-	-	2	0	0	125.02182	61.73860
55-2-17	0	-	-	-	-	2	0	0	125.02019	61.74022
55-2-18	0	0	-	-	-	2	0	0	125.01916	61.74086
55-2-19	0	0	-	-	-	2	0	0	125.01901	61.74175
55-2-20	0	0	-	-	-	2	0	0	125.01860	61.74262
55-2-21	0	0	-	-	-	2	0	0	125.01854	61.74352
55-2-22	0	-	-	-	-	2	0	0	125.01854	61.74441
55-2-26	0	-	-	-	-	2	0	0	125.01620	61.74780
56-1-11	0	0	0	-		1	0	0	125.07214	61.73690

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
56-1-12	0	0	0	-		1	0	0	125.07024	61.73684
56-1-14	0	0	0	-		1	0	0	125.06704	61.73707
56-1-15	0	0	0	-		1	0	0	125.06517	61.73728
56-1-16	0	0	0	-		1	0	0	125.06348	61.73757
56-2-03	0	0	0	-		2	0	0	125.05777	61.73990
56-2-04	0	0	0	-		2	0	0	125.05593	61.74018
56-2-06	0	0	0	-		2	0	0	125.05249	61.74025
56-2-07	0	0	0	-		2	0	0	125.05059	61.74028
56-2-09	0	0	0	-		2	0	0	125.04778	61.74068
56-2-10	0	0	0	-		2	0	0	125.04634	61.74122
56-2-12	0	0	0	-		2	0	0	125.04465	61.74282
58-1-03	0	-	-	-		1	0	0	124.94218	61.75694
58-1-09	1	0	0	-		1	1	0	124.93424	61.75348
58-1-113	0	0	0	0	0	1	0	1	124.91846	61.77225
58-1-66	1	1	1	1	1	1	1	0	124.85223	61.77660
58-1-70	1	0	0	0	0	1	1	0	124.84576	61.77623
58-1-77	1	0	0	0	0	1	1	0	124.83512	61.77261
58-1-79	0	0	0	0	0	1	0	0	124.83279	61.77165
58-1-901	0	-	-	-	-	1	0	0	124.83802	61.77364
58-2-02	0	0	-	-	-	2	0	0	124.95478	61.75533
58-2-23	0	0	-	-	-	2	0	1	124.92770	61.76562
58-2-34	0	1	-	-	-	2	1	0	124.91000	61.76656
58-2-36	1	0	-	-	-	2	1	1	124.90721	61.76740
58-2-40	0	-	-	-		2	0	0	124.90123	61.76883
58-2-43	1	0	-	-	-	2	1	0	124.89546	61.76909
58-2-45	1	0	-	-	-	2	1	1	124.89196	61.76896
58-2-50	1	1	-	-	-	2	1	1	124.88311	61.76899
58-2-60	1	0	-	-	-	2	1	1	124.87004	61.77432
58-2-901	0	-	-	-		2	0	0	124.93950	61.75950

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
58-2-902	0	-	-	-		2	0	0	124.92457	61.76617
58-2-903	0	-	-	-		2	0	1	124.92230	61.76629
58-2-904	1	-	-	-		2	1	0	124.89669	61.76898
58-2-905	1	-	-	-		2	1	0	124.89594	61.76909
58-2-906	1	-	-	-		2	1	0	124.88193	61.76928
58-2-907	0	0	0	-		2	0	0	124.86208	61.77961
58-2-908	1	-	-	-		2	1	1	124.86508	61.77597
61-2-03	1	1	1	-	-	2	1	1	124.90826	61.80887
61-2-04	1	1	1	-	-	2	1	1	124.90775	61.80972
61-2-08	1	1	1	-	-	2	1	1	124.90628	61.81320
61-2-11	1	1	1	-	-	2	1	1	124.90451	61.81566
61-2-15	1	1	1	-	-	2	1	1	124.90187	61.81898
61-2-18	0	1	1	-	-	2	1	1	124.89973	61.82120
61-2-20	0	0	0	-	-	2	0	1	124.89870	61.82295
61-2-22	0	0	0	-	-	2	0	1	124.89785	61.82455
61-2-24	0	0	0	-	-	2	0	0	124.89739	61.82635
61-2-25	0	0	0	-	-	2	0	1	124.89726	61.82731
61-2-29	0	0	0	-	-	2	0	0	124.90010	61.83036
61-2-30	0	0	0	-	-	2	0	1	124.90120	61.83111
61-2-36	0	0	0	-		2	0	0	124.90630	61.83539
61-2-42	0	0	0	-	-	2	0	1	124.91075	61.83964
61-2-44	0	0	0	-	-	2	0	1	124.91383	61.84031
6-3-06	1	1	0	-	-	3	1	0	124.96758	61.68869
6-3-07	0	0	1	-	-	3	1	1	124.96604	61.68827
6-3-08	1	0	0	-	-	3	1	0	124.96486	61.68766
6-3-13	1	0	1	-	-	3	1	0	124.95714	61.68516
6-3-14	0	0	0	-	-	3	0	0	124.95560	61.68465
6-3-20	0	0	0	-	-	3	0	0	124.94591	61.68389
6-3-23	0	1	0	-	-	3	1	0	124.94118	61.68386

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
6-3-27	0	0	0	-	-	3	0	1	124.93481	61.68439
6-3-37	0	0	0	-	-	3	0	0	124.91793	61.68383
6-3-38	0	0	0	-	-	3	0	1	124.91610	61.68377
6-3-42	0	0	0	-	-	3	0	0	124.90939	61.68323
6-3-43	0	0	0	-	-	3	0	0	124.90768	61.68308
6-3-48	0	0	0	-	-	3	0	0	124.89872	61.68194
6-3-49	0	0	0	-	-	3	0	0	124.89725	61.68154
6-3-52	1	0	0	-	-	3	1	0	124.89189	61.68141
66-03	0	0	-	-	-	1	0	0	124.88500	61.80708
66-06	0	0	-	-	-	1	0	0	124.88472	61.80930
66-13	0	0	-	-	-	2	0	1	124.89517	61.80758
66-15	1	1	-	-	-	2	1	0	124.90257	61.80644
66-16	0	-	-	-	-	2	0	0	124.90810	61.80681
66-18	1	0	-	-	-	2	1	1	124.90509	61.80658
66-20	1	1	0	-	-	2	1	0	124.89930	61.80666
66-21	1	1	-	-	-	2	1	0	124.90998	61.80732
66-22	0	0	-	-	-	2	0	0	124.90321	61.80661
66-23	0	0	-	-	-	2	0	0	124.88926	61.80851
68-01	0	0	-	-	-	1	0	0	125.03304	61.76461
68-03	0	-	-	-	-	1	0	0	124.99554	61.76230
68-04	0	-	-	-	-	1	0	0	125.04843	61.78431
68-05	0	0	-	-	-	1	0	0	125.01381	61.75982
68-06	0	-	-	-	-	1	0	0	124.99797	61.75815
68-07	0	0	-	-	-	1	0	0	125.02892	61.76503
68-08	0	0	-	-	-	1	0	0	125.02535	61.76352
68-10	0	-	-	-	-	1	0	0	125.05552	61.78351
68-11	0	-	-	-	-	1	0	0	125.03954	61.78337
68-12	0	-	-	-	-	2	0	0	125.02042	61.76822
68-13	0	-	-	-	-	2	0	0	125.02159	61.77446

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
68-14	0	-	-	-	-	2	0	0	125.03626	61.78231
68-15	0	0	-	-	-	2	0	0	125.00593	61.75871
68-16	0	0	-	-	-	2	0	0	125.01482	61.76292
68-17	0	0	-	-	-	2	0	0	125.02720	61.77889
68-18	0	-	-	-	-	2	0	0	125.02115	61.77357
68-19	0	0	-	-	-	2	0	0	125.01609	61.76428
68-20	0	0	0	-	-	2	0	0	124.99495	61.75608
68-21	0	0	-	-	-	2	0	0	125.00713	61.75906
68-22	0	0	-	-	-	2	0	0	124.98931	61.75322
71-901	0	-	-	-	-	2	0	1	125.04706	61.74402
7-3-01	0	-	-	-	-	3	0	0	124.89313	61.69187
7-3-02	0	-	-	-	-	3	0	0	124.89203	61.69261
7-3-03	0	-	-	-	-	3	0	0	124.89088	61.69315
7-3-04	0	-	-	-	-	3	0	0	124.89018	61.69398
7-3-05	0	-	-	-	-	3	0	0	124.88917	61.69474
7-3-06	0	-	-	-	-	3	0	0	124.88815	61.69550
7-3-07	0	-	-	-	-	3	0	0	124.88771	61.69634
7-3-09	0	-	-	-	-	3	0	0	124.88735	61.69812
7-3-10	0	-	-	-	-	3	0	0	124.88771	61.69897
7-3-12	0	-	-	-	-	3	0	0	124.88632	61.70059
7-3-14	0	-	-	-	-	3	0	0	124.88383	61.70183
7-3-15	0	-	-	-	-	3	0	0	124.88285	61.70260
7-3-16	0	-	-	-	-	3	0	0	124.88224	61.70340
7-3-17	0	-	-	-	-	3	0	0	124.88113	61.70407
7-3-18	0	-	-	-	-	3	0	0	124.87999	61.70467
9-3-05	0	0	0	-	-	3	0	0	125.03745	61.74488
9-3-06	0	0	0	-	-	3	0	1	125.03562	61.74517
9-3-07	0	0	0	-	-	3	0	1	125.03404	61.74565
9-3-10	0	0	0	-	-	3	0	1	125.03054	61.74749

SiteID	S1	S2	S3	S4	S5	SO	≤150mm	≥175mm	Longitude (DD)	Latitude (DD)
9-3-19	0	0	0	-	-	3	0	1	125.01534	61.74853
9-3-27	0	0	0	-	-	3	0	0	124.99915	61.75011
9-3-34	0	-	-	-	-	3	0	0	124.98625	61.75072
9-3-39	0	0	0	-	-	3	0	0	124.98458	61.74738
9-3-42	0	-	-	-	-	3	0	0	124.97947	61.74662
9-3-45	0	0	0	-	-	3	0	1	124.97379	61.74671
9-3-53	0	0	0	-	-	3	0	0	124.96092	61.74473
9-3-57	0	0	0	-	-	3	0	0	124.95658	61.74201
9-3-64	0	1	1	-	-	3	1	1	124.94815	61.73737
9-3-70	0	0	0	-	-	3	0	0	124.94219	61.73297
9-3-71	0	1	0	-	-	3	1	1	124.94046	61.73263
9-3-72	0	1	0	-	-	3	1	1	124.93892	61.73212
9-3-75	0	1	1	-	-	3	1	1	124.93548	61.73032

Chapter 5: Conclusion

This thesis has provided novel insights into the thermal ecology of a cold-water ectotherm, and bull trout was used as the model organism. The work presented in the previous chapters spanned multiple spatial scales. First, I focused on sampling methodology at local and regional scales to show how accounting for low detectability in fringe habitats near distributional boundaries can improve accuracy of distributional assessments and increase our ability to detect demographic shifts in bull trout. Next, I used full-year temperature records from montane streams, spanning a broad latitudinal gradient, to examine the thermal regimes that bull trout populations experience across both regional and global scales. Results show that all streams exhibit similar thermal stability and insensitivity to warming effects of air temperature throughout the year. Also, as latitude increases, the distribution of bull trout is constrained by cold-limiting streams in both the summer and winter. Finally, I defined the ecological niche and examined potential consequences of climate warming for a local population using data collected with the protocol developed in Chapter 2. Results show how the distribution of juvenile bull trout in a northern watershed is shaped by a combination of cold-limiting streams, prevalence of perennial groundwater, and stream geomorphology. Projections based on climate warming scenarios suggest two different outcomes. First, suitable habitat, based on both climatic and geomorphic factors, will decrease across all scenarios. Second, the availability of thermally suitable habitat (i.e., does not consider other habitat associations) will initially increase, and then either decline or remain stable. The latter projections are based only on the defined summer thermal niche that bull trout occupy in this watershed, and illustrate the importance of considering broader dimensions of the ecological niche when making climate change projections for northern stream fishes.

Implications for bull trout

Bull trout is a species of great societal and ecological importance found in lakes and streams across North America (COSEWIC 2012; see Chapter 1). Bull trout are highly sought after by recreational fishers and, as a top predator in most systems, they are a critical element of aquatic ecosystems. As latitude increases, the diversity of stream fish communities typically decreases, and higher trophic consumers become even more important for maintaining ecosystem structure and function (Layman et al. 2007; Tilman et al. 2014). In addition, chars are renowned for exhibiting exceptional phenotypic plasticity (Chavarie et al. 2010; Klemetsen 2010; Chavarie et al. 2016), and bull trout conform to this assertion, demonstrating intra-specific variability in both habitat use and biological traits (Al-Chokhachy et al. 2010; Warnock and Rasmussen 2014; Austin et al. 2019). Consequently, my findings have broad implications for the species.

Distributional patterns

The patchy distribution of juvenile bull trout across Prairie Creek, as reported in Chapters 2 and 4, is consistent what others have reported elsewhere (Wenger et al. 2011; Isaak et al. 2015; Rodtka et al. 2015); however, juveniles in Prairie Creek are even rarer than what others have observed. This finding provides further evidence that bull trout is a habitat specialist and suggests that, as one moves north across the range, the availability of suitable habitat at the sub-basin scale declines. Results from Chapter 3 show that few streams in this watershed do not completely freeze during winter, and Chapter 4 illustrates that juveniles are most likely to occupy streams with low-to-moderate thermal sensitivity. Through deductive reasoning, I show that perennial groundwater is the most likely mechanism responsible for low thermal sensitivity in the Prairie Creek watershed. This finding suggests that northern bull trout preferentially select streams with higher groundwater inputs. A similar affinity for habitat associated with perennial groundwater has been shown to be a key determinant of spawning site selection in other bull trout populations (Baxter and McPhail 1999; Baxter and Hauer 2000). Although I did not look directly at the spawning life stage, young-of-the year fish were captured in most streams that bull trout occupy in the Prairie Creek watershed, and this is a strong indication that fish successfully spawn in these streams. Improving understanding of the spatial heterogeneity in occupancy bull trout exhibit across this watershed will aid in management of populations and their habitat. It is important to note that the differences in distributional patterns between Prairie Creek and stream networks further south could be a local watershed effect. However, this seems unlikely as stream surveys across broader areas in the north suggest bull trout is relatively rare in this region (Mochnacz and Reist 2007a, 2007b; Mochnacz et al. 2013). Regardless, conducting similar watershed-level surveys in other northern watersheds would be useful to assess bull trout status elsewhere and determine if the distributional pattern I report is consistent across the region.

Assessment and monitoring

Results from Chapter 2 demonstrate that detectability of juvenile bull trout is not uniform across environmental gradients in the Prairie Creek watershed and is lowest in fringe habitats at downstream and upstream distributional limits. Low detectability in fringe habitats can affect the accuracy of initial assessments, ability to detect distributional changes, and inferences from species distribution models. However, the effect of imperfect detection can be mediated in fringe habitat by increasing the density of sampling sites, collecting at least three temporal replicates at a site, or a combination of both. Adopting this sampling strategy will increase the likelihood of finding juveniles in habitat at the edge of distributional boundaries resulting in greater accuracy during initial assessments and re-assessments. From a monitoring perspective this is an important finding, and shows how one can optimize assessments to increase power of detecting population trends over time. Although similar sampling frameworks exist, my results provide greater insight into the sensitivity of monitoring schemes that may be attained using site-level surveys which account for heterogeneity in detectability. My results are similar to what others report, whereby increasing sampling effort improves the ability to detect trends in population abundance (Al-Chokhachy et al. 2009). The monitoring framework I present is well-suited for tracking distributional changes in bull trout at sites within and across streams, and, as shown by others (Eby et al. 2014; LeMoine et al. 2020), extirpation is most likely to occur in sites near downstream distributional boundaries. These findings will give others the knowledge to implement sampling protocols that yield accurate geospatial status assessments of bull trout distributions, and can serve as a baseline for conducting long-term trend assessments.

Thermal regimes

Results from Chapter 3 support findings of other studies which demonstrate that bull trout occupy one of the narrowest and coldest thermal niches of stream-dwelling chars in North America (Selong et al. 2001; Benjamin et al. 2016; Isaak et al. 2017). Given that this species requires cold streams to persist, one would think that as latitude increases the amount of thermally suitable habitat would increase. However, results from Chapter 3 illustrate two important findings that challenge this notion. First, few streams in the Prairie Creek watershed provide year-round thermally suitable habitat for juveniles because most freeze during winter. Second, although some streams do not freeze during winter, they are extremely cold in the summer (i.e., August mean <3.0°C) and juveniles do not reside in these streams. This suggests that some streams are too cold to sustain juvenile populations at higher latitudes and initial evidence that the distribution of northern populations is driven primarily by cold-limiting thresholds. In addition, Chapter 4 shows that the thermal properties of streams are an important determinant of juvenile distribution in the Prairie Creek watershed. More specifically, the probability of juvenile occurrence is highest in streams with low-to-moderate thermal sensitivity and moderately warm mean August temperature (5.0-7.0°C). It is important to note that these streams are still relatively cold, but they represent warmer streams in the context of the thermal niche that the Prairie Creek population occupies. Together, these findings demonstrate that the distribution of juveniles at higher latitudes is driven by cold-limiting streams in both the summer and winter (i.e., do not freeze). This result is opposite to what others report for bull trout at the southern range extent, where distributional patterns and population demographics are governed by warm-limiting streams that approach upper thermal thresholds during the open water season (Isaak et al. 2015; Benjamin et al. 2016; Kovach et al. 2016). My results provide a broader understanding of how the thermal properties of streams that juvenile bull trout occupy differ across latitude and further insight into mechanisms that influence distributional patterns and persistence of a northern population.

Climate warming at the northern geographic range extent

In Chapter 4, results show that the extent of suitable juvenile habitat in the Prairie Creek watershed is projected to change in two ways as climate warms. In the first scenario, suitable habitat, based on both climatic and geomorphic factors, is projected to decline as climate warms, even though the thermal properties of these streams will mediate the coherent effect of climate warming. This finding is significant for two reasons. First, to my knowledge, this is the first study to assess potential effects of climate warming at this spatial resolution in a northern stream-dwelling salmonid. Other studies have assessed potential effects of climate change in northern fishes but at a much coarser spatial scale and from a narrative rather than a habitat perspective (Reist et al. 2006a, 2006b). Because my data set was spatially dense, I was able to develop accurate models and predict occurrence probabilities with precision across the watershed, which is not possible with sparse data sets that are common in remote northern watersheds. Second, the trajectory of habitat decline is contrary to most climate change predictions for northern freshwater fishes, which suggest that the extent and quality of habitat will improve as climate warms (Prowse et al. 2006; Reist et al. 2006a, 2006b). The notion that habitat will decline is similar to what others have reported for populations at the southern range extent and follows a similar pattern primarily driven by loss of thermally suitable downstream habitat as streams warm (Isaak et al. 2015). In the Prairie Creek basin, some mid- to-upstream habitat is predicted to initially improve in terms of thermal quality as climate warms, but eventually suitable habitats will shift upstream towards distributional boundaries rendering some streams inhabitable or others as small, isolated habitats. These predictions are based on the thermal adaptation hypothesis, which suggests that juvenile bull trout have adapted over time to occupy their current thermal niche, and will track this niche as climate warms.

In the second scenario, projections show that the amount of available suitable thermal habitat will increase across all scenarios into the 2040s, and then either decline or plateau. The calculations of suitable habitat for these projections are based solely on the defined summer thermal niche that bull trout currently occupy (4.7°C – 7.5°C) and an expanded thermal niche (4.7°C – 10.0°C), based on the assumption that this population is capable of occupying a broader thermal niche (i.e., niche evolution). There are two plausible hypotheses associated with niche evolution. First, juveniles are forced to occupy their current thermal niche due to limited availability of thermally suitable habitat, but possess the phenotypic plasticity to adjust to occupy a broader niche if it becomes available. Second, this population has undergone local adaptation to their current thermal niche, but will further adapt (i.e., genetically) to occupy a wider thermal niche as it becomes available over time. Although both hypotheses seem plausible, adjustment seems like the most likely mechanism given that chars exhibit great phenotypic plasticity (Klemetsen 2010). The predictions in both of these scenarios fail to account for other climatic (e.g., thermal sensitivity/groundwater) and geomorphic factors that I show influence juvenile distribution across the watershed. As shown by others, the dichotomy in the habitat trajectory projections I present, reinforce the importance of considering broader dimensions of the ecological niche in climate change vulnerability assessments (Snyder et al. 2015; Troia et al. 2019).

Based on the research completed in this thesis, I suggest that the following impacts of climate warming are most likely to occur for northern bull trout populations in montane watersheds:

1. The proportion of available suitable habitat will decline, further constraining opportunities for distributional expansion.
2. The structure and function of habitat with suitable thermal and geomorphic properties will remain intact for most core populations, but the size of these habitats will decrease and may result in local site extirpation at downstream distributional boundaries.
3. The winter season will be shorter and warmer, resulting in warmer thermal regimes throughout the incubation and growing seasons, and this change will provide better opportunities for juvenile growth before the onset of winter leading to improved survival and recruitment.

Implications for salmonids

Monitoring protocol

Accurately documenting and effectively tracking the status of populations is one of the greatest challenges of modern-day conservation (Noon et al. 2012). Collecting information on population demographics consistently over time provides a time series to assess natural variability in populations, which can then be used to detect deviation from normal conditions. However, collecting this type of information can be costly, time consuming, and is not feasible for many populations across large areas. Occupancy is now used as an alternative population metric for assessing the status of salmonids across larger stream and lake ecosystems (Falke et al. 2010; Haynes et al. 2014), as it is relatively inexpensive to gather samples and provides reliable data upon which robust inferences can be made (MacKenzie et al. 2018). The work presented in this thesis illustrates how occupancy can be used to assess the distributional status of juvenile salmonids across stream-networks and provides guidance on how to optimize sampling designs to reliably detect trends in occupancy of resident fish while accounting for imperfect detection. The latter element is lacking in occupancy studies as many identify factors responsible for imperfect detection (Falke et al. 2010; Rodtka et al. 2015), but few highlight how to effectively sample in these areas to reliably detect population trends (Reid and Haxton 2017). It is in this regard that I believe results from this thesis will be most useful, as I provide a method to effectively sample watershed-scale occupancy of a resident fish. Although it is difficult to sample fish at distributional boundaries, it is in these fringe habitats where populations are expected to be most vulnerable to extirpation (Eby et al. 2014; LeMoine et al. 2020). Therefore, effectively monitoring population trends requires accurate distributional assessments and reassessments. The sampling and monitoring framework that I present shows how accurate baseline assessments can be done to effectively track population trends, and could be easily transferred to other stream-dwelling salmonids (e.g., Dolly Varden). Also, as shown by others, the occupancy-based method has great flexibility for broader applications (Baker et al. 2017).

Thermal regimes and thermal ecology

This thesis has provided a deeper understanding of the thermal ecology of bull trout across a broad latitudinal gradient. The differences in thermal regimes that bull trout experience across this latitudinal gradient show that juvenile distribution is driven by cold-limiting streams in the north and warm-limiting streams in the south. These two divergent mechanisms explaining distributional patterns in each respective area raises some interesting questions relevant to salmonid research. This result fits with the thermal adaptation hypothesis, which states that growth and fitness is maximized at temperatures that an organism experiences most often in their native environment (Lonsdale and Levinton 1985). It follows that organisms at higher latitudes will have reaction norms for better growth potential at lower temperatures than those from lower latitudes (Levinton 1983; Angilletta 2009). Even though bull trout in the north successfully occupy streams that do not accumulate as many thermal units in the growing season as streams in the south, I show that temperatures in these streams are less variable throughout the year than streams in the south. The Prairie Creek bull trout population may have adapted to optimize growth and physiological performance in these colder, more thermally stable streams. Similar evidence of local adaptation to different environmental regimes is common in other salmonids (Eliason et al. 2011; Narum et al. 2013; Hecht et al. 2015; Sparks et al. 2017).

Conversely, the fact that juveniles in the Prairie Creek watershed are capable of surviving in streams where they experience colder thermal regimes and a shorter growing season than their southern counterparts could be explained by the countergradient hypothesis. This hypothesis suggests that organisms at higher latitudes exhibit compensatory growth to offset latitudinal differences in growth potential associated with different climatic conditions and phenology (Conover and Teresa 1990). Therefore, populations at higher latitudes often exhibit higher growth than those at lower latitudes, yielding an inverse relationship between growth rates and latitude. Differences in growth potential across similar latitudinal gradients has been reported in other chars and supports the countergradient hypothesis (Chavarie et al. 2010; Sinnatamby et al. 2015).

Determining which prevailing mechanism (i.e., thermal adaptation or countergradient variation) explains how the Prairie Creek bull trout population can occupy much colder streams than populations at southern latitudes is important from an evolutionary perspective. Salmonids that exhibit thermal adaptation may possess greater potential to evolve and occupy novel thermal niches (i.e., niche evolution), whereas salmonids that exhibit growth-compensation may have phenotypes that vary less but still possess adaptive potential (Conover and Schultz 1995). It is, however, important to recognize that local adaptation does not necessarily confer genetic differentiation and could reflect the broader phenotypic plasticity of bull trout. Using bull trout as a model organism, I provide further support that salmonids possess great intraspecific adjustment potential, allowing populations to survive across a range of different thermal environments. Despite the exceptional phenotypic plasticity and adaptation exhibited by salmonids (Klemetsen 2010; Narum et al. 2013; Hecht et al. 2015; Armstrong et al. 2016; Raby et al. 2016; Sparks et al. 2017), some of these cold-water ectotherms have difficulty overcoming upper thermal thresholds (Eliason et al. 2011; LeMoine et al. 2020). I encourage others to examine the adaptive capacity of bull trout populations across ecologically relevant temperature gradients using populations spanning the geographical range. This research will strengthen the foundational understanding of how North American salmonids will respond as our climate changes and broaden understanding of the adaptive potential of these cold-water fishes.

Implications for the study of thermal ecology and climate change

The study of thermal ecology is of fundamental importance for understanding the evolution and ecology of species geographic range limits as temperature affects nearly all biological rate processes (Kingsolver 2009; Sexton et al. 2009). The shape of thermal reaction norms for ectothermic organisms provide insight into the breadth and magnitude of thermal niches that individuals, populations, and species occupy (Kingsolver 2009). On the landscape, the thermal properties of a species' ecological niche act in concert with other dimensions of their niche (e.g., physical habitat, biological features) to govern habitat suitability for a given species (Angilletta 2009; Peterson 2011). Despite this, we still know relatively little about how temperature sets geographic range boundaries (Sexton et al. 2009). The results from this thesis, combined with other studies on bull trout, further support the claim that temperature is an important ecological dimension that controls the distribution of aquatic ectotherms at both regional and global scales. Chapters 3 and 4 provide further insight into potential mechanisms influencing the distribution of a cold-water stenotherm at southern and northern geographic range extents and the vulnerability of thermally suitable habitat to climate change. The results I present in Chapters 3 and 4 on thermal sensitivity is an important finding, as it provides further evidence that not all thermally suitable habitat is created equal and some habitat will be more vulnerable to climate warming than others. Such findings support similar patterns of habitat heterogeneity in climate vulnerability for other freshwater taxa (Troia et al. 2019). Additionally, recent studies have documented both range shifts and contractions associated with climate warming (Parmesan et al. 1999; Sunday et al. 2012; Comte et al. 2013); however, inadequate sampling and resampling at fine enough spatial scales has hampered efforts to precisely document distributional changes across taxa (Thomas et al. 2006). Results from Chapter 2 highlight the importance of documenting baseline distributions accurately if we are to successfully track population trends to understand consequences of climate warming. This will be especially important in regions with minimal perturbations, such as montane watersheds like Prairie Creek situated in remote sub-Arctic regions (Post et al. 2009). Accurately documenting species distributions across montane ecosystems, defining the thermal niche organisms occupy, and identifying ecological thresholds that limit population persistence, represent key elements of assessing risk and tracking distributional changes as our climate continues to warm.

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