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Salmonid life history, phenology, and distribution within a large river basin

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Abstract

Spatial and temporal patterns of salmonid distribution relative to thermal and physical characteristics of riverine habitats of Northwestern Washington

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Where fishes are found, and in what temporal patterns and under which physical conditions, are basic questions of biology and management. Salmonid species occupy distinct habitats across their life stages, usually reproduce only once, and are subject to intense anthropogenic pressures. Patterns of occupancy, life history, and phenology vary among and within species, which can be usefully explored at the watershed scale.

Otolith microchemistry reveals partial migration and life history variation in a facultatively anadromous, iteroparous salmonid, bull trout (*Salvelinus confluentus*)

Migration of fishes between habitats influences population dynamics and ecological interactions. Some “partially migratory” populations include both migratory and non-migratory individuals, adding complexity to these dynamics. For partially migratory fishes with diadromous life histories, freshwater and marine habitats can differ greatly in availability of prey and physical conditions conducive to growth, predation risk, and exposure to fisheries and to contaminants. Therefore, understanding patterns of migratory behavior can inform population biology and conservation. Using otolith microchemistry, we describe observations of partial anadromy in a threatened, iteroparous salmonid species, bull trout (*Salvelinus confluentus*), in the Skagit River basin of Washington State, USA. We found that 59% of the fish sampled (> 338 mm fork length) in the river had not been to marine water, despite easy access. The other 41% had migrated to salt water, typically every year beginning at age 2 or 3. We also observed overwintering in marine waters by some individuals, and extended time in fresh water between otherwise annual migrations to marine waters in others. Additionally, there was no obligatory relationship between anadromy in mothers and their offspring. The facultative nature of migration in this species, and the lack of tight connection between maternal and offspring life history patterns are consistent with studies of other *Salvelinus* species but contrast with the more rigid controls on migration in semelparous salmonids.

Spawning and emergence phenology of bull trout *Salvelinus confluentus* under differing thermal regimes

Median bull trout *Salvelinus confluentus* breeding was two weeks earlier in a cool stream than in a proximate warmer stream, aligning with expectations for salmonids, followed by

emergence timing calculated to be six weeks later in the cool stream than the warm stream. This pattern is consistent with both site-specific adaptation and thermal spawning threshold hypotheses for life history event timing in this threatened species.

Differential long-term shifts in the timing of spawning by wild and hatchery-derived Skagit River Chinook salmon under climate-driven increasing temperature regimes

The duration of reproduction within salmon populations often varies among years, but median timing is relatively consistent, reflecting long-term patterns of natural selection and the local environment. However, altered selection resulting from factors including climate change or human intervention might shift timing, with implications for the population's persistence. We modeled median timing of redd (nest) counts as an index of spawning timing by wild Chinook salmon in the Skagit River system in Washington State, USA. Over the last 2-6 decades, wild salmon have been spawning later by 0.03 – 0.48 d/yr, while a naturally spawning subset of one of these populations that is influenced by strays from a hatchery has been spawning earlier by 0.18 d/yr. Trends in the spawning timing of hatchery strays may reflect opposing selection from the hatchery, where egg take for propagation has become earlier by 0.58 d/yr. Concurrently, mean August river temperatures have risen, suggesting that hatchery timing trends may be moving in the opposite direction from the plastic or adaptive patterns expressed by wild fish.

Temperature, elevation, and discharge control the breeding distribution of six native salmonid species in tributaries within a single basin

The spatial distributions of organisms, among the most essential elements of their ecology and conservation, can be defined and studied at different scales. For example, at one end of the spatial continuum, the geographic ranges of salmonid species are well known and broadly overlapping. At the other end of the continuum, there is substantial overlap in fine scale spawning site selection among species, though differences in physical features (e.g., water depth, velocity, and gravel size) are known. However, within their ranges, many rivers and streams apparently suitable for reproduction and rearing are used by some salmonid species but not others. The conservation of species depends, in part, on the number and diversity of breeding populations. Consequently, it is important to determine why some apparently suitable sites are not used by species with ready access to them. In this study we examined the effects of physical factors on the watershed-scale spawning distribution of six native Pacific salmonids in the Skagit River basin, Washington: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), Chinook salmon (*O. tshawytscha*), steelhead (*O. mykiss*), and bull trout (*Salvelinus confluentus*). Annual mean temperature and catchment elevation had the strongest association with the assemblage's breeding distribution at the watershed scale, but stream length and annual discharge, seasonal hydrologic norms, and land use patterns were also influential. The distributions of pink and Chinook salmon were closely associated with each other and with common variables and bull trout displayed the most distinctive pattern among the species. Interspecific differences in habitat association remained despite broad thermal and elevational patterns, suggesting some fundamental constraints on species distributions within basins that have implications for their conservation and habitat restoration.

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DEDICATION

For all those who strive for their education with too little support; may there be room in science
for your voices and your passion.

Chapter 1. GENERAL INTRODUCTION

1.1 INTRODUCTION

Among the fundamental questions about fishes are what locations they occupy and when, and where and when they engage in the behaviors on which their survival depends. Biological understanding and sound resource management depend on the answers to these questions, particularly for salmonid species, which occupy distinct habitats across their life stages, usually reproduce only once, and are subject to intense anthropogenic pressures. Salmonids vary in patterns of occupancy, life history, and phenology among and within species, such that further exploration is warranted.

Many species migrate from one habitat to another as they balance feeding, growth, reproduction, and mortality across life stages (Gross 1987), but while some species are obligate migrants between habitats, others are partially migratory. Partial migration within a population represents multiple parallel solutions among individuals to the tradeoffs of food availability, energetics for growth, opportunities for reproduction, and predation avoidance (Chapman et al. 2011). The prevalence of partial migration in a population, the types of alternate patterns, and their heritability are important to population structure and persistence (Chapman et al. 2012).

Populations persist at a basic level because of successful reproduction for which fish behaviors have evolved in conjunction with physical habitat characteristics. Water temperature is a critical component of the physical habitat for ectotherms (Brett 1956) and reproduction in a species or population is often observed at consistent temperatures across seasons and sites (e.g., Heggberget 1988). This is thought to stabilize the timing of juvenile emergence in relation to environmental conditions conducive to growth and survival (Brannon 1987). Since reproductive

timing in salmonids is strongly heritable (Quinn et al. 2002), changes in thermal regimes may be associated with changes in reproductive phenology, potentially influencing juvenile emergence timing and survival.

Long term patterns of species distribution in a basin-wide salmonid assemblage are a function of both biological factors and a hierarchy of physical factors (Beechie et al. 2008). Among the physical factors, geology, hydrology, temperature, vegetation, and human land use have all been linked to salmonid use of freshwater habitats for reproduction (e.g., Feist et al. 2011; Moir et al. 2002; Pess et al. 2002). Disentangling those factors at an intermediate scale, among the tributaries of a large watershed, provides insights into similarities and differences among species, as well as a template to leverage restoration and conservation actions.

The purpose of this dissertation was to explore the migration, spatial distribution, and life history event timing of salmonid species occupying a large river basin. The largest source of freshwater to Puget Sound is the Skagit River, which supports all nine Pacific salmonid species native to the region (Lowery and Beauchamp 2015; Rybczyk et al. 2016). The first chapter discusses the movement patterns of Skagit River bull trout (*Salvelinus confluentus*) across their lifetimes, extracting patterns of partial migration between riverine and marine waters in bull trout from hard structures that contain the chemical signature of freshwater and saltwater environments. The second chapter assesses the difference in reproductive timing between bull trout spawning in tributaries with differing thermal regimes, as well as projects the possible implications of spawning timing for juvenile development and emergence under these thermal conditions. The third chapter takes a multi-decadal view of reproductive timing in Chinook salmon (*Oncorhynchus tshawytscha*), quantifying changes in phenology across multiple streams and populations that coincide with changing river temperatures. The fourth chapter evaluates the

habitat characteristics most strongly associated with the spawning distributions of six salmonid species: pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), Chinook salmon, steelhead (*O. mykiss*), and bull trout.

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Chapter 2. OTOLITH MICROCHEMISTRY REVEALS PARTIAL MIGRATION AND LIFE HISTORY VARIATION IN A FACULTATIVELY ANADROMOUS, ITEROPAROUS SALMONID, BULL TROUT (*SALVELINUS CONFLUENTUS*)

2.1 INTRODUCTION

Migration between habitats in fishes, as in other taxa, influences ecology and evolution at multiple scales (McDowall 1988; Dingle 1996; Chapman et al. 2012). It can affect growth and fecundity (Gross 1987), gene flow (Gyllensten 1985; Ward et al. 1994), top-down trophic cascades (Brodersen et al. 2011), and transfer of nutrients (Gende et al. 2002; Nislow and Kynard 2009; Walters et al. 2009) or contaminants (Ewald et al. 1998; O'Neill and West 2009) between ecosystems. Patterns of migration can vary between and within species and populations (Secor 2015), including what is known as partial migration – populations containing both migrants and residents (nonmigratory individuals). The ratio of migrants to residents in a partially migratory population reflects the tradeoffs between the energetic cost of movement and the relative risk of mortality and growth opportunities in multiple habitats (McDowall 1988). Partial migration is expressed across a wide range of fish species and spatial scales, and has long been recognized in Salmonidae (Rounsefell 1958). Some salmonids are obligate migrants, invariably moving to salt water at an early life stage (notably pink, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*), some are typically freshwater residents (e.g., lake trout, *Salvelinus namaycush*), and others fall along an intermediate continuum, such as Atlantic salmon, *Salmo*

salar, brown trout, *Salmo trutta*, and many char (*Salvelinus* spp.) (Rounsefell 1958; Quinn and Myers 2004; Jonsson and Jonsson 2011; Dunham et al. 2008; Dodson et al. 2013).

The expression of anadromy in char populations seems to be influenced both by genetics and environmental factors that vary with species and location, including latitude, distance from salt water, and prey availability (Thériault et al. 2007; Finstad and Hein 2012; Bond et al. 2015). Dolly Varden, *S. malma*, and Arctic char, *S. alpinus*, produce facultative migrant and resident individuals (Moore et al. 2014; Harris et al. 2015), while migratory life histories of lake trout can be genetically determined (Kissinger et al. 2018). Char are distributed in historically periglacial latitudes of the northern hemisphere, and Power (2002) suggested that migration could have facilitated persistence during repeated ice advances. Anadromous Arctic char and Dolly Varden mature at older age, larger size, and with more eggs than nonanadromous individuals, suggesting a reproductive advantage for those surviving their migration to sea (Blackett 1973; Tallman et al. 1996; Jonsson and Jonsson 2001). These benefits are balanced against the risks of anadromy: energetic expenditure, physiological adjustment, mortality from large marine predators, and exposure to marine fisheries.

A range of migratory life history patterns between and within populations has been observed in bull trout (*Salvelinus confluentus*), a char species whose distribution is limited to western North America from 42°N to 65°N (Haas and McPhail 1991; Reist et al. 2002; Mochnacz et al. 2013). Bull trout are mostly found in fresh water with stream-resident, fluvial (river-migrant), and adfluvial (lake-migrant) life histories (Fraley and Shepherd 1989; Rieman and McIntyre 1993; Swanberg 1997). They are also partially anadromous in parts of their range (Brenkman and Corbett 2005; Quinn et al. 2017), and anadromy may have allowed bull trout to persist through dynamic periods of glacial advance and retreat because long distance migration

provided access to marine resources and distributional flexibility (McPhail and Baxter 1996; Northcote 1997; Power 2002). Bull trout were once sufficiently numerous to be a food resource for indigenous people of the Pacific Northwest (Lord 1866), but in the last century the species has declined, in part due to habitat loss and regulations aimed at reducing bull trout predation on sympatric salmonids (McPhail and Baxter 1996). Bull trout are designated as threatened under the Endangered Species Act throughout their United States range (U.S. Fish and Wildlife Service 1999) and as threatened or of special concern in most of their Canadian range (COSEWIC 2012). By exploring migratory behavior in bull trout to the extent possible given their protected status, we increase our knowledge of their ecology as well as potential impacts of climate change and human activities.

Partial migration in fishes can be explored using otolith microchemistry, which provides a chronology of the fish's sequential seasonal occupancy of freshwater and marine habitats (Secor 1992). Over a fish's life, elements from the surrounding water are permanently incorporated into the calcified structure of aragonite otoliths. Some elements (e.g. strontium and barium) are incorporated at rates relative to their concentration in the surrounding water, which is typically distinctive between fresh and salt water (Campana 1999; Elsdon and Gillanders 2005; Doubleday et al. 2014). Maternal anadromy during vitellogenesis is detectable through signatures imparted in the natal portions of otoliths (Kalish 1990).

We explored partial migration using otolith microchemistry in bull trout in the Skagit River basin, Washington State, with a series of questions. First, does otolith microchemistry reveal both anadromy and residency in adult bull trout in this river system? Second, what ages did the anadromous individuals first migrate to marine waters? Third, did any anadromous fish deviate

from a pattern of annual migration to and from marine waters? Finally, did all fish adopt the maternal migration patterns of anadromy or residency?

2.2 METHODS

Study area

The Skagit River empties into the Salish Sea, draining parts of northwestern Washington State, U.S.A. and southern British Columbia, Canada (Figure 1.2). The basin drains over 8,500 km² of steep, rugged mountains whose precipitation regimes range from alpine glacier-dominated to lower elevation rain-only (Thompson and Beauchamp 2014). Mean annual discharge is 473 m³/s near the mouth at Mount Vernon (Pickett 1997), with higher flows in winter and spring, and lower in summer and early fall (USGS 2017). There is no physical barrier to fish passage for >100 rkm but above the confluences of several large, free-flowing tributaries, the main stem Skagit River is dammed for hydroelectric power production at river kilometer (rkm) 155 (Skagit Hydroelectric Project; Federal Energy Regulatory Commission Project Number 553). Water released from the reservoirs is hypolimnetic, lowering the river temperature above the confluence with the Sauk River in summer and raising it slightly in winter relative to historic conditions. The basin supports all nine species of Pacific salmonids native to the region: Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye salmon (*O. nerka*), steelhead-rainbow trout (*O. mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), Dolly Varden (*Salvelinus malma*), and bull trout (*S. confluentus*) (Lowery and Beauchamp 2015). In the Skagit River, bull trout express stream resident, fluvial, adfluvial (in reservoirs above dams), and anadromous migratory patterns (U.S. Fish and Wildlife Service 2015).

Sample collection

As bull trout are federally protected in the U.S.A., 44 sets of sagittal otoliths were obtained from a combination of sources in an opportunistic rather than systematic manner. First, 12 samples came from creel sampling of a legal recreational fishery that allows retention of bull trout over 20 inches (50.8 cm) during months and locations that have varied among years (Washington Department of Fish and Wildlife (WDFW) 2002-2016; WDFW Section 6 ESA exemption). Second, we obtained one sample of a fish taken illegally and retained by enforcement officers. Third, 22 fish had been sampled in prior studies, also obtained through the recreational fishery, and the otoliths were provided to us (Lowery and Beauchamp 2015; WDFW Section 6 ESA exemption; Figure 1). Finally, lethal sampling for a study of chemical contaminant load in bull trout by the U.S. Fish and Wildlife Service yielded two samples from the river and another seven from marine waters near the river that were determined to be of Skagit River system origin by genetic markers (Small and Bowman 2017; WDFW Section 6 ESA exemption). The 37 samples collected in the river system were caught in the main stem Skagit River above rkm 108, several major tributaries above this point (Sauk, Suiattle, Whitechuck and Cascade rivers, and Illabot Creek), or the fish trap at the Baker River hydropower project at rkm 91, across most months of the year. The remaining seven samples came from marine waters.

Otolith microchemistry

For otolith preparation, we embedded each whole otolith in epoxy (Pelco, Ted Pella, Inc.), took a 1.0 mm transverse section of the core area, mounted it on a petrographic glass slide, and polished the surface with increasingly fine sandpaper to 5 μm , exposing the core and inner matrix layers. Chemical analysis was performed using laser ablation inductively coupled plasma

mass spectrometry (LA-ICP-MS) at Oregon State University (Keck Laboratory) on a Thermo X-Series II ICP-MS (ThermoFisher Scientific, Waltham, MA) and a Photon Machines Analyte G2 (Photon Machines, Bozeman, MT). In each sample run we removed contamination along the intended transect on each otolith surface with a pre-ablation track 100 μm wide, then collected continuous count data for ^{43}Ca , ^{86}Sr , and ^{138}Ba from otolith matrix material ablated along a transect through the otolith core chosen for its readability (Figure 2). The laser diameter for data collection was 20 μm , pulse rate was 7 Hz, and ablation speed was 5 $\mu\text{m}\cdot\text{sec}^{-1}$. Three times during each set of 10 to 12 transect analyses, we collected NIST-612 glass standard reference values, which we averaged to find a NIST standard adjustment for those otoliths (Miller 2011). Washout data collected before and after sample ablation were removed and raw counts were background-adjusted, then converted to ratios to ^{43}Ca in the otolith matrix, and then molar ratios of $^{86}\text{Sr}:^{43}\text{Ca}$ in $\text{mmol}\cdot\text{mol}^{-1}$ and $^{138}\text{Ba}:^{43}\text{Ca}$ in $\mu\text{mol}\cdot\text{mol}^{-1}$ (Bond et al. 2015). To verify that the transect data had not missed a maternal signal laid down during vitellogenesis at the otolith core, we also drilled 24 sample cores on an iCAP Qnova Series ICP-MS (ThermoFisher Scientific, Bremen, Germany) at University of Washington (Dennert et al. 2016). For this ablation, spot size was larger (85 μm) to ensure capture of core material. We used 10 Hz and 5.44 $\text{J}\cdot\text{cm}^{-2}$ laser fluence to drill for 1000 pulses, which comprised most of the depth of the transverse sections. These analyses corroborated the transect results, i.e. did not detect any missed elevated maternal Sr:Ca values (one-tailed paired $t_{24} = -2.88$, $p = 0.996$).

We aged each fish by visually identifying the terminal edge of translucent bands indicative of slower winter growth in the sectioned otoliths using transmitted light and a dissecting microscope, using two different readers on at least two separate occasions each, with a third referee called for differing readings until convergence was reached (Brenkman et al. 2007;

Figure 2). We digitally photographed each otolith and measured the distances to the locations of annuli along the ablated transect of each otolith using Image Pro Premier (Media Cybernetics) and Image J (Rasbund) software, although some annulus distances at early ages could not be measured precisely. The overlain annulus designations allowed us to identify age specific timing of chemical signature changes to estimate lifetime migratory histories for the sampled fish with the precision of several weeks (Miller 2011; Bond et al. 2015) as plotted against LA-ICP-MS 9 point rolling mean data.

Freshwater residency was established using baseline Sr:Ca values around the otolith core (Brenkman et al. 2007). Steeply inflected deviations $> 1 \text{ mmol} \cdot \text{mol}^{-1}$ Sr:Ca from this baseline were identified as salt water migrations, with the inflection point in the first marked increase Sr:Ca values termed the first migration and matched to the corresponding age of the fish in the otolith transect (Brenkman et al. 2007; Bond et al. 2015). We corroborated visual detection of maternal anadromy (difference in Sr:Ca $> \sim 0.5 \text{ mmol} \cdot \text{mol}^{-1}$ between the central $100 \mu\text{m}$ of the core transect and the juvenile growth values found between the steep decline marking the edge of the core and the subsequent annulus) using one-tailed *t*-tests (Zimmerman and Reeves 2002). All analyses were conducted in the statistical software R (R Development Core Team 2015).

Skagit River bull trout utilize estuarine habitats which may experience marine salinities (Beamer et al. 2004), but intermediate salinities (5-15 ppt) typically reflect the elevated Sr:Ca of full strength marine water (Phillis et al. 2011). All bull trout from freshwater were sampled at sites in the river well above tidal influence, beyond the location where the 10-yr mean monthly salinity was recorded as 0.0 ± 0.0 ppt (Skagit County Public Works). Sites at rkm 5 and rkm 7 also measured 0.0 ± 0.0 ppt, whereas a site at rkm 4 measured 0.3 ± 0.2 ppt. Estuary channel salinity near the mouth of the Skagit River increased abruptly to 21.2 ± 4.2 ppt, making us

confident in the capacity to detect anadromous migration in this system by analysis of bull trout otoliths.

2.3 RESULTS

Microchemical analysis indicated that the sampled fish included both anadromous and nonanadromous individuals (Figure 3). Fifteen of the 37 bull trout sampled in fresh water (41%, 95% confidence interval (CI) 26% – 57%) had migrated to salt water, in addition to the seven fish collected in marine waters which were evidently anadromous. Mean age at sampling of anadromous fish (4.9+ years (SD = 1.0)) did not differ from nonanadromous fish (5.0+ years, SD = 1.3; two-sample $t_{39} = 0.54$, $p = 0.59$).

Of the 22 anadromous fish, all commenced migration at age 4 or younger, with a mean age at first migration of 2.5+ years (SD = 0.8, range 1-4). Nine percent (95% CI 3% - 28%) migrated first at age 1, 36% (95% CI 20% - 57%) at age 2, 41% (95% CI 23% - 61%) at age 3, and 9% at age 4 (95% CI 3% - 28%). No sampled fish was older than 7 years, but 73% ($n = 16$) of the nonanadromous fish were older than age 4. The maximum number of lifetime migrations to salt water observed was 6 (an age 7 fish caught in Illabot Creek in September).

Exceptions to regular annual marine migrations were detected; two fish appeared to have remained in salt water through the fall and winter (i.e., did not return to spawn; Figure 1.4). A third fish apparently skipped a year of migration (i.e., migrated to sea in one year, remained in fresh water the following year, and then migrated again), and a fourth fish migrated to salt water at age 2, spent a prolonged time there, then returned to fresh water for two years without returning to the marine environment.

Of the 39 fish for which maternal anadromy could be assessed, nine showed evidence of maternal marine migration in the year prior to spawning (23% (95% CI 13% – 38%); Figure 1.5).

Of these nine, three individuals made anadromous migrations themselves, one sampled in fresh water and two sampled in marine water, over 38 cumulative years (combined ages of all fish with maternal anadromy) in which to do so (Figure 1.3).

2.4 DISCUSSION

Despite a relatively small sample size, we detected substantial diversity in the migratory behavior of Skagit River basin bull trout. We found anadromous migration beginning at ages 1-4 (primarily 2 and 3), as well as presumed residency in fish old enough to have migrated to marine environments that had not done so by the time of capture. Since temperate latitude marine environments are generally more conducive to growth than fresh water ones, and faster growth tends to generate higher fecundity, one might expect population-wide expression of anadromy in a migratory population with unimpeded access to salt water. Nevertheless, fewer than half the fish sampled (41%) had been to marine waters at all, and even fewer (only 23%) had evidence that their mother had been to sea on the season prior to spawning. Residency in bull trout with easy access to marine water might suggest high cost to migration or low benefit relative to remaining in fresh water (Gross 1987). High migratory cost due to physical distance in this study system is unlikely, given that the Skagit River is not an arduous migration corridor relative to many salmonid habitats, gaining ~84 m in elevation over 100 km in the main stem. However, bull trout that undertake anadromous migrations may face predation by marine mammals such as harbor seals, *Phoca vitulina* (Chasco et al. 2017; Thomas et al. 2017) or incidental capture in fisheries. Incentives for freshwater residency could include relative prey abundance and favorable thermal regimes. The 130 km main stem reach with salt water access is regulated by hydropower projects, making the water cooler in summer relative to tributaries and adjacent watersheds (Goetz 2016; U.S. Geological Survey 2017). Bull trout are associated with cold water

(< 16°C) throughout their range (Dunham et al. 2003), and adfluvial bull trout in the Skagit River basin occupied water as cool as 6°C in summer where prey were abundant in a reservoir, despite alternative habitats with higher temperatures (Eckmann et al. 2016). The Skagit River basin also supports substantial populations of all native Pacific salmon species, whose eggs, flesh, and fry are important contributors to annual energy budgets for adult bull trout (Lowery and Beauchamp 2015). The importance of salmon subsidies to the life histories of char populations was illustrated in Iliamna River, Alaska Dolly Varden, whose heavy reliance on a seasonal subsidy of salmon eggs can still be detected after months of winter fasting; that population does not migrate to sea despite the absence of physical barriers (Jaecks and Quinn 2014). Seasonal marine subsidies and favorable thermal conditions for metabolism or gametogenesis may thus increase the benefit of residency in such populations (Armstrong and Bond 2013).

Our second objective was to explore age at first migration for anadromous individuals. In this sample, most fish commenced migration at age two or three, which is consistent with Skagit River smolt trap data for presumed migrants of fork length 124 to 143 mm (Zimmerman and Kinsel 2010). Most bull trout first migrate to sea from the coastal Washington State at ages 3 or 4 but some as old as 6 (Brenkman et al. 2007), suggesting that further work could compare the demographics of partial anadromy in bull trout from different rivers.

There is wide variation in migration regularity, distance, and duration among *Salvelinus* species; anadromous Dolly Varden may spawn every other year, and frequently overwinter at sea (Bernard et al. 1995; Brown et al. 2014) or in lakes (Armstrong 1974), and white-spotted char, *S. leucomaenis*, can use intermediate salinity environments or make multiple trips to sea in a year (Arai and Morita 2005). In the present study, most anadromous fish made annual migrations until

capture but some did not. A prior study using acoustic tagging also inferred overwintering at sea in a few fish (Goetz 2016). Skipped anadromous migration is a pattern previously undocumented in bull trout but consistent with the migratory plasticity of the genus (Figure 1.4). Skipped spawning events occur in salmonids (Rideout and Tomkiewicz 2011; e.g. Johnston et al. 2007), and skipped migrations have been observed in Arctic char with seasonal habitat access due to low stream flow (Gyselman and Broughton 1991; Quinn et al. 2016). In contrast to the thermal habitats of Arctic char, Puget Sound presents a mild range of mean offshore temperatures, from 7.2°C in the winter to 12.8°C in the summer (Reum et al. 2011; Goetz 2016). Summer temperatures in estuaries are higher than those offshore, but bull trout are seldom found in estuary temperatures above 17-18°C (Goetz 2016). Acoustic telemetry indicates that individual bull trout use Skagit River estuarine habitats for about of two months between March and August (Hayes et al. 2011; Goetz 2016), much like the short and variable saltwater migrations in Alaskan Dolly Varden under similar conditions (Bond and Quinn 2013). Since anadromous bull trout from the Skagit basin were collected in fresh water sites throughout the year, our data also suggest variability in migration timing, contributing to an overall picture of plasticity in bull trout migration tactics (Table 1.1).

Lastly, otolith analysis did not detect maternal anadromy in some fish that had gone to marine waters. This result might have arisen from either of two processes. First, there may indeed be little or no genetic control over anadromy, such that parental and progeny patterns are not linked. Alternatively, if a female migrated to sea in one year but then not in the subsequent year prior to spawning, offspring from that latter season would reflect only maternal freshwater Sr:Ca. Our data suggest that such “skipped migration” indeed occurred, though this was rare. Elsewhere, Dolly Varden may “retire from anadromy” late in life, and such fish would also

produce offspring whose otoliths would give no indication of the mother's earlier migration history (Bond et al. 2015). Low correspondence between maternal and offspring migration patterns in bull trout was also detected in a coastal Washington river; all 15 nonanadromous fish examined were the offspring of anadromous mothers, and the four bull trout with nonanadromous mothers all eventually migrated to salt water themselves (Brenkman et al. 2007). These patterns imply little or no genetic control over migratory behavior within breeding populations, and likely the contingency of migration on growth patterns or some other environmental induction. From a conservation standpoint, these results indicate that the anadromous and fluvial components of the population complex should continue to be managed as an integrated whole rather than as separate units.

Given our small sample size, it is unlikely that we captured the full suite of migratory and life-history diversity of Skagit River Basin bull trout. Nevertheless, the diversity we observed indicated a wide range of migratory patterns in the basin. The study basin is physically and biologically diverse, with a strong salmon subsidy over many months of the year compared to adjacent watersheds. The relative strength and duration of that resource subsidy may contribute to migratory tradeoffs between marine and fresh water environments, providing another motivator for wider fish conservation efforts.

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Table 1.1. Collection date, site name, river km of capture, length, age, and life history patterns of Skagit River system bull trout either captured in fresh water or genetically assigned to the Skagit River Basin (Small and Bowman 2017)

Collection date	Water body	River km	Fork length (mm)	Age	Maternal anadromy	Offspring anadromy	Age at first migration
4/28/2006	Skagit River	112	421	6	no	no	
6/9/2006	Skagit River	118	519	5	no	yes	2
8/18/2006	Skagit River	131	492	4	no	no	
8/19/2006	Cascade River	125+	660	6	no	no	
8/29/2002	Sauk River	108+	498	4	no	yes	3
9/2/2002	Cascade River	125+	560	4	no	yes	2
9/13/2002	Illabot Creek	115+	643	7	no	yes	2
11/9/2002	Skagit River	108+	533	6	yes	yes	3
3/14/2006	Skagit River	108	500	3	no	no	
9/28/2003	Illabot Creek	115+	660	5	no	yes	2
8/4/2006	Skagit River	130	398	2	yes	no	
6/9/2006	Skagit River	118	456	5	yes	no	
8/19/2006	Cascade River	125+	558	6	no	no	
11/9/2002	Skagit River	108+	711	6	no	yes	2
8/3/2002	Whitechuck River	108+	526	5	no	yes	3
11/22/2002	Skagit River	108+	546	6	no	no	
2002	Cascade River	125+	533	5	no	yes	2
9/28/2003	Illabot Creek	115+	508	6	no	no	
9/19/2006	Skagit River	135	581	5	no	no	
4/7/2007	Skagit River	125	510	6	no	yes	3
10/13/2007	Skagit River	118	584	6	no	no	
6/15/2008	Skagit River	112	516	6	no	no	
9/15/2016	Suiattle River	108+	338	3	no	yes	1
7/11/2011	Cascade River	125+	620	6	no	yes	3
6/30/2011	Cascade River	125+	650	5	no	yes	3
4/7/2007	Skagit River	118	510	3	yes	no	
4/6/2007	Skagit River	112	585	6	no	no	
4/6/2007	Skagit River	112	530	3	yes	no	
2/3/2007	Skagit River	108	467	6	no	no	
2/3/2007	Skagit River	108	590	5	no	yes	1
10/13/2006	Skagit River	108+	533	6	no	no	
10/28/2007	Skagit River	125+	500	4	no	yes	2
6/15/2008	Skagit River	125-	509	6	no	no	
6/9/2006	Skagit River	118	446	5	yes	no	

6/14/2008	Illabot Creek	115+	500	6	no	no
4/25/2012	Puget Sound		560	4	unknown	yes
4/25/2012	Puget Sound		555		unknown	unknown
4/30/2012	Baker River	91	503	4	unknown	no
4/30/2012	Baker River	91	517	5	yes	no
5/2/2012	Puget Sound		520	5	unknown	yes
5/14/2012	Puget Sound		530	5	yes	yes
5/29/2012	Puget Sound		510	4	no	yes
5/29/2012	Puget Sound		490	4	unknown	yes
5/29/2012	Puget Sound		500	4	yes	yes

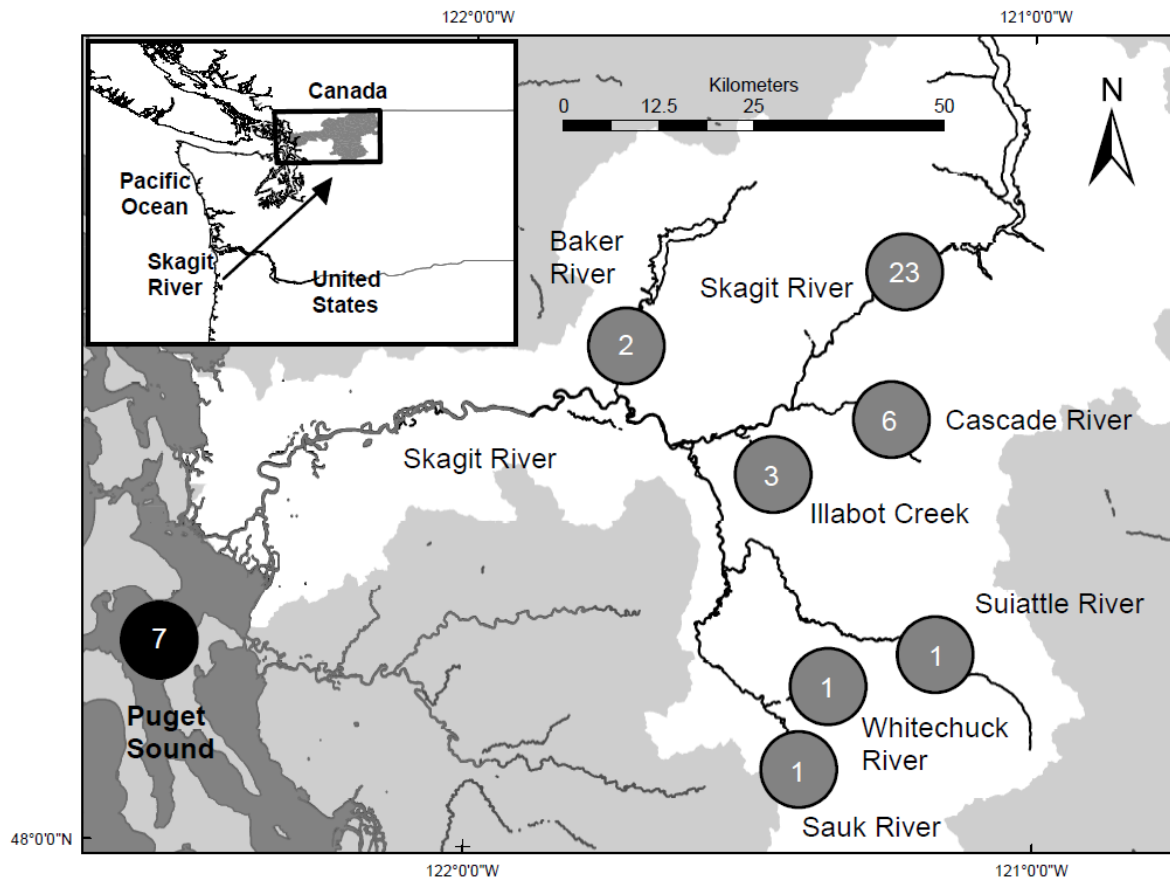


Figure 2.1. Coastal North America and the Skagit River basin. Bull trout otoliths were collected from reaches and tributary rivers as indicated by clear circles and those sampled in marine waters by black circles; numbers indicate sample sizes

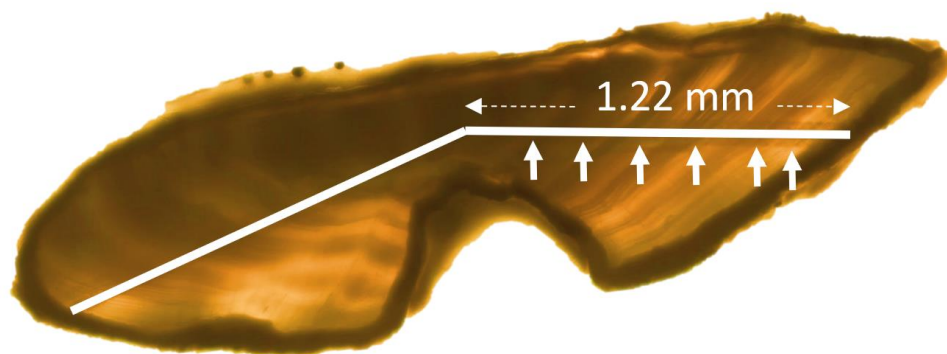


Figure 2.2. Polished transverse section of sagittal bull trout otolith with laser ablation track and arrows indicating denser winter growth rings representing annuli

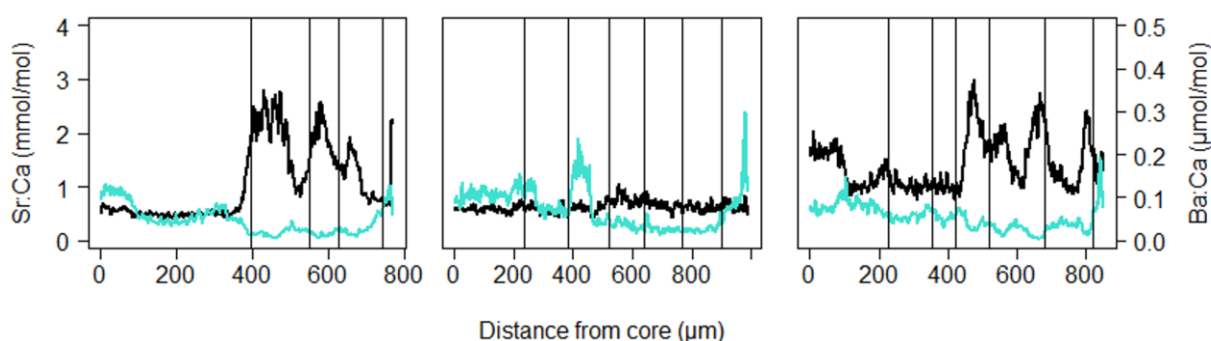


Figure 2.3. Otolith microchemistry plots with 9 point moving average Sr:Ca ($\text{mmol} \cdot \text{mol}^{-1}$) in black and 9 point moving average Ba:Ca ($\mu\text{mol} \cdot \text{mol}^{-1}$) in turquoise, where the vertical bars represent winter annuli. The left panel shows the microchemistry of a typical anadromous bull trout, in this case a 560 mm fish caught in the South Fork Cascade River, which made three marine migrations over its four-year life. The middle panel shows a typical resident bull trout, a 660 mm fish caught in the Cascade River, which did not migrate to sea over six years. In neither case did the fish's mother apparently migrate to sea in the year prior to spawning. The right panel shows the only fish sampled in fresh water whose mother had been to sea in the year of spawning (with elevated core Sr:Ca) which subsequently made anadromous migrations; it was 6 years old and 533 mm at its capture in the Skagit River

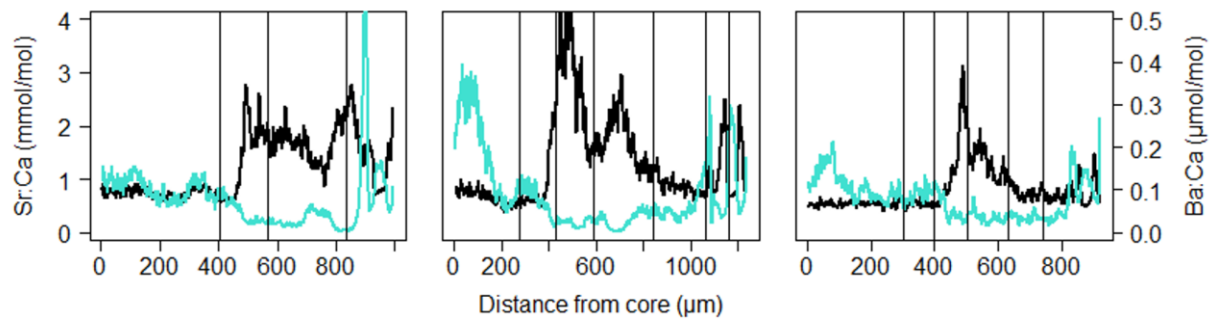


Figure 2.4. Otolith microchemistry plots with 9 point moving average Sr:Ca ($\text{mmol} \cdot \text{mol}^{-1}$) in black and 9 point moving average Ba:Ca ($\mu\text{mol} \cdot \text{mol}^{-1}$) in turquoise, where the vertical bars represent winter annuli. The three panels show possible life history variations detected in Skagit River basin bull trout on the basis of otolith chemical analysis, indicated by arrows: Left panel: a 526 mm fish caught in the Whitechuck River that overwintered in marine waters, middle panel: a skipped migration (i.e., anadromy, followed by a year in freshwater without migration to marine waters, followed by resumption of anadromy) in a 711 mm fish caught in the Skagit River, and right panel: cessation of anadromy for three years after a single year of migration, including Sr:Ca peaks below our threshold for interpretation as anadromy, in a 519 mm fish, caught in the Skagit River

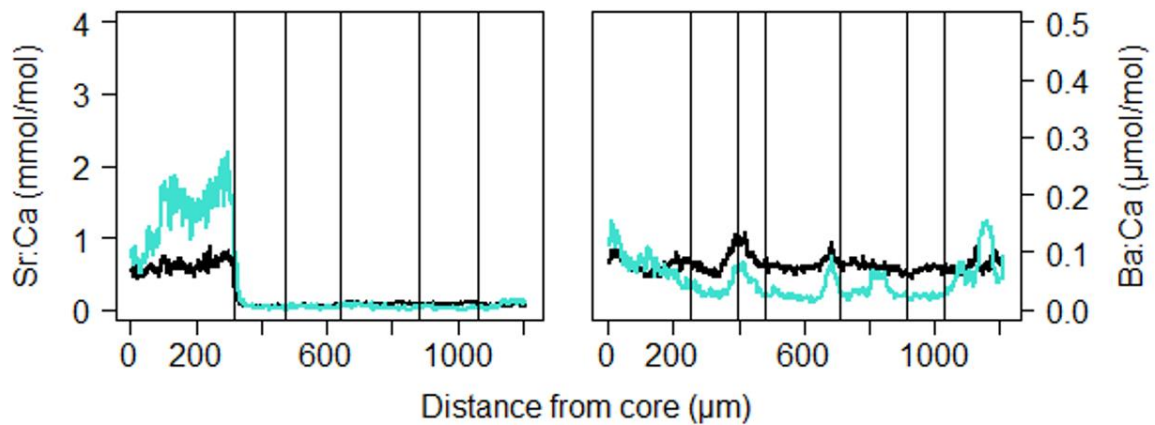


Figure 2.5. Otolith microchemistry plots with 9 point moving average Sr:Ca ($\text{mmol} \cdot \text{mol}^{-1}$) in black and 9 point moving average Ba:Ca ($\mu\text{mol} \cdot \text{mol}^{-1}$) in turquoise, where the vertical bars represent winter annuli. The left panel shows the microchemistry of a fish with the elevated core Sr:Ca indicative of maternal anadromy but this fish itself (a 446 mm individual caught in the Skagit River) did not migrate. The right panel shows a fish (558 mm, caught in the Cascade River) with no signal for anadromy whose mother apparently did not migrate in the season prior to spawning

Chapter 3. SPAWNING AND EMERGENCE PHENOLOGY OF BULL TROUT *SALVELINUS CONFLUENTUS* UNDER DIFFERING THERMAL REGIMES

3.1 INTRODUCTION

Parental breeding date and rate of larval development drive the timing of progeny hatching and initiation of feeding, which strongly affect growth and survival (Sogard, 1997). Larval development rates increase with temperature in many aquatic taxa (O'Connor *et al.*, 2007), such that the combination of mean temperature and duration of development in days (often referred to as temperature units [TUs] or degree days) yields approximately the same stage of development after fewer days in warmer water. However, salmonids typically require more TUs to reach a given stage in warmer than in colder water (Beacham & Murray, 1990). This compensation is generally thought to stabilize juvenile emergence timing to coincide with favourable conditions many months later (Alderdice & Velsen, 1978; Tallman, 1986; Brannon, 1987), though in some cases different relationships between temperature and development are observed at high temperatures (Jonsson & Jonsson 2011). Salmonids show strong genetic control over breeding date (Jonsson & Jonsson, 2011; Quinn, 2018), and populations tend to breed later in the year where temperatures are warmer (within basins: Hartman *et al.*, 1962; Webb & McLay, 1996; among basins: Hodgson & Quinn, 2002). These observations are consistent with the hypothesis that breeding timing evolves to synchronize juvenile emergence timing. However, such synchronous emergence may not be the rule. For example, fry from proximate sockeye salmon *Oncorhynchus nerka* breeding populations emerge over a wide range of dates despite experiencing the same thermal regime and food resources in the lake (Abrey, 2005; Sparks *et al.*, 2017).

Alternatively, thermal thresholds experienced by adults may trigger the initiation of breeding, as has been suggested for the fall spawning, cold water char, bull trout *Salvelinus confluentus*, when water temperatures fall below 9 °C (McPhail & Baxter, 1996; Selong *et al.*, 2001). This species is considered threatened in much of its range (U.S. Fish and Wildlife Service, 1999; COSEWIC, 2012) and may be susceptible to range contractions due to climate change and anthropogenic influences on stream temperatures and hydrologic regimes that can affect salmonid spawning and emergence phenology (Crozier *et al.*, 2008; Eby *et al.*, 2014). Spawning migrations in bull trout have been correlated with thermal thresholds (Swanberg, 1997; Fraley and Shepherd, 1989; Brenkman *et al.*, 2001; Sinnatamby *et al.*, 2017) and spawning phenology may be similarly thermally controlled.

3.2 METHODS

The Skagit River basin connects southern British Columbia and northwestern Washington State to the Salish Sea, draining > 8,500 km² of mountains with a range of precipitation regimes (Liermann *et al.*, 2012) and mean annual river discharge of 473 m³/s near the mouth (Pickett, 1997). Bull trout are entirely wild and native in the basin, and two spawning streams were selected for study that have similar topography, basin aspect, drainage area, vegetation, and salmonid species assemblage (Table 1). Both streams are hydrologically snow and rain dominated (Liermann *et al.*, 2012), surrounded by mature conifer forest, and contain bull trout, Chinook *O. tshawytscha*, coho *O. kisutch*, pink salmon *O. gorbuscha* and steelhead *O. mykiss* (WDFW, 2017). The lower reach of the warm stream (below bull trout spawning) also supports a spawning population of chum salmon *O. keta*. Temperature data from the mouths of the two streams indicated that one is warmer than the other. While stream temperatures can differ from intragravel temperatures in redd sites, they provide a reasonable proxy (Bean *et al.*, 2014).

We collected water temperature data in the surveyed bull trout spawning reaches of both streams at 30 minute intervals from September 2016 to May 2017 using Hobo V2 temperature loggers (Onset Corporation, Bourne, MA) anchored in well-mixed pools, inspected the raw data for accuracy (Dunham *et al.*, 2005), and calculated daily means. For 8 d of missing data in the cool stream, affecting one of six site-time combinations, modelled data were substituted from a linear regression using corresponding temperature data from a site 10 km downstream (full model $F = 2.43_{(1, 3274)}$, $P < 0.0001$). The year 2016 provided the only fine scale temperature data available for comparison between spawning reaches, and was determined to be indicative of the types of conditions forecasted for the region under climate change (Elsner *et al.*, 2010). August 2016 fell above the 75th percentile for 1987-2017 August mean daily maximum air temperature in the basin (USGS 2018) and below the 25th percentile for annual maximum daily river discharge (NOAA 2018). An additional year of data was excluded because environmental conditions compromised viewing conditions for redd observations at one site and temperature loggers were lost due to flooding.

New bull trout redd observations were recorded on non-sequential surveys of both streams every 7-14 d over the spawning season, September-November, 2009-2016 (WDFW, 2017). Bull trout in this system are typically large (400-550 mm; Lowery *et al.*, 2015) migratory fluvial or anadromous fish (Austin *et al.*, *in review*), which construct readily identifiable redds in the study streams. No other species spawns at the same time in the cold stream. The only heterospecific spawning occurs during the last 1-2 surveys of the season in the warm stream. Observers were experienced in differentiating redds made by bull trout from the only other alternative, coho salmon, and conservative in their assessment. We estimated the median spawning date for each year using a multi-level hierarchical Bayesian model (Appendix A) that related new redd counts

to run size, day of year, and stream. Count of redds in stream i , on day t , in year y was denoted $e_{i,t,y}$. The expected number of new redds in any time interval t to $t+\Delta t$ is assumed to be **Error!**

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$$\hat{e}_{i,t,y} = r_{i,y} \int_t^{t+\Delta t} f(t)_{i,y} dt^2 \quad (3.1)$$

where $r_{i,y}$ is the run size in year y in stream reach i (assumed to be independent across stream reaches and years); $f(t)$ is a normal distribution with mean μ_{iy} and standard deviation σ . The parameter μ_y gives the median spawning date for stream reach i in year y .

Posterior probability densities for model parameters were numerically estimated using the no-U turn Hamiltonian MCMC sampler, implemented in Stan (Stan Development Team 2017). Three replicate MCMC chains were generated for 10,000 iterations plus a 5,000 iteration burn in period using standard diagnostics for convergence (\hat{R} ; Gelman & Rubin, 1992) and model fit as described by Gelman and Rubin (1995). The supplemental information provides more information on prior probability specification.

We estimated hatching and emergence timing for fish spawning at median timing using a variation of McPhail and Murray's (1979) British Columbia thermal sums model, developed experimentally using bull trout in the Arrow Lakes, which experience similar thermal regimes to those studied here, and tested under a range of temperatures that span our thermal regimes. McPhail and Murray reported that at 2, 4, 6, 8, and 10 °C, respectively, bull trout hatching required 124, 96, 74, 57, and 44 d, and emergence required 208, 162, 126, 98, and 76 d. Using a similar thermal relationship to calculate hatching and emergence time for Pacific salmon, Sparks *et al.* (2018) used a reciprocal format to account for variable natural thermal regimes when the length of the incubation period is inherently unknown. The following equation expresses embryonic

development using bull trout data and McPhail and Murray's bull trout thermal sums model in a reciprocal format **Error! Reference source not found.:**

$$E_i = \frac{1}{\exp(a - (Ti - b))} \quad (3.2)$$

where a and b are bull trout-specific parameters as calculated by McPhail and Murray from their experimental data, such that $a = 5.086$ and $b = 0.131$ for time to hatching and $a = 5.590$ and $b = 0.126$ for time to emergence, T is mean temperature, and 50% hatching or emergence occurs at the date for which $E_i = 1$. All analyses were conducted in the statistical software R (R Development Core Team 2017).

3.3 RESULTS

Water temperatures at the stream mouth were consistently higher in the warm stream across the period of record (December 2015 – November 2017); > 95% of daily mean observations were higher in the warm stream with an average difference of $1.6^\circ\text{C} \pm \text{SD } 0.9$ ($t_{(1416)} = 9.7$, $P < 0.0001$). The warm stream was also warmer than the cool stream throughout the study year 2016; the mean 30 min interval water temperature at the mouth of the warm stream in August was 1.4°C higher than the cool stream ($t_{(2723)} = 27.49$, $P < 0.0001$) and in January, 4.0°C higher than the cool stream ($t_{(1883)} = 153.81$, $P < 0.0001$). All 30 minute observations from the spawning and incubation season (28 September 2016 – 13 May 2017) were higher in the warm stream with an average difference of $2.8^\circ\text{C} \pm \text{SD } 1.2$ ($t_{(20716)} = 123.92$, $P < 0.0001$).

In all eight years of spawning time data, spawning was earlier in the cool stream (range: 4 – 28 d; Table 2). In 2016, median spawning date was 25 d earlier (27 September; Figure 1) in the cool stream than the warm stream (22 October). Estimated median hatching in 2016 occurred only 8 d apart (14 December in the cool stream and 22 December in the warm stream). Fish in

the warm stream were projected to emerge 23 d earlier (15 February) than fish in the cool stream (9 March), with duration of incubation of 165 d in the cool stream and 117 d in the warm stream. Water temperature was always higher in the warm stream over the life history event periods, by 1.4°C during spawning, 4.4°C during hatching, and 2.3°C during emergence.

3.4 DISCUSSION

The hypothesis that bull trout spawning would occur earlier in a cool stream was supported, as expected from patterns of breeding timing in other salmonids. Both streams demonstrated later spawning than in other parts of the species' range, although at similar water temperatures, supporting the hypothesis of a threshold spawning temperature consistent with other observations of spawning at $< 9^{\circ}\text{C}$ (McPhail & Murray, 1979; Fraley & Shepherd, 1989; Baxter, 1997; Guzevich *et al.*, 2017). Estimated emergence was later in the cool stream, demonstrating divergence in total larval development time between fish in the two streams consistent with faster development in warmer temperatures. This result differs from some other salmonid studies, in which emergence is synchronous despite different thermal regimes (e.g., Campbell *et al.* *in press*). Empirical data would be needed to test site-specific adaptation in juvenile bull trout emergence timing. The results of this study suggest a few lines of speculation for further research to explore. There may be some advantage to emerging early in a warm stream, although a range of conditions appears to be suitable for juvenile bull trout growth and survival. If observed emergence occurs earlier in the warm stream, in accordance with our predictions, this would suggest neither an extreme degree of site-specific adaptation, nor a completely generalized regionally consistent pattern of environmental drivers, but perhaps a response to thermal threshold for the initiation of spawning.

As this region is dominated by both rain and snow, the opposing factors of high temperatures in the fall and scouring snowmelt runoff in the spring potentially drive a common developmental pattern of developmental timing. If juvenile experience drives spawning time, multiple factors could be involved, including ambient thermal regime, flow dynamics, and timing of invertebrate hatch (Naman *et al.*, 2016). Downscaled climate models for Puget Sound drainages forecast a $\sim 1^{\circ}\text{C}$ increase in water temperature by the end of the century (Mantua *et al.*, 2010). Increasing empirical thermal regimes by 1°C during bull trout larval development would decrease time to median emergence by 2 weeks in the warm stream and 3 weeks in the cool stream. However, phenological impacts are hard to predict, as they result from interactions between variable regional and stream-specific hydrology and water temperature, particularly at freezing level thresholds as in the basin of study, and climate velocities may be slower than initially predicted at higher elevations (Isaak *et al.*, 2016). Thermal regime variation can shift emergence timing and development at emergence (Steel *et al.*, 2012), and larval development in cold water fishes could be affected in complex ways. Food sources for juvenile fish in headwater streams such as macroinvertebrates can be impacted by multiple factors including regional climate cycles and climate change (Durance & Ormerod, 2007). Thus baseline understanding of the relationships between water temperature and reproductive and early life history phenology are critical.

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Table 2.2. Physical habitat characteristics for a cool stream (Downey Creek) and a warm stream (Bacon Creek), in the Skagit River basin, Washington State, USA. Drainage area, mean basin elevation, and mean annual precipitation were calculated from National Hydrography Dataset Plus Version 2. Summer water temperatures ($^{\circ}\text{C} \pm \text{SD}$) recorded at 30 min intervals with Hobo Water Temp Pro V2 loggers (Onset Corporation, Bourne, MA) anchored in well-mixed pools near the stream mouth, where adult fish must pass prior to spawning. Winter water temperatures ($^{\circ}\text{C} \pm \text{SD}$) were recorded farther upstream of the mouth, where bull trout *Salvelinus confluentus* spawn and embryos incubate

	Cool	Warm
Drainage area (km^2)	92.6	132.1
Mean basin elevation (m)	1296	1085
Mean annual precipitation (cm)	351	282
Mean August temperature in 2016	11.8 ± 1.2	13.2 ± 1.6
Maximum August temperature in 2016	14.6	17.0
Mean January temperature in 2017	1.7 ± 0.9	5.7 ± 0.3
Minimum January temperature in 2017	0.1	4.0

Table 2.2. Estimated median bull trout *Salvelinus confluentus* spawning date (day of year) in a cool stream (Downey Creek) and a warm stream (Bacon Creek), in the Skagit River basin, Washington State, USA, and difference in days between these estimates. Empirical data consisted of redd surveys, from which a multi-level hierarchical Bayesian model related new redd counts to run size, day of year, and stream (Appendix A)

Year	Cool	Warm	Difference
			(warm-cool)
2009	280	284	4
2010	287	291	4
2011	286	293	7
2012	276	288	12
2013	287	294	7
2014	275	297	23
2015	270	297	28
2016	270	295	26

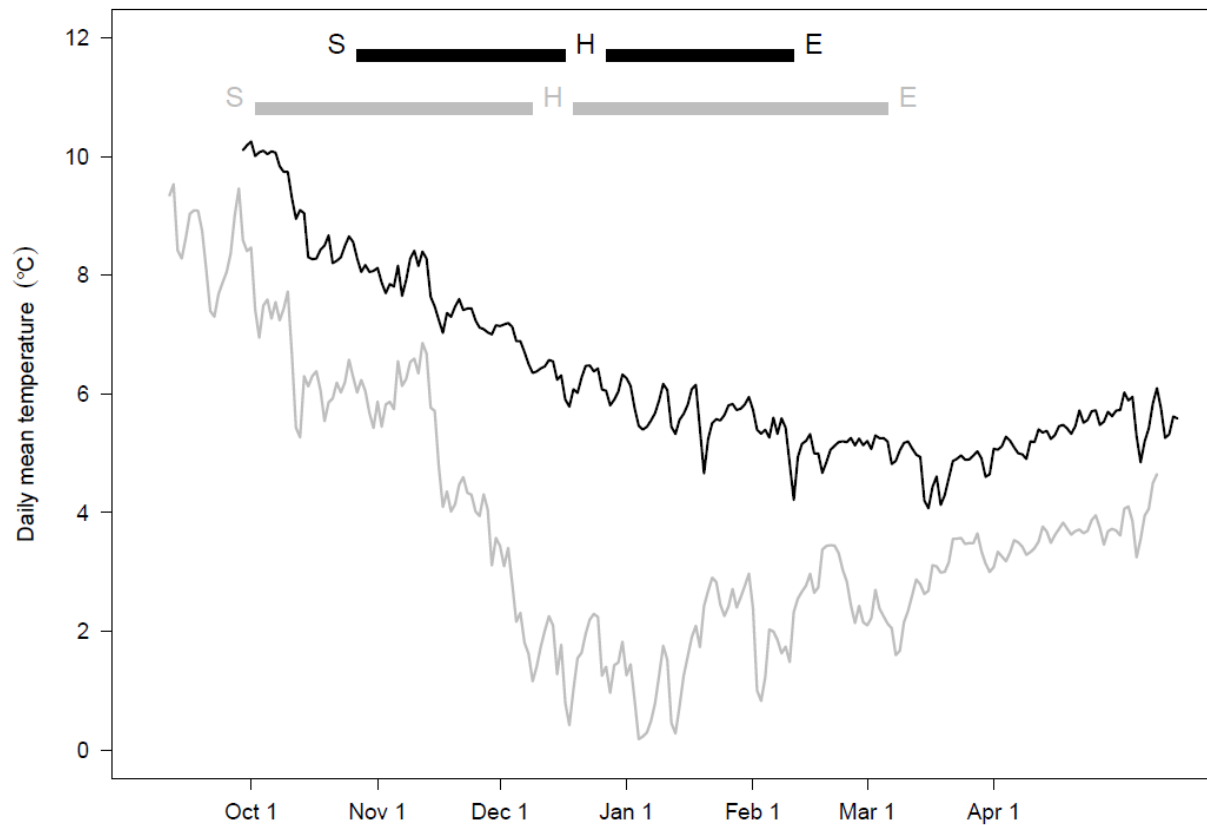


Figure 2.1. Observed daily mean water temperatures in 2016-2017 in a warm stream (Bacon Creek) shown in black, and a cool stream (Downey Creek), shown in grey, in the Skagit River basin, Washington State, USA. Horizontal bars show median dates of bull trout *Salvelinus confluentus* life history events in the warm stream (black) and cool stream (grey). The letter “S” marks median spawning date as estimated from weekly field observations over eight years. The letter “H” indicates estimated median hatching dates in each stream, and the letter “E” marks estimated median emergence dates. Hatching and emergence were estimated for 2016-2017 from thermal relationships reported for bull trout by McPhail and Murray (1979). The total estimated duration of incubation from the median spawning date was 117 d in the warm stream and 165 d in the cool stream.

Chapter 4. DIFFERENTIAL LONG-TERM SHIFTS IN THE TIMING OF SPAWNING BY WILD AND HATCHERY- DERIVED SKAGIT RIVER CHINOOK SALMON UNDER CLIMATE-DRIVEN INCREASING TEMPERATURE REGIMES

4.1 INTRODUCTION

The timing of reproduction in fish populations is an adaptation to long-term patterns of natural selection on adults and offspring (Cushing 1969). Across a wide range of species, temperature is a critical environmental condition affecting breeding timing, e.g., in capelin, *Mallotus villosus* (Carscadden et al. 1997), damselfish, *Dascyllus albisella* (Danilowicz 1995), and smallmouth bass, *Micropterus dolomieu* (Ridgway et al. 1991). Spawning and migration timing are frequently linked, and may both be tied to thermal conditions, as in American shad, *Alosa sapidissima* (Leggett and Whitney 1972). Timing of reproduction has implications for juvenile success, e.g., in seasonal and interannual growth of fathead minnow, *Pimephalus promelas* (Divino and Tonn 2007), and growth and overwinter survival in bluegill sunfish, *Lepomis macrochirus* (Cargnelli and Gross 1996).

In many bodies of water, fish breeding dates are shifting in association with progressive increases in water temperature (e.g., Warren et al. 2012; Lyons et al. 2015) and shifts in flow regime, which is often associated with temperature (Krabbenhoft et al. 2014). Fishes with highly plastic responses may track these environmental changes whereas those with a greater degree of genetic control will change more slowly, with selection from one generation to the next (e.g., American shad vs. sockeye salmon, *Oncorhynchus nerka*: Quinn and Adams 1996). In salmonids, artificial propagation in hatcheries has also been associated with earlier breeding over

decades due to deliberate or inadvertent selection (Quinn et al. 2002; McLean et al. 2005; Ford et al. 2006). Hatchery propagation may select for earlier breeding but, simultaneously, climate warming may select for later breeding, producing conflicting pressures on spawning timing (Quinn et al. 2002; Tillotson et al. 2018). Understanding the reproductive link between generations, then, is vital for determining the current adaptations of populations to their habitat and the consequences of climate and human activities for population persistence.

In salmonids, spawning phenology varies greatly among discrete populations (e.g., sockeye salmon: Hodgson and Quinn 2002; Chinook salmon, *O. tshawytscha*: Brannon et al. 2004). The timing of spawning interacts with the thermal regime experienced by incubating embryos to determine the timing of juvenile emergence months later (Beacham and Murray 1990; Murray and McPhail 1988). Emergence timing, in turn, is adapted to local temperature and prey availability that determine growth, and the risk of predation in the environment where the juveniles emerge (Quinn 2018). For example, Chinook salmon vary greatly in the timing of return from the ocean, even within a given watershed, and often exist as distinct populations with separate river entry times and spawning destinations that could respond differently to varying natural and anthropogenic pressures. These populations are classified as spring, summer, or fall according to their migration timing (Healey 1991) but they may also differ in the timing of reproduction in the fall.

The Skagit River in Washington, USA (Figure 1), supports six population groups of Chinook salmon, each utilizing multiple breeding areas, that collectively migrate from the ocean from May to October and spawn from August to November (Figure 2). These populations are part of the Puget Sound Evolutionarily Significant Unit listed as Threatened under the U. S. Endangered Species Act (Federal Register 1999; Ruckelshaus et al. 2006). The watershed

contains hydroelectric dams that modulate the temperature of mainstem fish habitats in various ways that could impact life history event timing but the tributaries used by Chinook salmon are free-flowing and thus subject to climate-driven processes.

The purpose of this study was to explore spawning phenology of Skagit River Chinook salmon populations in relation to multi-decadal water temperature patterns. Our objectives were to, *i.*) Estimate current median spawning timing for six wild population groups and one naturally spawning group, a subset of one of the populations, that has substantial input of strays from a nearby hatchery, as well as the timing of egg take in the hatchery itself, *ii.*) Determine whether there is evidence for change in spawning timing in any of these populations over the period of record as a possible reflection of climate change. We then used the ensuing results to compare phenology estimates from hierarchical models with calculations based on peak counts from an area-under-the-curve escapement methodology, determine the extent to which patterns in timing are associated with basin level variation in exposure to river temperatures during the period of spawning, and estimate fry emergence timing given empirical thermal data for each population.

4.2 METHODS

Study sites

The Skagit River drains an 8,500 km² basin originating in British Columbia, Canada, passing through rugged mountains and a series of three reservoirs with impassable dams, joined by a number of unregulated small tributaries and the larger Sauk River and its tributaries at river kilometer (rkm) 106 before reaching urban and agricultural alluvium in Washington State, United States (Figure 1). It is the largest watershed in Puget Sound, with upper elevation precipitation regimes dominated by snow and seasonal glacial melt, and lowlands by rain (Beechie et al. 2006). Mean annual discharge near the mouth at Mount Vernon is 473 m³/s

(Pickett 1997), averaged over higher flows in winter and spring, and lower flows in summer and early fall (U.S. Geological Survey 2019). The Skagit Hydroelectric Project (Federal Energy Regulatory Commission Project Number 553) above rkm 155 regulates downstream flow and releases hypolimnetic water from project reservoirs, most strongly affecting the 49 km above the Sauk River confluence. The basin supports all salmonid species native to the region: Chinook, coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye salmon, steelhead/rainbow trout (*O. mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), and bull trout (*Salvelinus confluentus*), as well as Dolly Varden (*S. malma*) in the reservoirs above rkm 155 (Lowery and Beauchamp 2015). Hydrologic regimes have been shifting in the Skagit River basin, consistent with climate change, due to changes in precipitation form and timing within and among years (Riedel and Larrabee 2016; Stumbaugh and Hamlet 2016).

Population groups

Our analysis of spawning phenology considered the six Skagit River Chinook salmon population groups described using genetic analysis by National Oceanic and Atmospheric Administration (NOAA) Fisheries (Ruckelshaus et al. 2006). These populations are named by a combination of the part of the basin where they spawn and their arrival timing in the river system: Suiattle River spring, Cascade River spring, Sauk River spring, Sauk River summer, Skagit River summer, and Skagit River fall (Ruckelshaus et al. 2006; Figure 1). Each population group displays a quasi-normal distribution of spawning timing, and distribution tails are not thoroughly sampled, but the populations are divided spatially and temporally for management purposes and sampled accordingly during their respective spawning seasons (Table 1; Figure 1). The Suiattle River spring population is sampled in tributaries to the Suiattle River in August and September, as the mainstem is turbid with glacial runoff and cannot be surveyed. The Cascade

River spring population is sampled in the Cascade River above rkm 13 in August and September. The Sauk River spring population is sampled in the Sauk River and its tributaries above rkm 52 from August through October, whereas the Sauk River summer population is sampled in the river's mainstem and tributaries below rkm 52 from September through November. The Skagit River summer population is sampled in the river's mainstem and tributaries (including the Cascade River below rkm 6) above Skagit rkm 108 and after a management cutoff date of September 1 through October. The Skagit River fall population is sampled in the mainstem and tributaries below rkm 108 in September and October, a less well defined spatial and temporal separation relative to the Skagit River summer population than the other population groups are from each other, although genetic analyses support the separation (Ruckelshaus et al. 2006).

These population groups generally have little hatchery influence. Musslewhite and Hayman (2007) concluded that the hatchery component in each population group's spawning adults ranged from 0.2-7%, depending on the number of hatchery juveniles released, except for the Cascade River spring population, which ranged from 7-25%. Clark Creek Hatchery at Marblemount, located on the Cascade River 0.8 rkm above its confluence with the Skagit River, is the only source of propagated Chinook salmon in the system (Musslewhite and Hayman 2007; Figure 1). Hatchery origin fish were first noted spawning in the upper Skagit River and tributaries in the early 2000's and have been monitored since 2006 (Musslewhite and Hayman 2007). This naturally spawning hatchery spring group is surveyed in the lower 1.4 km of the Cascade River (near the hatchery itself) and in several tributaries to the upper Skagit River, overlapping in space with the Skagit River summer population group (Figure 1). Hatchery origin fish are identified by coded wire tags and adipose fin clips, which in the case of the hatchery-influenced group recorded in July and August, comprise 50-90% of the individuals on the

spawning ground (WDFW unpublished data). Since there is no discrete spatial and temporal divide between spawning of the hatchery influenced group and the Skagit summer population, we considered a continuous distribution of spawners in the Skagit summer population for all dates of record (July-October), and then separately analyzed a subset of the data (July and August records) as a rough proxy for the tail of the distribution that consists of greater hatchery influence. Therefore, we include analysis for a hatchery spring group consisting of naturally spawning wild and hatchery origin fish that are sampled in the Skagit mainstem and tributaries (including the Cascade River below rkm 6) above Skagit rkm 108 starting in July, prior to the management cutoff date of September 1.

Data analysis

To estimate median spawning date in population groups of Chinook salmon, we used visual redd count data from 28 discrete spawning sites in the mainstem Skagit River and tributaries that each had nonzero redd counts for at least 8 years and up to 66 years (Table 1). Each of the six population groups was represented in the dataset by 1-8 separate spawning sites that were typically surveyed every 7-10 days over 4-8 weeks each year (Table 1). To ensure redd survey data compatibility, analysis was conducted on data from spatially consistent surveys performed by comparable observation methods (i.e., visual counts from ground level made on foot and by boat, or aerial counts from fixed wing aircraft and helicopter; Table 1).

Rather than estimate separate median spawning timing for each population group, in each site, in each year, we employed a hierarchical Bayesian model tailored for each spawning site which used data from all years and dates simultaneously to improve parameter estimation over single year calculations (Adkison and Su 2001). The hierarchical method allowed us to use data rich years to improve model estimates for other years that were data poor for each site, missing

late season surveys as seasonal rainfall increased water turbidity, reducing visibility for aerial surveys, and when high flows made foot and boat surveys unsafe. Counts were conducted by experienced observers and so, the purposes of this analysis, we assumed that interannual observation bias was minimal and variation in precision was consistent among years, as in Walsworth and Schindler (2015). Deviations from this assumption, likely related to autumn high flow events, would only bias estimates if there was a trend in discharge during the spawning season over the period of record. August discharge (cms) at the U.S. Geological Survey Newhalem gage (rkm 150) has not changed significantly over the study period (1962-2018), but discharges in September and October have increased (September slope 17.8 (SE 4.2), adjusted R^2 0.23, $p < 0.01$; October slope 26.6 (SE 7.8), adjusted R^2 0.16, $p < 0.01$). However, surveys are not performed when visibility is estimated to be $< 80\%$, which means that survey frequency, but not survey accuracy, is likely to be reduced by increased discharge later in the season. Any bias due to decreased survey frequency late in the season is likely to be in the direction of failing to detect later spawners, and thus if anything create the false impression of progressively earlier spawning – the opposite of what was observed.

In addition to redd survey data, we also evaluated data on the timing of spawning at the hatchery since 1984, when the current broodstock was obtained. Date, number of females spawned, and number of eggs taken were recorded for the spring Chinook salmon hatchery program from 1984 to 2018. For 20 events when egg take was recorded but number of fish was not, we estimated number of females based on linear regression of the relationship between number of females and number of eggs per female in hatchery records (adjusted $R^2 = 0.89$).

Analysis of median reproductive timing was performed using a model that predicts the expected number of new redds in a survey site for population i , year y , on day t ($\hat{e}_{i,t,y}$) is **Error!**

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$$\hat{e}_{i,t,y} = r_{i,y} \int_t^{t+\Delta t} f(t)_{i,y} dt \quad (3.3)$$

Where $r_{i,y}$ is run size of population i in year y , Δt is the number of days since the last survey, $f(t)_{i,y}$ is a normal probability density function with parameters μ_{iy} and $\bar{\sigma}_I$ (thus, mean timing data varies by year but standard deviation does not).

Aerial surveys were handled differently, as the data consisted of total visible redds rather than new redds. We introduced a new parameter that represents the duration that a redd is visible after spawning. Thus, the expected number of redds observed from these surveys equals **Error!**

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$$\hat{e}_{i,t,y} = r_{i,y} \int_{t-t_{max}}^t f(t)_{i,y} dt \quad (3.2)$$

We relate the model expected values to the new redds observed by foot or boat, denoted $e_{i,t,y}$ for each site i , day t , and year y , using a Poisson likelihood **Error! Reference source not found.:**

$$L(e_{i,t,y}) = \frac{\exp(-\hat{e}_{i,t,y})}{e_{i,t,y}} \hat{e}_{i,t,y}^{e_{i,t,y}} \quad (3.3)$$

The parameters μ_{iy} were modeled hierarchically and assumed to be drawn independently from a normal distribution, with estimated parameters μ_i and $\bar{\sigma}_i$ (the mean and standard deviation of the μ_{iy}) for each site. Broad, bounded, user-defined hyperparameters included uniform priors, with μ_i set to day of year >160 and $\bar{\sigma}_i$ set to 0-50. No covariance among the μ_{iy} was assumed, due to insufficient information in the data. We used a uniform prior on t_{max} from 14 – 28 days (Orrel 1976), but our intention was not to estimate this parameter (as there is little information in these

data to this end) but rather to ensure that our estimates of median spawning date integrated over the uncertainty in how long redds were visible **Error! Reference source not found.:**

$$L(e_{i,t,y}) = \frac{\exp(-\hat{e}_{i,t,y})}{e_{i,t,y}} \hat{e}_{i,t,y}^{e_{i,t,y}} \quad (3.4)$$

We numerically estimated posterior probability distributions using the No-U Turn Hamiltonian sampler implemented in Stan (Stan Development Team 2017; www.r-project.org). We wished to model variance in timing in addition to peak timing, but the data insufficiently captured zero counts pre- and post-spawning season and model convergence was not possible with the inclusion of variance. For the same reason we did not model observer error. Focusing on peak timing, then, the sampler was allowed to warm up for 5,000 iterations, followed by 3 chains of 10,000 iterations for most sites, and 2 for sites with high redd counts and high count variability, then checked using standard convergence diagnostics (\hat{R} ; Gelman and Rubin 1992) and model fit (Gelman and Rubin 1995).

Finally, we compared the results from the hierarchical model with results obtained using linear model fits to raw peak redd counts for each site in each year, a method that is often used in the estimation of salmon population escapement using area-under-the-curve methods (Orrel 1976; English et al. 1992; Smith and Castle 1994; Millar et al. 2012).

Simple linear models were fit to estimated posterior median spawning dates for each spawning site and for the population groups that consisted of a single site (Cascade River spring, and the hatchery egg take). To assess population group trends where multiple sites were involved, we fit robust linear mixed effects models to the estimated dates, weighted by the inverse of the standard error of the date estimates. Candidate models included random effects for population only, site only, and population-site interaction with the most parsimonious chosen according to Akaike's Information Criterion (AIC).

We used the relationship between water temperature and Chinook salmon embryo incubation rate reported by Beacham and Murray (1990), and the reciprocal equation format suggested by Sparks et al. (2017; Austin et al. 2019) to estimate a scenario for median juvenile emergence timing for each population. For this scenario, we used a “current” value for estimated median spawning date (mean of the last five annual values) and population-specific empirical experienced thermal regime from sub-basin temperature gages. Few long-term water temperature data are available for the Skagit River basin. The only datasets of < 4-year duration were from USGS gages in the lower Skagit River at rkm 26 below significant tributary inputs and rainfed lowland catchments (Mount Vernon, 1963-2018, where the metric with the longest record was daily maximum; e.g., Figure 2), and in the upper Skagit River at rkm 127 where the dominant hydrologic influence is the hypolimnetic water released from the hydropower project dams (Marblemount, 1986-2018, for continuity, daily maximum). For these two sites we calculated linear model slopes over time for mean monthly temperatures in August, September, and October, when most Chinook salmon spawn in the basin. For all other sub-basin gages with short time series data, daily mean temperatures were available for the most recent water year, beginning October 1, 2018, allowing us to compare thermal regimes among sites in that year. Daily mean water temperatures were also available for the 2017-2018 spawning and incubation year at USGS gages corresponding to each population, except for the Suiattle spring population, which had data from a gage maintained by the Sauk Suiattle Indian Tribe. All analyses were conducted in the statistical software R (R Core Team 2017).

4.3 RESULTS

Skagit River Chinook salmon population groups varied in median spawning date from August 26 to September 30 in last-five-year averages taken to represent the current period

(ANOVA $F = 6.48$, $p < 0.01$; Table 2). Model comparison of annual medians from the entire temporal span of the datasets (as far back as 1952) indicated that all six wild populations showed progressively later spawning over time (0.03 – 0.48 d/yr; Figure 3). Five of six trends were significant (Table 3); of these, the Sauk River spring population demonstrated the fastest rate of change (0.48 d/yr, SE 0.06) and the Skagit River fall population the slowest (0.22 d/yr, SE 0.04). The Cascade River spring population, monitored at a single spawning site and with fewer redds than other populations, had a trend towards later spawning that was not significant (0.03 d/yr, SE 0.10). Over the entire datasets, wild Chinook salmon now spawn later in the year than in the past at 13 of 23 individual spawning sites, ($p < 0.05$; Figure 3); later trends at seven sites and earlier trends at three sites were not significant (Table 1; Figure 3). Trends derived from annual peak redd counts also revealed later spawning over time but tended to underestimate changes in spawning phenology relative to hierarchical estimation (Figure 4; linear model significance < 0.01 , slope estimate 0.69, slope p -value < 0.01).

Hatchery fish demonstrated the opposite trend from the wild populations. The naturally spawning, hatchery-influenced spring Chinook salmon group, consisting of a subset of the Skagit River summer population, had a last-five-year median spawning date of August 12. The hatchery-influenced group trended earlier in timing, unlike the wild populations (-0.18 d/yr, SE 0.05; Table 2). At the Clark Creek hatchery facility on the Cascade River, the average of last-five-year median egg take date at the hatchery was August 3, 23 d before the earliest wild population group's spawning date. Median timing of egg take for spring Chinook salmon propagation since 1984 also trended earlier, by -0.58 d/yr (SE 0.06).

Thermal regimes varied between sub-basins used for spawning and incubation of Chinook salmon populations in the water year beginning October 1, 2017 (Figure 5). The lowest

mean annual temperature was in the Suiattle River (7.4°C), where the Suiattle River population group spawns, followed by the Sauk River above the Whitechuck (7.5°C), used by the Sauk spring population group. In increasing order, the next lowest temperatures were in the Cascade River at Marblemount (7.8°C) corresponding to the Cascade spring population and the Skagit River at Marblemount (7.8°C) corresponding to the hatchery spring group and the Skagit River summer population. The highest temperatures were in the Sauk River at Sauk (8.7°C) corresponding to the Sauk summer population, followed by the Skagit River at Mount Vernon (9.4°C) corresponding to the Skagit River fall population. Monthly means of daily mean temperatures revealed that the relative ranking of warm and cool sites varied over the Chinook spawning season (Table 5). In August and September, the lowest temperatures were observed in the upper Skagit River mainstem close to the hydropower project and the highest temperatures in the lower Sauk and lower Skagit Rivers. In October, the lowest temperatures were observed instead in the major tributaries: the Suiattle, Cascade, and Sauk rivers, while the lower Skagit River was the warmest, followed by the upper Skagit River. October mean of daily mean temperature in each sub-basin was correlated with median spawning date of the respective population spawning in that sub-basin (adjusted R^2 0.74, $p=0.01$).

Long term temperature trend data were available for two sites in the Skagit River mainstem, demonstrating that water temperature during the Chinook salmon spawning season rose over the decades of study. At rkm 26, daily maximum temperature was measured 1982-1970, 1974-1981, and 2016-2019, over which period mean of daily maximum temperature in August, the warmest month of the year, rose by 0.5 °C/decade (95% CI 0.2 – 0.8, p -value <0.01; Table 3), for an estimated total change of 2.8°C. Closer to the dams, at rkm 127, daily temperature was measured starting in 1986, over which period mean daily maximum August

temperature rose by 0.3 °C/decade (95% CI 0.0 – 0.7, p-value 0.03; Table 3; Figure 2) , or for a total change of 1.1°C. Subsequent monthly mean temperatures also rose over this period of record, but less so (Table 3).

4.4 DISCUSSION

The general sequence of spawning in the fall by the wild population groups followed the predictions based on thermal regimes – earlier in cooler water and later in warmer water. Analysis of the long-term data revealed progressively later spawning by wild fish, contrasting with the trend towards earlier hatchery egg take and redd counts for the naturally spawning hatchery-influenced group. These two patterns were consistent with the intermediate pattern (no change) in the Cascade River population that has received more hatchery-origin fish than the other populations designated “wild.” The direction of timing trends in wild populations was consistent with the prediction that increasing temperature trends in the Skagit River would be met with progressively later spawning to prevent or retard the advancement of juvenile emergence in the absence of hatchery influence.

The greatest rates of change in timing were in the Sauk River populations. While long term data were not available to assess interdecadal changes in temperature in most sub-basins, interannual comparison among sites showed that the warmest spawning season temperatures are in the lower Skagit River, where the population already spawns latest, and in the Sauk River, which has less snow and glacial input from the headwaters than the Cascade or Suiattle rivers (Beechie et al. 2006; Table 6; Figure 6). The populations spawning in the mainstem Skagit River changed less, and these reaches are cooled in August and September relative to adjacent rivers by cool and less variable hypolimnetic water released from the hydroproject dams (Table 6). The Skagit River summer population analysis also included data from the hatchery influenced group,

and therefore captured a combined trend even if hatchery origin fish are spawning earlier than wild origin fish. However, the numerical importance of hatchery influenced individuals would be smaller in the Skagit River summer population (mean annual redd count 3058) relative to the Cascade spring population (mean annual redd count 98).

The wild Cascade spring population, which did not show significant phenological change, spawns in a river that may be cooled in summer relative to historic conditions by glacial meltwater from the South Cascade Glacier, which is rapidly retreating (maximum elevation ~2300 m) (Marcinkowski and Peterson 2015). While recent data do not suggest that the Cascade River is the Chinook spawning location with the lowest temperature (Table 6), trends in basin warming in the mainstem Skagit River may not apply equally to the Cascade River due to glacial influence. Several sources of evidence also suggest that there may be hatchery influence on spawning phenology in the Cascade spring population. Musslewhite and Hayman (2007) reported higher proportions of hatchery-origin fish in this population than the other wild populations. Moreover, the hatchery is located downstream of Cascade River spring spawning grounds. Carcass identification data to further explore the prevalence of hatchery bred individuals on the spawning grounds were limited. Of 349 carcasses recovered in Cascade spring surveys since 1961, 4% were hatchery fish based on coded wire tags and adipose fin clips, 26% were unmarked and presumed wild, and 69% were unknown (WDFW unpublished data). Given the impossibility of disentangling hatchery and environmental influences on the wild Cascade spring Chinook salmon population with current data, further exploration is warranted.

Anadromous fish other than salmonids (e.g. river herring, *Alosa* spp.; Quinn and Adams 1996; Lombardo et al. 2019) have demonstrated changing spawning timing associated with warming water. These species spawn in the spring, as temperatures are increasing, and spawn

earlier in the year with warming trends. In contrast, fall-spawning salmon such as those we studied in the Skagit River spawn as temperatures are descending. Skagit River temperatures, particularly in August, have become warmer over the period of record, and all pooled wild population groups are spawning progressively later. However, hatchery timing trends are moving contrary to adaptive or plastic response patterns in the basin. Because spawning date is highly heritable (Carlson and Seamons 2008), hatchery fish timing can rapidly shift in response to deliberate and/or inadvertent selection (Quinn et al. 2002; Ford et al. 2006; Tillotson et al. 2018), as appears to have happened since 1984 in this system. This selection arises from the fact that the fish that arrive early are more likely to be spawned in the hatchery, since the number and quality of late arrivals are uncertain. Even slight unintentional biases toward earlier spawning timing compound over generations (McLean et al. 2005). Additionally, the progeny of earlier spawning adults may also experience a competitive advantage over the progeny of later adults owing to the body size differential resulting from earlier initiation of feeding. Management considerations should include the impact of such divergence on hatchery runs as well as potential impacts on natural spawning by such fish.

Temperature is an important influence on breeding timing in fishes with impacts across generations. Small changes in temperature (e.g., an average of 1°C) can shift juvenile emergence timing by a month (McCullough 1999). However, temperature and timing interact, such that if thermal regimes during spawning season increase but spawning occurs later in the year, juvenile emergence timing in salmon could remain steady, presumably continuing to optimize conditions for growth and survival in spring. In our juvenile Chinook salmon development scenario, the estimated date of emergence among populations spanned four months, with the predominant difference between the naturally spawning hatchery-influenced group and the natural origin

populations. Theoretically, the range of emergence timing in a given populations may be wide and buffered relative to the magnitude of change in spawning timing (Sparks et al. 2018). But the effects on hatchery-influenced fry emerging in November, like any population of an early emerging fall spawning species, could include the advantages of growth and survival in spring compared to later emerging individuals, as well as the disadvantages of low winter temperatures, volatile storm-driven flows, and limited prey availability (Shuter et al. 2012). For example, wild steelhead trout spawned later in the spring and their progeny emerged later, when flows are lower, than did hatchery-origin steelhead in Forks Creek, Washington, and high discharge was associated with lower reproductive success by the hatchery origin fish (Mackey et al. 2001; Seamons et al. 2012). Across fishes, larger juveniles tend to survive better, although environmental conditions, predation, and other factors can reverse the trend (Sogard 1997). More research is still needed on the energetic consequences of juvenile emergence at different developmental states and times as climate change drives riverine thermal regime change (Beer and Anderson 2001; Campbell et al. 2019).

Changes in salmon phenology may produce ecosystem effects in addition to the effects on the focal species. Rubenstein et al. (2018) found that chum and coho salmon spawning migrations were getting later in the Skagit River basin, increasing the exposure of carcasses to floods and thereby reducing foraging opportunities for bald eagles (*Haliaeetus leucocephalus*). Diverse expression of migration and spawning timing are also linked to regional life history diversity that provides spatial and temporal ecological buffering, which can be compromised by environmental change and anthropogenic impacts, especially at lower latitudes (Hilborn et al. 2003; Satterthwaite and Carlson 2015). A wide range of factors including streamflow and ocean conditions can influence population dynamics in adjacent locations and the scale of the impacts

can vary (Crozier and Zabel 2006), although the Skagit River basin is cooler than adjacent watersheds, suggesting that regional trends be examined for coherence (Goetz 2016). In North American fish populations, changing reproductive phenology is among the responses that have been linked to trends in temperature, stream flow, and hydrologic regime, although anthropogenic factors such as dams, hatchery programs, harvest, land use, pollution, and others, can have compounding or dampening effects (Lynch et al. 2016). However, where warming freshwaters are prompting later breeding in fall spawning fishes, managers should consider the impact of dams and hatchery programs on wild populations, as well as explore the consequences of phenological change for the persistence of threatened fish populations.

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Table 3.3. Chinook salmon (*Oncorhynchus tshawytscha*) redd count survey sites in the Skagit River watershed, Washington State, USA, used in data analysis. River km distances indicate lower and upper bounds of surveyed area, as measured from the mouth of the named site, that were used in analysis; in some cases a slightly truncated range of rkm were analyzed than have been recently surveyed due to data insufficiency. Surveys were typically performed every 7-10 days over 4-8 weeks each year from the ground, by foot or boat unless marked ^a, indicating aerial surveys completed by airplane or helicopter. Trends in median spawning date and significance from estimated median spawning date in each year at each site were estimated using a hierarchical sampling algorithm, to which a linear model was fit; asterisks denote p-values < 0.05

Population	Site	Survey location (river km)	First survey yr	n yr	Mean annual redd count	CV	Median spawn day of year	Slope	p
Suiattle spring	Big Creek	0-1.0	1959	42	23	162.1	250	0.43	<0.01 *
Suiattle spring	Tenas Creek	0-0.5	1959	40	13	110.6	238	0.34	<0.01 *
Suiattle spring	Straight Creek	0-1.1	1965	33	8	295.6	233	0.10	0.60
Suiattle spring	Buck Creek	0-1.3	1959	47	72	126.8	242	0.30	<0.01 *

Suiattle spring	Lime Creek	0-0.3	1966	36	18	114.7	234	0.18	0.08	
Suiattle spring	Downey Creek	0-0.2	1990	17	26	77.3	240	0.42	0.16	
Suiattle spring	Sulphur Creek	0-0.5	1959	46	32	78.1	229	0.21	0.03	*
Suiattle spring	Milk Creek	0-0.2	1959	23	11	68.3	237	0.31	0.07	
Cascade spring	Cascade River	13-31	1965	33	98	54.5	246	0.08	0.57	
Sauk spring	Sauk River	52-64	1964	41	200	79.5	257	0.44	<0.01	*
Sauk spring	Falls Creek	0-0.5	2010	8	5	106.6	270	1.80	0.23	
Sauk spring	South Fork Sauk R.	0-5.6	2000	16	38	71.1	257	-0.09	0.82	
Hatchery spring	Illabot Creek	0-4.2	2007	10	10	55.5	227	-0.20	0.79	
Hatchery spring	Cascade River	0-1.4	1990	20	97	85.8	224	-0.23	0.13	
Hatchery spring	Boulder Creek	0-0.5	2006	12	8	57.6	225	-0.59	0.51	
Hatchery spring	Bacon Creek	0-2.4	1990	16	6	56.7	236	-0.20	0.38	
Hatchery spring	Goodell Creek	0-1.1	2006 1984	12	1	152.1	273	-1.33	0.08	
Sauk summer	Dan Creek	0-0.6	1956	13	3	105	288	0.15	0.66	
Sauk summer	Sauk River ^a	21-34		44	356	167.8	265	0.26	<0.01	*
Skagit summer	Skagit River ^a	108- 126	1952	57	3058	80.3	268	0.31	<0.01	*
Skagit summer	Illabot Creek	0-3.1	1966	35	68	107.4	253	-0.08	0.70	
Skagit summer	Cascade River	0-1.4	1969	31	118	99.7	229	-0.60	0.02	*
Skagit summer	Bacon Creek	0-2.4	1974	40	32	66.8	263	0.26	0.10	
Skagit summer	Goodell Creek	0-1.1	1960	29	8	88.6	258	0.28	0.12	
Skagit fall	Skagit River ^a	39-108	1955	35	787	85.5	272	0.27	0.03	*
Skagit fall	Day Creek	0-3.5	1984	30	29	82.2	291	0.24	0.22	
Skagit fall	Finney Creek	0-6.7	1974	33	34	114.9	331	0.39	0.02	*
Skagit fall	Jackman Creek	0-0.8	1980	14	3	114.2	272	0.50	0.13	
Hatchery egg take		NA		25	NA	NA	216	-0.45	<0.01	*

Table 4.2. Mean date for hatchery egg take is the mean annual median egg take date over the last five years of record (2014-2018) and mean date for the Cascade spring population is the mean annual median spawning date over the last five years of record (2014-2018), where ^a denotes a single site or data source for the group. Mean date for all other groups, one hatchery influenced group and five wild populations, is the population-wide average of site-specific estimates of mean annual median spawning date over the last five years of record, as weighted by mean annual redd count contribution to the population total (2014-2018). Estimate (d/yr) and standard error (SE) are calculated using robust linear models weighted by the standard error of the annual date estimates; trend indicates the direction of change of estimated median spawning timing, if any, that is supported by model results

Population	Mean date	Estimate (d/yr)	SE	Trend
Hatchery egg take ^a	3-Aug	-0.58	0.06	earlier
Hatchery spring	12-Aug	-0.18	0.05	earlier
Suiattle spring	26-Aug	0.28	0.03	later
Cascade spring ^a	2-Sep	0.03	0.10	none
Sauk spring	13-Sep	0.48	0.06	later
Sauk summer	21-Sep	0.30	0.06	later
Skagit summer	22-Sep	0.29	0.03	later
Skagit fall	30-Sep	0.22	0.04	later

Table 4.3. Water temperature trends over time (d/yr) at two United States Geological Survey gages located on the mainstem Skagit River: Mount Vernon, rkm 26 (1963-2018, daily maximum) and Marblemount, rkm 127 (1986-2018, daily maximum). F statistics, degrees of freedom, and adjusted R^2 refer to the overall model, while slope, 95% confidence interval, t statistics, and p-values describe the coefficient year in linear models of the format Temperature ~ Year

Month	F	df	Adj R2	Slope	95% CI	t	p	
<hr/>								
Mount Vernon								
<hr/>								
August	12.25	1, 15	0.41	0.05	0.02 - 0.08	3.5	<0.01	*
September	7.17	1, 14	0.29	0.03	0 - 0.05	2.68	0.02	*
October	5.83	1, 15	0.23	0.02	0 - 0.04	2.42	0.03	*
<hr/>								
Marblemount								
<hr/>								
August	5.47	1, 24	0.15	0.03	0 - 0.07	2.34	0.03	*
September	1.17	1, 23	0.01	0.01	0 - 0.03	1.08	0.29	
October	0.67	1, 27	-0.01	0.01	-0.01 - 0.25	0.82	0.42	

Table 4.4. Estimated juvenile Chinook salmon emergence timing in Skagit River populations based on median population-specific spawning dates averaged over 2014-2018, population-specific water temperature from United States Geological Survey gage data from 2018, and thermal development relationships reported in Beacham and Murray (1990)

Population	Date of emergence	Time from fertilization to emergence (d)	Mean water temperature (°C) on emergence date
Hatchery spring	23-Nov	103	6.0
Suiattle spring	20-Jan	147	4.1
Cascade spring	20-Jan	140	5.3
Skagit summer	17-Feb	148	4.2
Skagit fall	25-Feb	147	3.0
Sauk spring	3-Mar	171	3.4
Sauk summer	5-Mar	165	4.7

Table 4.5. Monthly mean of daily mean temperatures in 2017 at United State Geologic Survey and Sauk Suiattle Indian Tribe stream gages

Population	Gage location	August	September	October
Hatchery spring	upper Skagit River	11.8	10.8	9.5
Suiattle spring	Suiattle River	12.7	11.0	7.4
Cascade spring	Cascade River	13.0	11.1	8.2
Sauk spring	upper Sauk River	14.3	12.2	8.1
Sauk summer	lower Sauk River	15.7	13.1	8.8
Skagit summer	upper Skagit River	11.8	10.8	9.5

Skagit fall	lower Skagit River	15.8	13.8	10.7
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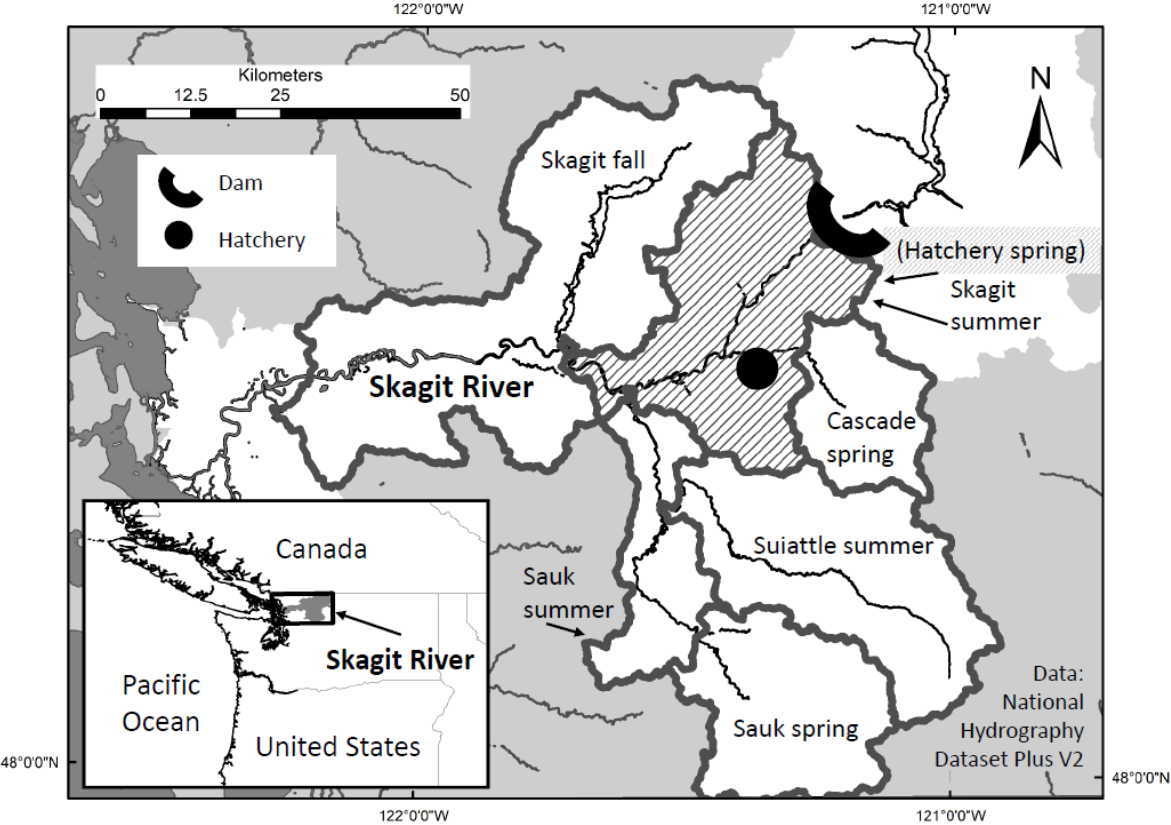


Figure 3.1. The Skagit River study area, Washington State, USA. Black bars indicate hydroelectric dams; star indicates hatchery location; boundaries indicate spawning locations for wild Chinook salmon populations. Naturally spawning hatchery fish are found in the lower Cascade River and tributaries to the upper Skagit River

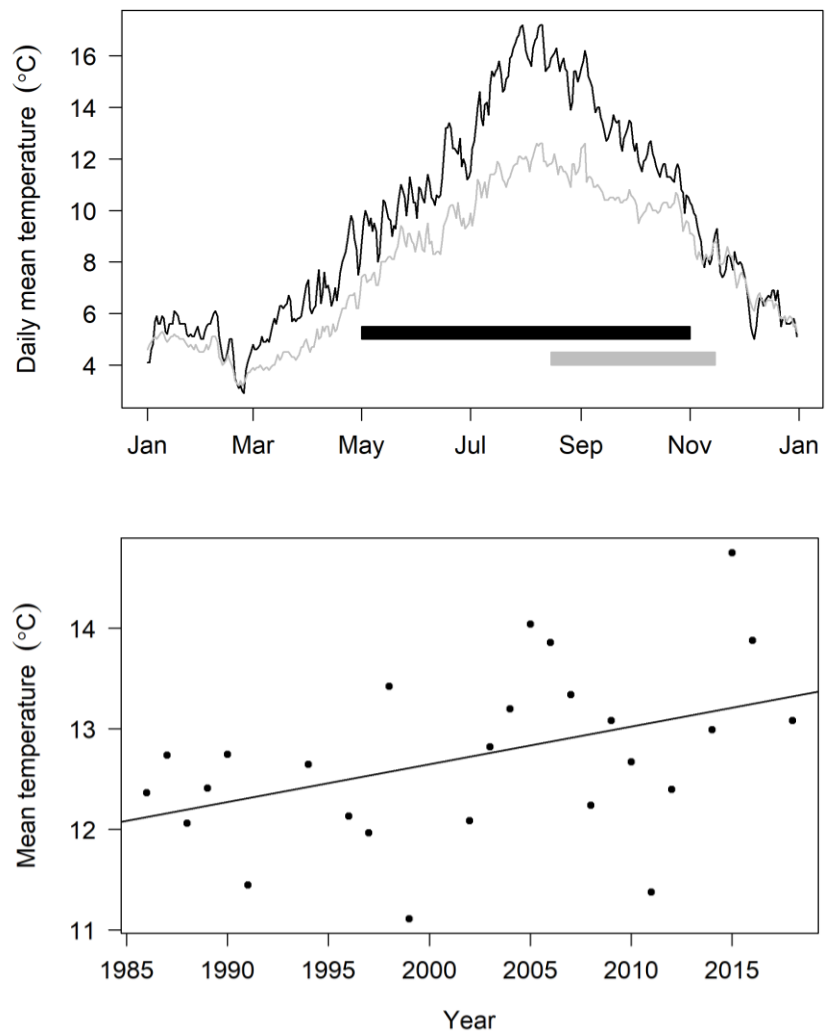


Figure 3.2. In upper panel, Skagit River daily mean water temperature for 2018 at U.S. Geological Survey gages at Mount Vernon (rkm 26) in black, and Marblemount (rkm 127) in gray. Black bar indicates generalized duration of river entry for combined Skagit Chinook populations; gray bar indicates generalized duration of spawning for combined populations. In lower panel, Skagit River mean of daily August maximum temperature over the period of record at Marblemount

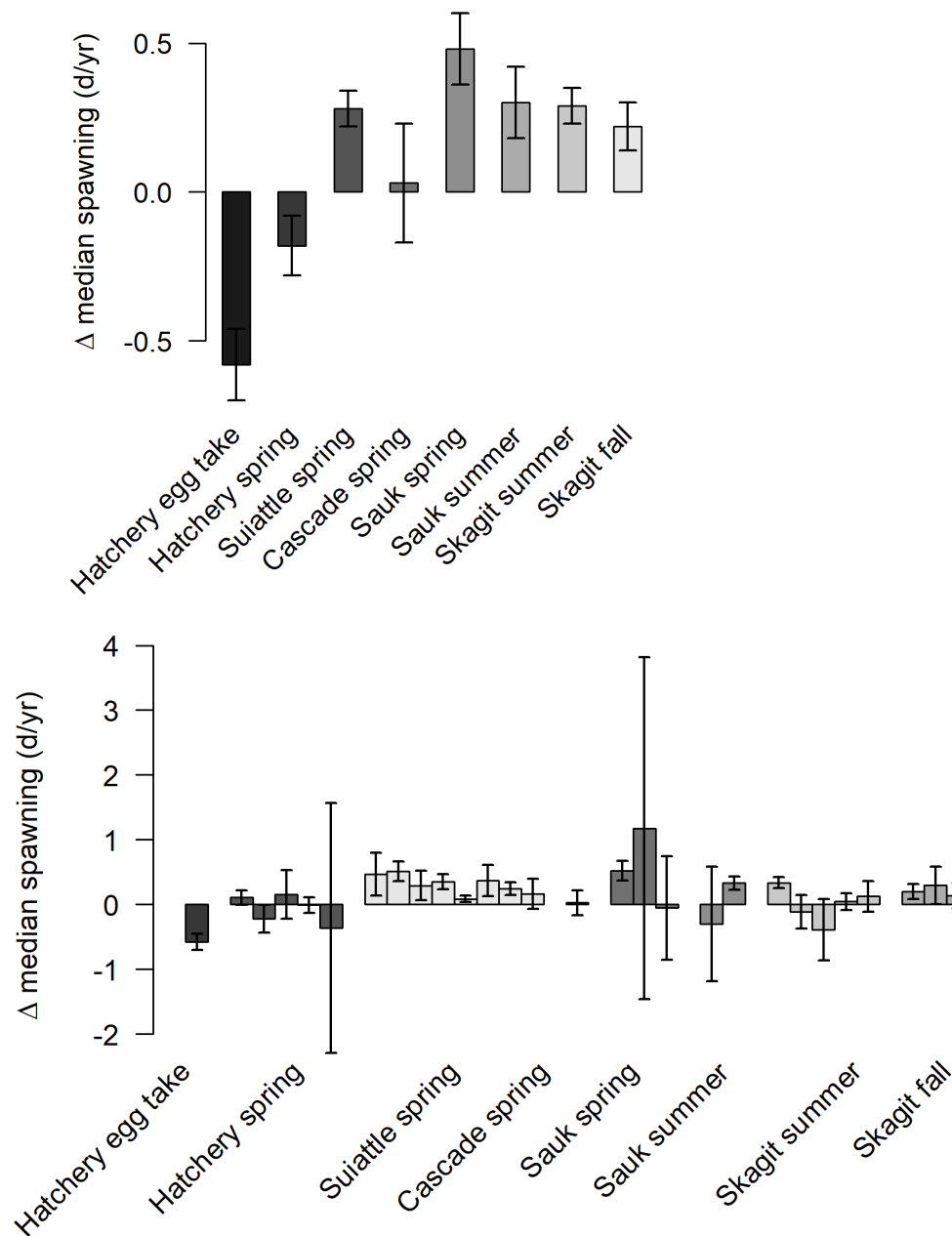


Figure 3.3. The upper panel depicts the slope of robust linear regression models weighted by the standard error of annual estimates indicating rate of change in median spawning date per year over the period of record for populations of Skagit River Chinook salmon. Hatchery egg take refers to the timing of Chinook propagation in the Clark Creek Hatchery. The hatchery spring group is a naturally spawning combination of 50-90% hatchery origin fish with the remainder wild fish, a subset of the Skagit summer population. Suiattle, Cascade, Sauk, and Skagit River populations are differentiated by river entry date and spawning location. The lower panel depicts

linear model slopes for individual survey sites for each population

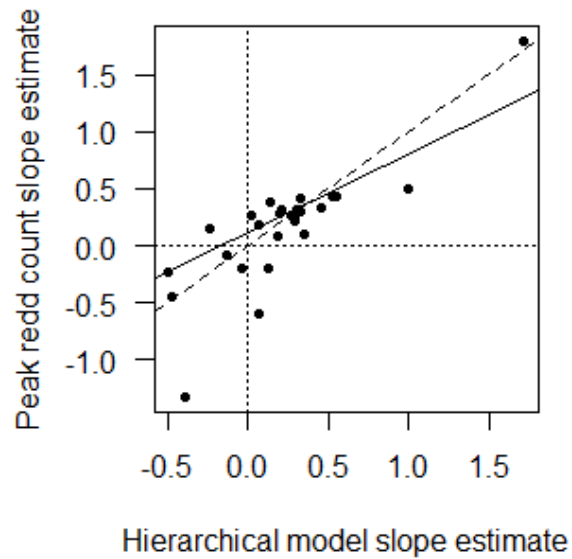


Figure 3.4. Comparison between estimated rate of change (d/yr) in median Chinook salmon spawning date over the study duration in 28 study sites in the Skagit River basin using two methods: hierarchical modeling and annual peak redd count selection. The dashed line depicts the 1:1 ratio; the solid line depicts the linear model fit showing that peak counts underestimate change in spawning timing relative to hierarchical estimates (intercept estimate 0.12, p-value 0.02; slope estimate 0.69, p-value <0.01; overall p-value <0.01)

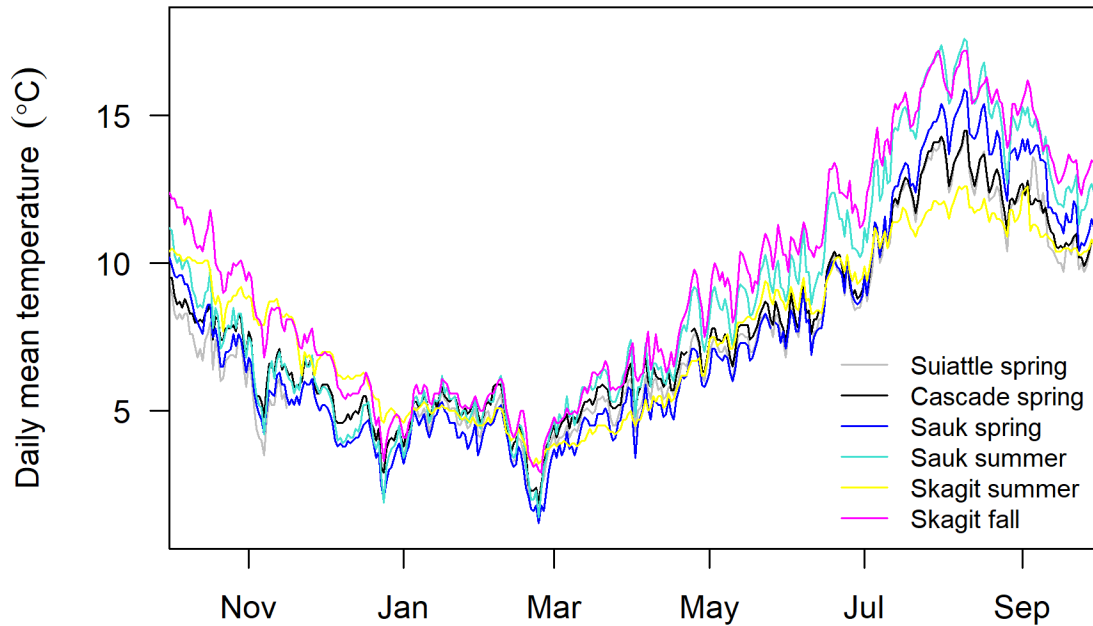


Figure 3.5. Thermal regimes relevant to spawning and incubation of Skagit River basin Chinook salmon populations for the water year October 1, 2017 – September 30, 2018. Data from United States Geologic Survey gage sites: Skagit River at Marblemount (hatchery spring and Skagit summer), Cascade River at Marblemount (Cascade spring), Sauk River above Whitechuck River (Sauk spring), Sauk River at Sauk (Sauk summer), and Skagit River at Mount Vernon (Skagit fall), and from Sauk Suiattle Indian Tribe gage site: Suiattle River at All Creek (Suiattle spring)

Chapter 5. TEMPERATURE, ELEVATION, AND DISCHARGE

CONTROL BREEDING DISTRIBUTION OF SIX NATIVE SALMONID SPECIES IN TRIBUTARIES WITHIN A SINGLE BASIN

5.1 INTRODUCTION

Groups of fishes found together in freshwater are often studied as non-random communities, associated with biotic and abiotic factors (Jackson et al. 2001). The existence of such organized communities has been investigated with different approaches, including correspondence between fish and benthic communities (Kilgour and Barton 1999), temporally consistent patterns in common fish species (Grossman et al. 1982), and analysis of null models (Jackson et al. 1992). As a general principle, environmental gradients are a template on which biological interactions occur, resulting in species distributions (e.g., Schlosser 1990). Following these principles, lotic waters support fish communities whose organization relative to physical habitat features may be understood at multiple spatial scales (e.g., Smith and Powell 1971). Early stream research understandably focused on habitat and species distribution at scales most readily perceptible to the human observer, those of reaches and streams (e.g., Burton and Odum 1945). Distribution of fish species among microhabitats has been considered in relation to habitat characteristics like water depth, substrate type, and cover (e.g., Brown 1991), as well as extrinsic factors like trophic separation and temporal segregation (Ross 1986). Expanding the perspective of stream studies, Vannote et al. (1980) emphasized the directionality and dendritic character of rivers and the consequent downstream changes in physical attributes, sources of carbon, and community composition of consumers. Poff et al. (1997) advocated testing mechanistic hydrologic hypotheses about community patterns in lotic systems while Lapointe (2012) related

river habitat geomorphology to sites selected for fish reproduction along a spatial gradient ranging from substrate to landscape. These spatial template lenses on species distribution can be complemented by perspectives that includes species traits (Jackson et al. 2001) and interactions within and among populations (e.g., Schlosser 1987; Peres-Neto 1994).

Salmonids (salmon, trout, and char) are among the most closely studied fishes breeding in fresh water (Jonsson and Jonsson 2011; Quinn 2018). Notwithstanding this wealth of information, and the importance of breeding distributions for the conservation and restoration of the species, they also exemplify the challenges of determining the factors controlling breeding distributions. The spatial distribution of salmonid spawning and rearing in a watershed is likely to be a function of multiple habitat characteristics operating at nested spatial and temporal scales, such as water temperature, discharge, and topographical features, as well as human land use practices, reflecting the sum of factors acting on all life stages of each species. However, the spatial distribution patterns of salmonids at the scales most relevant to conservation have not been well explained despite a conceptual understanding of habitat use (Beechie et al. 2008) and a wealth of information on the basic ecology of each species. At regional scales within the overall ranges of each species, comparisons among watersheds reveal that physical controls such as channel morphology and hydrologic regime affect breeding distribution and life history patterns (Chinook salmon: Beechie et al. 2006; multiple species: Montgomery et al. 1999). At the finest spatial scale of the habitat spectrum, there has been detailed research on the physical features of specific sites used for spawning (depth, velocity, gravel size, etc.). For instance, Chinook salmon spawn in deeper, faster water, with larger substrate than other salmon (e.g., Groves and Chandler 1999), coho salmon use pebble substrates in pools and run tails (Mull and Wilzbach 2007), sockeye salmon spawning sites are related to substrate composition and water temperature

(Hoopes 1972), and bull trout *Salvelinus confluentus* (Guzevich and Thurow 2017) and Dolly Varden *S. malma* (Kitano and Shimakazi 1995) use shallower, lower velocity water than other species. However, Fausch et al. (2002) observed “it is at the scale [of 1 to 100 km stream segments], which humans must view by walking or low-altitude flight in an aircraft, that stream habitat features become most important to fish.” This intermediate scale, so important to fish, is also the most logistically difficult to study and the most poorly represented in literature.

Intermediate scale habitat use, where much of the conservation and restoration activity takes place, may to be linked to several physical and life history characteristics in salmonids, including adult body size, juvenile stream rearing duration, and timing of spawning. Many physical features of spawning sites (e.g., substrate size and water depth), scale with female body size, which varies among species. Females can excavate gravel for redds with a median diameter up to 10% of body length (Kondolf and Wolman 1993). Substrate size, in turn, is associated with water velocity and scale-related hydrologic features of stream catchments, suggesting that at the ends of the size spectrum, species occupancy might be limited by the availability of suitable physical habitat. Like adult body size, the duration of rearing in streams by juveniles varies among species (Quinn 2018): chum salmon, *O. keta*, pink salmon, *O. gorbuscha*, and ocean-type Chinook salmon, migrate to the ocean to feed more or less immediately after emerging from the gravel, and sockeye salmon, migrate to lakes or, in some populations, to the ocean. Juveniles of other species remain in streams and rivers for several months to a year (stream-type Chinook salmon), a year or two (coho salmon, *O. kisutch*), or one to two or more years (rainbow trout, *O. mykiss*, cutthroat trout, *O. clarkii*, bull trout, and Dolly Varden). Consequently, some streams might be more conducive to occupancy than others, and this might affect spawning distribution as well. Salmonids also vary in spawning season, with successive reproductive windows for

different species occurring over much of the year. Phenology could affect the distribution of spawning if, for example, access to streams early in the season was limited by low flows or high temperatures.

Many studies have detailed habitat use by single species, but far fewer have examined habitat use by multiple species in the same river basin, and they often reveal considerable overlap in the physical features of selected redd sites (e.g., Fukushima and Smoker 1998; Smith 1973). Differences in distribution are, at least in some cases, related to female size (e.g., Witzel and MacCrimmon 1983). Studies have also been conducted at broader spatial scales to determine what geomorphic features are most consistently associated with spawning distributions but, again, these studies typically report a single species in a single river (e.g., bull trout: Baxter and Hauer 2000; Bean et al. 2015; and Chinook salmon: Cram et al. 2017; Hanrahan 2007; Klett et al. 2013, but see also Nelson et al. 2015).

Our goal was to determine whether intermediate scale habitat characteristics predict species habitat use by salmonids in the Skagit River basin of western Washington, USA. We compared stream-scale physical characteristics of breeding habitat in tributaries occupied by six native, naturally-reproducing salmonid species in the basin: Chinook, coho, chum, and pink salmon, steelhead, and bull trout. We identified the most important habitat characteristics describing breeding distribution of the salmonid assemblage at multiple scales, then used ordination techniques to explain variation in species occupancy at each stream in terms of these characteristics (e.g., temperature, precipitation, stream discharge, soil characteristics, vegetation type, land use categories, and topography). We asked whether any of three life history traits was reflected in spatial patterns of distribution of each species: 1) adult body size, 2) seasonal timing of breeding, and 3) length of time juveniles feed in the stream. At the reach scale, larger fish

spawn in deeper, faster water, with larger substrate (Bjornn and Reiser 1991), so we hypothesized that lower elevation catchments would have more of these habitats and thus be more likely to support larger bodied fish. Additionally, larger bodied fish would be less likely to be able to physically access small streams, which dominate total habitat length in small catchments. Therefore, if body size is an important driver of intermediate-scale distribution, we expected to find larger-bodied species would occur in catchments with higher stream order, lower elevation, higher mean annual velocity, and higher mean annual discharge. Generalized female fork length at maturity, from large to small, is Chinook salmon = 871 mm, steelhead = 721 mm, chum salmon = 683 mm, coho salmon = 643 mm, pink salmon = 522 mm, and bull trout ~ 425 mm (Skagit River basin bull trout in Beamer et al. 2004; salmon data collected from sources in Quinn 2018). In addition or alternatively, given the strong relationship between embryo development and temperature that controls emergence timing (Brannon 1987; Webb and McLay 1996), we hypothesized that if spawning timing is important to species distribution, the dominant covariates will be related to seasonal temperature regimes at the catchment scale, which represents a strong temporal pattern across fine-scale site variability. From early to late in the study basin, the annual order of median spawning date is Chinook salmon (range: August-September), pink salmon (range: August-September), bull trout (range: September-November), chum salmon (range: November-December), coho salmon (range: October-January), and steelhead (range: January-May) (Washington Department of Fish and Wildlife, unpublished data). Finally, the distribution of spawning may vary with the duration of juvenile stream rearing, along a continuum of minimal to maximal time spent in freshwater before migrating. Since juveniles increasingly disperse from their natal sites over time, it is immediate post-emergence growth and survival that is likely to be linked to spatial patterns of spawning. Thus, we expect

that if stream rearing duration drives spatial habitat use, the species with longer duration (coho, steelhead, and bull trout, as well as stream-type Chinook) will be found in a subset of sites with adequate conditions for year-round residence, while the species with shorter duration stream rearing (pink, chum, and ocean-type Chinook) will be found in a different subset, since they do not have to find suitable juvenile feeding territories or overwinter in freshwater. The following generalizations about species inherently group together such intraspecific differences in life history as partial anadromy in bull trout (Austin et al. 2019a), diverse migratory patterns in steelhead (Kendall et al. 2015), and rearing dichotomies in Chinook salmon, in which most individuals spend little time rearing in freshwater, while others remain for a year (Zimmerman et al 2015). Nevertheless, characteristic juvenile stream rearing time, from least to most, is pink salmon (days), chum salmon (days-weeks), ocean-type Chinook salmon (days-months), stream-type Chinook salmon (1 year), coho salmon (1 year), steelhead (2-3 years), and bull trout (2-5 years) (Zimmerman et al. 2015; Austin et al. 2019a; Quinn 2018).

We looked for a preponderance of analytical and qualitative evidence to evaluate these options, knowing they may not be mutually exclusive. We considered measures of support including overlap in occupancy status among species pairs, rank order comparisons between species pairs along the three hypothesized continua, multivariate analysis of species distributions and habitat variation, and side-by-side visualization of modeled single species occupancy patterns as a function of habitat variables to shed light on species-specific habitat relationships and multi-species distribution.

5.2 METHODS

Study location

Our study basin lies in the middle latitudes of the Pacific salmonid range in North America, 48-49° N, beginning in the mountains of southwestern Canada and reaching marine waters in the northwestern United States (Figure 1). Over an area of 8,500 km², the Skagit River basin covers rugged and glaciated peaks under public land protection, reservoirs with impassable dams, middle elevations with timber harvest rotations, unregulated tributary rivers, alluvial agriculture, diking, urbanized floodplains, and modified estuary distributary channels. Upper elevation hydrology is snow-dominated and lowland hydrology is rain-dominated (Beechie et al. 2008). Mean annual discharge near the river mouth is 473 m³/s (Pickett 1997), with high flows in late fall and early winter from seasonal rainfall (November to January), lower flows in late winter and early spring, another peak in May through July from the melting of snow deposited in higher elevations, and low flows in summer and early fall (USGS 2018). Dams above rkm 155 regulate downstream flow and release hypolimnetic reservoir water, most strongly affecting the main channel for 49 km above the confluence with the Sauk River. The basin supports all salmonid species native to the region as well as mountain whitefish (*Prosopium williamsoni*), suckers (*Catostomus* spp.), dace (*Rhinichthys* spp.), lampreys (*Entosphenus tridentata* and *Lampetra* spp.), threespine stickleback (*Gasterosteus aculeatus*), and sculpins (*Cottus* spp.) (Lowery and Beauchamp 2015).

Data sources

Salmonid occupancy data were compiled for 46 free-flowing tributaries with lengths of 3 to 30 km throughout the Skagit River watershed (Figure 1). For scale comparability we did not include mainstem river reaches, even though pink, chum, and Chinook salmon breed in

mainstem rivers. Occupancy data were summarized from 1943-2018 Washington Department of Fish and Wildlife (WDFW) foot and boat surveys documenting spawning Chinook, coho, chum, and pink salmon, steelhead, and bull trout. The basin also supports sockeye salmon but they are almost exclusively restricted to the Baker River system which is strongly affected by a hydroelectric dam and so not representative of the other streams, all of which are free-flowing. The spawning distribution of coastal cutthroat trout in the basin is not mapped so they were excluded from analysis, as were Dolly Varden because they have only been observed above impassable dams, where Pacific salmon are absent. Ocean and stream type Chinook salmon were pooled in the study because ultimate life histories of offspring are not reliably known from adult spawning characteristics. For all species, index reaches in study streams were surveyed every 7 to 14 d throughout the respective spawning seasons, e.g., July-September for Chinook, and September-November for bull trout. When the repeated surveying of all index reaches in a stream failed in all years to detect a given species, that species was considered absent from the stream. When one of the *Oncorhynchus* species was documented infrequently, defined as 1.) fewer than 2 redds/year on average or 2.) observation of fewer than 5 live or dead fish/year in fewer than 10 years of the 75 year dataset, expert opinion was used to determine whether the species occupied that reach, whether these observation result from straying from another breeding population or whether they represent a small and difficult to detect population (Brett Barkdull, Washington Department of Fish and Wildlife, and Scott Morris, Sauk-Suiattle Indian Tribe, personal communication).

Bull trout have been less frequently surveyed than the other species and tend to inhabit more remote streams that are difficult to survey on foot, but some streams might still host low-density spawning populations. For 16 streams in our dataset with unknown bull trout occupancy

status, environmental DNA was collected in July 2016, a time of year when juveniles would typically be in streams and adults could begin to stage prior to spawning in October (Austin et al. 2019b), and seasonally low water levels would maximize detection probability. In each stream, at suitable sites 1 km apart as predicted by a United States Geological Survey gradient and air temperature model, a 5 L sample of stream water was filtered through a 1.5 μ m glass microfiber filter (USFS and NGS 2015). From these filters, the combined environmental DNA was extracted, amplified, and tested for the presence of *Salvelinus*-specific markers (Carim et al. 2016). *Salvelinus* DNA was detected in 12 of 16 streams, indicating the presence of juveniles or adults representing a spawning population. No definitive record exists for Dolly Varden below the impassable dams in the basin, so we used these data to indicate the strong likelihood of bull trout presence.

Environmental variables for the streams in the dataset were considered from among those known to influence regional salmonid distribution (Burnett et al. 2007; Fullerton et al. 2015; Pess et al. 2002; Table 1). We also included those relevant in a changing climate, such as percentage ice cover in a watershed, which can affect stream flow and temperature in summer, and other anthropogenic factors such as population density. A broad range of likely and less likely candidate variables was considered, given the comprehensive salmonid assemblage data being considered. We considered physical habitat related variables for each stream including catchment area, elevation metrics, soils and permeability data, percent cover of major vegetation types, and human land use metrics, as well as hydrologic variables including Strahler stream order, calculated catchment air temperature metrics, base flow index, calculated precipitation, average stream discharge, and average velocity metrics in several months of the year ecologically relevant to salmonid spawning and susceptible to change under climate-impacted temperature

and discharge conditions (Table 1). Variables were grouped into categories, e.g., watershed position, catchment elevation, and watershed elevation, from which multivariate analysis could be conducted to select the best descriptor. Variable values were obtained from 1:100,000 scale stream reach data in the National Hydrography Dataset Plus Version 2, as derived from digital elevation models, the National Land Cover Database, the State Soil Geographic Database, and Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate data (USGS 2019). Raster data, e.g., forest cover, were calculated over the entire study catchment and hydrologic data, e.g., calculated discharge, were calculated at the most downstream point in the catchment. Of the 46 streams for which occupancy data were available, 39 could be assessed for the habitat variables in question and 36 of those supported breeding by at least one salmonid species (Figure 1).

Data analysis

Data screening and initial exploration included determining, for each species, the relative frequency of occurrence in the dataset, the percentage of streams occupied, and its stream-specific overlap with each other species. The independence of the occupancy patterns of each pair of species in each stream was analyzed with Chi-square tests of independence to ask, for instance, whether Chinook salmon presence or absence in each of the study sites was independent of pink salmon presence or absence in those sites, and so forth for all combinations of species.

Environmental data were screened by examining empirical cumulative distribution functions and histograms for all environmental variables to look for outlier sites and values. Environmental data were not transformed due to a relatively small ranges of values and adherence to assumptions of normality (Legendre and Gallagher 2001). Principal component

analysis (PCA), which uses weighted linear combinations of variables to extract the major patterns of variation from a correlation matrix, was used to select variables for subsequent analysis (Goodall 1954). From each group of autocorrelated variables (for example, those related to watershed elevation), the best descriptor was selected in the following way: 1) consideration was given to variables included in the statistically significant principal components ($P < 0.05$) based on 999 Monte Carlo simulations of the randomized dataset; 2) each eigenvector coefficient was converted into a Pearson product-moment correlation; 3) the chosen variable was the one with the highest correlation between its Pearson product-moment correlation and its original value, e.g., mean catchment elevation (m) (variable selection procedures, e.g., Hering et al. 2006).

We sought to explain salmonid occupancy using the variation in the selected environmental characteristics of the study streams. Constrained ordination techniques address this type of comparison between two matrices. First, detrended correspondence analysis (DCA) was applied to the species data to determine whether canonical correlation analysis or redundancy analysis was more appropriate, given the range of the original data (ter Braak 1986). The first DCA axis length was 2.99 standard deviations, indicating that the variable response was unimodal and canonical correspondence analysis (CCA) was appropriate. Monte Carlo tests of 999 permutations of the original dataset were used to assess the significance of the overall CCA ordination model and of each of the CCA axes in sequence. Results were visualized in a CCA triplot along the first two axes as weighted averages of site scores and with site and species scores scaled symmetrically by the square root of their eigenvalues (ordination sequence, e.g., Wang et al. 2003).

To highlight the habitat relationships for each species individually, fixed effects generalized linear models were used to explore the relationship between each species' occupancy and continuous environmental variables across all sites, with the integer category Strahler stream order removed (e.g., Guisan et al. 1999). We visualized relationships by plotting scaled single main effects for each species from a model that included all PCA selected variables with their standard error and significance level, such that positive variable values indicated association with occupancy by that species. Recognizing that the assumption of independence among variables was not met, these results were considered exploratory. All analyses were conducted in R (R Core Team 2018), using the *vegan* (v2.5-6) and *pastecs* (v1.3.21) packages.

5.3 RESULTS

On average, the 46 study streams supported breeding by 3 Pacific salmonid species with a median of 3 and a mode of 5 (10 of 46). Longer streams supported breeding by more species (linear model slope 0.14, SE 0.03, $P < 0.01$). The percentage of streams occupied by each species ranged from 28% (chum salmon) to 72% (steelhead), with variable proportions of overlapping occupancy by each species pair (Table 2). Steelhead and coho salmon shared occupancy status, i.e., both present, or both absent, in the greatest number of streams, 52%, whereas bull trout and chum salmon shared occupancy status in the fewest, 2%. Some individual species-habitat associations were evident from individual comparisons (e.g., chum salmon and water temperature and velocity; Figure 5).

Linear predictors of environmental variables captured a large amount of the variation in habitat features in our dataset. In the PCA of environmental variables only, the first three principal components were significant, explaining 45%, 19%, and 7% of the variation, respectively. Principal component scores for individual environmental variables were converted

to Pearson-product moment correlations, yielding 13 environmental variables for subsequent analysis (Table 1).

Environmental variables explained almost half of salmonid stream occupancy patterns, emphasizing the influence of temperature and elevation. The global CCA demonstrated a nonrandom association between habitat characteristics and species presence (model $df = 13$, $\chi^2 = 0.50$, $F = 2.22$, $P < 0.01$). The primary axis explained 37% ($P < 0.01$) of the variance in species stream occupancy along a gradient between higher November and annual mean temperatures on one end and mountain-related metrics on the other: higher elevation, deeper water tables, higher autumn velocity and discharge, and more conifer forest and ice cover (Figure 2; Table 4). The secondary axis explained much less, 8%, of the variance in site occupancy, defined on one end by road density and on the other by stream length and October and annual discharge, and was not significant. The third and fourth axes were not interpreted, as they were not significant and explained little variance (7% and 3%, respectively) with no clear axis pattern.

Since bull trout occupancy appeared to be related to quite different habitat variables from that of the salmon species, we considered the possibility that bull trout occupancy patterns were obscuring patterns for the other species. Therefore, we also analyzed a reduced dataset including only chum, pink, coho, and Chinook salmon, and steelhead, which required eliminating 6 stream sites only occupied by bull trout, leaving 30 streams and shorter gradients of environmental variation. We analyzed the salmon-only dataset using redundancy analysis (RDA) because DCA yielded 1.73 standard deviations for the first axis, indicating RDA was appropriate. For the salmon-only dataset, as well, habitat variables were non-randomly associated with patterns of species occupancy (model $df = 13$, variance = 0.65, $F = 1.96$, $P < 0.01$; Figure 3), although in the primary axis explained less of the variance (27%, $P < 0.01$) in salmon site occupancy than did

the primary CCA axis that included all six species. Generally, the removal of bull trout did not affect the habitat associations of the other species. Individual species orientations in the triplot relative to each other and to covariate vectors did not change dramatically with the removal of bull trout, although steelhead and coho salmon habitat associations became further differentiated from each other. Chum salmon remained tightly connected to higher temperatures; Chinook and pink salmon remained close together and both linked to higher October discharge, annual discharge, and stream length, and steelhead aligned more with higher elevation variables including increased velocity and precipitation. Therefore, we focused the remainder of our interpretation on the initial analysis that included all six species.

Temperature was also a dominant feature related to individual species distributions according to scaled single main generalized linear model effects (Figure 4). For five of the species in our dataset, occupancy was positively correlated with temperature, whereas bull trout presence was negatively correlated with temperature (Figure 6). The largest effect sizes were in Chinook and pink salmon associations with longer streams and higher annual and October discharge. Chinook and pink salmon were also associated with lower elevation catchments. Coho salmon and steelhead were likewise present more often at lower elevations, but with generally smaller effect sizes; both species were positively associated with road density and negatively associated with October precipitation, water table depth, September velocity, conifer cover, and base flow. Chum salmon exhibited similar habitat associations and effect sizes to those of coho salmon and steelhead, except that road density and discharge were not significant, and nearly the inverse of the associations for bull trout, for which greater upstream ice extent had a large effect size.

No salmonid life history characteristic emerged as a compelling explanation for intermediate scale distribution. There were mixed results when species pairs were sorted by occupancy status and the absolute value of ranked difference in body size, breeding timing, and juvenile life history (Table 3). Strong support for the spatial structuring of spawning distribution by body size would have included the species with the smallest difference in body size (e.g., large species Chinook salmon and steelhead, intermediate species chum salmon and coho salmon, or small species pink salmon and bull trout) occupying more streams in common. However, a pattern to this effect did not emerge. For instance, Chinook salmon and bull trout shared occupancy status in a quarter of streams despite being the most different in body size. Nor was there a pattern in the ranked difference timing of spawning relative to shared occupancy (Table 3). The earliest and the latest spawners, Chinook salmon and steelhead, shared one of the highest rates of occupancy, despite reproductive timing of late summer-fall, and winter-spring, respectively. Similarly, pink salmon and bull trout, and chum salmon and bull trout, with the fewest shared occupancy streams, reproduce at more similar times than other pairs. The third comparison, generalized juvenile stream rearing duration, also yielded ambiguous results (Table 3). Species with more similar duration of stream rearing shared breeding occupancy patterns in some cases (e.g., coho salmon and steelhead, and Chinook salmon and steelhead), relative to species with very different juvenile life history patterns (e.g., chum salmon and bull trout, and pink salmon and bull trout), but the pattern was not pronounced. Further investigating Chinook salmon, which were otherwise pooled across life histories, we divided Chinook salmon between sites thought to produce more stream-type versus more ocean-type individuals based on distance from river mouth and population migration timing (Ruckelshaus et al. 2006). Sites with these two life history patterns were then compared to sites with pink salmon habitat use; 11 of 24 sites

had shared pink and ocean-type Chinook salmon breeding and 8 of 22 sites had shared pink and stream-type Chinook salmon breeding.

5.4 DISCUSSION

The six salmonid species studied in the Skagit River watershed spend time ranging from days to years in fresh water as juveniles before migrating to sea, span mean adult body sizes from 425 to 871 mm, and reproduce from August to May, with substantial overlap yet distinct variation in their breeding locations. None of the three hypothesized organizing biological characteristics, juvenile stream rearing, body size, or timing of spawning, was clearly associated with breeding distribution among streams in the watershed. Ranked differences of the extent of juvenile stream rearing among species pairs had slightly fewer outliers in occupancy patterns than did ranked differences related to adult body size or spawning timing. However, temperature and elevation, the most important environmental variables for assemblage-level variation in occupancy, are associated with both timing of spawning and juvenile stream rearing. Water velocity and discharge, likely to be linked to adult body size at the time of spawning, were also associated with occupancy for multiple species, although not all. The two species with the closest association in multivariate analysis were species that overlap in timing of spawning, pink and Chinook salmon.

From among the generally suitable streams (i.e., used by at least one salmonid species), breeding distribution across the basin was linked to habitat features at a range of spatial and temporal scales. Elevation and temperature explained the most variation in breeding assemblages among tributaries across multiple forms of analysis, both including and excluding bull trout, which were strongly associated with cold water. The distributions of many species were influenced by smaller scale hydrologic and topographic variables related to stream size,

groundwater, and autumn climate regime. These findings correspond with variables known to affect reach-scale spawning site selection (e.g., in bull trout: Bean et al. 2015; coho salmon: McRae et al. 2012; chum salmon: Poirier et al. 2012). Road density and the area of watershed ice cover mattered for fewer species and were less important associations, although both variables may be important in other systems (e.g., Beschta 1978; Power 2002). Longer streams supported breeding by more species, likely because larger catchments can offer greater diversity of spawning and rearing habitats (Pess et al. 2014). Despite this scale-dependency, there were overarching patterns of sympatry and differentiation in stream use among the six species studied that superseded the effect of stream length.

Pink and Chinook salmon overlapped most among the study species. These species have similar spawn timing (late summer and early fall), but different juvenile rearing duration (shorter in pink salmon) and very different adult body size. Large bodied Chinook salmon would be expected to use larger streams with higher discharge, consistent with a body size hypothesis (Kondolf and Wolman 1993), but pink salmon, the smallest Pacific salmon (Quinn 2018), broadly overlapped with Chinook salmon in the Skagit River basin across both Chinook salmon life histories. In parts of its range such as southeastern Alaska, pink salmon characteristically spawn in very small streams and even inter-tidal areas (Heard 1991), often in sympatry with chum salmon. This combination, consistent with a juvenile rearing hypothesis, was not observed in our study watershed. Pink salmon commonly spawn in great numbers in the mainstem of the Skagit River and other large Puget Sound rivers, often overlapping in reach-scale space and time with Chinook salmon. These species typically spawn in late August and September in the Puget Sound region, when many small streams (including tributaries of large rivers) experience prohibitively low flows. In contrast, chum salmon spawn later, typically in November, when fall

rains make the small streams accessible. Chum and pink salmon require the least juvenile rearing in freshwater, but in the Skagit River basin the two species did not closely correspond in stream use.

Pink and chum salmon occupancy did align with low elevation variables reflecting agriculture and human land uses that dominate the flood plain. This is consistent with chum salmon spawning in regions of ground water exchange at the reach scale (Mouw et al. 2014), which could be required for embryo ventilation in streams with lower velocity-driven oxygenation. High discharge can deter chum salmon from spawning, as in the Columbia River when Bonneville Dam velocity increased beyond 0.8 m s^{-1} (Tiffan et al. 2010). None of our study streams had mean velocity in this range, but some had November velocity around 0.6 m s^{-1} , suggesting that peak discharge during storm events could prevent chum spawning in those sites. In the Skagit River basin, chum salmon spawned in streams that were warmer and slower than average in the fall (Figure 5). The importance of November and annual temperature and elevation could be interpreted as support for the timing of spawning hypothesis, as they are general proxies for multiple factors that affect physical stream conditions at the time of breeding for chum and other salmonids.

Coho salmon and steelhead were closely associated across our analyses, which could align with all three hypotheses, as the species share extended stream rearing and overlap in adult body size. Coho salmon spawn before steelhead, although nearly overlapping in season, and both species have protracted breeding seasons with distinct subgroups throughout the basin returning to fresh water at different times (WDFW unpublished data), enabling them to take advantage of a range of physical and hydrologic conditions. In other basins, coho salmon and steelhead overlap in stream habitat occupied by juveniles (Bisson et al. 1988), though steelhead are

characteristically found at higher densities in steeper streams (Hicks and Hall 2003), and adults choose similar spawning locations relative to woody debris (House and Boehne 1985).

Positive and negative habitat associations for bull trout were completely opposite those of the *Oncorhynchus* species (Figure 6). Bull trout breeding locations were associated with cold water, which was unsurprising given the species' peri-glacial range (Power 2002). Low temperature was the only predictor of bull trout presence from a suite of habitat variables including instream cover, channel form, substrate, and other fish abundances in a reach-scale study by Dunham et al. (2003). The importance of low temperature and ice cover to bull trout in our analyses suggest possible mechanisms of impact including summer cooling from glacier and snowmelt for pre-spawning adults, rearing juveniles, or both, consistent with laboratory work demonstrating lower thermal tolerance and growth optima in bull trout than in other salmonids (Selong et al. 2001; Mesa et al. 2013). Bull trout occupancy was also negatively associated with road density. Although our data were undifferentiated in terms of road surface, Baxter et al. (1999) found evidence that bull trout redd abundance declined with increasing gravel logging road density.

In the Skagit River basin, upland catchments tend to be more forested and have fewer roads, resulting from historical state and federal land protection of rugged higher elevation areas, whereas floodplains were developed for agriculture and urban uses (Rakestraw 1955; Wilderness Act of 1964; Washington State Wilderness Act of 1984). This legacy of land use may explain why many metrics were positively covaried in this watershed: catchment base flow index, catchment conifer cover, watershed ice cover, October precipitation, September stream velocity, and water table depth, and why several others were negatively associated: road density, November temperature, and annual temperature. In addition to being shaped by human land use

history, human actions may affect some environmental variables going forward. Seasonal streamflow and precipitation are liable to be affected by climate change, particularly in low elevation streams (Mantua et al. 2010; Stumbaugh and Hamlet 2016). It will be important in the coming decades to monitor the effects of changing hydrologic patterns on salmonid occupancy across the species' range.

Naiman et al. (1992) described a temporal scale of factors controlling stream habitat conditions ranging from proximate (10^{-1} yrs) to ultimate (10^6 yrs). Our study focused on the middle of that range. While capturing multi-decadal patterns in salmonid breeding distributions, we also attempted to capture some intra-annual variation in our habitat metric selection process, e.g., by including seasonal stream discharge and temperature metrics to allow PCA to sort. Nevertheless, we recognize that a different choice of environmental variables emphasizing temporal variation in conditions across salmonid life history stages might yield additional insights into breeding distribution.

We aimed to address the knowledge gap in salmonid-habitat relationships at intermediate scales – coarser than redd site selection or reaches within streams but finer than species range distributions or among-basin scales. Therefore, we used stream catchment as our unit of measure, even though fish use within a stream is typically organized on the reach scale, such that large bodied Chinook salmon and chum salmon spawn in lower reaches and smaller bull trout use lower order headwater sections in the same catchment. One effect of this choice is that we avoided the complications of continuous sampling (e.g., Brenkman et al. 2012) by treating each tributary as a discrete unit, but we left out mainstem river habitats where pink, chum, and Chinook salmon spawn. Inclusion of such mainstem spawning would have increased spawning site overlap estimates between these species, which otherwise shared few streams, and reduced

percent overall site overlap between some other pairs of species. Nevertheless, elevation and temperature would have remained important overall, since all three mainstem spawning species use low elevation stream sites, and mainstem river temperatures are closer to stream temperatures during the autumn spawning season than during summer or winter. A second consequence of the choice of streams as the study unit is that they inherently generalize across reach-scale patterns in habitat use, as does the application of coarse-grained GIS data, which were calculated but not always measured at the stream catchment scale. We did not include sub-reach scale variables like pool density, which can be important to salmonid occupancy (Anlauf-Dunn et al 2014). However, Ward et al. (2012) found that large scale habitat variables covaried with each other across Oregon coastal streams, suggesting that watershed scale analyses accurately express scaled up patterns found in streams. Nevertheless, Pacific coastal watersheds do not represent all salmon-producing watersheds. For example, in an eastern Oregon basin, adult spawning migrations take place when seasonal temperatures are near upper thermal limits, limiting habitat use by Chinook salmon (Torgersen et al. 1999). For this reason, we recommend comparative analyses among watersheds to determine similarities and differences.

One difference among watersheds in the study region is in the role of snowmelt in the hydrologic regime. This facet of physical habitat has been linked to the prevalence of particular life histories in salmonids: Chinook salmon, which commonly express ocean type life histories (little stream rearing), more often express stream type life histories (one year of stream rearing) in basins with more snowmelt, such as the Skagit River (Beechie et al. 2006). However, our occupancy data were not distinguished by life history type, so our habitat association results apply to the species as a whole. Splitting out life history differences would have only affected the

qualitative interpretation of life history impacts on distributions, but not sufficiently to clarify the already ambiguous results.

Recent research in a watershed with diverse thermal regimes, closely associated with climate variables (air temperature, precipitation, and snow pack), showed that thermal regime options appear to be narrowing with climate warming for native salmon species in Alaska (Shaftel et al. 2020). Our work highlights the central importance of temperature in salmonid distribution across a diverse watershed farther south, far outstripping the role of road density or other immediate human impacts, suggesting that species distribution within watersheds should continue to be assessed as regional climate patterns change. Our results also indicate that intermediate scale habitat use by a suite of related species is a function of multiple nested physical and hydrological variables, without a single, clear biological characteristic driving the pattern. Strong covariation in variables and limited support for juvenile stream rearing duration, as well as timing of spawning and body size as biological organizing principles, underscore the idea that habitat is composed of a suite of tightly linked characteristics operating at interconnected scales to determine which species occur where across a diverse landscape.

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Table 4.4. Environmental variables explored as predictors of salmonid species occupancy patterns, sorted by Pearson-product moment correlations from significant principal component analysis axes based on 999 Monte Carlo simulations of the randomized dataset. Autocorrelated variables were grouped; the bolded variable listed first in each group was retained. Data sources:

NHDPlusV2 snapshot of the National Elevation Dataset, State Soil Geographic Database, National Land Cover Database, U.S. Census, PRISM Climate Data, U.S. Geological Survey

Base Flow Index (United States Geological Survey 2019)

Pearson product-moment	Environmental variable	Description	Mechanism (general: Taylor 1990; Moir et al. 2002; Shellberg 2002; Gibbins 2008)
-0.88	Stream length	Catchment-scale cumulative network stream length (km)	Longer streams are more likely to provide a range of habitats to support more species (Pess et al. 2014)
0.83	Catchment area	Cumulative upstream drainage area of the catchment (km ²)	Larger basins are more likely to provide a range of habitats to support more species (Pess et al. 2014)
0.65	Stream order	Modified Strahler stream order for stream segment at bottom of catchment (integer)	Higher order streams have more confluence complexity and generally higher discharge
0.93	Elevation (catchment)	Mean catchment elevation (m)	Associated with discharge, precipitation and temperature metrics affecting migration and spawning (Beechie et al. 2006)
0.88	Watershed position	River distance from the watershed mouth to the bottom of stream catchment (km)	Channel types with disproportionate use distributed generally downstream (Moir et al. 2004)

0.85	Elevation (watershed)	Mean watershed elevation (m)	Associated with discharge, precipitation and temperature metrics affecting migration and spawning (Beechie et al. 2006)
0.85	Water table depth	Mean water table depth in the catchment (cm)	Ground water inputs associated with spawning site selection (Bean et al. 2014)
-0.84	Bedrock depth	Mean depth of soil to bedrock in the catchment (cm)	Contrasting valley floor alluvium and the shallow soils of upper watershed drainages (Church 2002)
-0.81	Organic matter	Mean soil percentage organic matter in the catchment by weight	Resulting from land use and topography, indicating allochthonous inputs for stream rearing juvenile food sources (Bilby and Bisson 1992)
-0.70	Soil permeability	Mean soil permeability in the catchment (cm/hour)	Related to hydrograph stability, buffering, and maintenance of sufficient flows for spawning and rearing (Church 2002)
0.86	Conifer cover	Catchment area land cover classified as evergreen forest, 2011 (%)	More conifer cover linked to more intact habitat including large woody debris in channels and spawning gravel (House and Boehne 1985; Buffington et al. 2004)
-0.38	Deciduous cover	Catchment area land cover classified as deciduous forest, 2011 (%)	More deciduous cover related to conifer forest removal and subsequent regrowth or riparian corridor area (Merz 2001)
0.54	Mixed forest cover	Catchment area classified as mixed deciduous/evergreen forest, 2011 (%)	Intermediate forestry classification encompassing both types
0.32	Shrub cover	Catchment area classified as shrub/scrub, 2011 (%)	Shrub cover is not common for the region except as vegetation above tree line, or in disturbed low elevation landscapes (Jones and Grant 2996)
0.39	Ice cover	Watershed area classified as ice/snow, 2011 (%)	Likely to cool streams downstream with summer meltwater (Power 2002)
-0.69	Road density	Mean road density in the catchment (km/km ²)	Paved roads provide impervious surface and contaminants; gravel roads leach sediment (Beschta 1978; Trombulak and Frissel 2001)

-0.68	Housing density	Mean housing unit density in the watershed, 2010 (housing units/block group area)	Impervious rooftops and built housing reduce ecosystem functions (Booth et al. 2002)
-0.49	Population density	Mean population density in the catchment (block group population/block group)	Number of humans provides a collective proxy for more impacts of many types: housing, transportation, runoff, fishing, etc. (Wohl et al. 2017)
-0.41	Impervious surfaces	Catchment area land cover classified as anthropogenic impervious surfaces (e.g., parking surfaces, roads, building roofs), 2006 (%)	Impervious surface area linked to rapid runoff after precipitation events, ecotoxicity, loss of habitat (e.g., Booth et al. 2002; Feist et al. 2011)
-0.95	Annual mean temperature	Mean annual mean catchment air temperature, 1981-2010 (C°)	Average air temperature provides a proxy magnitude metric for water temperature
-0.93	Annual maximum temperature	Mean annual maximum catchment air temperature, 1981-2010 (C°)	Maximum air temperatures are reached in summer, when migrating adults are vulnerable to water temperature maxima
-0.95	Annual minimum temperature	Mean annual minimum catchment air temperature, 1981-2010 (C°)	Minimum air temperatures are reached in winter, when incubating embryos and stream rearing juveniles would be limited
-0.95	November temperature	Mean November catchment temperature (C°)	Late spawning season temperature
-0.92	October temperature	Mean October catchment temperature (C°)	Mid spawning season temperature
-0.87	September temperature	Mean September catchment temperature (C°)	Early spawning season high temperature for most species
0.66	Base flow index	Ratio of catchment base flow to total flow (%)	Higher BFI generally required for migration and spawning in smaller order streams (Vadas 2000)
0.92	Annual discharge	Mean annual gage-adjusted discharge at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (cfs)	Average discharge at the catchment scale provides a general magnitude metric, likely scaled for spawning with fish body size

0.70	Annual precipitation	Mean annual catchment precipitation, 1981-2010 (mm) Mean annual gage-adjusted velocity at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (fps)	Average precipitation provides a general magnitude metric; precipitation, discharge, and velocity allowed a time-independent selection of mechanism Average velocity at the catchment scale provides a general magnitude metric, possibly prohibitive at either extreme depending on fish body size
0.62	Annual velocity		
0.97	October discharge	Mean October gage-adjusted discharge at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (cfs) Mean September gage-adjusted discharge estimate at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (cfs)	Discharge metric capturing intermediate flows midway through the fall spawning season for most species Discharge metric capturing intermediate flows midway through the fall spawning season for most species; one month was selected to include temporal variation for the metric
0.94	September discharge	Mean November gage-adjusted discharge at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (cfs)	
0.90	November discharge		Discharge metric capturing volatile storm flows late in the fall spawning season for most species
0.86	September velocity	Mean September gage-adjusted velocity at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (fps) Mean October gage-adjusted velocity at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (fps)	Velocity metric capturing low flows midway through the fall spawning season for most species; one month was selected to include temporal variation for the metric Velocity metric capturing intermediate flows midway through the fall spawning season for most species
0.82	October velocity		

0.59	November velocity	Mean November gage-adjusted velocity at the downstream end of the stream segment calculated with the Enhanced Runoff Method, 1971-2000 (fps)	Velocity metric capturing volatile storm flows early in the spawning season for most species
0.87	October precipitation	Mean October catchment precipitation (mm)	Mid spawning season precipitation
0.83	September precipitation	Mean September catchment precipitation (mm)	Precipitation metric capturing early spawning season dry weather; one month was selected to include temporal variation for the metric
0.75	November precipitation	Mean November catchment precipitation (mm)	Late spawning season precipitation

Table 4.2. Percent occupancy overlap among pairs of salmonid species (Salmonidae, *Oncorhynchus* and *Salvelinus*) in 46 tributary sites in the Skagit River basin, Washington. Occupancy of streams by one species was found to be independent of occupancy by another for one of two reasons, either because species are found together more often than expected by chance (shown in green), as in steelhead and coho salmon, or because species are found together less often than expected by chance (shown in yellow), as in chum salmon and bull trout. Asterisks indicate significance according to Chi square tests of independence ($P < 0.05$)

	Pink	Chum	Chinook	Coho	Steelhead
Pink					
Chum	20				
Chinook	41 *	17			
Coho	37 *	24 *	35		
Steelhead	43 *	26	43 *	52 *	
Bull trout	20	2 *	24	20	26

Table 4.3. Pairs of Pacific salmonid species, their percent of streams with observed occupancy status in common, ordered from most to least, and three columns of biological characteristics showing the absolute value of the difference in ranks between the species pairs, conditionally coded such that green represents the most alike and yellow the most different. Characteristics with more green at the top of the column and more yellow at the bottom are closer to the observed pattern in species overlap

Species pair	Percent shared presence or absence	Body size (largest to smallest)	Spawning timing (earliest to latest)	Stream rearing (least to most)
Coho - steelhead	52	2	1	1
Chinook - steelhead	43	1	5	2
Pink - steelhead	43	3	4	4
Pink - Chinook	41	4	1	2
Pink - coho	37	1	3	3
Chinook - coho	35	3	4	1
Chum - steelhead	26	1	2	3
Steelhead - bull trout	26	4	3	1
Chinook - bull trout	24	5	2	3
Chum - coho	24	1	1	2
Pink - chum	20	2	2	1
Coho - bull trout	20	2	2	2
Pink - bull trout	20	1	1	5
Chum - Chinook	17	2	3	1
Chum - bull trout	2	3	1	4

Table 4.4. Biplot scores for constraining variables in canonical correspondence analysis axes of variation in salmonid assemblage distribution in 36 streams, ordered from most negative to most

positive for CCA1

Variable	CCA1	CCA2
November temperature	-0.84	0.22
Temperature	-0.80	0.20
Road density	-0.34	0.40
Stream Length	-0.22	-0.46
Discharge	-0.21	-0.45
October discharge	0.02	-0.60
Base flow index	0.48	-0.57
Conifer cover	0.50	-0.34
Ice cover	0.59	-0.34
October precipitation	0.60	-0.28
September velocity	0.64	-0.48
Water table	0.65	-0.47
Elevation	0.74	-0.15

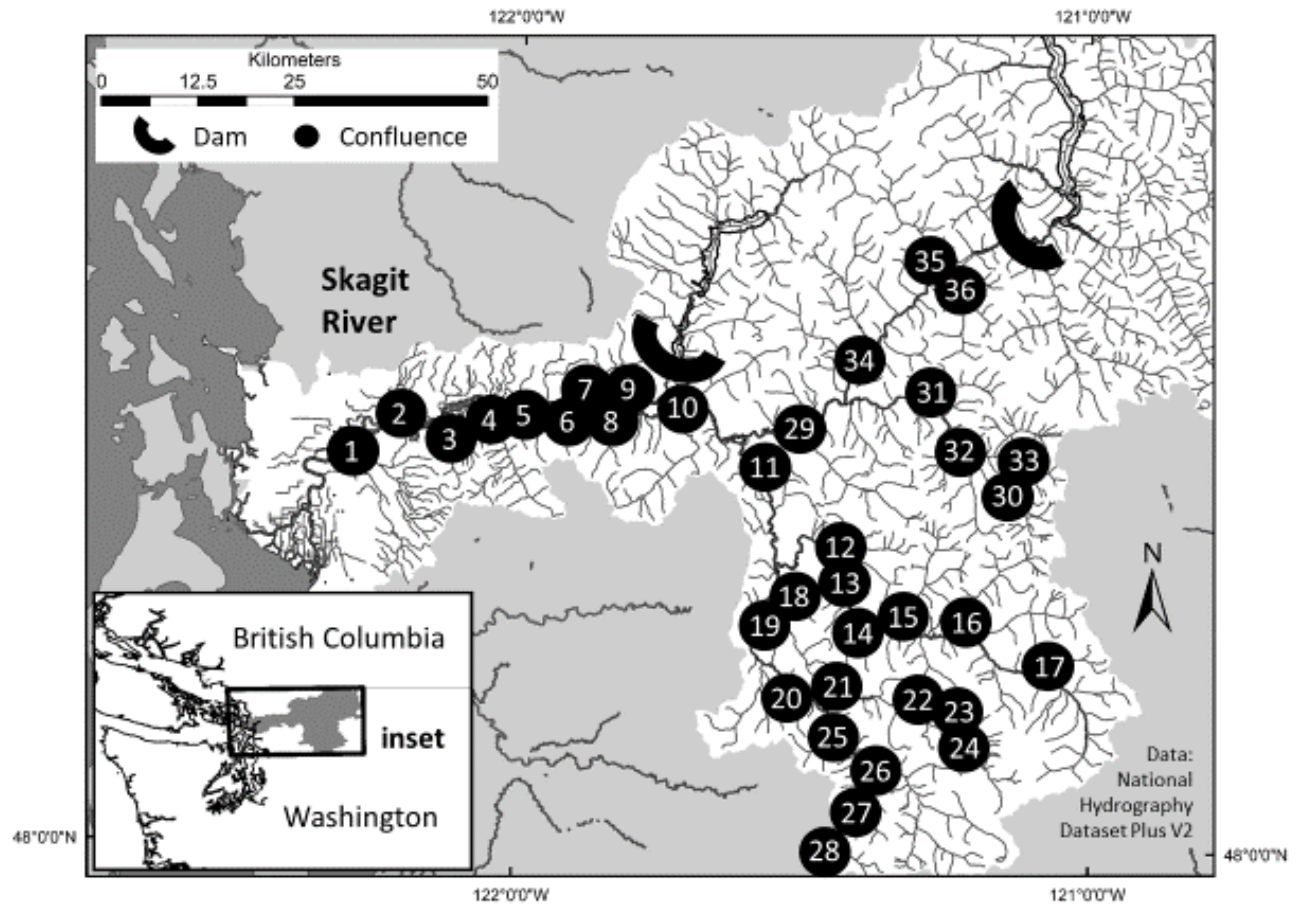


Figure 4.1. Approximate locations of study streams shown as black dots (n=36) with catchments measured as all upstream land draining to the confluences in the Skagit River basin, Washington State, USA. Numbers correspond to stream names in Appendix B **Error! Reference source not found..**

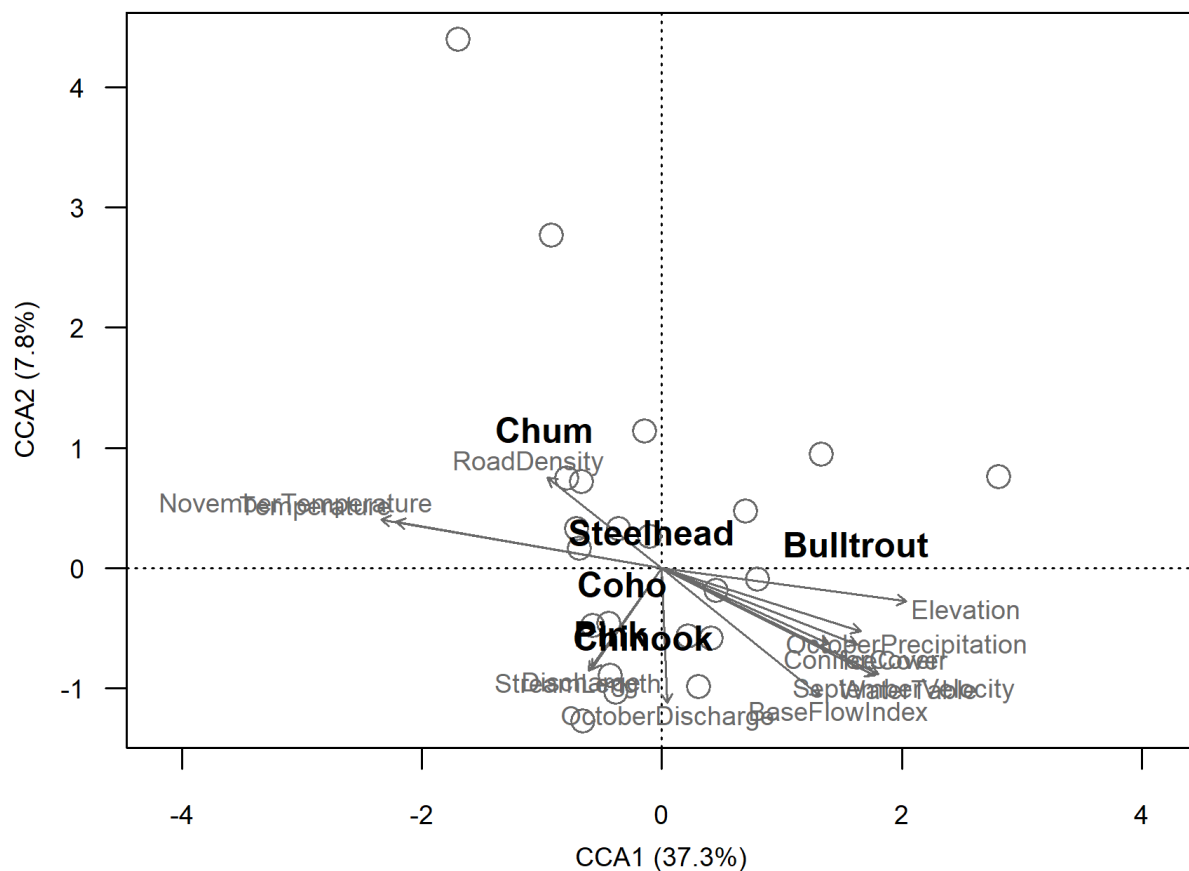


Figure 4.2. Variation in occupancy by six salmonid species in the Skagit River basin, shown in black text, at 36 stream sites, shown as gray points, as explained by linear correlations of variation in environmental characteristics shown in gray arrows, along the first and second canonical correspondence analysis axes plotted in ordination space. Note overlapping species names, “Pink” and “Chinook.” **Error! Reference source not found..**

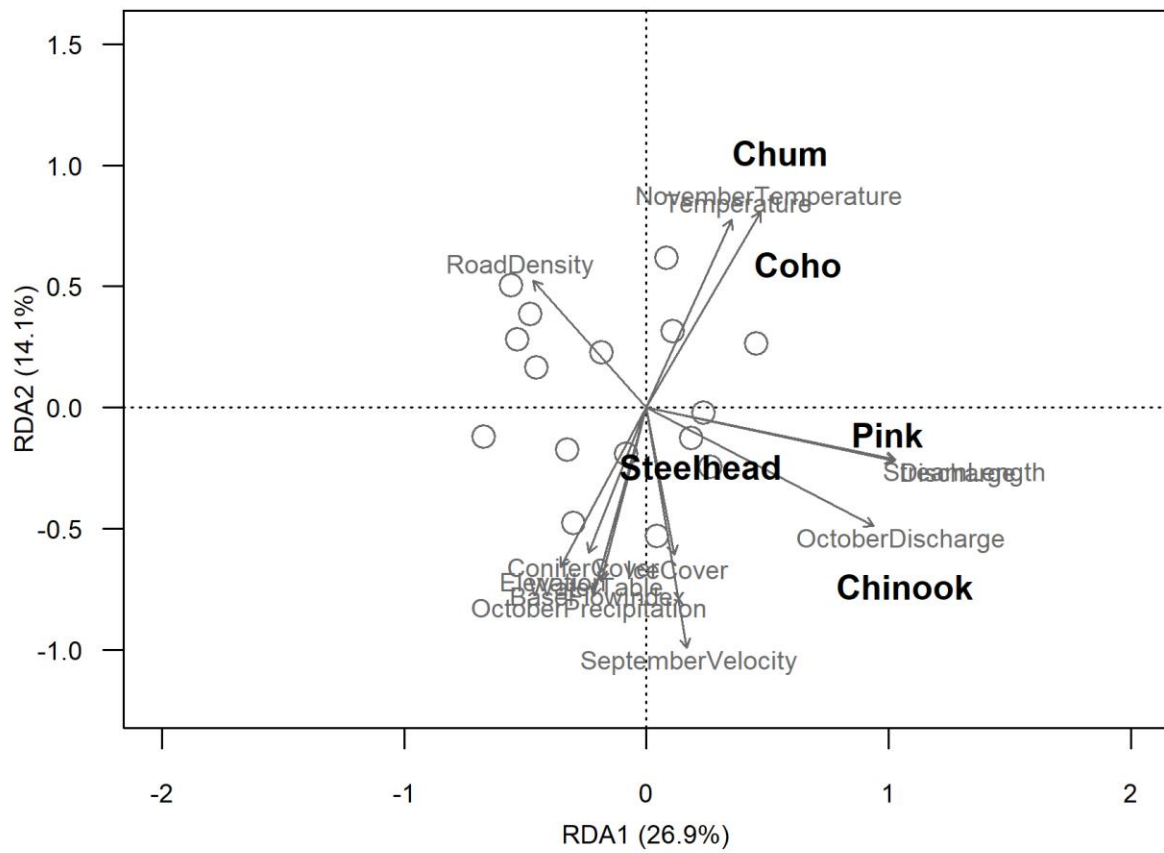


Figure 4.3. Variation in occupancy by five species of *Oncorhynchus*, shown in black text, at 30 stream sites, shown as gray points, in the Skagit River basin as explained by linear correlations of variation in environmental characteristics shown in gray arrows, along the first and second redundancy analysis axes plotted in ordination space **Error! Reference source not found..**

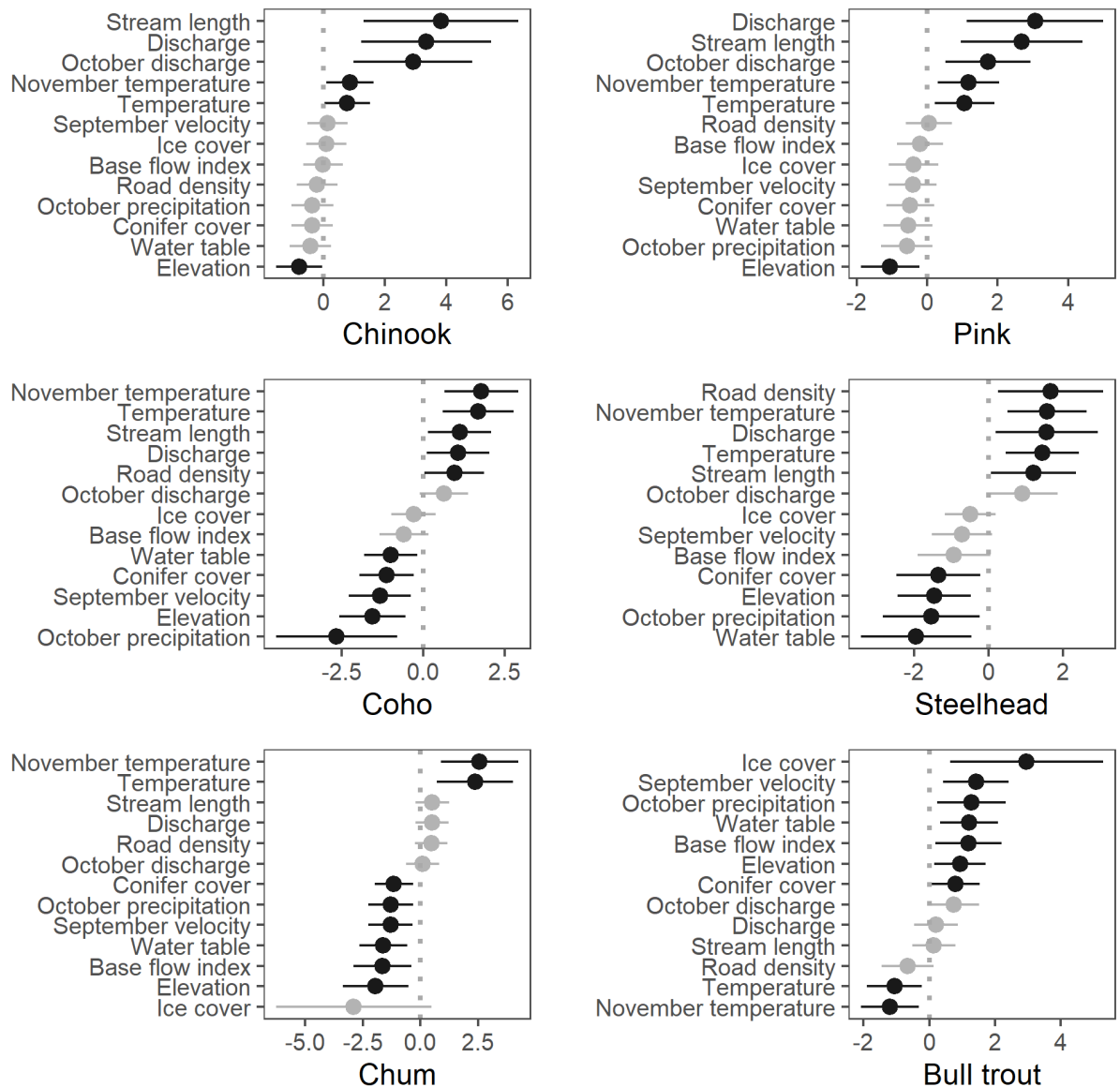


Figure 4.4. Scaled single main effects and standard errors from generalized linear models explaining individual species occupancy given a suite of environmental variables in 36 tributary sites in the Skagit River basin, Washington. Black dots indicate $p < 0.05$, gray dots indicate $p \geq 0.05$, and positive variable values indicate association with occupancy by that species **Error!**

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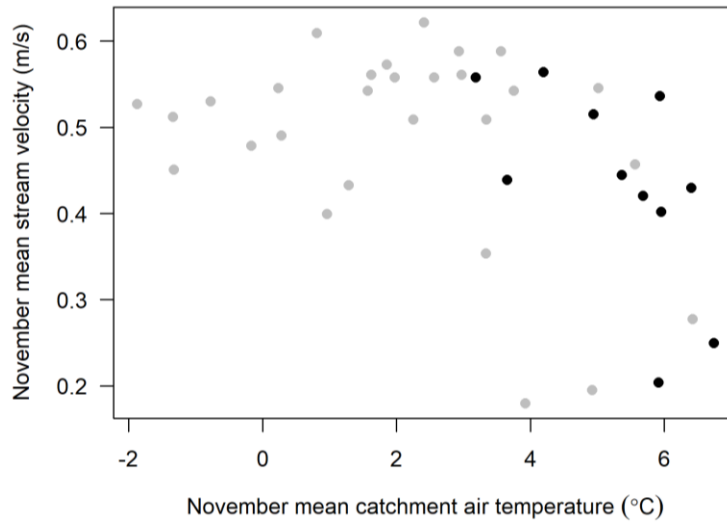


Figure 4.5. Relationship between November mean catchment air temperature and mean stream velocity, divided into streams where chum salmon breed (black dots), and other Skagit River basin streams (gray dots) **Error! Reference source not found..**

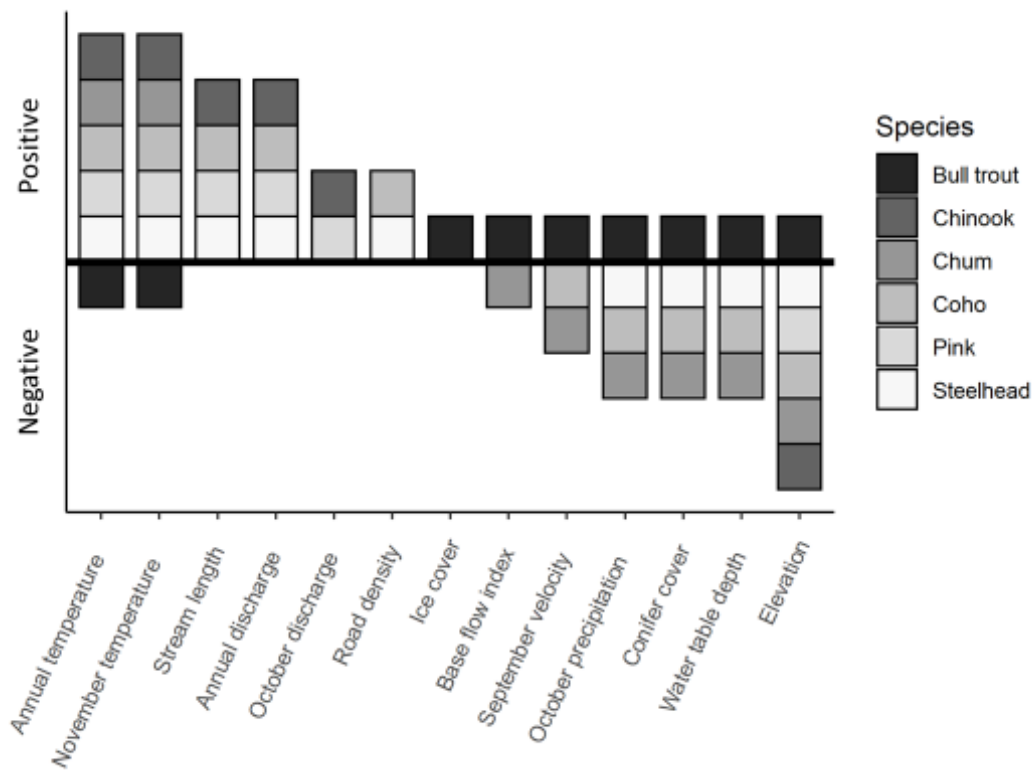


Figure 4.6. Directionality of the significant ($p < 0.05$) positive and negative associations between habitat variables and species occupancy in 36 tributary sites in the Skagit River basin, Washington, from generalized linear models **Error! Reference source not found.**

APPENDIX A

Estimation method for median spawning date of bull trout *Salvelinus confluentus* in 2009-2016 in a cool stream (Downey Creek) and a warm stream (Bacon Creek) in the Skagit River Basin, Washington State, USA.

The median spawning date for each year was modeled using a multi-level hierarchical model. In that way, years with more information assist the estimation of median spawning date in years with less information. The data consist of newly observed redd counts on non-sequential surveys of different streams. Count of redds in stream i , on day t , in year y was denoted $e_{i,d,t}$. We assume that redds are created following a normal distribution throughout the year, with a mean (μ_{iy}) that describes the median day of spawning, and standard deviation that describes the duration of the spawning period (Eq 1). We presume that the median spawning date varies across years by stream, but that the variance (duration) is identical across years (but unique for each stream).

The parameters μ_{iy} are modeled in a hierarchical fashion, assumed to be drawn independently from a normal distribution, with estimated parameters μ_i and $\bar{\sigma}_i$ (the mean and standard deviation of the μ_{iy}) for each stream. Uniform (flat) priors were assigned on each, from Julian day 250 to 350 and 0 to 50 for μ_i and $\bar{\sigma}_i$, respectively. No covariance among the μ_{iy} was assumed because there was insufficient information in the data to estimate covariance.

Finally, we assumed that the observed counts followed a Poisson distribution, using the expected redd counts as the mean of the Poisson probability density function. Thus, the likelihood of the data equals **Error! Reference source not found.:**

$$L(e_{i,t,y}) = \frac{\exp(-\hat{e}_{i,t,y})}{e_{i,t,y}} \hat{e}_{i,t,y}^{e_{i,t,y}} \quad (\text{A.4})$$

We used a Bayesian model to estimate the parameters, because integration of the multi-level parameters is difficult in a maximum likelihood framework. Posterior probability densities for model parameters were numerically estimated using the no-U turn Hamiltonian MCMC sampler, implemented in Stan (Stan Development Team 2017). Three replicate MCMC chains were generated for 10,000 iterations plus a 5,000 iteration burn in period using standard diagnostics for convergence (\hat{R} ; Gelman & Rubin 1992) and model fit as described by Gelman and Rubin (1995).

APPENDIX B

Study streams in the Skagit River basin, Washington State, USA.

Number	Stream
1	Nookachamps Creek
2	Hansen Creek
3	Anderson Creek
4	Day Creek
5	Cumberland Creek
6	O'Toole Creek
7	Grandy Creek
8	Pressentin Creek
9	Finney Creek
10	Jackman Creek
11	Hilt Creek
12	Big Creek
13	Tenas Creek
14	Straight Creek
15	Buck Creek
16	Downey Creek
17	Canyon Creek
18	Dan Creek
19	Mouse Creek
20	Murphy Creek

21	Black Oak Creek
22	Owl Creek
23	Fire Creek
24	Pumice Creek
25	Falls Creek
26	South Fork Sauk River
27	Elliot Creek
28	Weden Creek
29	Illabot Creek
30	South Fork Cascade River
31	Marble Creek
32	Kindy Creek
33	Middle Fork Cascade River
34	Bacon Creek
35	Goodell Creek
36	Newhalem Creek

VITA

Catherine Austin, born in Seattle, is a product of much time spent in the mountains and rivers of Western Washington, aided in fisheries understanding by regional research and participation in the research of the University of Washington's Alaska Salmon Program. She obtained her B.A. in Environmental Studies with a concentration in Conservation Biology from Lewis & Clark College, followed by work with the U.S. Forest Service and the Washington Department of Fish and Wildlife, before studying under the expert guidance of Dr. Thomas P. Quinn at the University of Washington, exploring questions in salmon and char ecology. She works in fisheries research and management in human impacted river systems, with aspirational dreaming of pristine systems.