USING REMOTE SENSING, OCCUPANCY ESTIMATION, AND FINE-SCALE HABITAT CHARACTERIZATION TO EVALUATE FALL CHUM SALMON (*ONCORHYNCHUS KETA*) SPAWNING HABITAT USAGE IN ARCTIC ALASKA

By

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Abstract

Groundwater upwellings provide stable temperatures for overwinter salmon embryo development and this process may be particularly important in cold, braided, gravel-bed Arctic rivers where rivers may freeze solid in the absence of upwellings. Aerial counts and remote sensing were used during 2013-2015 to estimate fall chum salmon (*Oncorhynchus keta*) spawner abundance states (e.g., low or high), classify river segments by geomorphic channel type (primary, flood, and spring), and map thermal variability along a 25.4 km stretch of the Chandalar River in interior Alaska. Additionally, I used on-the-ground examination of fine scale variation in physical habitat characteristics at 11 representative sites to characterize habitat variability, placed temperature loggers to assess overwinter thermal conditions in redds, and used a developmental model to predict hatching and emergence timing given known spawning dates and incubation temperatures. I delineated 330 unique river segments (mean length = 536 m) and used a multi-season multistate occupancy model to estimate detectability, occupancy, and local colonization and extinction rates. Triplicate surveys performed in 2014 allowed me to estimate detectability and the influence of observer bias. I found that detectability did not vary by observer, channel type, or segment length, but was better for high abundance (0.717 ± 0.06 SE) relative to low abundance (0.367 ± 0.07 SE) aggregations. After correcting for imperfect detection, the proportion of segments occupied by spawning fall chum salmon was highest in 2014 (0.41 ± 0.04 SE), relative to 2013 (0.23 ± 0.04) and 2015 (0.23 ± 0.04). Transition probabilities indicated unoccupied segments were likely to remain so from year to year ($2013 \rightarrow 2014 = 0.67$; $2014 \rightarrow 2015 = 0.90$), but low abundance spawning segments were dynamic and rarely remained in that state. One-third of high abundance sites remained so, indicating the presence of high quality spawning habitat. Mean segment temperatures ranged from -0.5 to

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4.4°C, and occupancy varied positively with temperature. I predicted a 50% probability of occupancy in segments with temperatures of 3°C. With my on-the-ground work, I found that habitat characteristics varied among the three channel types, with most significant differences between main channel and off-channel habitats. Dissolved oxygen and pH decreased with increasing temperature, and conductivity increased with temperature. Predicted hatching and emergence timing ranged from 78 and 176 days (December 11th and March 18th) to 288 and 317 days (July 8th and August 6th), respectively, post-spawning, and were highly variable within sites and among channel types owing to high habitat thermal heterogeneity. Because the Chandalar River supports 30% of the fall chum salmon run in the Yukon River Basin, information such as provided by this study will be critical to allow resource managers to better understand the effects of future climate and anthropogenic change in the region.

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General Introduction

Pacific salmon (*Oncorhynchus* sp.) spawn across a wide range of habitat conditions in locations that have physical and chemical characteristics (e.g., temperature, dissolved oxygen, substrate size) suitable for embryo incubation and survival (Groot and Margolis 1991; Quinn 2005). Because the rate of salmon embryo development increases with temperature, salmon spawn at the time of year and in locations with appropriate temperatures to ensure that progeny hatch and emerge into conditions that are conducive to survival and growth (Sheridan 1962; Brannon 1987; Kazakov 1971; Murray and McPhail 1988). Interpopulation differences in spawning timing are often related to water temperature variability, and the timing of hatching and emergence of young salmonids is thought to reflect locally adapted timing of reproduction (Hodgson and Quinn 2002; Lisi et al. 2013) to the temperature regime under which development occurs (Beacham and Murray 1990; Groot and Margolis 1991; Quinn 2005). There is a non-linear compensatory relationship between temperature and rate of development, therefore individuals developing under colder regimes require more days but fewer accumulated thermal units (ATUs) to hatch relative to embryos incubating under warmer conditions (Brannon 1987; Beacham and Murray 1990). Dissolved oxygen (DO) concentration is also a critical habitat feature for incubating salmon, and is important for embryo oxygen uptake and release of metabolic wastes (Quinn 2005). As embryos grow, their DO requirements increase, and reach a peak just before hatching, with critical levels of DO estimated at 1 mg/L just after fertilization to 7 mg/L prior to hatching (Alderdice et al. 1958). Low, but non-fatal DO levels can delay hatching (at 10°C) by as much as 50 days in coho salmon, and sudden drops in DO can induce premature hatching (Shumway et al. 1964). Whereas temperature is the primary determinant of salmon embryo development rate and survival, DO is an important secondary effect. Given the

interrelationships between salmon spawning habitat selection, water temperature, and dissolved oxygen, it is critical to consider all these factors when managing high-latitude fish species, especially those that occur across a broad and varied landscape.

Riverscapes (i.e., riverine landscapes; Wiens 2002; Fausch et al. 2002) are dynamic features that contain a diverse mosaic of terrestrial and aquatic ecosystems (Stanford and Ward 1992; Tockner et al. 2006). Local-scale variability in water temperature, along with other physical habitat variables, influences the type and distribution of species present (Montgomery et al. 1999; Ebersole et al. 2001; Cram et al. 2017). Adult salmonids and their embryos are highly intolerant of temperature extremes (Gibson 1966; Kaya et al. 1977), and take advantage of thermal variability throughout the riverscape for thermoregulation and selection of appropriate spawning site conditions (Berman and Quinn 1991; Torgersen et al. 1999). Such thermal refugia are often the result of groundwater upwellings, resulting in temperatures that are cooler than the main channel during the summer months (Arscott et al. 2001; Poole and Berman 2001; Acuna and Tockner 2009). Conversely, in high latitude areas that experience extreme cold in winter months, groundwater upwellings provide salmonids with warmwater thermal refugia characterized by warmer and more stable water temperatures and protection from freezing (Reynolds 1997; Geist and Dauble 1998; Baxter and Hauer 2000; Geist et al. 2002). Groundwater emerging from long-residence flow paths is warmer than the main channel in winter, and tends to emerge at distinct locations along the channel that persist through time (Stanford and Ward 1993; Poole et al. 2008). Groundwater is generally characterized by low dissolved oxygen content as a result of chemical reduction as the water percolates though soils (Youngson et al. 2005), and as groundwater residence time increases, dissolved oxygen content decreases (Geist et al. 2002; Malcolm et al. 2009). Therefore, while groundwater upwellings may

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provide warmer overwinter water temperatures for salmon embryo incubation, the dissolved oxygen content of groundwater may drop below optimum levels for development.

Groundwater has different physicochemical properties from surface water, and temperature can be used as a proxy to identify groundwater-fed channels (Wawrzyniak et al. 2013). Primary, flood, and spring channels (Mouw et al. 2014) characterize the complex channel network of northern-latitude braided rivers, and represent a gradient of hydrologic connectivity that provides a variety of salmon habitat across multiple scales (Olsen and Townsend 2003; Poole et al. 2008; Malcolm et al. 2009). Primary channels constitute the majority of water flow, and flood channels are connected to the primary channel during high flows, supplemented by water from alluvial aquifers (Kuzischin et al. 2010). Spring channels remain disconnected from the primary channel network except in extreme high water events, and their flow is exclusively derived from groundwater inputs (Stanford and Ward 1993; Mouw et al. 2014). Spatial variation in groundwater inputs along the river continuum provides habitats that differ in temperature, dissolved oxygen content, and water chemistry, providing a patchwork of potentially suitable spawning habitat, although little is known about how spawning salmon utilize this habitat heterogeneity in the Arctic.

The identification of warmwater thermal refugia and the patterns of usage by high latitude fishes are key elements for managing these species under a changing environment. Wandering gravel-bed rivers are common throughout the Arctic and sub-Arctic, and combine the features of braided and meandering, single threaded channels (Church 1983; Hey et al. 1982; Church 2002). These dynamic rivers move a large bedload, with common midchannel bar deposition and channel avulsions through forested riparia, resulting in a complex array of habitats (Church 1983; Lord et al. 2009; Mouw et al. 2014). The often remote nature of large

Arctic rivers fosters significant logistical challenges for monitoring salmon spawning habitats as these regions are inaccessible by road and contain few human settlements. However, these high latitude rivers provide critical habitats for Pacific salmon, and more information is needed to improve management and conservation of these important ecological, economic, and subsistence resources (Geist and Dauble 1998; Burril et al. 2010; Flannery et al. 2010). Remote sensing techniques may provide a solution as a relatively low cost method for data acquisition of fluvial landscapes. Additionally, thermal imagery shows great potential for mapping spatial patterns in water temperature variability. For example, Forward Looking Infrared (FLIR) has been used to detect coldwater thermal refugia for Chinook salmon (*Oncorhynchus tshawytscha*) in Oregon (Torgersen et al. 1999; Torgersen et al. 2001), and Atlantic salmon (*Salmo salar*) in Quebec (Dugdale et al. 2013; 2015), thermal patterns in a braided river in the French Alps (Wawrzyniak et al. 2013), and warm groundwater winter refugia for chum salmon in Alaska (Wirth et al. 2012).). Riverscape-scale (10^3 - 10^5 m; Geist and Dauble 1998; Torgersen et al. 1999; Baxter and Hauer 2000) habitat mapping (e.g., via aerial surveys, remote sensing, etc.; Torgersen et al. 2001; Dugdale et al. 2015) can provide information, for example, about trends in thermal and geomorphic conditions, but fine scale examination (10^1 – 10^3 m) is necessary to adequately characterize conditions experienced by individual spawning salmon (Malcolm et al. 2008).

The remote nature of Arctic rivers also complicates estimation of spawning salmon abundance. Aerial surveys allow for relatively easy access, and the ability to cover large territories in a short period of time (Eicher 1953; Cousens et al. 1982). However, aerial counts have a high degree of error, and often significantly underestimate population sizes through imperfect detection or under-counting of target species (Cousens et al. 1982; Jones et al. 1998). Estimation bias resulting from aerial population surveys can be addressed using several methods.

First, occupancy (i.e., probability of site use, given presence) can be used as a surrogate for abundance (Bart and Klosiewski 1989; Hall and Langtimm 2001), thus simplifying metrics from a count of individuals to occurrence likelihood of the species of interest. The second approach is to account for imperfect detection of the species of interest, because non-detection does not equate to species absence (MacKenzie et al. 2003). Statistically rigorous models have been developed to use multiple surveys at the same site to directly estimate detection probabilities, which are then incorporated into unbiased occupancy estimates (MacKenzie et al. 2003; MacKenzie et al. 2006). Third, expansion of simple presence-absence models to include multiple states such as a categorical indices of breeding/non-breeding (Nichols et al. 2007) or relative abundance (e.g., few/some/many individuals; Falke et al. 2010; Jensen and Vokoun 2013) provide additional information about occupied sites. Such multistate occupancy models can be fit over multiple seasons to generate likelihoods of local colonization and extinction contingent on state, allowing estimates of site quality and the relative contribution of individual sites to the population (Nichols et al. 2007; MacKenzie et al. 2009). Estimation of changes in occupancy states through time while accounting for uncertainty that results from imperfect detection may contribute toward a better understanding of habitat use dynamics, valuable information for conservation and management of sensitive species (MacKenzie et al. 2006).

Many tributaries in the Yukon River Basin of Alaska and Canada provide vital spawning habitat for fall chum, Chinook, and coho salmon, all of which are important subsistence and commercial resources for Yukon River Basin residents (Bue et al. 2009). Recent drastic declines in Chinook salmon runs have increased subsistence dependence on fall chum salmon (JTC 2015). Basin-wide recruitment of fall chum is highly variable through time (low of 239,299 fish in 2000 to a record high of 2,286,883 in 2005; Bue et al. 2009), and among tributaries. For

instance fall chum escapement on the Chandalar River has surpassed the maximum escapement goal of 152,000 fish every year since 2003, but escapement on the Fishing Branch River has been consistently below minimum escapement (50,000 fish) since 1974 (Bue et al. 2009; JTC 2015). Environmental stressors, such as resource extraction and shifting hydrological regimes, have raised concerns with resource managers and local communities that depend on salmon throughout the Yukon River Basin.

In this thesis, I used remote sensing techniques, multistate occupancy estimation modeling, on-the-ground habitat surveys, and predicted timing of hatching and emergence to provide information and management tools to improve the understanding of the habitat needs of spawning fall chum salmon. The overall goal of my research was to understand how spatial variability in habitat conditions, namely groundwater, affects the spawning distribution of fall chum salmon in a braided, Arctic river system, and to investigate whether aquatic habitat characteristics hypothesized to be important for spawning fall chum salmon and developing embryos (e.g., temperature, DO, groundwater) differed among representative channel types. Specifically, in Chapter 1 I (1) used thermal and orthoimagery to delineate habitats and map thermal variability across spawning areas to identify warm groundwater thermal refugia, (2) conducted aerial spawner count surveys over multiple years to evaluate detectability and site occupancy, and (3) assessed the relative importance of thermal variability and geomorphic channel type to spawning habitat selection. In Chapter 2 I (1) measured physical habitat, groundwater influence, and water chemistry in representative channel types, (2) characterized incubation thermal regimes within and among channel types, and (3) predicted hatching and emergence timing based on observed daily water temperature using an empirical model. My results provide insights into the characteristics of fall chum salmon spawning habitats in the

Arctic, and contribute toward a broader understanding of the habitat needs of high-latitude

salmon in a changing environment.

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Chapter 1: A Remote Sensing and Occupancy Estimation Approach to Quantify Spawning Habitat Use by Fall Chum Salmon (*Oncorhynchus keta*) Along the Chandalar River, Alaska[1]

ABSTRACT

Groundwater upwellings provide stable and relatively warm temperatures for developing salmon embryos and this process may be particularly important in cold, braided, gravel-bed Arctic rivers. Aerial counts and remote sensing were used during 2013-2015 to estimate fall chum salmon spawner abundance states (e.g., low or high), classify river segments by geomorphic channel type (primary, flood, and spring), and map thermal variability along a 25.4 km stretch of the Chandalar River in interior Alaska. We delineated 330 unique river segments (mean length = 536 m) and used a multi-season multistate occupancy model to estimate detectability, occupancy, and local colonization and extinction rates. Triplicate surveys performed in 2014 allowed us to estimate detectability and the influence of observer bias. We found that detectability did not vary by observer, channel type, or segment length, but was better for high abundance (0.717 ± 0.06 SE) relative to low abundance (0.367 ± 0.07 SE) aggregations. After correcting for imperfect detection, the proportion of segments occupied by spawning fall chum salmon (*Oncorhynchus keta*) was highest in 2014 (0.41 ± 0.04 SE), relative to 2013 (0.23 ± 0.04) and 2015 (0.23 ± 0.04). Estimated escapement was highest in 2013 with 227,145 fall chum salmon, slightly lower in 2014 with 214,396, and lowest in 2015 with 162,538. We found that unoccupied segments were likely to remain unoccupied from year to year (2013→2014 = 0.67; 2014→2015 = 0.90), but low abundance spawning segments were dynamic and rarely remained in that state. One-third of high abundance sites remained so, indicating the presence of high quality spawning habitat.

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Mean segment temperatures ranged from -0.5 to 4.4°C, and occupancy varied positively with temperature. We predicted a 50% probability of occupancy in segments with temperatures of 3°C. The Chandalar River supports 30% of the fall chum salmon run in the Yukon River Basin, an important commercial and subsistence resource. This study identifies habitat characteristics that are important for spawning site selection and trends in spawning habitat usage by fall chum salmon. This information will assist resource managers in making informed land use decisions and evaluating the potential impacts of future climate and anthropogenic change on fall chum salmon populations.

INTRODUCTION

Pacific salmon (*Oncorhynchus* sp.) spawn across a wide range of habitat conditions, selecting locations where physical and chemical characteristics (e.g., temperature, dissolved oxygen, substrate size) will ensure successful egg incubation and maximize embryo survival (Groot and Margolis 1991; Quinn 2005). Water temperature is one of the primary physical factors influencing salmon life history (Beacham and Murray 1985; Groot and Margolis 1991; Richter and Kolmes 2005), and because the rate of salmon embryo development increases with temperature, salmon spawn at the time of year and in locations with appropriate temperatures to ensure that progeny hatch and emerge into optimal survival and growth conditions (Sheridan 1962; Brannon 1987; Kazakov 1971; Murray and McPhail 1988). In high latitude areas that experience severe winter conditions, low water temperatures and freezing may negatively impact embryo survival (Beacham and Murray 1987). Given the interrelationship between salmon spawning habitat selection and water temperature it is critical to consider both when managing high-latitude fish species, especially those that occur across a broad and varied landscape.

Riverscapes (i.e., riverine landscapes; Wiens 2002; Fausch et al. 2002) are dynamic

features that contain a dynamic patchwork of terrestrial and aquatic ecosystems (Stanford and

Ward 1992; Tockner et al. 2006). Local-scale variability in water temperature, along with other

physical habitat variables, influences the type and distribution of species present (Montgomery et

al. 1999; Ebersole et al. 2001; Cram et al. 2017). Adult salmonids and their embryos are highly

intolerant of temperature extremes, and take advantage of thermal variability throughout the

riverscape for thermoregulation and selection of appropriate spawning site conditions (Gibson

1966; Kaya et al. 1977; Berman and Quinn 1991; Torgersen et al. 1999). Such thermal refugia

are often the result of groundwater upwellings, resulting in temperatures that are cooler than the

main channel during the summer months (Arscott et al. 2001; Poole and Berman 2001; Acuna

and Tockner 2009). Conversely, in high latitude areas that experience extreme cold in winter

months, groundwater upwellings provide salmonids with warmwater thermal refugia

characterized by warmer and more stable water temperatures and protection from freezing

(Reynolds 1997; Geist and Dauble 1998; Baxter and Hauer 2000; Geist et al. 2002). Even in the

extreme climate of the Arctic where winter air temperatures commonly remain below -20°C for

weeks (U. S. Fish and Wildlife Service 1987), groundwater upwellings may result in ice-free

river areas and provide stable, relatively warm water temperatures for salmon embryo incubation

(Leman 1993; Burril et al. 2010; Wirth et al. 2012; Mouw et al. 2014). Groundwater emerging

from long-residence flow paths is warmer than the main channel in winter, and tends to emerge

at distinct locations along the channel that persist through time (Stanford and Ward 1993; Poole

et al. 2008). Long-residence groundwater discharge on alluvial floodplains is often related to

bedrock outcrops or encroaching canyon walls (knickpoints) that restrict the downstream end of

the floodplain (Stanford and Ward 1993). Because the locations of groundwater-based

warmwater refugia remain stable throughout time (Winter 2007), but spawning is a shorter term process, past reproductive success and homing behavior of preceding generations likely factor into spawning site selection (Dittman and Quinn 1996; Keefer and Caudill 2014). Thus, the identification of warmwater thermal refugia and the patterns of usage by high latitude fishes are key elements for managing these species under a changing environment.

Wandering gravel-bed rivers are common throughout the Arctic and sub-Arctic, and combine the features of braided and meandering, single threaded channels (Church 1983; Hey et al. 1982; Church 2002). These dynamic rivers move a large bedload, with common midchannel bar deposition and channel avulsions through forested riparia, resulting in a complex array of habitats (Church 1983; Smikrud et al 2008; Lord et al. 2009; Mouw et al. 2014). Floodplains with extensive channel networks have strongly three-dimensional bedforms that drive hydrostatic pressure gradients that circulate river water through the alluvial aquifer (Stanford and Ward 1993; Geist and Dauble 1998; Woessner 2000). Although there is localized flux of river water through bedforms via advective pore water flow, river water also flows laterally and downslope through large floodplain bars in relation to topography and hydraulic head gradients, often within or adjacent to the main channel (Poole et al. 2008). Longer flow paths (>100 m) are point sourced through a network of high porosity paleochannels, and emerge as spring channels within the forested riparia (Stanford and Ward 1993; Mouw et al. 2014).

Groundwater has different physicochemical properties from surface water, and temperature can often be used as a proxy to identify groundwater-fed channels (Wawrzyniak et al. 2013). Primary, flood, and spring channels (Mouw et al. 2014) characterize the complex channel network of northern-latitude braided rivers, and represent a gradient of hydrologic connectivity that provides a variety of salmon habitat across multiple scales (Olsen and

Townsend 2003; Poole et al. 2008; Malcolm et al. 2009). Primary channels constitute the majority of water flow, and flood channels are connected to the primary channel during high flows, supplemented by water from alluvial aquifers (Kuzischin et al. 2010). Spring channels remain disconnected from the primary channel network except in extreme high water events, and their flow is exclusively derived from groundwater inputs (Stanford and Ward 1993; Mouw et al. 2014). Spatial variation in groundwater inputs along the river continuum provides habitats that differ in temperature, dissolved oxygen content, and water chemistry, providing a patchwork of potentially suitable spawning habitat, although little is known about how spawning salmon utilize this habitat heterogeneity in the Arctic. Braided rivers provide a mosaic of habitat conditions, but are difficult to map due to the extensive area of multiple, braided channels.

The remote nature of large Arctic rivers fosters significant logistical challenges for monitoring salmon spawning habitats as these regions are inaccessible by road and contain few human settlements. However, Arctic rivers are critical habitats for Pacific salmon, and more fine-scale information is needed to improve management and conservation of these important ecological, economic, and subsistence resources (Geist and Dauble 1998; Burril et al. 2010; Flannery et al. 2010). Remote sensing techniques may provide a solution through a relatively low cost method for data acquisition of fluvial landscapes. Satellite imagery such as WorldView is commercially available, and can provide resolutions of up to 1.25 m for multispectral imagery (Mallison and Nagrid 2015), but even this resolution is generally too coarse for fine-scale fish habitat mapping. Airborne imagery can provide much finer resolutions of up to 10 cm allowing for fine scale analysis of riverine habitats (Smikrud and Prakash 2006; Hugue et al. 2016). Thermal imagery also shows great potential for mapping water surfaces. For example, Forward Looking Infrared (FLIR) has been used to detect coldwater thermal refugia for Chinook salmon

(*Oncorhynchus tshawytscha*) in Oregon (Torgersen et al. 1999; Torgersen et al. 2001), and

Atlantic salmon (*Salmo salar*) in Quebec (Dugdale et al. 2013; 2015), thermal patterns in a

braided river in the French Alps (Wawrzyniak et al. 2013), and warm groundwater winter refugia

for chum salmon in Alaska (Wirth et al. 2012). Fall chum salmon spawn on the descending limb

of the annual thermograph in September and October, when primary river flows are cold and

groundwater upwellings comparatively warm (Reynolds 1997). As a result, remote sensing via

thermal imagery may be a good candidate for detecting and mapping groundwater upwellings

critical for sustaining fall chum salmon populations.

The remote nature of Arctic rivers also complicates estimation of spawning salmon

abundance. Aerial surveys allow for relatively easy access, and the ability to cover large

territories in a short period of time (Eicher 1953; Cousens et al. 1982). However, aerial counts

have error, often significantly underestimating population sizes through imperfect detection or

under-counting of target species (Cousens et al. 1982; Jones et al. 1998). Estimation bias

resulting from aerial population surveys can be addressed using several methods. First,

occupancy (i.e., probability of site use, given presence) can be used as a surrogate for abundance

(Bart and Klosiewski 1989; Hall and Langtimm 2001), thus simplifying metrics from a count of

individuals to occurrence likelihood of the species of interest. The second approach is to account

for imperfect detection of the species of interest, because non-detection does not equate to

species absence (MacKenzie et al. 2003). Statistically rigorous models have been developed to

use multiple surveys at the same site to directly estimate detection probabilities, which are then

incorporated into unbiased occupancy estimates (MacKenzie et al. 2003; MacKenzie et al. 2006).

Third, although simple presence-absence observations provide useful data, expansion of models

to include multiple states such as a categorical indices of breeding/non-breeding (Nichols et al.

2007) or relative abundance (e.g., few/some/many individuals; Falke et al. 2010; Jensen and Vokoun 2013) provide additional information about occupied sites. Such multistate occupancy models can be fit over multiple seasons to generate likelihoods of local colonization and extinction contingent on state, allowing estimates of site quality and the relative contribution of individual sites to the population (Nichols et al. 2007; MacKenzie 2009). Estimation of changes in occupancy states through time while accounting for uncertainty that results from imperfect detection may contribute toward a better understanding of habitat use dynamics, valuable information for conservation and management of sensitive species (MacKenzie et al. 2006).

Remote Arctic riverscapes pose unique challenges for habitat monitoring, but are vital spawning grounds for fall chum salmon, an important commercial and subsistence resource. We used remote sensing techniques and multistate occupancy estimation modeling to provide information and management tools to improve our understanding of the habitat needs of spawning fall chum salmon. The overall goal of our research was to understand how spatial variability in habitat conditions, namely groundwater, affects the spawning distribution of fall chum salmon in a braided, Arctic river system. Specifically, we (1) used thermal and optical imagery to delineate habitats and map thermal variability across spawning areas to identify warm groundwater thermal refugia, (2) conducted aerial spawner count surveys over multiple years to evaluate detectability and site occupancy, and (3) assessed the relative importance of thermal variability and geomorphic channel type to spawning habitat selection.

MATERIALS AND METHODS

Study area

This study was conducted on the Chandalar River, a fifth order tributary of the Yukon River that drains the southern slopes of the Brooks Range in Alaska (Fig. 1.1). The region

experiences some of the most extreme temperatures in Alaska, with an annual average range of -59°C to 38°C (U. S. Fish and Wildlife Service 1987). The Chandalar River flows south from the Arctic National Wildlife Refuge through State and Tribal lands to its confluence with the Yukon River on the Yukon Flats National Wildlife Refuge, and consists of three major branches, the East, Middle and North Forks. The Chandalar River drainage area is 24,165 km^2, and principal water sources are rainfall, snowmelt, and to a lesser extent, perennial springs (Craig and Wells 1975; Brabets et al. 2000). A USGS stream gauge located downstream from the confluence of the East Fork and the main stem operated from 1963-1973, during which time mean daily open water season (June – September) discharge was 359 m^3/s ± 289 SD, with peak streamflow up to 1,733 m^3/s. Data collection and aerial imagery focused on the approximately 40-km stretch of river from the village of Venetie upstream to the confluence of the East Fork and main stem of the Chandalar River (Fig. 1.1).

The Chandalar River system produces over 30% of the total Yukon River Basin fall chum salmon run (Melegari 2012) and 3-5% of Chinook salmon (Eiler et al. 2006; Eiler et al. 2006b). The Chandalar River is at the northern edge of the distribution of fall chum salmon; the species spawns in September and October in this region (Buklis and Barton 1984). River freeze-up typically occurs in early October, so almost all egg incubation occurs over winter when the main river channel is frozen. The U.S. Fish and Wildlife Service (USFWS) conducted pilot aerial surveys across the entire Chandalar river network in 2013, and found that 83% of the spawning aggregations of fall chum salmon were located between the village of Venetie and the confluence of the East Fork and main stem of the Chandalar River (A. Martin and J. Rose, *unpublished data*). Based on these results, data collection for the current study occurred within the 40 km of river from Venetie to the East Fork – main stem confluence (Fig. 1.1).

Fish surveys

Sonar counts

The USFWS operates a sonar counting station on the Chandalar River, approximately 22 km upriver from its confluence with the Yukon River that estimates annual fall chum salmon run timing and passage during early August through the end of September (Melegari 2014). Data from this enumeration project are used to estimate annual passage of fall chum salmon, as well as describe annual variability in run size and timing. Annual passage estimates from 1995 to 2013 averaged 194,802 ± 92,820 SD fall chum salmon (Melegari and McGuire 2017). A staff gauge was installed at the sonar site and used to measure daily water levels. Levels were calibrated using a benchmark established in 1989 (Melegari 2014).

Aerial spawner counts

Fixed-wing aerial surveys were used to quantify the size and location of fall chum salmon spawning aggregations between Venetie and the confluence of the East Fork and main stem of the Chandalar River in late fall of 2013, 2014 and 2015 (Figure 1). Surveys were timed to maximize spawner detectability during the short window in late September when fish actively spawn, and freeze-up, which typically occurs during early October. Surveys occurred on September 23rd, September 25th, and October 13th in 2013, 2014 and 2015, respectively, and completed redds were observed on all surveys. During each survey, spawning aggregations were georeferenced and categorized as small, medium, or large (1-150, 151-500, >500 individuals). The observer noted survey time (hours), visibility conditions (wind disturbance, turbidity, glare, ice, obstructions such as shadows or timber), and cloud cover. Multiple passes were conducted in braided sections of the river. Triplicate surveys were conducted in 2014 to assess observer bias and aggregation detectability. These surveys were conducted within a 48 hour period to reduce

the likelihood of fish movement between replicate surveys, and each survey was conducted by a different observer-pilot combination. Although surveys in all years covered a larger extent, survey data were truncated to the extent of the 2014 imagery collection (see below) for all analyses.

Spawning habitat

Optical imagery

High spatial resolution optical imagery was collected on October 8th, 2014 using a fixed-wing mounted Nikon D700 digital camera with a 35 mm Nikkor lens to collect optical images in the visible spectrum. Imagery collection was timed to maximize temperature differences between groundwater inputs and the main river flow before river freeze-up in early October. The aircraft flew at approximately 1 km above ground level, resulting in a spatial resolution of 10 cm. Flying speed was 185 km/hr, and 35 flight lines were flown for a total flight length of approximately 800 km. Optical images had approximately 40% side lap and 70% forward lap to facilitate precision during the mosaicking process. Optical imagery was orthorectified and mosaicked using Agisoft software (Agisoft LLC, St. Petersburg, Russia).

Spawning habitat classification

Optical imagery from 2014 was used to categorize river habitats based on the classification scheme of Mouw et al. (2014) of primary, flood, and spring channels. Primary channels constitute the river mainstem, remain connected throughout the year, and may contain either the majority of water flow or smaller side channels that receive a smaller portion of flow. Flood channels are connected to the primary channel network during high flows, and their configuration may change after each high flow event (Kuzischin et al. 2010). When disconnected from the primary channel network, portions of flood channels may remain flowing if they remain

hydraulically connected to alluvial aquifers (Stanford et al. 2005; Kuzischin et al. 2010; Mouw et al. 2014). Spring channels remain disconnected from the primary channel network except in extreme high water events, and their flow is exclusively derived from groundwater inputs (Stanford and Ward 1993; Mouw et al. 2014). They are long (>500 m), and cut deeply into the floodplain, with well-established trees (greater than 50 years old) on their banks (Kuzischin et al. 2010). River channels were further visually separated into geomorphic units (hereafter referred to as segments) using natural breaks such as riffle-pool sequences, channel splits, and tributary inputs. We created two-dimensional representations of each segment by drawing unique, non-overlapping polygons around the wetted area of each segment, then measured the length of each segment along the channel midline. Segment widths were measured along three transects perpendicular to the channel mid-line, one at the midpoint of the segment, and the other two were half the distance from the midpoint to the up- and downstream boundaries, respectively. Because in two spring channels there were long stretches of uniform flow without obvious natural breaks, we divided them into reaches of uniform length based on the average lengths of other spring channel segments. All measurements and polygon delineations were done in ArcGIS version 10.3 (Esri LLC, Redlands, California).

Thermal imagery

Airborne thermal imagery was collected concurrently with optical imagery on October 8th, 2014 using a fixed-wing mounted FLIR A320 automation series camera with a built-in 25 degree lens that acquired imagery in a TIR broadband (7.5-13.0 μm) spectral range, with an image capture rate of 30 images/s (FLIR Systems 2016). The flight height of 1 km above ground level resulted in a spatial resolution of 1 m. Ten low emissivity reflective tarps were placed in highly visible locations along the study area, and a Trimble GeoExplorer GPS unit was used to

record their locations as ground control points to assist in georectifying the geolocation of aerial images (Woll et al. 2011). Tarps were prominent in the thermal image as a dark spot with low emissivity values.

The thermal imagery was orthorectified, geometrically and radiometrically corrected, seamed, and mosaicked using EnsoMOSAIC and FLIR Examin IR (MosaicMill Ltd, Helsinki, Finland; FLIR Systems, Redlands, California). Radiosounding (temperature and relative humidity) data from the NASA Atmospheric Correction Parameter Calculator (http://atmcorr.gsfc.nasa.gov/) were used for radiometric correction of the 2014 thermal imagery (Barsi et al. 2003; Barsi et al. 2005).

We converted the thermal imagery from 1.0×10^2 K to Celcius degrees. Thermal imagery was classified into water and non-water (e.g., sand, rocks, and vegetation) values, using optical imagery to inform decision making, and the non-water pixels were eliminated from analysis. Water pixels had values ranging from -2.65°C to 15.5°C. In 2014, there were no concurrent on-the-ground water temperature measurements available to corroborate or correct the thermal imagery. Inspecting the 2014 image-derived temperature values along with the concurrent optical imagery we figured that the image-derived temperatures were consistently lower as free-flowing water on optical images showed temperature values below zero. After examining the entire study area we empirically determined that bias was 2.1 degrees C and we added 2.15°C to all water temperature values. Using the histogram of pixel values, we eliminated 108 pixels above 10°C as outliers. The water values were then classified into one degree increments from 0 to 10°C, with an additional class from -0.5 to 0°C. Although there was some overlap in pixel values between wet sand and water, segment polygon boundaries were drawn using optical imagery ensuring that subsequent temperature analysis encompassed only water pixels. We calculated temperature

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zonal statistics (mean, standard deviation, minimum, maximum, range and area) for each

segment polygon using ArcGIS version 10.3 (ESRI 2014)

Data analyses

Detection and occupancy estimation

We used a two-stage analysis to estimate detectability and multistate occupancy of fall

chum salmon spawning aggregations by first investigating how detectability varied as a function

of covariates (while holding all occupancy parameters constant) using triplicate survey data

collected in 2014 (MacKenzie et al. 2003; Bailey et al. 2004). Second, we incorporated the

results of detection models into a multistate multi-season occupancy analysis to assess

occupancy and relevant covariates across the three years. Because very few instances of > 500

individuals were observed, and only by a single observer, we collapsed the abundance categories

into three states (not detected = 0; detected at low abundance = 1; detected at high abundance =

2) to reduce the number of model parameters and facilitate estimation.

For the first stage of analysis, we used a single-season, multistate occupancy model to

estimate the probability of detecting spawning salmon aggregations when present at low ($p_t^{[1]}$),

and high ($p_t^{[2]}$) abundance, and the probability of observing the true state, given the species has

been detected and is truly present at high abundance (δ_t), for time period t (Nichols et al. 2007;

Jensen and Vokoun 2013; Pregler et al. 2015). Additionally, two occupancy parameters were

estimated: the probability that site i was occupied by spawning fish (ψ_i^1) and the conditional

probability that the fish were present at high abundance given occupancy (ψ_i^2) (Nichols et al.

2007). Models in the candidate set tested the effect of channel type (primary, flood, or spring)

and segment length (m) as individual site-specific covariates on $p_t^{[1]}$ and $p_t^{[2]}$. Because surveys

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were performed by different observers we also fit candidate models where $p_t^{[1]}$ and $p_t^{[2]}$ were allowed to vary by observer.

In the second stage, the model(s) that best described detection probabilities, given the data, were incorporated into a second candidate set of models in a robust design multistate, multi-season occupancy estimation conditional binomial model (MacKenzie et al. 2006). The occupancy parameters estimated in this analysis were initial probability of occupancy for each primary session t (ϕ_t), the probability of transitioning from unoccupied to occupied, given that the site is not currently occupied (ψ_t^0), the probability of remaining occupied, given that the site is currently occupied at low abundance (ψ_t^1), and the probability of remaining occupied, given that the site is currently occupied at high abundance (ψ_t^2). Conditional parameters estimated included the probability of high abundance, given that the site is currently unoccupied ($R_t^{[0,2]}$), the probability of high abundance, given the site is currently occupied at low abundance ($R_t^{[1,2]}$), and the probability of high abundance, given that the site is currently occupied at high abundance ($R_t^{[2,2]}$). The detection parameters in the model parameterization were similar to those examined in stage one, and were the probability of detecting the species when present at low abundance ($p_t^{[1]}$), the probability of detecting the species when present at high abundance ($p_t^{[2]}$), and the probability of correctly classifying the species when it is truly present at high abundance (δ_t) (MacKenzie et al. 2009). Detection parameters in the multi-season model were fixed based on the results from the 2014 detection analysis (above). Segment mean temperature and channel type were tested as individual site-specific covariates on ϕ_t. The parameters ϕ_t, ψ_t^0, ψ_t^1, ψ_t^2, $R_t^{[0,2]}$, $R_t^{[1,2]}$, and $R_t^{[2,2]}$ were used to construct transition probability matrices, which represent the probabilities of a segment remaining in its current state or transitioning from one state to another

between seasons (e.g., 0 → 0, 2 → 1, etc.; MacKenzie et al. 2009). Rows represented the true state of a segment at time t and columns the true state of the segment at time $t + 1$ (Mackenzie et al. 2009).

Model selection

In both stages of analysis, the best supported models were selected using AIC_c, a modification of Akaike's information criterion that corrects for small sample sizes (Burnham and Anderson 2002). Models with a difference in AIC_c from the top model (ΔAIC_c) from 0 to 2 were considered to have substantial support, those with values from 4 to 7 had minor support, and models with values larger than 10 were not supported by the data (Burnham and Anderson 2002). The model with the lowest AIC_c and the highest Akaike weight (w_i) was considered to be the top model. Akaike weight (w_i) represents the relative likelihood of the model, and is the ΔAIC_c of the individual model divided by the summed ΔAIC_c values for all models. Because model uncertainty existed, we considered other models that had $w_i \geq 0.05$ (Falke et al. 2010). Models with $\Delta AIC_c \leq 3$ and $w_i \geq 0.05$ were considered plausible competing models, and to account for model selection uncertainty model averaging was used to generate unconditional parameter estimates (Burnham and Anderson 2002; Jensen and Vokoun 2013). The level of support for a particular covariate was determined by summing the w_i of all models that included it (Williams and Fabrizio 2011). All analyses were conducted using Program MARK version 8.1 (White and Burnham 1999).

RESULTS

Imagery

Optical and thermal imagery collection in 2014 was 25.43 km long and 3.60-4.54 km wide for a total area of 102.43 km^2. Optical and thermal imagery resolutions were 9 cm and 1 m,

respectively (Fig. 1.2; Fig. 1.3). We delineated 330 unique and non-overlapping segment polygons, of which 161 were primary channels, 82 flood channels, and 87 spring channels (Table 1.1). Using ANOVA to examine segment length, mean width, and mean temperature by channel type, we found significant differences in mean segment width (df = 2, F = 5.10, P = 0.007) and mean segment temperature (df = 2, F = 8.80, P = 0.0002). Mean segment widths were different between spring and primary channels; spring channels were narrower than primary. Mean segment temperatures were significantly different between primary and spring channels, with spring channels warmer than primary (Table 1.1).

Fish Surveys

Sonar data

The sonar station enumerated fall chum salmon from August 8th to September 26th in 2013, August 6th to September 28th in 2014, and August 8th to September 27th in 2015. Final passage estimates were 227,145 fish in 2013, 214,396 fish in 2014, and 162,538 fish in 2015 (Melegari 2014; Melegari 2015; Melegari and McGuire 2017). In 2013, average stage height was 1.77 m, and ranged from 1.39 to 2.70 m, with peak water level on August 23rd (Melegari 2014). In 2014, average stage height was 2.31 m, with a range of 1.87 m to 2.89 m, and peak water level occurred on August 25th (Melegari 2015). Average stage height in 2015 was 2.59 m, with a range of 1.80 to 3.92 m, and peak water level occurred on August 29th (Melegari and McGuire 2017).

Aerial spawner counts

The naïve observations of spawner abundance, where imperfect detection has not been accounted for, were 22 low abundance and 22 high abundance aggregations in 2013, for a total of 44 observations. Low abundance aggregations occurred in primary channels 50% of the time, and high abundance aggregations were in primary channels 80% of the time. In 2014, there were

51 low abundance and 54 high abundance aggregations detected, for a total of 105 observations. Similar to 2013, the highest proportion of low abundance aggregations was in primary channels (47%). High abundance aggregations occurred in primary channels 48% of the time. In 2015, there were 23 low abundance and 19 high abundance aggregations detected, for a total of 42 observations. The trend of naïve occupancy changed this season, with 47% of low abundance aggregations occurring in flood channels. Primary channels still accounted for the majority of high abundance aggregations, with 53%. The proportions of low and high abundance observations were similar across all years. In progress and completed redds were observed during aerial surveys in all three years, indicating that aggregations were spawning groups, not holding aggregations. Naïve estimates of spawning aggregations by abundance, year and channel type are shown in Fig. 1.4.

Detection and occupancy estimation

Detection

The detection analysis resulted in 11 candidate models with $w_i \geq 0.05$ (Table 1.2), all of which had ΔAIC_c values from 0 to 2, indicating substantial support (Williams and Fabrizio 2011; Burnham and Anderson 2002). The simplest model, with no covariates and constant parameters, was present in the candidate set, with a ΔAIC_c value of 1.42, and a w_i of 0.09 (Table 1.2). Segment channel type CHAN (primary, flood, spring) and segment length LEN (m) were present in the candidate set of models as covariates on $p_t^{[1]}$ and/or $p_t^{[2]}$. The summed w_i of all models where channel type was a covariate of $p_t^{[1]}$ was 0.48, which was the largest summed w_i for any covariate on either $p_t^{[1]}$ or $p_t^{[2]}$. Neither covariate (CHAN or LEN) on either $p_t^{[1]}$ or $p_t^{[2]}$ possessed majority weight in the top set of models, thus we did not include them as covariates to detection in the next stage of analysis. Detection probabilities across all three surveys had overlapping

confidence intervals, indicating no significant difference in detectability by observer (Fig. 1.5).

The candidate models all had $p_t^{[1]}$ as constant throughout time, with the model averaged

parameter estimated at 0.38. Model-averaged estimates of $p_t^{[2]}$ ranged from 0.69 to 0.76, and δ_t

ranged from 0.77 to 0.80 (Table 1.3).

Occupancy

Based on detection analysis estimates from stage 1, detection parameters were fixed to

the 2014 values, where $p_t^{[1]}$ = 0.367, $p_t^{[2]}$ = 0.717, and δ_t = 0.754. This resulted in six models

with $w_i \geq 0.05$, all of which contained temperature as a covariate on ϕ_0 (Table 1.4). All top

models contained temperature as a covariate on ϕ_0, and the model-averaged relationship

between ϕ_0 and segment mean temperature (°C) was positive (Fig. 1.7) indicating that the

likelihood of occurrence of fall chum salmon spawning aggregations was higher in warmer

segments. The 95% confidence interval was narrow for lower temperatures, and wider at the

upper end of the temperature distribution. At 0°C, ϕ_0 was 0.12, with a 95% CI of 0.07 to 0.20.

At 4°C, ϕ_0 was 0.67, with a 95% CI of 0.42 to 0.86. The predicted temperature when $\phi_0 = 0.50$

was 2.94°C.

Unoccupied sites tended to remain so from year to year (0.67 and 0.90 for 2013 to 2014,

and 2014 to 2015, respectively; Fig. 1.6). However, sites occupied at low abundance were

dynamic, and were unlikely to remain in that state from year to year. From 2013 to 2014, low

abundance segments had a high probability of transitioning to high abundance (0.88), but from

2014 to 2015 we found the reverse pattern (0.13). Sites occupied at low abundance in 2014 were

highly likely to become unoccupied in 2015 (0.85), yet from 2013 to 2014 this probability was

zero. In both transition periods, about one-third of all sites occupied at high abundance remained

so, suggesting the presence of persistent, high quality spawning habitats. Estimated proportion of

segments occupied was 0.41 in 2014, almost twice as high as 2013 and 2015, which were both 0.23. Low abundance aggregations made up 30% of occupancy in 2013, 57% in 2014, and 54% in 2015 (Fig. 1.8).

DISCUSSION

Our observations and analysis indicate that water temperature influences spawning site selection by fall chum salmon, and that spawning sites are dynamic between years. While there are sites consistently occupied by high abundance aggregations, there are many more sites that change in occupancy state from year to year. Our research showed that aerial surveys and remote sensing are useful tools for identifying habitats and mapping spawning areas of fall chum salmon along remote Arctic riverscapes. Aerially collected thermal and optical imagery provide high resolution imagery that can be used for detailed habitat classification and analysis, a novel solution for extensive systems with limited access. Multistate occupancy modeling has not been extensively utilized in aquatic systems (see Jensen and Vokoun 2013; Falke et al. 2010; Pregler et al. 2015), but this study demonstrates the utility of these methods for evaluating unbiased estimation of Pacific salmon spawning habitat dynamics.

Remote sensing

Aerial remote sensing has clear advantages for data gathering in remote systems. For example, detailed imagery for large areas can be collected in short periods of time (< 16 hrs of flight time for this study), and at very high resolutions (9 cm for this study). Systems that are remote and inaccessible by road can still be easily reached by plane. However, collecting concurrent atmospheric conditions on the ground (e.g., wind speed, temperature, and relative humidity) enables the most accurate correction of thermal imagery (Torgersen et al. 2001); thus, a field crew must be available for on-the-ground measurements for accurate correction. If

necessary, corrections can be made with data from nearby weather stations or with satellite imagery (Barsi et al. 2003; 2005). This was our adopted approach, as there were no concurrent ground measurements available during our imagery collection in 2014. This could have been the cause of the error in temperature values for our imagery, where the temperature values for flowing water in the primary channel were frequently as low as -2.65°C. Additionally, we only had a single year of imagery and three years of aerial surveys, so we assumed that segment water temperatures were consistent over all three years.

The process of correcting and mosaicking the imagery is labor intensive and time consuming, and requires specialized skills and computer software, but this time input is compensated for by the continuous, detailed coverage that would not be able to be obtained by on-the-ground data collection. Our optical imagery processing was complicated by the presence of large ice chunks on the river that moved between images, making it difficult for the computer program (AgiSoft) to find stable common points with which to stitch together overlapping images. The fine resolution (9 cm) of the optical imagery made the moving ice more problematic relative to the coarser resolution of the thermal imagery (1 m). Despite this complication, the resulting imagery provided spatially continuous, detailed information across the riverscape for only 2 days of field effort.

The ability to map water temperature and habitat conditions at fine and coarse scales across large areas is an important management tool. Conventional methods of temperature measurement such as in-stream data recorders provide data that are temporally continuous but spatially limited. The opposite is true of remote sensing thermal imagery, where data are spatially continuous but temporally limited, providing only a snapshot of the conditions at that

particular time. Repeated thermal mapping over time would allow analysis of the stability and persistence of thermal refuges, but was beyond the scope of this study.

Detection and occupancy

Repeated aerial surveys allowed for quantitative estimates of factors influencing detectability of fall chum salmon spawning aggregations and provided useful information for future population evaluations. The differing detection probabilities for low and high abundance aggregations (0.367 and 0.717, respectively) are logical, since large numbers of grouped fish would be easier to detect relative to smaller aggregations. A single aerial survey would likely be adequate to detect high abundance aggregations, but if the population of interest is likely to spawn in smaller aggregations, multiple surveys increase the chance of observing the majority of spawning groups. The triplicate surveys for fall chum salmon in 2014 demonstrated this advantage, as 25% more low abundance aggregations were detected with three surveys than with a single survey (41 unique observations in a single survey vs. 55 unique observations with all three surveys combined). The difference in high abundance aggregation detection was not as pronounced, but the number of unique observations still increased by 13% with three surveys as opposed to one (45 vs. 52). Effective aerial surveys are contingent upon water conditions that are conducive to spotting fish from the air, such as during the open water season on a non-glacial river. Aerial surveys are most suited to rivers and seasons with a single spawning species of interest, such as fall on the Chandalar River, to avoid the complication of species identification. Multiple surveys conducted within a short time frame provide multiple opportunities to detect the true occupancy state. For aggregations of spawning salmon, repeated surveys must be conducted within in a relatively short period of time and once the majority of fish have reached the spawning grounds in order to accurately evaluate the true occupancy state. In suitable

systems, aerial surveys provide an efficient, cost-effective way to monitor salmon populations. Multiple surveys within a single season are necessary to evaluate detection, observer bias, and potential covariates to detection. Once detectability has been quantified, a single survey each year would suffice, provided that no observer bias exists and influential covariates are accounted for in the occupancy model.

Incorporating imperfect detection into occupancy analysis ensures unbiased estimates of population status and trends (MacKenzie et al. 2002). When detection is imperfect, occupancy is underestimated unless accounted for in the statistical model. Our naïve estimates of occupancy were generally below the 95% unconditional confidence interval of the model averaged estimates from the imperfect detection occupancy model (Fig. 1.7.). If imperfect detection had not been incorporated into the multi-season multistate occupancy model, occupancy would have been underestimated, potentially leading to overestimates of regression coefficients reflecting association of occurrence with habitat factors (MacKenzie et al. 2009). As with all methods of estimation, the reliability of the results depends on the reliability of the initial input information. Because of imperfect detection, greater improvements to parameter estimates may be obtained by increasing the number of repeated surveys, but at some point this becomes too costly in terms of money and effort to collect additional data (Guillera-Arroita and Lahoz-Monfort 2012; Matter 2016). Because multiple surveys within a season were only available for 2014, we used detection probabilities from that year to fix estimates for the other years. If there had been multiple surveys in each of the three seasons, we could have generated detection probabilities for each year, which would have allowed us to investigate if climatic conditions affected detection among years. Although we aimed to conduct aerial surveys in similar weather and water conditions every year, water levels were higher in 2015, which could have negatively affected visibility and thus

detection. The survey in 2015 was conducted later in the year than the previous two due to weather conditions, and ice cover had formed on the upper stretch of the survey area, impeding detection. If multiple surveys had occurred in each season, we could have investigated the effects of ice cover on detection. For our study area a short window of time exists in which fall chum salmon have reached their spawning grounds but before river freeze-up occurs, thus data collection is difficult if weather conditions are not conducive to aerial surveys within that short window.

Interestingly, the predicted occupancy was much lower in 2013 than in 2014, despite similar escapement estimates from the USFWS sonar project (227,145 in 2013 and 214,396 in 2014). This could be a result of the imprecise categorical classification of spawning aggregation size, since a high abundance aggregation was any group greater than 100 fish. It is possible that river conditions in 2013 were conducive to very large aggregations, and that river conditions in 2014 forced fish to disperse into more different locations, although still in groups larger than 100 fish. Another possibility is that detection probabilities were lower in 2013, but without multiple surveys in each season, we assumed constant detection probabilities across the three seasons. The lower escapement for 2015 (162,538 fish) was reflected in the predicted occupancy and transition estimates from 2014 to 2015, with lower overall predicted occupancy in 2015 and a high proportion of sites occupied at low abundance in 2014 transitioning to unoccupied in 2015 (0.85).

The incorporation of multiple states into occupancy analysis provides additional information about the value of different habitats, and enables managers to make state-dependent decisions, assess progress towards management objectives, and discriminate among competing hypotheses about population responses to management actions (Franklin et al. 2004; Nichols and

William 2006; Martin et al. 2009). Multistate models can also be viewed as an approach for dealing with heterogeneous probabilities of detection (MavKenzie et al. 2002). The detection probabilities of low abundance and high abundance aggregations were very different (0.367 versus 0.717), and accounting for these different levels of imperfect detection resulted in more accurate estimates. State-specific occupancy is a potentially useful tool for population monitoring, especially for geographically extensive management and conservation programs. Multiple states can be used to consider multiple biologically relevant states, such as breeding/non-breeding or categorical abundance, to provide more information on how the species is using a particular site throughout time.

High abundance segments were more likely to remain occupied from year to year than low abundance segments. The model-averaged transition matrices estimated that about one-third of segments remained occupied at high abundance from year to year (Fig. 1.6.). However, 20% and 42% of high abundance segments transitioned to low abundance from 2013 to 2014, and 2014 to 2015, respectively. On the Chandalar River, these consistently high abundance segments are likely valuable and stable spawning habitats for fall chum salmon. They were utilized by large numbers of fish in each year of our three year study, suggesting that embryo survival is high since adult fish home to their natal site to spawn. For example, Quinn et al. (2006) demonstrated that sockeye salmon will bypass 1.5 km of suitable spawning area to return to the small (~510 m^2) pond in which they were born, indicating that natal homing occurs on a fine scale (1,000 m). Although these segments are likely critical spawning habitats, other dynamic, low abundance habitats should not be discounted since they also provide extensive spawning habitat with less competition. Spawning salmon are often tightly packed into high abundance segments on the Chandalar River (C. Clawson, *personal observation*), which could result in

redds from early arriving fish being buried or excavated by later arrivals (i.e., superimposition; Essington 1998; Essington 2000). Thus, low abundance spawning segments, while not consistently occupied from year to year, may provide extensive spawning habitat without the risk of superimposition in high abundance segments. Spawning fall chum salmon clearly use dynamic, low abundance habitats; over half of the habitats used by spawning salmon in 2014 and 2015 were low abundance segments (Fig. 1.7). Density may not be a suitable proxy for habitat quality, and the occurrence of high abundance spawning aggregations does not necessarily indicate successful incubation and survival for all embryos (Van Horne 1983). However, repeated use of these sites by large numbers of fish over multiple years indicates a substantial degree of reproductive success, since it is likely that many of the fish spawning in these locations were born there.

Habitat

Fall chum salmon were more likely to spawn in areas with relatively warmer water temperatures, likely indicative of groundwater input, as evidenced by the positive relationship between initial probability of occupancy (ϕ_0) and temperature (°C). Channel type (primary, flood, or spring) did not emerge as an influential covariate to occupancy although our data suggested that temperatures varied with channel type. Spring channel segments were 0.27°C warmer, on average, than flood channel segments, which in turn were 0.22°C warmer than primary channel segments, although mean segment temperature was only found to be significantly different between primary and spring channels (1.00°C versus 1.49°C). There was wide variability in mean temperatures within channel types indicating that channel type alone was not the sole determinant of segment temperature and thus presence or absence of groundwater input. Importantly, we found that fish spawned in all channel types, and

temperature was a more important determinant of spawning location. This may have to do with the mechanisms of groundwater influx in a wandering, gravel bed river, where groundwater inputs are present regardless of channel type. The thermal effect of groundwater input in the primary and flood channels is quickly mediated by the primary water flow, but localized thermal refugia may be sufficient to provide appropriate incubation conditions for chum salmon embryos. Groundwater based thermal refugia were more evident within spring channels, likely because thermal effects were not mediated by primary channel water flow. The primary and flood channels may shift within the floodplain between and among years, changing flow patterns and accessibility to certain areas. In contrast, spring channels are more stable, as indicated by their narrow, deeply incised channels with mature tree growth on the banks.

Implications

Fall chum salmon on the Chandalar River utilize a diverse array of habitats for spawning habitat, with water temperature playing an important role in spawning site selection. While some locations hosted spawning salmon across all three years of this study, many more locations were dynamic, and changed in occupancy level from year to year. Wandering, gravel-bed rivers are changeable systems, therefore individual site habitat quality also changes, but the aggregate of floodplain habitat is stable because the component parts are out of sync – habitat units are always changing, but rarely in a coordinated direction (Whited et al. 2007). In braided river systems the proportion of floodplain exhibiting habitat turnover can reach 60% in a single year (Arscott et al. 2002). This implies that there will be some amount of high quality habitat available each year, although changing environmental conditions may cause the habitat type or location of the quality spawning habitat to change. Although there were some segments occupied at consistently high levels throughout the span of this study, those alone are not what makes the Chandalar River a

strong producer of fall chum salmon. The variety of habitats available to spawning fish makes the population as a whole resilient to change since some of the floodplain provides suitable spawning conditions each year, although shifting environmental conditions may change the distribution of the suitable spawning habitats. The mosaic of connected but variable habitats buffers the fall chum salmon population from changing environmental conditions, but any activity (such as natural resource extraction) that degrades a subset of these habitats lessens the ability of the riverscape as a whole to buffer change. Protecting the diversity and interconnectedness of riverine habitats is key to sustaining this salmon population for future generations.

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Table 1.1. Summary of segment characteristics, by channel type, for the 25.4 km study area along the Chandalar River, Alaska.

Channel Type	Total Area (km^2)	Total Length (km)	N	Mean Length (m)	Mean Width (m)	Mean Temp (°C)
Primary	21.5	91.4	161	567.7 (228.5)	32.1 (25.7)	1.0 (0.9)
Flood	4.0	43.3	82	527.8 (183.5)	26.5 (21.9)	1.2 (1.1)
Spring	2.3	44.7	87	513.8 (220.5)	22.1 (23.8)	1.5 (1.4)

Note: The number of segments (N), along with mean (standard deviation) lengths (m), widths (m), and temperatures (°C) are shown.

Table 1.2. Summary of model selection statistics for top multistate, single season detection models for fall chum salmon on the Chandalar River, Alaska.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	K	Deviance
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.)\,p_t^{[2]}(t) + \text{LEN }\delta_t(.)$	751.44	0	0.17	1.00	10	730.37
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{CHAN }p_t^{[2]}(.)\,\delta_t(.)$	751.91	0.47	0.14	0.79	7	737.37
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{CHAN }p_t^{[2]}(.) + \text{CHAN }\delta_t(.)$	752.05	0.62	0.13	0.74	9	733.18
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{CHAN }p_t^{[2]}(t)\,\delta_t(.)$	752.36	0.92	0.11	0.63	9	733.48
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.)\,p_t^{[2]}(.) + \text{CHAN }\delta_t(.)$	752.84	1.40	0.09	0.50	7	738.30
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.)\,p_t^{[2]}(.)\,\delta_t(.)$	752.86	1.42	0.09	0.49	5	742.58
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{CHAN }p_t^{[2]}(.)\,\delta_t(t)$	753.02	1.58	0.08	0.45	9	734.14
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.)\,p_t^{[2]}(t)\,\delta_t(.)$	753.20	1.76	0.07	0.41	7	738.66
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{CHAN }p_t^{[2]}(.) + \text{CHAN }\delta_t(t)$	753.32	1.88	0.07	0.39	11	730.03
$\psi_i^1(.)\,\psi_i^2(.)\,p_t^{[1]}(.) + \text{LEN }p_t^{[2]}(t) + \text{LEN }\delta_t(.)$	753.45	2.01	0.06	0.37	11	730.15

Note: ΔAIC_c is the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model, and w_i is the AIC_c weight. Model likelihood is the w_i for the model of interest divided by the w_i of the best model, and represents the strength of evidence for this model relative to other models in the set. K is the number of parameters. Covariates are abbreviated as follows: LEN = length (m) of stream segment and CHAN = categorical channel type (primary, flood, or spring) of the stream segment. Parameters with (.) were held constant across all surveys, and parameters with (t) were allowed to vary.

Table 1.3. Detection parameters from the top multistate, single season detection models for fall chum salmon on the Chandalar River, Alaska.

Parameter	Estimate	SE	LCI	UCI
$p_1^{[1]}$	0.38	0.07	0.26	0.52
$p_2^{[1]}$	0.38	0.07	0.26	0.52
$p_3^{[1]}$	0.38	0.07	0.26	0.52
$p_1^{[2]}$	0.76	0.08	0.56	0.89
$p_2^{[2]}$	0.70	0.06	0.56	0.81
$p_3^{[2]}$	0.69	0.07	0.53	0.81
δ_1	0.80	0.06	0.64	0.89
δ_2	0.78	0.06	0.65	0.87
δ_3	0.77	0.07	0.61	0.87

Note: Model-averaged estimates, unconditional standard errors (SE), lower (LCI) and upper (UCI) 95% confidence intervals are shown. Estimates are derived from the confidence set of models with $w_i \geq 0.05$ (Table 1.2).

Table 1.4. Summary of model selection statistics for the top multistate, multi-season occupancy models for fall chum salmon on the Chandalar River, Alaska.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	K	Deviance
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(.)\ R_t^{[0,2]}(.)\ R_t^{[1,2]}(.)\ R_t^{[2,2]}(.)$	1455.25	0.00	0.29	1.00	11	1432.97
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(t)\ R_t^{[0,2]}(.)\ R_t^{[1,2]}(.)\ R_t^{[2,2]}(t)$	1455.31	0.06	0.28	0.97	13	1428.92
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(t)\ R_t^{[0,2]}(t)\ R_t^{[1,2]}(.)\ R_t^{[2,2]}(t)$	1457.06	1.81	0.12	0.40	14	1428.61
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(t)\ R_t^{[0,2]}(.)\ R_t^{[1,2]}(t)\ R_t^{[2,2]}(.)$	1457.26	2.01	0.11	0.37	13	1430.87
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(t)\ R_t^{[0,2]}(.)\ R_t^{[1,2]}(.)\ R_t^{[2,2]}(.)$	1457.32	2.07	0.10	0.36	13	1430.93
$\phi_0(t) + \text{TEMP}\ \psi_t^0(t)\ \psi_t^1(t)\ \psi_t^2(t)\ R_t^{[0,2]}(.)\ R_t^{[1,2]}(t)\ R_t^{[2,2]}(t)$	1457.34	2.09	0.10	0.35	14	1428.89

Note: ΔAIC_c is the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model, and w_i is the AIC_c weight. Model likelihood is the w_i for the model of interest divided by the w_i of the best model, and represents the strength of evidence for this model relative to other models in the set. K is the number of parameters. Covariates are abbreviated as follows: TEMP = individual segment mean temperature (°C). Parameters of $p_t^{[1]}$, $p_t^{[2]}$, and δ_t have been omitted from the model descriptions since they were held constant at 0.367, 0.717, and 0.754, respectively, for all models. Parameters with (.) were held constant across all years, and parameters with (t) were allowed to vary.
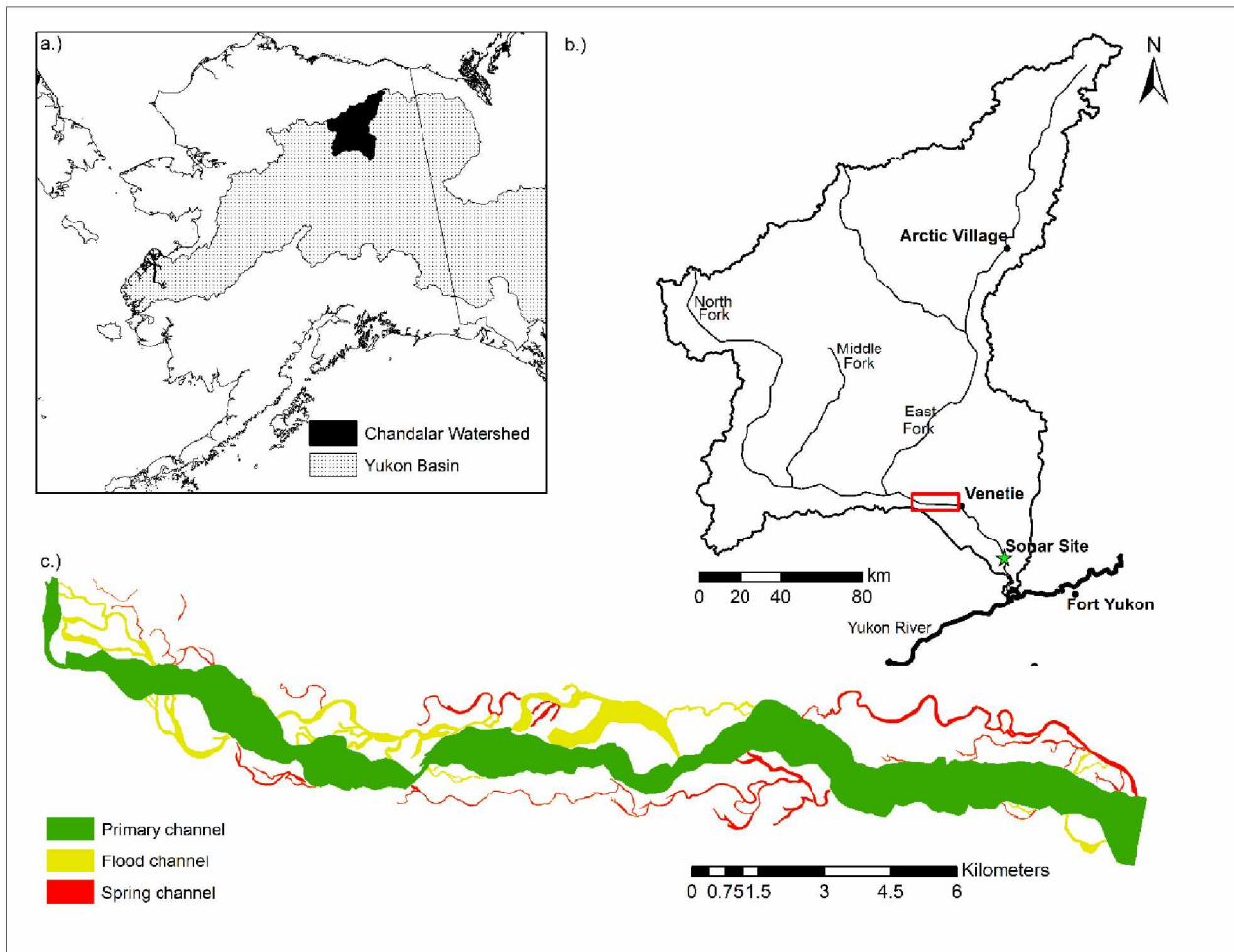
Fig. 1.1. a.) Location of the Chandalar River watershed in Alaska, and b.) branches of the Chandalar River with the location of the village of Venetie, the USFWS Sonar Site, and the 25 km study area (red box) shown. In c.) geomorphic channel types (primary, flood, and spring) are shown for the study area.
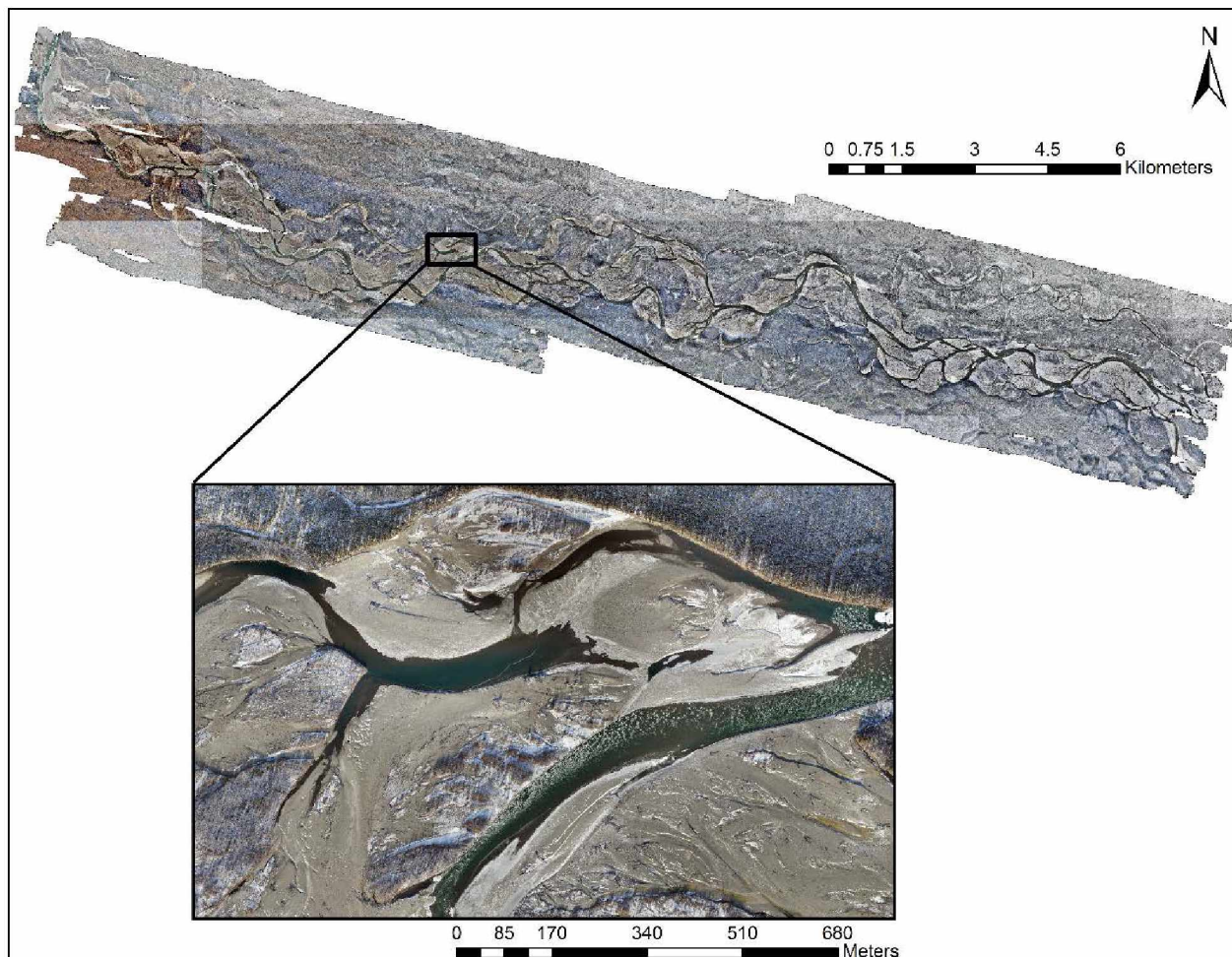
Fig. 1.2. Optical imagery collected by fixed-wing plane at a flight height of 1 km in 2014. Detailed inset shows the primary channel in the bottom right and a flood channel across the upper half of the image. River flow is from left (west) to right (east).
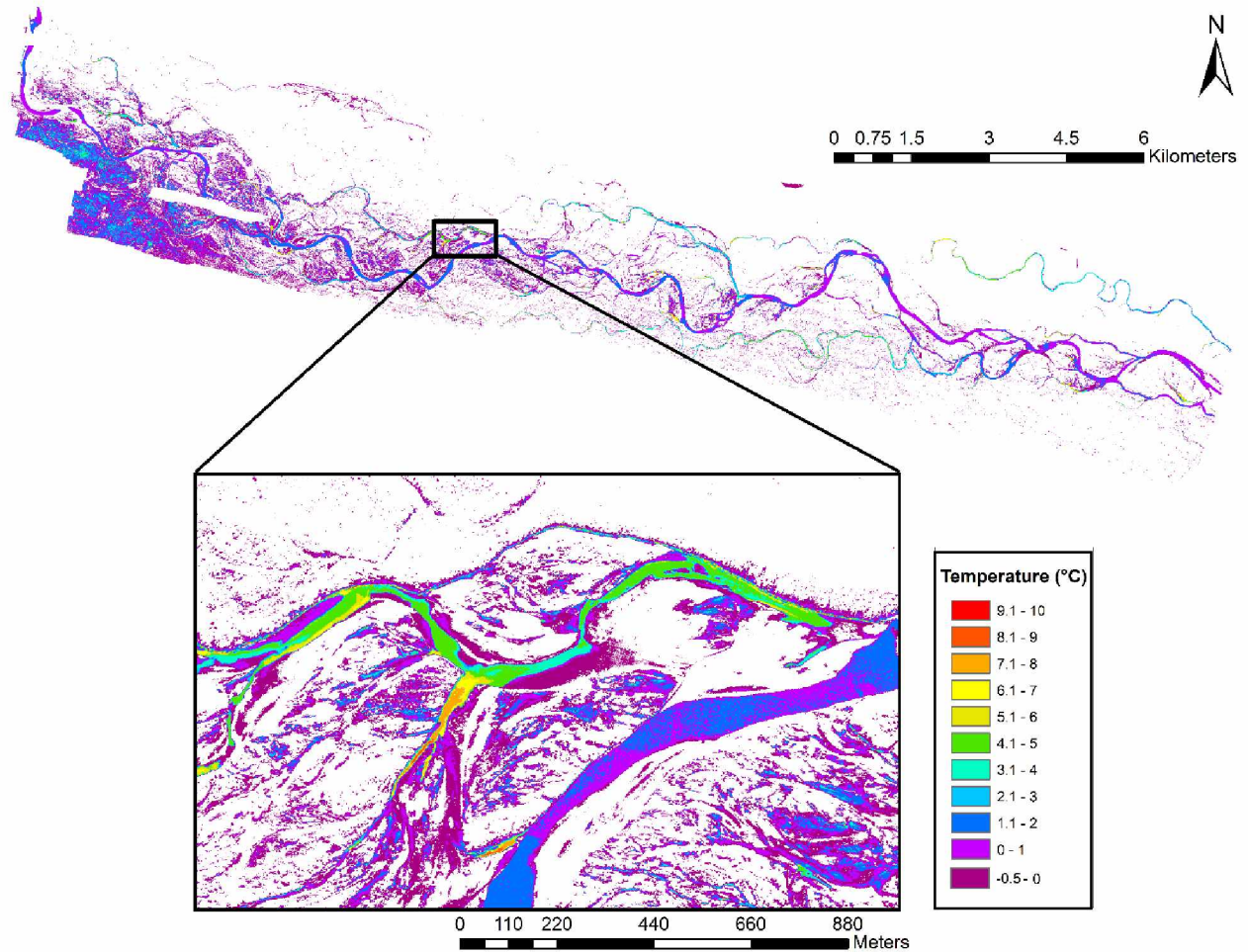
Fig. 1.3. Thermal imagery collected by fixed-wing plane at a flight height of 1 km in 2014. Detailed inset shows the cooler primary channel in the bottom right corner, flowing from left to right. A flood channel is shown in the upper portion of the image, with a warmer groundwater upwelling present in the center of the image.
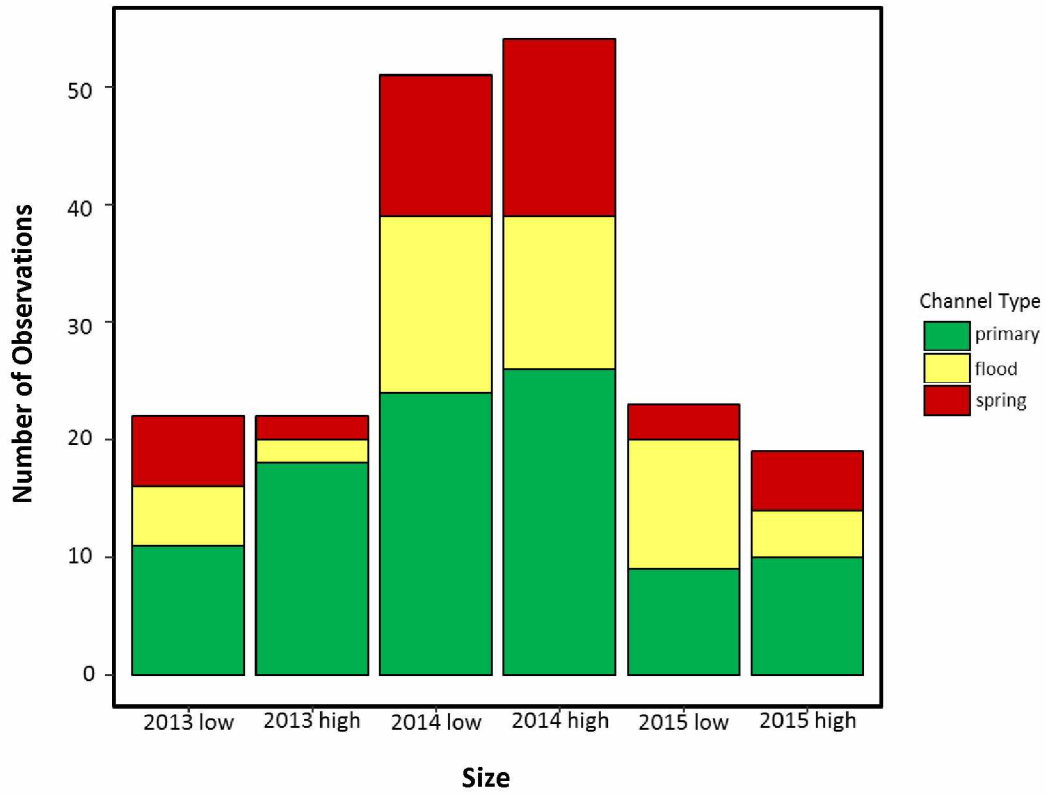
Fig. 1.4. Observed (naïve) estimates of spawning aggregation distribution, by abundance category (low or high), year (2013-2015), and channel type (primary, flood, or spring).
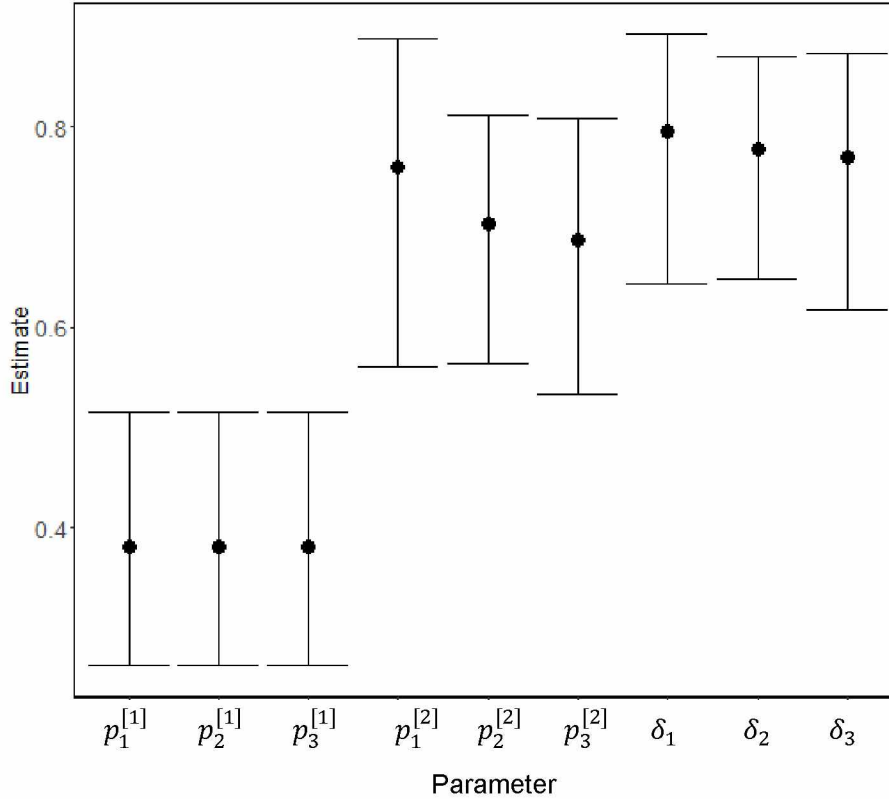
Fig. 1.5. Model-averaged estimates (± 95% unconditional confidence limits) of detection parameters from the top single season, multistate detection models. Parameters are as follows: probability of detecting low abundance on survey 1($p_1^{[1]}$); probability of detecting low abundance on survey 2 ($p_2^{[1]}$); probability of detecting low abundance on survey 3 ($p_3^{[1]}$); probability of detecting high abundance on survey 1 ($p_1^{[2]}$); probability of detecting high abundance on survey 2 ($p_2^{[2]}$); probability of detecting high abundance on survey 3 ($p_3^{[2]}$); probability of classifying the aggregation as high abundance, given the species has been detected and is truly present at high abundance on survey 1 (δ_1); probability of classifying the aggregation as high abundance, given the species has been detected and is truly present at high abundance on survey 2 δ_2; and probability of classifying the aggregation as high abundance, given the species has been detected and is truly present at high abundance on survey 3 (δ_3).

$$\begin{bmatrix} unoccupied \rightarrow unoccupied & unoccupied \rightarrow low & unoccupied \rightarrow high \\ low \rightarrow unoccupied & low \rightarrow low & low \rightarrow high \\ high \rightarrow unoccupied & high \rightarrow low & high \rightarrow high \end{bmatrix}$$

$$\begin{bmatrix} 1 - \psi_t^0 & \psi_t^0 * (1 - R_t^{[0,2]}) & \psi_t^0 * R_t^{[0,2]} \\ 1 - \psi_t^1 & \psi_t^1 * (1 - R_t^{[1,2]}) & \psi_t^1 * R_t^{[1,2]} \\ 1 - \psi_t^2 & \psi_t^2 * (1 - R_t^{[2,2]}) & \psi_t^2 * R_t^{[2,2]} \end{bmatrix}$$

$$A = \begin{bmatrix} 0.67 & 0.25 & 0.08 \\ 0.00 & 0.12 & 0.88 \\ 0.47 & 0.20 & 0.33 \end{bmatrix}$$

$$B = \begin{bmatrix} 0.90 & 0.08 & 0.03 \\ 0.85 & 0.03 & 0.13 \\ 0.24 & 0.42 & 0.34 \end{bmatrix}$$

Fig. 1.6. Transition probability matrices calculated using model averaging of the top multistate, multi-season occupancy models for fall chum salmon on the Chandalar River, Alaska. The upper matrix shows which state transition is displayed in each element of the matrix. The second matrix shows how each element was derived. Matrix A is the transition from 2013 to 2014, and matrix B is the transition from 2014 to 2015.
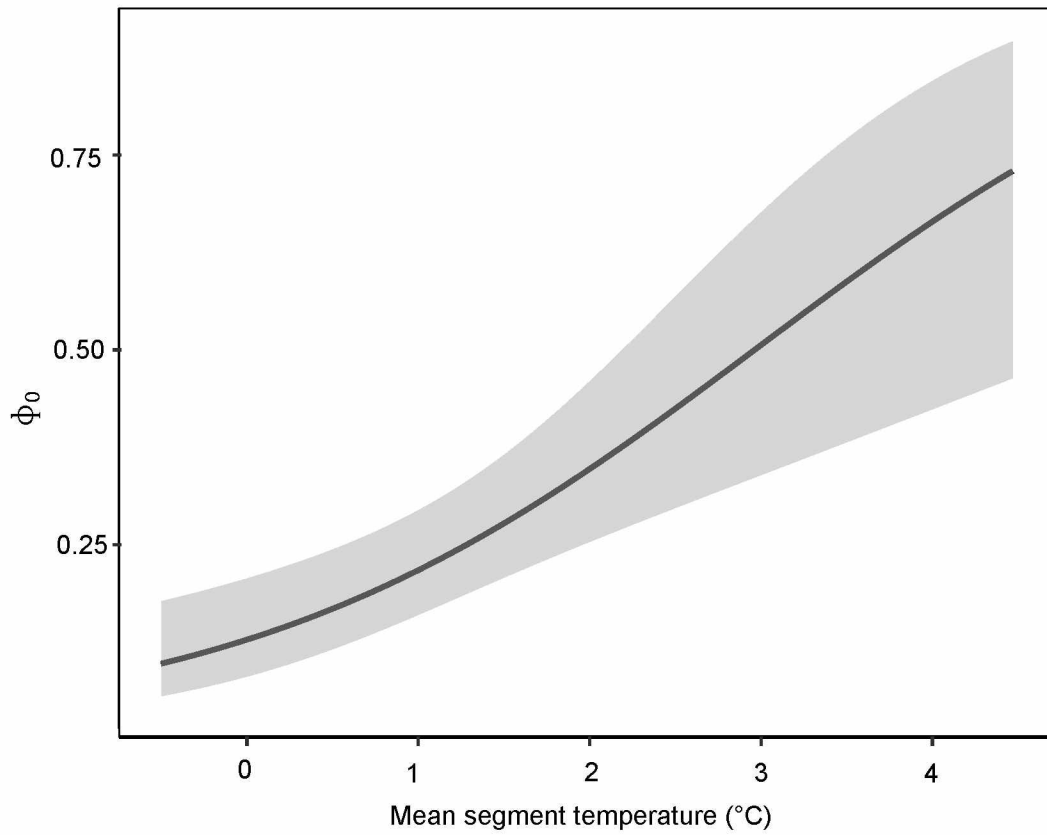
Figure 1.7. Estimated initial probability of occupancy (ϕ_0, y-axis) by fall chum salmon, based on three seasons of aerial spawning surveys, as a function of mean segment temperature (°C, x-axis). Shaded area is the 95% confidence envelope.
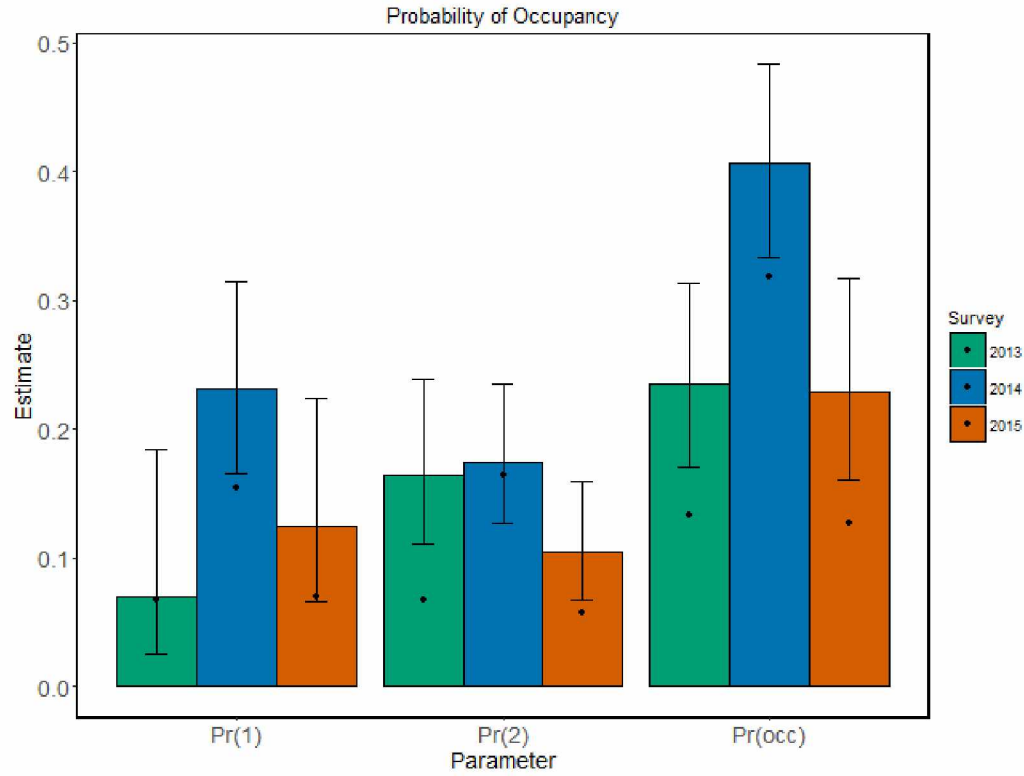
Fig. 1.8. Model-averaged estimates (± 95% unconditional confidence intervals) of derived parameters (Pr(1) = probability of occupancy at low abundance, Pr(2) = probability of occupancy at high abundance, and Pr(occ) = Pr(1) + Pr(2) = overall probability of occupancy). Black dots are the naïve estimates of occupancy.

Chapter 2: Spawning Habitat Characteristics and Phenology of Fall Chum Salmon

(*Oncorhynchus keta*) on the Chandalar River, Alaska.[2]

ABSTRACT

Spawning site selection by Pacific salmon is influenced by physical and chemical habitat

characteristics that influence embryonic developmental rates and can result in variation in

hatching and emergence timing within and among species. In Arctic rivers, groundwater-surface

water interactions result in a wide variety of thermal habitat conditions, but the effects on early

life history phenology are unknown. We measured water chemistry (conductivity, dissolved

oxygen, and pH) and physical habitat characteristics (water temperature, water velocity, and

substrate composition) at 11 sites representative of three geomorphic channel types (primary,

flood, and spring), and used continuous water temperature data to assess overwinter thermal

trends experienced by incubating fall chum salmon (*Oncorhynchus keta*) embryos along the

Chandalar River, Alaska. Spawning habitat characteristics including mean temperature,

conductivity, and vertical hydraulic gradient differed by channel type. Temperature was

negatively correlated with dissolved oxygen and pH, and positively correlated with conductivity.

Predicted hatching timing for primary, flood, and spring channels was 121 d, 142 (± 68 SD) d,

and 149 (± 23 SD) d, respectively. The temporal extent of our data were only sufficient to predict

emergence in flood channels, resulting in a mean predicted emergence of 222 (± 49 SD) d. The

Chandalar River is a consistently strong producer of fall chum salmon in the Yukon River Basin,

but nearby tributaries such as the Fishing Branch River have experience drastic declines in fall

chum numbers. Information provided by this study will assist natural resource managers in

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[2] Clawson, C. M., Falke, J. A., Westley, P. A. H., Martin, A., and Rose, J. 2017. Physical habitat characteristics influencing spawning site selection and reproductive success of fall chum salmon (*Oncorhynchus keta*) along the Chandalar River, Alaska. Formatted for the *Canadian Journal of Fisheries and Aquatic Sciences*.

understanding the causes of this regional variation, and help them prepare for the effects of future climate and anthropogenic change in the region.

INTRODUCTION

Pacific salmon exhibit extensive variation in life history characteristics, including spawning timing, which varies within and among species (Sheridan 1962: Brannon 1987; Groot and Margolis 1991). Interpopulation differences in spawning timing are thought to reflect locally adapted timing of reproduction (Hodgson and Quinn 2002; Lisi et al. 2013) to the temperature regime under which development occurs (Beacham and Murray 1990; Groot and Margolis 1991; Quinn 2005). Salmon reproduction is expected to occur at the time of year that given the long-term average water temperatures will result in hatching and emergence into favorable conditions (Brannon 1987; Kazakov 1971). As a result, and because water temperature is one of the primary factors that influence embryo development (Beacham and Murray 1985; Groot and Margolis 1991; Richter and Kolmes 2005), salmon tend to spawn earlier in high latitude and elevation environments that are cooler than low latitude and elevation environments where spawning tends to occur late in the season (Hodgson and Quinn 2002; Brannon et al. 2004). Although rate of development increases with higher water temperatures, there is a non-linear compensatory relationship between temperature and rate of development such that embryos developing under colder regimes require more days but fewer accumulated thermal units (ATUs) to hatch than embryos incubating under warmer conditions (Brannon 1987; Beacham and Murray 1990). However, little is known of salmon hatching/emergence timing and temperature relationships in high latitude systems, where incubation often occurs over winter and under ice.

Dissolved oxygen (DO) concentration is also a critical habitat feature for spawning and incubating salmon and is important for embryo oxygen uptake and release of metabolic wastes

(Quinn 2005). The concentration of DO in water at saturation decreases with increasing temperature, from 14.23 mg/L at 1°C to 11.33 mg/L at 10°C (Davis 1975). As water temperatures increase, rate of development accelerates, increasing the metabolic demand for oxygen, but warmer waters hold less dissolved oxygen. As embryos grow, their DO requirements increase, and reach a peak just before hatching, with critical levels of DO estimated at 1 mg/L just after fertilization to 7 mg/L prior to hatching (Alderdice et al. 1958). Sowden and Power found rainbow trout embryos failed to survive in the field at DO concentrations below 5 mg/L (1985). Low, but non-fatal DO levels can delay hatching (at 10°C) by as much as 50 days in coho salmon (Shumway et al. 1964), and abrupt drops can induce early emergence (Alderdice et al. 1958). As a result, whereas temperature is the primary determinant of salmon embryo development rate and survival, DO is an important secondary effect.

The spatial variation of groundwater inputs in a wandering gravel bed river provides a patchwork of habitats that differ in water temperature, dissolved oxygen content, and water chemistry (Mouw et al. 2014). Primary, flood, and spring channels (Mouw et al. 2014; CH1) characterize the complex channel network of Northern-latitude braided rivers, and represent a gradient of hydrologic connectivity that provides a variety of salmon habitat across multiple scales (Olsen and Townsend 2003; Poole et al. 2008; Malcolm et al. 2009). Primary channels constitute the majority of water flow, and are always connected to the main body of flow at the upstream and downstream ends (Mouw et al. 2014). Flood channels are connected to the primary channel at the upstream end during high flows, and are supplemented by water from alluvial aquifers (Kuzischin et al. 2010). Spring channels remain disconnected from the primary channel network except in extreme high water events, and their flow is exclusively derived from groundwater inputs (Stanford and Ward 1993; Mouw et al. 2014). Riverscape-scale (10^3 - 10^5 m;

Geist and Dauble 1998; Torgersen et al. 1999; Baxter and Hauer 2000) habitat mapping (e.g., via aerial surveys, remote sensing, etc.; Torgersen et al. 2001; Dugdale et al. 2015; CH1) can provide information about trends in thermal and geomorphic conditions. However, fine scale examination ($10^1 - 10^3$ m) is necessary to adequately characterize conditions experienced by individual spawning salmon (Malcolm et al. 2008).

Ground-surface water interactions occur within and among channel units (e.g., pools, riffles) and at finer scales within salmon spawning habitats (Malcolm et al. 2009). The chemical and physical characteristics of groundwater differ from those of surface water (Wondzell and Swanson 1996; Brunke and Gonser 1997; Malcolm et al 2004; Poole et al. 2006). Groundwater is generally characterized by low dissolved oxygen content as a result of chemical reduction as the water percolates though soils (Youngson et al. 2005). As groundwater residence time increases, dissolved oxygen content decreases (Geist et al. 2002, Malcolm et al. 2009). Therefore, depending on residence time, upwelling groundwater may have much lower dissolved oxygen concentrations than the surrounding surface river water. The temperature of upwelling groundwater can differ from the surrounding surface water, although the specific influence of groundwater discharge on channel water temperature varies over spatial and temporal scales (Ward et al. 1999; Cozetto et al. 2006; Arrigoni et al. 2008). In temperate climates, groundwater is usually cooler than surface water in the spring and summer, and warmer in the winter and fall (Acuna and Tockner 2009; Poole et al. 2008). In high latitude climates differences between groundwater and surface water temperatures are particularly pronounced during winter when air temperatures drop well below freezing for long periods. In these extreme climates, groundwater provides warmwater thermal refugia for fall spawning salmon during the winter incubation

period and may buffer developing embryos from cold temperatures (Kuzishchin et al. 2010; Mouw et al. 2014).

The tradeoff between warmer over winter water temperature and lower dissolved oxygen content in groundwater upwellings can result in different spawning tactics by salmon (Montgomery et al. 1999; Geist and Dauble 1998; Geist et al. 2002). For example, on the Kwethluk River, Alaska, summer chum salmon (*Oncorhynchus keta*) spawning in the primary channel avoided hyporheic upwelling and spawned in areas of downwelling river water, while in off-channel habitats the salmon spawned in areas of groundwater upwelling (Mouw et al. 2014). Similar spatial segregation in chum salmon spawning in primary and off-channel habitats has been observed on the Kol River, a wandering gravel-bed river on Russia's Kamchatka Peninsula (Leman 1993; Kuzischin et al. 2010). Spawning in areas of downwelling provides embryos with a constant supply of oxygen-rich water, but in extreme climates eggs may freeze or develop too slowly for appropriately timed emergence (Greig et al. 2007). However, if dissolved oxygen concentrations are sufficient for embryo development, the continual upwelling of groundwater through redds may provide ideal conditions for oxygenation of embryos and flushing of metabolic wastes (Malcolm et al. 2004).

The Yukon River is one of only a few rivers in North America with two seasonal races of chum salmon that are spatially and temporally separated (Groot and Margolis 1991). Summer chum salmon are found in the lower and middle reaches of the Yukon River Basin, and enter freshwater in early June. Fall chum salmon spawn in the middle and upper reaches of the Yukon River Basin, with some migrating over 1,678 miles, and enter freshwater after mid-July (Flannery et al. 2010). These extensive freshwater migrations are in marked contrast to more southerly chum populations, where freshwater migration distances are typically much shorter

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(Groot and Margolis 1991). Migration timing is likely controlled by water temperature rather than migration distance, as thermal unit requirements for developing embryos are probably similar for both races and outmigration occurs at similar times (Buklis and Barton 1984). Summer chum salmon typically spawn in colder runoff streams, while fall chum salmon spawn in warmer groundwater upwellings and thus require fewer days to acquire sufficient ATUs to hatch (Buklis 1981; Buklis and Barton 1984). Adult fall chum salmon have larger bodies, higher fat content, and a more fusiform shape than summer chum, all of which are characteristics better suited for long freshwater migrations (Buklis and Barton 1984; Beacham et al. 1988). Chum salmon fry migrate downstream soon after emergence, and do not rear for extended periods in their natal streams (Quinn 2005).

Many tributaries in the Yukon River Basin of Alaska and Canada provide vital spawning habitat for fall chum, Chinook, and coho salmon, all of which are important subsistence and commercial resources for Yukon River Basin residents (Bue et al. 2009). Recent drastic declines in Chinook salmon runs have increased subsistence dependence on fall chum salmon (JTC 2015). Basin-wide recruitment of fall chum salmon is highly variable through time (low of 239,299 fish in 2000 to a record high of 2,286,883 in 2005; Bue et al. 2009), and among tributaries. For instance fall chum escapement on the Chandalar River has surpassed the maximum escapement goal of 152,000 fish every year since 2003, but escapement on the Fishing Branch River (an adjacent tributary to the Porcupine River) has been consistently below minimum escapement (50,000 fish) since 1974 (Bue et al. 2009; JTC 2015). Environmental stressors, such as resource extraction and shifting hydrological regimes, have raised concerns with resource managers and local communities that depend on salmon throughout the Yukon River Basin.

In light of these impacts, the overall goal of this study was to evaluate whether aquatic habitat characteristics, hypothesized to be important for spawning fall chum salmon and developing embryos (e.g., temperature, DO, groundwater), differed among representative channel types used by spawning salmon along an Arctic wandering, gravel-bed river in Alaska. Specifically, we (1) measured physical habitat, groundwater influence, and water chemistry in representative channel types, (2) characterized incubation thermal regimes within and among channel types, and (3) predicted hatching and emergence timing based on observed daily water temperature using an empirical model. Our results provide insight into the characteristics of fall chum salmon spawning and rearing habitats in the Arctic, and contribute toward a broader understanding of the habitat needs of high-latitude salmon in a changing environment.

MATERIALS AND METHODS

Study area

This study was conducted on the Chandalar River, a fifth order tributary of the Yukon River that drains the southern slopes of the Brooks Range in Alaska (Fig. 2.1). The region experiences some of the most extreme temperatures in Alaska, -59°C to 38°C (U. S. Fish and Wildlife Service 1987). The Chandalar River flows south from the Arctic National Wildlife Refuge through State and Tribal lands to its confluence with the Yukon River on the Yukon Flats National Wildlife Refuge, and consists of three major branches, the East, Middle and North Forks. The Chandalar River drainage area is 24,165 km^2, and principle water sources are rainfall, snowmelt, and to a lesser extent, perennial springs (Craig and Wells 1975; Brabets et al. 2000). A USGS stream gauge located downstream from the confluence of the East Fork and the main stem operated from 1963-1973, during which time mean daily open water season (June – September) discharge was 359 m^3/s ± 289 SD, with peak streamflow up to 1,733 m^3/s.

The Chandalar River system produces over 30% of the total Yukon River Basin fall chum salmon run (Melegari 2012) and is at the northern edge of the distribution of the species. In this region, fall chum salmon spawn in late September and early October (Buklis and Barton 1984). River freeze up typically occurs in early October, so almost all egg incubation occurs over winter when the main river channel is frozen. U.S. Fish and Wildlife Service (USFWS) conducted pilot aerial surveys across the entire Chandalar river network in 2013, and found that 83% of the spawning aggregations of fall chum salmon were located between the village of Venetie and the confluence of the East Fork and Middle Fork of the Chandalar River (A. Martin and J. Rose, *unpublished data*). Based on these results, study sites were selected from within the 40 km of river between Venetie and the confluence (Fig. 2.1).

Fine-scale habitat assessment

On-the-ground study sites were selected in September 2015 based on extensive boat and foot reconnaissance surveys. After visual identification of sites with actively spawning fall chum salmon, we established the upper and lower bounds of the concentrated spawning area and placed four equally spaced transects perpendicular to the channel midline. Along each transect water chemistry, temperature, and substrate measurements were taken at the right wetted edge, middle, and left wetted edge. Each measurement location consisted of paired measurements near the river bottom and just below the water surface. Water temperature (°C), dissolved oxygen (mg/L), conductivity (µS/cm), and pH were measured using a multimeter (YSI Pro Plus; YSI Inc., Yellow Springs, OH). Substrate composition was visually assessed and categorized by dominant/subdominant bed sediment size (Kondolf et al. 2008; Davis et al. 2013).

Piezometers were installed to quantify vertical hydraulic gradient (VHG) at four redd clusters throughout each spawning site (Geist et al. 2002; Burril et al. 2010; Mouw et al. 2014;

Bean et al. 2015). Piezometers were constructed and installed following the methods of Baxter et al. (2003). A steel capped 3.175 cm diameter steel pipe within a slightly longer drive rod was used to install the piezometers to a depth representing the average extent to which fall chum salmon excavate redds (approximately 35 cm; Zimmerman and Finn 2012). The piezometers were allowed 30 minutes to equilibrate after which the water level height (mm) within the piezometer and the height of the stream surface outside the piezometer were recorded. The VHG is a unitless measure that is positive under upwelling conditions and negative under downwelling and was calculated as:

$$VHG = \frac{\Delta h}{L},$$

where Δh is the difference in hydraulic head between the water level in the piezometer and the level of the stream surface (L). Water velocity was measured immediately above the river substrate adjacent to the piezometers using an acoustic Doppler velocity meter (FlowTracker, Sontek Corp., San Diego, CA) attached to a wading rod. Water depth (cm) was also recorded. All data points were georeferenced and entered in Trimble GeoExplorer handheld computers (Trimble Inc., Sunnyvale, CA).

At spawning sites, six continuous water temperature loggers with ± 0.2°C accuracy (Hobo Tidbit V2, Onset Corp., Bourne, MA) were placed in the substrate in redd clusters throughout each study site to record intergravel over-winter water temperatures. Loggers were calibrated prior to deployment (Mauger et al. 2015) and set to record temperature every hour. We used the same piezometer installation drive rod setup to install temperature loggers at redd depths. Each temperature logger was attached to a 40 cm length of 1/16" steel cable with a pink survey marker to aid in location and retrieval of the temperature loggers. The location of each logger was georeferenced and noted on a site sketch to aid in retrieval. Initial temperature logger

retrieval occurred in March 2016, to avoid losing loggers to spring breakup and bed

mobilization, and additional retrieval occurred in September 2016. Once retrieved, the loggers

were downloaded using HOBOWare (Onset Corp., Bourne, MA), and mean daily temperature

was calculated. Instrumentation and data collection processes at non-spawning sites were

identical as for spawning sites, with the only difference being placement of instrumentation and

water velocity measurements. Because non-spawning sites did not contain redds, piezometers,

temperature loggers, and velocity measurements were spaced throughout the study site in

configurations similar to those in spawning areas.

Data analysis

Physical habitat and water chemistry characteristics were compared individually among

channel types using one-way analysis of variance (ANOVA). If significant differences were

detected by the ANOVA, we used Tukey's honestly significant difference post hoc test for

multiple comparisons. Response variables were log transformed as needed to meet assumptions

of ANOVA. To address the potential for bias induced by non-normality of data and an

unbalanced design, we compared results of the ANOVA with those from a randomized

permutation test (Manly 2007) based on the same main effects. Results of permutation tests were

identical to one-way ANOVAs. Based on those results, we felt justified that the ANOVA

analysis did not influence our results in substantial ways to warrant a different analysis.

Statistical significance was evaluated at the $\alpha < 0.05$ level.

Mean daily temperatures were used to predict hatching and fry emergence dates for fall

chum salmon embryos at each temperature logger location. We modified an empirical model

commonly used to predict hatching and emergence timing in Pacific salmon (Beacham and

Murray 1990). This model was among those with a best fit for chum salmon ($r^2 = 0.985$ for

hatch, $r^2 = 0.973$ for emergence) based on a suite of candidate models (see Table A.2 in Beacham and Murray 1990). The general formula of the model is:

(1)

$$\log_e(D) = \log_e(a) - \log_e(T - b),$$

where D is the observed hatching time after fertilization, T is the mean temperature (°C) over the incubation period, and $\log_e(a)$ and b are constant parameters specific to British Colombia chum salmon (Beacham and Murray 1990). For hatch prediction, $\log_e(a) = 6.413$ and $b = -1.079$, and for predicting emergence, $\log_e(a) = 6.982$ and $b = -1.447$.

To evaluate the suitability of the British Colombia chum salmon parameters to Yukon River fall chum salmon, we compared known incubation and emergence times of Kluane River (Yukon River basin) fall chum salmon embryos and alevins incubated under 3 different constant thermal regimes (Beacham et al. 1988) to the timing generated by the empirical model described above (Beacham and Murray 1990). The values generated by the empirical model were within 2 standard deviations of the Kluane River hatch timing, and within 3 standard deviations of the Kluane River emergence timing.

Because the length of the incubation period was unknown for our dataset, we modified Model 1 to incorporate daily mean temperature instead of mean temperature across the entire incubation period using methods developed by Sparks (2016). The formula for this model (termed the Effective Value model) is:

(2)

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

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where $\log_e(a)$ and b remain the same, but E_i is an effective value (range $0-1$), which describes the relative daily temperature contribution, and T_i is the mean daily temperature (°C). According to the Effective Value model, fish will hatch (or emerge) when the sum of $E_i = 1$.

RESULTS

Eleven sites were surveyed, eight of which were occupied by actively spawning fall chum salmon (spawning sites), and three sites were unoccupied (non-spawning sites). Two sites were in the primary channel, five were in flood channels, and four were in spring channels. Site length ranged from 46 m to 112 m (mean = 75 m ± 21 SD). Point estimates from field work in late September resulted in temperatures that ranged from 1.88°C to 4.87°C, dissolved oxygen that ranged from 8.10 mg/L to 12.78 mg/L, pH that ranged from 8.14 to 8.52, conductivity that ranged from 192.83 µS/cm to 224.69 µS/cm, vertical hydraulic gradient that ranged from -0.01 to 0.21, and water velocity that ranged from 0.02 m/s to 0.52 m/s (Table 2.1; Fig. 2.2).

Habitat characteristics

Habitat characteristics hypothesized to be important for fall chum salmon spawning site selection and incubation varied among the three channel types on the Chandalar River (Fig. 2.2). Using ANOVA to test for differences among habitat characteristics by channel type, we found significant differences in temperature (df = 2, F = 5.73, P = 0.03), pH (df = 2, F = 5.70, P = 0.03), conductivity (df = 2, F = 7.10, P = 0.02), and vertical hydraulic gradient (df = 2, F = 9.80, P = 0.01). Dissolved oxygen (df = 2, F = 3.84, P = 0.07) and velocity did not differ among channel types (df = 2, F = 0.80, P = 0.49). Primary channels were colder than flood and spring channels (P = 0.04, P = 0.03, respectively) and pH was higher in primary channels relative to flood (P = 0.04) and spring (P = 0.03) channels. Mean conductivity in primary channels was lower than spring channels (P = 0.01), but did not differ from flood channels (P = 0.06). Vertical

hydraulic gradient was higher in flood channels relative to spring and primary channel types (P = 0.01, P = 0.02, respectively; Fig. 2.2). Habitat characteristics by channel type are summarized in Table 2.2.

We also examined Pearson correlations among habitat characteristics (Fig. 2.3), and evaluated differences at the $\alpha < 0.05$ level. Temperature was negatively correlated with dissolved oxygen (-0.78, P < 0.01) and pH (-0.78, P < 0.01), and positively correlated with conductivity (0.76, P < 0.01). Dissolved oxygen was positively correlated with pH (0.97, P < 0.01) and negatively correlated with conductivity (-0.84, P < 0.01). The pH and conductivity were also negatively correlated (-0.89, P < 0.01).

In primary channels, the dominant substrate was cobble in 100% of observations, but cobble was less prevalent (63% and 56%) in flood and spring channels, respectively. The subdominant substrate was gravel in 100% of primary channel observations, 59% of flood channel observations, and 45% of spring channel observations (Fig. 2.4). Cobble-gravel was the most common dominant-subdominant substrate composition among channel types. We observed no fine grained substrate (silt) in primary channels.

Hatching and emergence timing

In total, 30 temperature loggers were retrieved from 9 of the 11 sites. Mean, minimum, and maximum daily temperatures for each site are plotted in Fig. 2.5. Primary and flood channels exhibited the greatest daily range within a single site. Spring channels, and some flood channels, had consistently low diel variation. Two flood channels had temperatures drop below freezing in December and January, and incubating embryos at those locations were assumed to have died. Site F2 exhibited the largest variation in temperature over the incubation period, beginning at an average temperature of 7.34°C in September, and dropping to -2.26°C in February. Site F5, a

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spring channel site, had an average temperature of 4.00°C in September, and only declined to 2.46°C in March. Flood site F5 exhibited very little variation over winter, beginning at 4.90°C in September, and only declined to 2.80°C by the end of March.

The temperature loggers were placed in completed redds at all spawning sites between September 20th and September 25th, 2015. For ease of comparison, we used September 25th as the spawn date for all hatch and emergence predictions. The predicted number of days required to hatch by fall chum salmon varied substantially within and among habitat types (Table 2.3; Fig. 2.5), reflecting the variety of experienced temperature regimes. Fish were predicted to hatch as early as 78 d following spawning (December 11, 2015) or as late as 288 d post spawning (July 8, 2016). The overall mean predicted hatching date was 144 (± 60 SD) d following spawning, which corresponded to February 15, 2016. Mean predicted hatching timing for primary, flood, and spring channels were 121 d, 142 (± 68 SD) d, and 149 (± 23 SD) d, respectively. Sites with less variable regimes had tighter predicted hatch windows. We were unable to estimate hatching dates from 7 of the loggers that were retrieved in March 2016, since hatching was not projected to occur before the loggers were retrieved (Fig. 2.5).

The predicted number of days required for emergence by fall chum salmon varied substantially across the three flood sites for which we were able to predict emergence timing (Table 2.3; Fig. 2.6), reflecting the variety of experienced temperature regimes. Fish were predicted to emerge as early as 176 d following spawning (March 8, 2016) or as late as 317 d post spawning (August 6, 2016). Mean predicted emergence was 222 (± 49 SD) d following spawning, which corresponds to May 3, 2016. In the middle of May 2016, our data indicated a pulse of warmer water that moved through all three sites, likely indicating break up and

accompanying high water conditions that connect the flood channels to the primary body of flow.

DISCUSSION

We found that water chemistry and physical habitat characteristics varied among channel types, highlighting the mosaic of habitat conditions available to spawning fall chum salmon along the Chandalar River, but only a subset were suitable for embryo incubation. Temperature, dissolved oxygen, and vertical hydraulic gradient varied substantially among the three channel types and highlight spatial variability in incubation conditions across habitats. Measurement of within-redd incubation thermal regimes revealed substantial variability within sites and among channel types. The wide range of hatch and emergence dates predicted from these thermal regimes illustrates how variation in incubation temperatures can affect hatch and emergence timing.

Habitat characteristics

Water chemistry and habitat characteristics within primary channels differed substantially from those of off-channel flood and spring channels. Primary channels were always connected to the surface water flow, and groundwater input effects are quickly mediated by the main surface flow. However, spawning habitat conditions in spring and flood channels were more similar than expected. This could be due to the temporal limitation of our habitat data. In late September, when the point measurements were collected, water level was low on the Chandalar River, and therefore the flood channels were not well connected to the primary flow at their upstream ends. As a result, water flow in flood channels was being sustained by groundwater inputs, thus the similarities to spring channels. Flood channels connect to the primary channel at the upstream end during high flows, unlike spring channels, which are only

connected to the primary flow at the upstream juncture in extreme high water events. If these measurements had been taken during high spring flows, the flood channels would have likely been much more similar to the primary channel, and spring channels would have been distinct from both.

The correlation between temperature and dissolved oxygen was high with dissolved oxygen content decreasing with increasing temperature, although none of the dissolved oxygen measurements were low enough to negatively impact embryos. However, the decrease in dissolved oxygen was steeper than what would have been expected based solely on the water temperature (°C) and barometric pressure (mm Hg) (Fig. 2.7.; Benson and Krause 1984). This was likely due to groundwater input, as long residence groundwater has low dissolved oxygen content as a result of chemical reduction as the water percolates though soils (Geist et al. 2002; Youngson et al. 2005). Primary channels were colder, with no thermal influence from groundwater. Spring channels were entirely fed by groundwater, and flood channels were intermediate between the two, although due to low water conditions during data collection, flood channel flow was likely predominantly groundwater based. As temperature is a proxy for groundwater, warmer water temperature indicates a higher proportion of groundwater to surface water. This increasing proportion of groundwater was also the likely cause of pH (-) and conductivity (+) changing with increasing temperature. The filtration of groundwater through the substrata results in different concentrations of solutes which affects pH and conductivity (Geist et al. 2002). Contrary to expectation, vertical hydraulic gradient did not correlate with temperature (groundwater). VHG is positive under upwelling, and negative under downwelling, but this measurement does not differentiate between localized upwelling of river water (short term and shallow) and groundwater upwelling (long term and deep). For example, it is possible

that the positive VHG measured in the primary channel was the result of localized, short term, river water flux, but it is impossible to tell without water chemistry tests of water from inside the piezometer.

Hatching and emergence timing

Our analysis of predicted hatching and emergence timing within Chandalar River fall chum salmon revealed substantial variation in early life history phenology. Based on a spawning date of September 25th, 2015, hatching was predicted to occur over a broad period from December to July the following year, and emergence was predicted to occur from March to August. Our temperature data indicated that breakup and accompanying high spring flows occurred in the middle of May in 2016. This is shortly after our average predicted emergence of May 3, 2016. Alevins that were still in the gravel at this point could have been harmed by the accompanying scour of this flow pulse, but fry that are free swimming could use this environmental cue to begin their downstream migration. Scour during high flow events is thought to be a major cause of salmon embryo mortality (Lisle and Lewis 1992; Montgomery et al.1996). In an investigation into scour on two chum salmon spawning streams in the Pacific Northwest, Montgomery et al. (1996) concluded that close correspondence between chum salmon egg burial depths and scour depths during typical annual high flows implies high salmon population sensitivity to variations in scour depth. Bean et al. (2015) found that bull trout (*Salvelinus confluentus*) reproductive success in the Flathead River Basin, Montana, was linked to non-overlapping timing of embryo incubation and high flows, whereby bull trout embryo and emerging fry are resilient to redd scour under typical high spring flow timing. Local populations have become adapted to scour caused by high flows either through increasing egg burial depth or by timing reproduction to avoid scour during the incubation period. However, changes to either

the depth of scour or the timing of scour events could have substantial negative impacts on embryo survival.

The patchwork of habitat conditions within sites and among channel types on the Chandalar River indicates a mosaic of spawning habitat conditions that leads to a wide spread of hatching and emergence dates. The observed broad range of life history phenology exhibited in this small sample of representative habitats indicates that this population is likely resilient to changing hydrologic conditions. Assumed reproductive success varied across even the small sample of redds that were observed in this study, with some freezing, others becoming so cold they were not predicted to hatch until July, and occasional stranding due to dewatering (C. Clawson *personal observation*). However, the variety of predicted hatch and emergence dates implies that at least some of the fry will emerge into suitable conditions for growth and downstream migration, making the population as a whole resilient to some changes to flow magnitude and timing.

Air temperatures in the Arctic fall well below 0°C for months in the winter, during which time fall chum salmon embryos are incubating. Channels primarily sustained by groundwater exhibited relatively stable thermal regimes that remained above freezing throughout the winter. This groundwater is likely long-term residence groundwater, based on lower dissolved oxygen concentrations, lower pH, and higher conductivities relative to water in primary channels. Long hyporheic flow paths are not sensitive to daily temperature variations, and even annual air temperature warming trends would not affect long residence groundwater output temperature in the near term (Poole et al. 2008). Accordingly, thermal regimes in these groundwater dominated habitats may be less sensitive to recent and near-term climate change. However, a potential mismatch could occur if breakup and high spring flow timing are shifted earlier by warmer air

temperatures yet within-redd incubation temperatures remain the same (Reist et al. 2006). If timing of suitable conditions for downstream migration becomes earlier than normal, emerging fry may be stranded in channels that no longer connect at the downstream end to the main body of flow. Additionally, fall chum salmon born on the Chandalar River must migrate over 1600 km downstream to reach the ocean. If incubation conditions shift and alter the timing of hatch, emergence, and migration, the downstream river conditions may no longer be suitable for migration, and ocean conditions may not provide adequate thermal conditions and food sources once the smolt reach the saltwater. Alternatively, if incubation conditions are stable due to groundwater inputs, migration timing will remain the same, but ocean conditions may be altered by changing climate, again resulting in a mismatch between juvenile chum salmon and their saltwater rearing habitat.

Thus one channel type is not necessarily superior to another with respect to fall chum salmon reproductive success; it is this diversity of habitats that buffer the population against hydrologic and thermal change and contribute to population stability and sustain the high abundance of fall chum salmon spawners in the Chandalar River. In ecology this is termed the portfolio effect, where biological diversity stabilizes ecosystem processes and dampens variance (Hooper et al. 2005). In Bristol Bay, Schindler et al. (2010) demonstrated that the population and life history diversity in sockeye salmon results in 2.2 times lower variability in annual returns than if the system consisted of a single homogenous population. Additionally, strong shifts in climatic conditions of the North Pacific Ocean during the last century should have induced synchrony in the population dynamics of the stock complex, but had little effect, indicating that individual populations fluctuate mostly independently of one another (Schindler et al. 2008; Schindler et al. 2010). The long term strength of the Chandalar River fall chum salmon stock is

dependent on the variation in habitats and incubation conditions present throughout the spawning area. Any anthropogenic change that degrades portions or types of habitats on the Chandalar River could restrict the population's ability to withstand changes in climate. The important message for natural resource managers is to protect the diversity of habitats available to spawning salmon on the Chandalar River in order to sustain this population for future generations.

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Table 2.1. General habitat characteristics for 11 sites along the Chandalar River, Alaska.

CHAN	SITE	OCC	LEN	TEMP	DO	PH	COND	VHG	VELOC
primary	F6	spawning	73	2.58	11.85	8.41	201.88	0.09	0.52
primary	NF2	non-spawning	56	1.88	12.78	8.52	192.83	-0.01	0.17
flood	F1	spawning	53	3.65	8.83	8.20	219.55	0.14	.
flood	F2	spawning	77	4.87	9.18	8.25	213.07	0.14	0.03
flood	F3	spawning	46	3.92	8.10	8.14	223.88	0.21	0.03
flood	F4	spawning	112	2.74	12.06	8.42	198.33	0.12	0.36
flood	NF1	spawning	54	4.48	10.02	8.29	226.11	0.15	0.13
spring	F5	spawning	97	4.44	10.11	8.24	222.94	0.09	0.30
spring	F7	spawning	74	4.33	9.69	8.25	224.69	0.04	0.02
spring	F8	spawning	107	2.92	10.19	8.26	224.36	0.06	0.26
spring	NF3	non-spawning	77	4.59	9.10	8.16	224.19	0.01	0.22

Note: CHAN = channel type, OCC = site occupancy, LEN = site length (m), TEMP = mean site temperature (°C), DO = mean site dissolved oxygen (mg/L), PH = mean site pH, COND = mean site conductivity (μS/cm), VHG = mean site vertical hydraulic gradient, and VELOC = mean site water velocity (m/s).

Table 2.2. Mean (± 1 SD) habitat characteristics by channel type along the Chandalar River Alaska from data collected in September 2015.

CHAN	TEMP	DO	PH	COND	VHG	VELOC
primary	2.23(0.35)	12.32(0.47)	8.47(0.05)	197.36(4.53)	0.04(0.05)	0.35(0.18)
flood	3.92(0.73)	9.64(1.36)	8.26(0.09)	216.19(10.00)	0.15(0.03)	0.14(0.13)
spring	4.07(0.67)	9.77(0.43)	8.23(0.04)	224.05(0.66)	0.05(0.03)	0.20(0.11)

Note: CHAN = channel type, TEMP = temperature (°C), DO = dissolved oxygen (mg/L), PH = pH, COND = conductivity (μS/cm), VHG = vertical hydraulic gradient, and VELOC = water velocity (m/s). N = 2 (primary), N = 5 (flood), and N = 4 (spring).

Table 2.3. Projected number of days to hatch and emerge based on observed mean daily temperature along the Chandalar River, Alaska.

CHAN	SITE	TEMP	EH	LH	EE	LE
primary	F6	2.58	121	AR	AR	AR
flood	F1	3.65	104	122	200	245
flood	F2	4.87	202	288	269	317
flood	F3	3.92	104	113	176	205
flood	F4	2.74	78	103	176	AR
flood	NF1	4.48	122	AR	AR	AR
spring	F5	4.44	126	150	AR	AR
spring	F7	4.33	dead	dead	dead	dead
spring	NF3	4.59	167	180	AR	AR

Note: CHAN = channel type, TEMP = temperature (°C), EH = earliest modeled hatch date (days after spawning), LH = latest modeled hatch date (days after spawning), EE = earliest modeled emergence date (days after spawning), and LE = latest modeled emergence date (days after spawning). AR = after retrieval, indicating that data collection was terminated before projected hatch//emergence. If temperature dropped below 0°C, the embryos are assumed to have died.
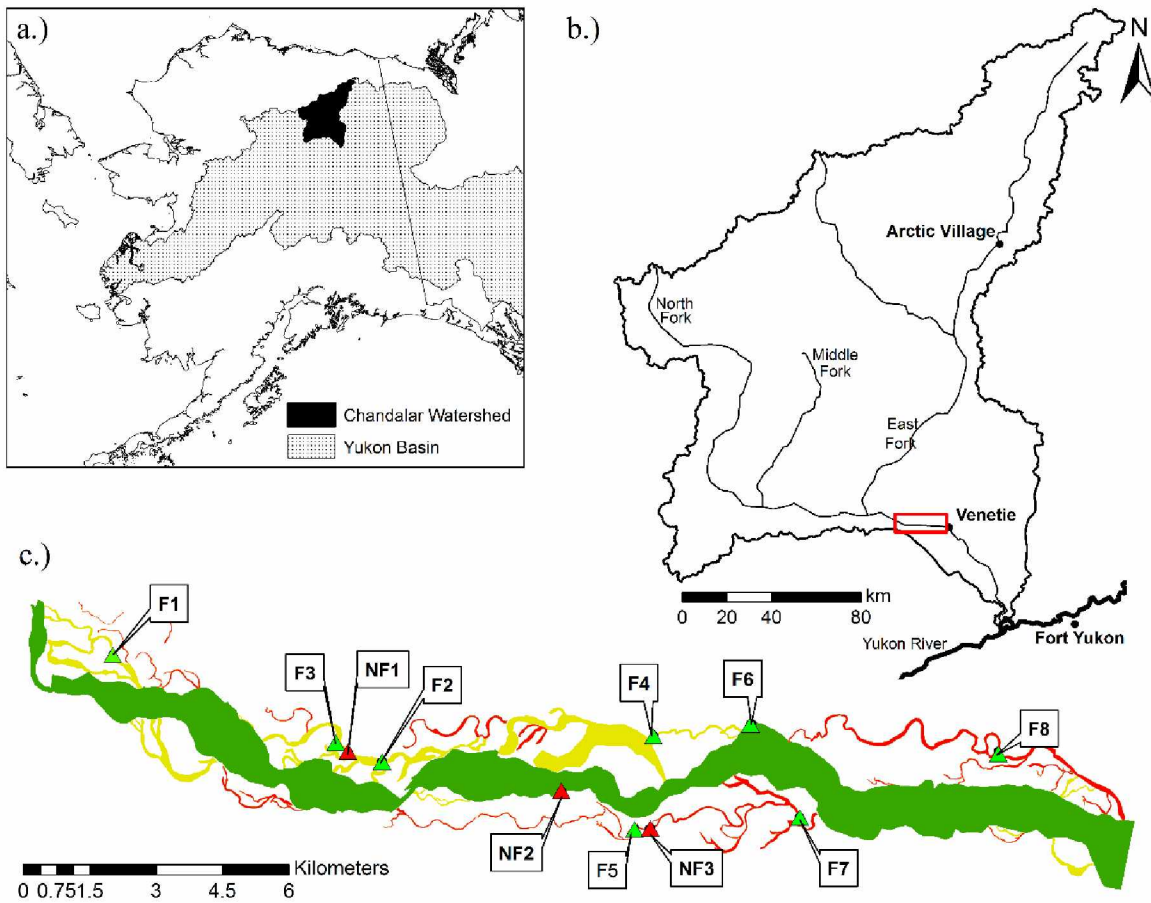
Fig. 2.1. a.) Location of the Chandalar River watershed in Alaska, and b.) branches of the Chandalar River with the location of the village of Venetie, and the 25 km study area (red box) shown. In c.) locations of the 11 study sites are shown, and F = spawning site and NF = non-spawning site. Primary channel is green, yellow is flood channel, and red is spring channel. Spawning sites are shown with green triangles, and non-spawning sites are shown in red triangles.
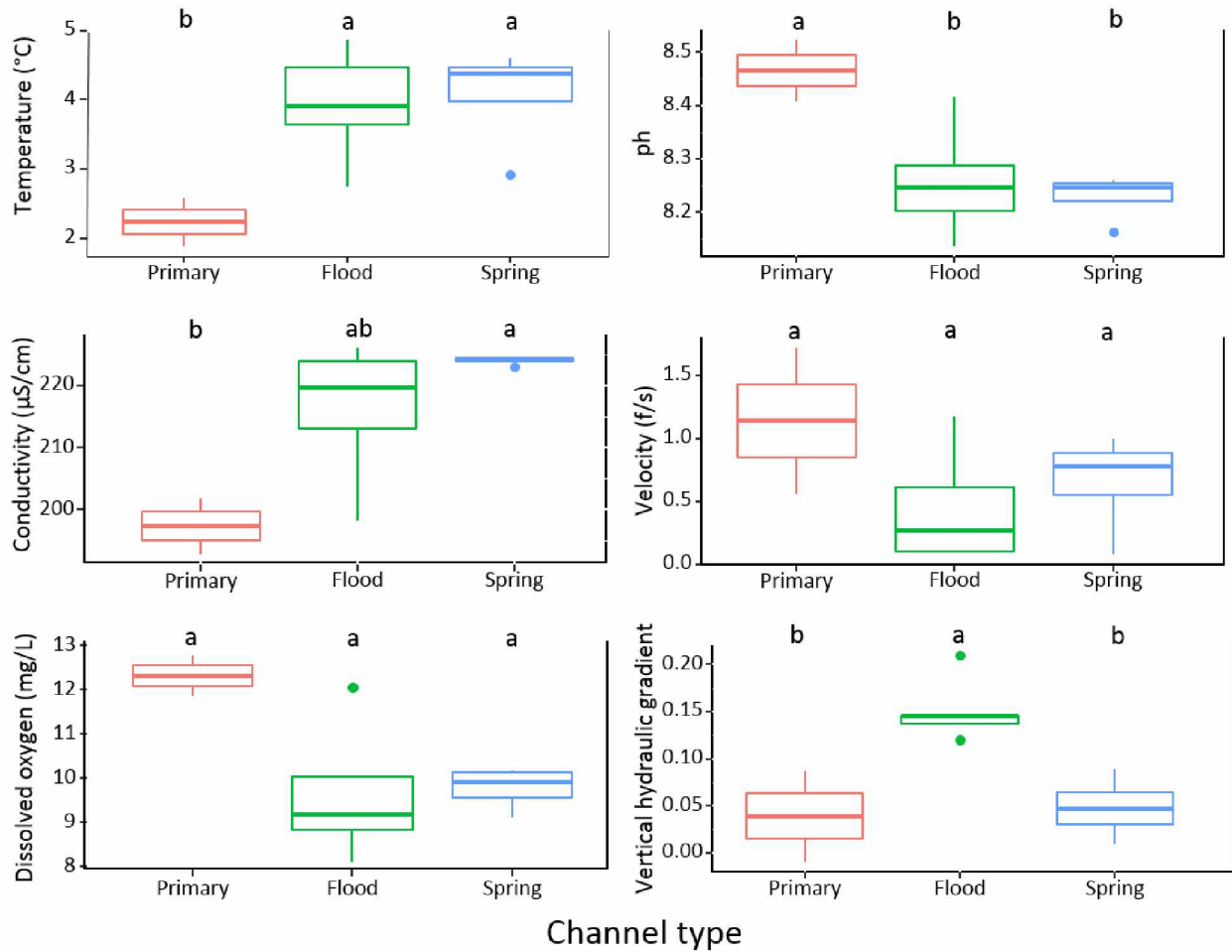
Fig. 2.2. Water chemistry, temperature, and vertical hydraulic gradient from 11 sites on the Chandalar River, Alaska, separated by channel type. Treatments sharing the same letter were not significantly different at the $\alpha < 0.05$ level.
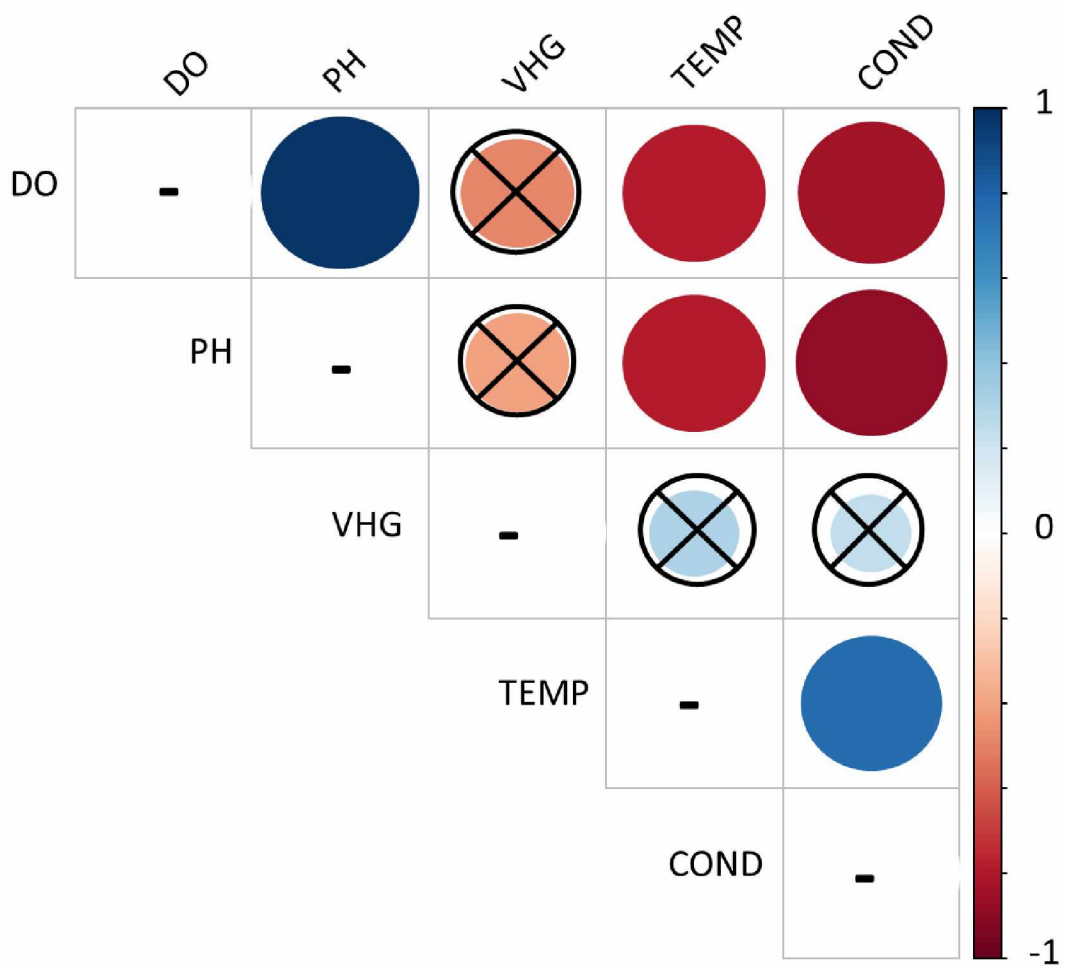
Fig. 2.3. Corellelogram of Pearson correlations for physical habitat characteristics among eleven sites along the Chandalar River, Alaska. Positive correlations are displayed in blue and negative correlations in red. Color intensity and the size of the circle are proportional to the correlation coefficients. Insignificant correlations have been crossed out.
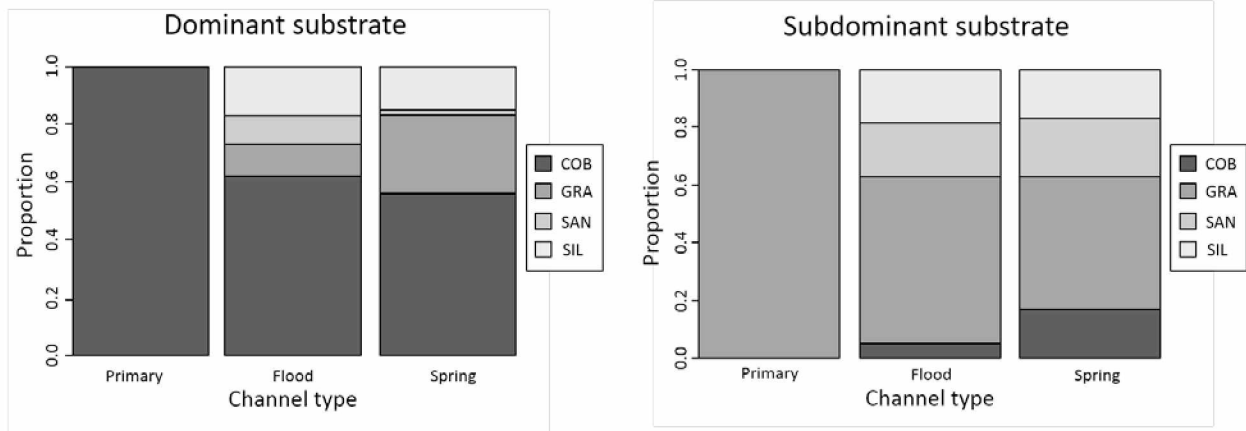
Fig. 2.4. Dominant and sub-dominant substrate by channel type at 11 sites on the Chandalar River, Alaska. COB = cobble, GRA = gravel, SAN = sand, SIL = silt.
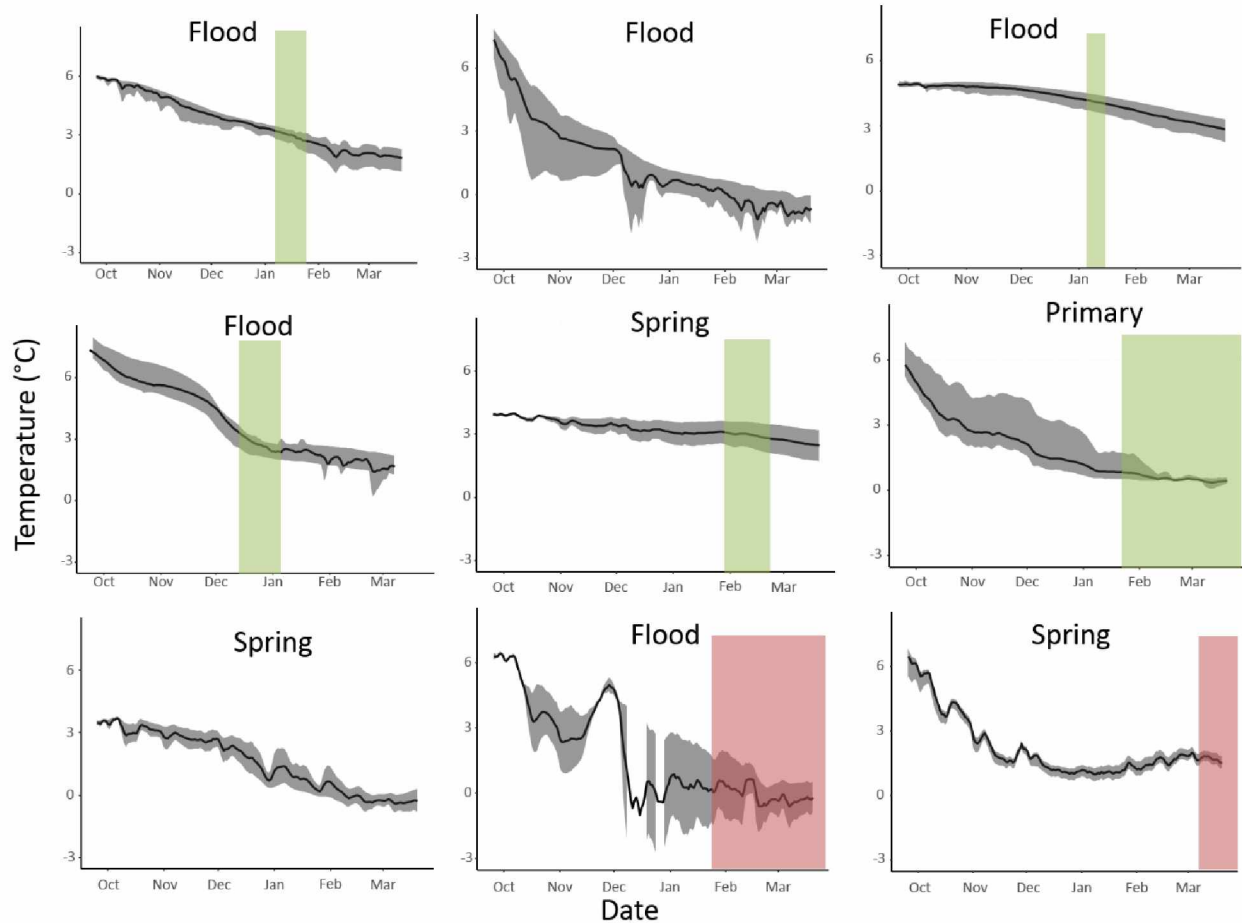
Fig. 2.5. Temperature at redd depth from late September 2015 to late March 2016, at nine sites representing primary, flood, and spring channel types on the Chandalar River, Alaska. Mean temperature at each site is shown by the black line, and minimum and maximum observed daily temperature at that site are the bounds of the shaded areas. Estimated range of hatch dates for that site are shown in green bars. Red bars are for non-spawning sites, where no observed spawning occurred. Sites with no bars would not have hatched before temperature collection was terminated.
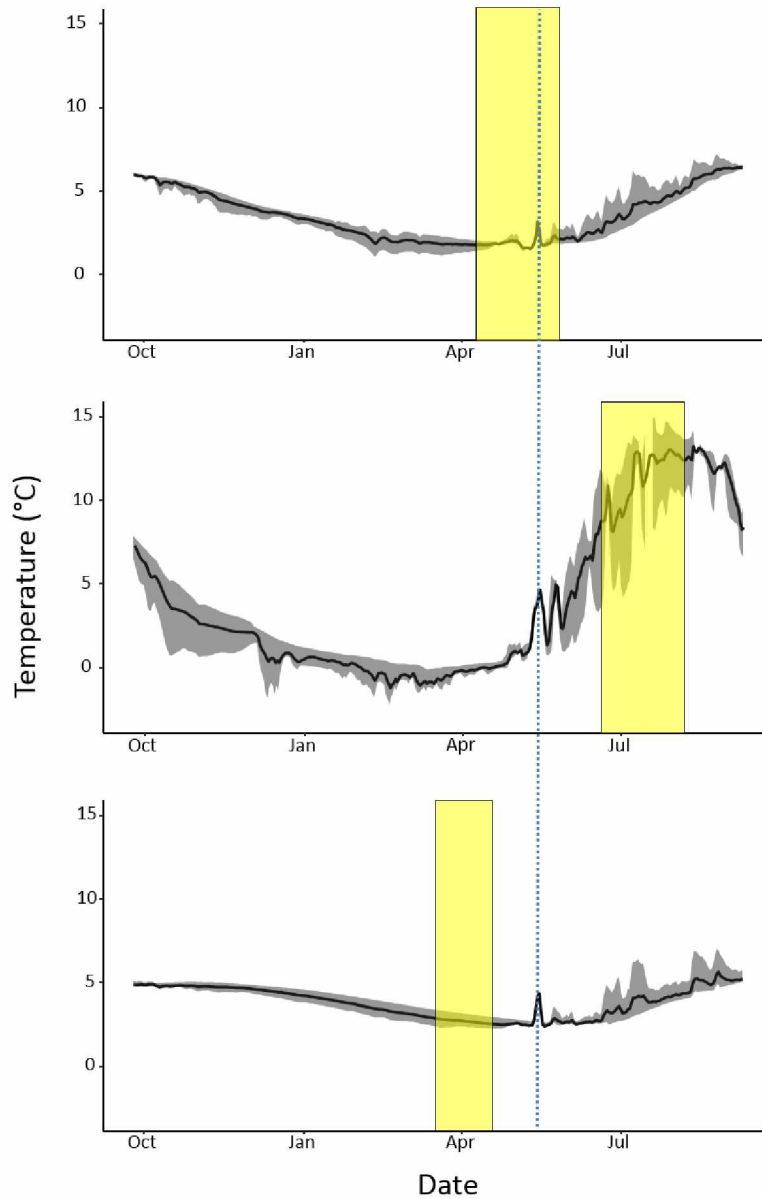
Fig. 2.6. Substrate temperature and estimated emergence dates from late September 2015 to early September 2016, at three flood channel sites on the Chandalar River, Alaska. Mean temperature at each site is shown by the black line, and minimum and maximum observed temperature at that site are the bounds of the shaded areas. Estimated range of emergence dates for that site are shown in yellow bars. Breakup is shown by the blue dashed line.
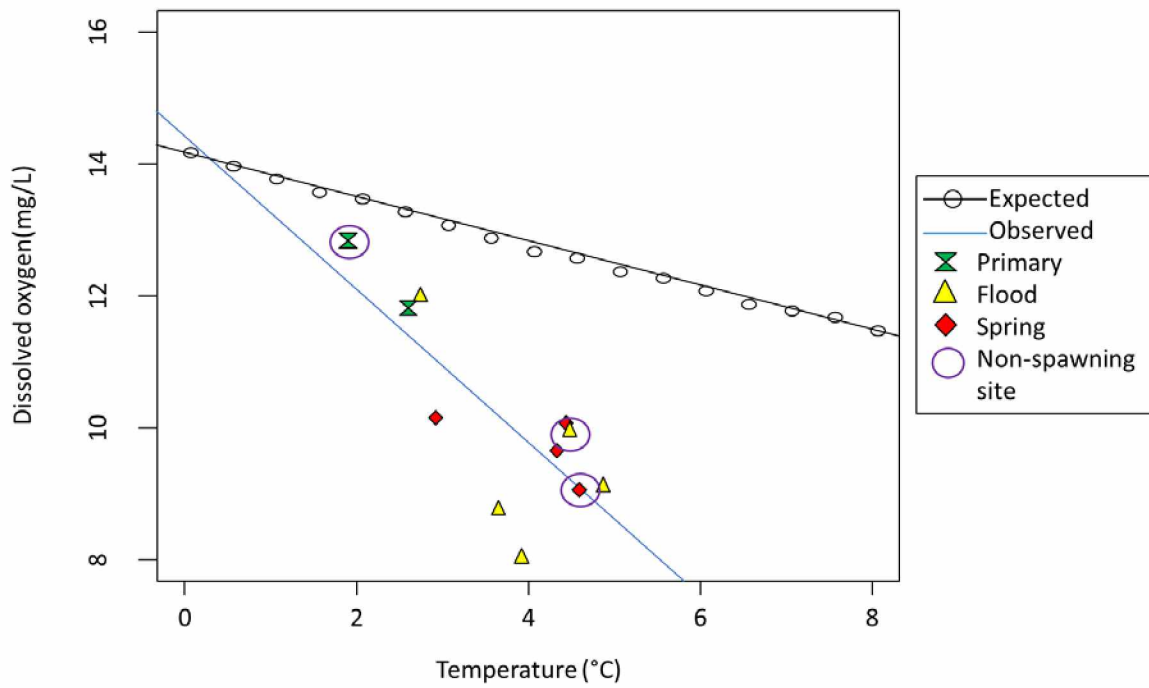
Fig. 2.7. Expected and observed relationships between dissolved oxygen solubility and water temperature at the average observed barometric pressure during data collection (745 mm Hg).

General Conclusions

With this work I demonstrated the utility of applying remote sensing and multistate occupancy techniques to a salmon population in Arctic Alaska, and investigated physical habitat variables hypothesized to affect spawning site selection by fall chum salmon on the Chandalar River, Alaska. The main findings of this work were as follows:

- Optical and thermal imagery were used to classify spawning habitats into three channel types (primary, flood, and spring) and delineate 330 unique and non-overlapping river segments, of which 161 were primary channels, 82 were flood channels, and 87 were spring channels.

- Detection analysis of the 2014 aerial spawning surveys resulted in a probability of detecting low abundance aggregations of 0.38 ± 0.07, and probability of detecting high abundance aggregations ranged from 0.69 ± 0.07 to 0.876 ± 0.08.

- All top multi-season (2013-2015) multistate (low, high abundance) occupancy models contained mean segment temperature as a covariate on initial probability of occupancy (ϕ_0) by spawning fall chum salmon, with ϕ_0 increasing with segment temperature. At 0°C, $\phi_0 = 0.12$ (95% CI = 0.07 - 0.20). At 4°C, $\phi_0 = 0.67$ (95% CI = 0.42 - 0.86). The predicted temperature when $\phi_0 = 0.50$ was 2.94°C.

- Water quality and spawning habitat characteristics varied among the three channel types used by fall chum salmon, with most differences occurring between main channel and off-channel habitats. Primary channels were colder, on average, than flood and spring channels ($P = 0.04$, $P = 0.03$, respectively), and pH was higher in primary channels ($P = 0.04$, $P = 0.03$). Conductivity was lower in primary

channels than in spring channels (P = 0.01), but did not differ from flood channel (P = 0.06). Vertical hydraulic gradient was higher in flood channels relative to spring and primary channel types (P = 0.01, P = 0.02).

- Dissolved oxygen was negatively correlated with temperature, but the slope of the relationship was steeper than what would have been expected based solely on the water temperature (°C) and barometric pressure (mm Hg), indicating that the input of long-term residence groundwater was driving the decrease in dissolved oxygen.

- Fall chum salmon embryos were predicted to hatch, on average, 144 (± 60 SD) d following spawning, which corresponded to February 15, 2016. Mean predicted hatching timing for primary, flood, and spring channels were 121 d, 142 (±68 SD) d, and 149 (±23 SD) d, respectively.

- Mean predicted emergence in flood channels was 222 (±49 SD) d following spawning, which corresponded to May 3, 2016.

Based on the occupancy modelling in chapter one, water temperature, and therefore groundwater upwelling, had a significant effect on spawning site selection by fall chum salmon on the Chandalar River. In high latitude areas that experience extreme cold in winter months, groundwater upwellings provide salmonids with warmwater thermal refugia characterized by warmer and more stable water temperatures and protection from freezing (Reynolds 1997; Geist and Dauble 1998; Baxter and Hauer 2000; Geist et al. 2002). However, while the three different channel types had different mean segment temperatures, channel type did not emerge as a significant covariate in the occupancy models. Warm groundwater upwelling occurs throughout the Chandalar River riverscape, and it appears that spawning salmon are attracted to the warmer

temperatures regardless of habitat type. Thus conservation and protection of spawning areas within all channel types will be key to successful management of fall chum salmon in this system.

Aerial spawning surveys proved to be an effective tool for detecting aggregations of spawning fall chum salmon. Detection probabilities of 0.38 and 0.69-0.80 are high, indicating that even a single aerial survey could collect sufficient data for occupancy analysis. I also found that there was no observer bias to detection by aerial survey. This is an important improvement to aerial surveys that seek to estimate abundance, which are often subject to observer bias and underestimation (Cousens et al. 1982; Jones et al. 1998). While occupancy data cannot be used to determine population abundance, they do provide useful information about trends in habitat usage and spawning distribution. For example, the USFWS sonar counting project on the lower Chandalar River provides estimates of population abundance, but does not provide information about upstream fall chum salmon spawning distribution. For clear water systems that do not have escapement monitoring via sonar, weir, or counting tower, aerial surveys may provide a cost effective and low effort means to assess trends in habitat usage and identify spawning distribution. The Yukon River Basin is extensive, extending across Alaska and into Canada, and encompasses over 832,700 km^2. Using aerial surveys to investigate fall chum salmon distribution on tributaries without escapement monitoring, such as the Teedraanjik (Salmon Fork River) or Draanjik (Black River) would provide additional distribution and habitat information to natural resource managers, enabling more informed and comprehensive management decisions.

Remote sensing allowed me to collect a spatially continuous dataset with relatively low effort in a remote, inaccessible area. The large extent of the data ($\approx$ 102 km^2) enabled me to evaluate temperature trends in a spatially continuous manner, at a fine spatial scale, over the

entire core spawning area. Satellite imagery such as Landsat is easily available via online

platforms, but the resolution of Landsat imagery is 15 m and 100 m for panchromatic and

thermal imagery, respectively. The resolution of aerial imagery is much finer (9 cm and 1 m, in

this study), which is critical for characterizing riverscapes where individual channels are often

narrower than 15 m but may be heavily utilized by spawning salmon. The spatial continuity of

aerial imagery is also important, since it allows the various habitats to be examined holistically

and on a variety of different scales. The on-the-ground work performed for this thesis was

important for evaluating water chemistry and physical habitat characteristics that could not be

gleaned from the optical or thermal imagery, but these data were limited to isolated sites

scattered across the riverscape. Remote sensing is an ideal method for collecting large, spatially

continuous data in remote areas such as the Arctic.

My analysis of predicted hatching and emergence timing within Chandalar River fall

chum salmon revealed substantial variation in early life history phenology. Hatching was

predicted to occur over a broad period from December to July the following year, and emergence

was predicted to occur from March to August. Breakup typically occurs in May on the Chandalar

River, and embryos or alevins that were still in the gravel at this point could have been

negatively impacted by the accompanying scour of this flow pulse. However, free swimming fry

could have used this flow pulse to begin their downstream migration (Quinn 2005). Local

populations have become adapted to scour caused by high flow either through egg burial depth

or by timing reproduction to avoid scour during the incubation period. However, changes to

either the depth of scour or the timing of scour events could have substantial negative impacts on

embryo survival. Warming climate patterns could result in earlier ice breakup, altering the timing

of high spring flows. Decreases or increases to snowpack and precipitation due to climate change would affect river flows, altering the historic hydrologic regime (Prowse et al. 2006).

The patchwork of habitat conditions within and among channel types on the Chandalar River provide a mosaic of spawning habitat, that may result in a wide spread of hatch and emergence dates. My occupancy modelling results indicated that the presence of groundwater upwelling, as inferred by water temperature variation, is an important factor for spawning site selection, across channel types. Even with this preference for groundwater upwellings that are assumed to provide warmer water temperatures over winter, the over winter thermal data indicated a substantial range of experienced thermal regimes. The broad range of life history phenology exhibited in this small sample of representative habitats indicates that this population may be resilient to changing hydrologic conditions. There was extensive variation in hatch timing and reproductive success across the small sample of redds that were observed in this study, with some freezing, others becoming so cold they were not predicted to hatch until July, and occasional stranding owing to dewatering (C. Clawson *personal observation*). However, the variety of predicted hatch and emergence dates implies that at least some of the fry will emerge into suitable conditions for growth and downstream migration, making the population as a whole resilient to hydrologic change.

The groundwater influx on the Chandalar River is likely long-term residence groundwater, based on the lowered dissolved oxygen and differing pH and conductivity from water in primary channels. Long hyporheic flow paths are not sensitive to daily temperature variations, and even annual air temperature warming trends would not affect long residence groundwater output temperature in the near term (Poole et al. 2008). Accordingly, thermal regimes in these groundwater dominated habitats may be less sensitive to recent and near-term

climate change. However, a potential mismatch could occur if breakup and high spring flow timing is shifted by warmer temperatures yet incubation temperatures remain the same. If suitable hydrologic conditions for downstream migration occur earlier than normal, but incubation temperatures have not warmed, hatching and emergence may occur after the ideal flow conditions for downstream migration have passed.

In summary, primary, flood, and spring channels provide a spectrum of spawning and incubation habitat conditions. The varying influence of groundwater, from absent in primary channels to dominating in spring channels, affects the thermal, chemical, and physical conditions experienced by spawning and incubating fall chum salmon in the Chandalar River. This population has been historically strong, perhaps due to the patchwork of spawning habitats that buffer the population against hydrologic and thermal change. Any anthropogenic change that degrades portions or types of habitats on the Chandalar River could restrict the population's ability to withstand changes in climate. There is not a single habitat type that is more important than other habitats to spawning fall chum salmon; it is the patchwork of habitats along the Chandalar River that make it a consistent producer of fall chum salmon.

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