THERMAL LIMITATIONS ON CHINOOK SALMON SPAWNING HABITAT IN THE NORTHERN EXTENT OF THEIR RANGE

By

Samantha Kristin Strom Decker

RECOMMENDED:

Mr. Matthew Evenson

Dr. Amanda Rosenberger

Dr. F. Joseph Margraf, Advisory Committee Chair

Dr. Trent Sutton, Academic Program Head, Fisheries Division

APPROVED:

Dr. Denis Wiesenburg
Dean, School of Fisheries and Ocean Sciences

Dr. Lawrence Duffy, Dean of the Graduate School

April 6, 2010

Date

THERMAL LIMITATIONS ON CHINOOK SALMON SPAWNING HABITAT IN THE NORTHERN EXTENT OF THEIR RANGE

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Samantha Kristin Strom Decker, B.S.

Fairbanks, Alaska

May 2010

Abstract

Pacific salmon (Oncorhynchus) habitat models attempt to balance research efficiency with management effectiveness, however, model transferability between regions remains elusive. To develop efficient habitat models, we must understand the critical elements that limit habitat. At the northern edge of the geographic range for Chinook salmon, O. tschawytscha, water temperature is a probably a limiting habitat factor. This study investigated the spatial and temporal correspondence between water temperature and Chinook salmon spawning on the Chena River, Alaska. Water temperatures were monitored at 21 stations across 220 river kilometers during the 2006 and 2007 spawning seasons and compared to known thermal requirements for egg development. While an absolute upstream thermal boundary to spawning was not discovered, we describe potential temporal limitations in thermal conditions over the spawning season. Our results show that 98.5% of Chinook salmon selected spawning habitat in which their eggs have a 90% probability of accumulating 450 ATUs before freeze up. This suggests not only temperature conditions limit salmon spawning habitat, but also, as expected, water temperatures temporally limit accessible Chinook salmon spawning habitat at the northern edge of their range. This project documents new spawning habitat for the Anadromous Waters Catalog and broadens the geographical range of Chinook salmon thermal habitat research. It also contributes to the understanding of the processes that define salmon habitat, while providing a baseline for further investigations into water temperature in other thermal regimes.

Acknowledgements

Funding for this project was provided by the Alaska Department of Fish and Game through the Alaska Cooperative Fish and Wildlife Research Unit. I thank my committee members Joseph Margraf, Amanda Rosenberger, and Matthew Evenson for their support and guidance. Thank you also to Nicholas Hughes (deceased) for his early help as a member of my advising committee; he provided inspiration and detailed guidance at a critical point in the project. Thank you to Jiaqi Huang at the Alaska Department of Fish and Game, Fairbanks office and to Jason Neuswanger at the University of Alaska Fairbanks for statistical and programming support in data analysis. Thank you to the many technicians who helped with field work and the Alaska Cooperative Fish and Wildlife Research Unit and School of Fisheries staff for their attention to detail. I would also like to thank my family and friends who have helped me in so many ways.

Table of Contents

Page

List of Tables

Page

List of Figures

Introduction

Salmon are an important component of northern Pacific ecosystems and have value to humans for sport, commercial, subsistence, and personal uses (Groot and Margolis 1991). Their semelparous life history provides marine nutrients to both aquatic and terrestrial food webs before winter (Quinn 2005). Fishery managers in Alaska manage salmon returns to achieve fixed escapements as dictated by the *Policy for the Management of Sustainable Salmon Fisheries* (AAC 2000), and information on salmon productivity and system carrying capacity is needed to set escapement goals. Management therefore depends upon research and salmon enumeration locations that are sometimes remote. Alaska's large size and transportation limitations exacerbate the expense of research. Further, enumeration studies often ignore other interactions between salmon and habitat which can be complex and nuanced.

Both simple models based on enumeration (e.g., stock and recruitment model; Ricker 1975) and complex statistical models attempting to integrate ecological concerns (e.g., those reviewed in Fausch et al. 1988) require expensive and time-consuming data collection. However, models remain desirable management tools for fish population projections and identification of limiting habitat. The creation of region-specific habitat carrying capacity models would be prohibitively expensive and impractical over an entire species range; managers instead require models that can be applied widely. This goal has proven elusive; for example, a meta-analysis by Fausch et al. (1988) found 99 unique habitat-based carrying capacity models (for many fish species in diverse regions) published between 1950 and 1985. These models described 150 unique population limiting habitat characteristics that were statistically significant. The most precise models lacked universality and could not be applied to other, even nearby, rivers, while more general models lacked sufficient precision (Fausch et al. 1988). Researchers have also raised concerns regarding transference of thermal requirements across a species range. Myrick and Cech (2004) recognized that the majority of the published studies on Chinook salmon *Oncorhynchus tschawytscha* and water temperature were from Washington, Oregon and British Columbia which raised concerns about the applicability of these models to different thermal regimes and thermal acclimation of fish in their study of California Chinook salmon. Similar concerns exist for the transference of thermal regime models to Chinook salmon populations in the northern extent of their range, as the geographical distance of transferance is even greater. The interaction of limiting factors are more likely to be simple as habitat is less modified, and habitat suitability (as measured by presence/absence) is more likely to be apparent on northern rivers that sustain large wild Pacific salmon stocks. This project assumes that Chinook salmon spawning habitat requirements and preferences are the same across the species range, but critical limiting factors change from region to region. At the northern extent of the range, we anticipate the coolest temperature regimes experienced by the species. In fact, limitations brought about by both colder temperatures and a contracted growing season, have probably prevented northward expansion rather than lack of physical habitat for spawning (e.g., gravel).

Water temperature has been recognized as a critical component of survival and fitness for Chinook salmon (Brett 1956; Heming 1982; Burger et al. 1985; Murray and McPhail 1988). Thermal regimes have a strong effect on fish survival and energetic demands (e.g., lethal thermal limits and metabolic rates; Brett 1956; Heming 1982) and on development timing (differing rates of development depending on water temperature; Quinn 2005), which vary based on life stage (e.g., egg, alevin, fry; Table 1; Alderdice and Velsen 1978) and individual acclimation (Brett 1952). Sub-lethal thermal conditions can also have long-term effects that can negatively impact fitness and survival, including decreased disease resistance (Snieszko 1974), altered growth and smoltification (Zaugg and McLain 1976), and increased vulnerability to predation (Brett 1952; Marine and Cech 2004).

Table 1. Water temperatures for optimal survival, upper incipient lethal limit (UILL), and lower incipient lethal limits (LILL) by life stage for Chinook salmon.

Lifestage	Optimal T for survival	UILL	LILL
Egg	14?C[2] 6-12?C[1]	15.5?C[5]	3?C[3]
Alevin	5-8?C[2] 6-12?C[3]		
Fry	<17?C[3]	20?C[3]	
Adult	4-11?C[6]	20-21?C avoidance[4] 22-25?C death[4]	

Summarized from Alderdice and Velsen (1978)[1], Murray and McPhail (1988)[2], Myrick and Cech(2004) [3], Richter and Kolmes (2005)[4], Seymour (1959)[5] and Zaugg and McLain (1976) [6].

Pacific salmon have evolved such that they will select specific spawning habitat with appropriate thermal conditions that maximize offspring survival (e.g., chum salmon *O. keta* in the Chena River, Maclean 2002). While previous laboratory thermal experiments tested survival at water temperatures as low as 3°C (Table 1), it is commonly assumed that salmonid eggs comes to a developmental standstill around 0°C in Alaska (C. Skaugstad, Alaska Department of Fish and Game, personal communication). Given the short ice-free season in Alaska, there are a limited number of days after fertilization in which eggs can achieve the 450-500 accumulated thermal units (ATUs) (Quinn 2005) necessary to hatch before water temperature approaches zero for the duration of winter. Chinook salmon have actively spawned in the Nunti River, a tributary of the Chandalar River, Alaska, as late as mid August (personal observation), but this late summer spawning exposes the eggs to cooler water temperatures and delayed development. Late hatching and smaller body size (Brannon et al. 2004) lowers juvenile survival (Murray and McPhail 1987; Beer and Anderson 2001) during the long outmigration (as far as 1,700 km for Chena River salmon, via the Tanana and Yukon rivers).

Water temperature can greatly influence survival of Chinook salmon in Alaska, particularly during the immobile juvenile life stages. Offspring survival relies upon the parent fish selecting adequate spawning habitat. The goal of this study was to determine if Chinook salmon spawning habitat was thermally limited in rivers near the northern edge of their range. Relating water temperature characteristics to spawning habitat selection and run timing for Chinook salmon spawning, based on known thermal preferences, will improve our understanding of the river conditions that drive habitat limitations of this species and will fill a geographic gap in Pacific salmon thermal habitat research. We determined whether Chinook salmon were thermally restricted by investigating two hypotheses: First, spawning habitat of northern populations has a theoretical absolute upstream thermal boundary beyond which eggs cannot accumulate enough thermal units to develop to hatching before freeze up. Second, upstream habitat provides sufficient ATUs to Chinook salmon that arrive early in the spawning season but not to those that arrive later within the spawning season, creating a temporal compression of thermally suitable spawning grounds. Based on these findings, this study also explores the potential for Chinook salmon range expansion under a warming scenario.

The short-term benefits of this research include identifying the boundaries of potential Chinook salmon spawning in an important tributary of the Yukon River spawning population, determining if a thermal spawning boundary exists, and understanding how interannual variability in thermal conditions result in a spatially variable boundary. Long term benefits of this work include establishing detailed baseline data for the thermal regime of a lotic environment in interior Alaska, thereby facilitating future research. This project lays the groundwork for future investigations such as predicting the effects of a warming thermal environment on salmon distribution, conducting thermal modeling of Alaskan rivers, describing thermal tolerances of northern Chinook salmon populations, and developing habitat carrying capacity models to aid in setting salmon escapement objectives.

Methods

Study Area

The Chena River is a clearwater tributary that originates in the Tanana Uplands in the interior region of Alaska and flows approximately 250 km to the Tanana River, a tributary of the Yukon River (Frey et al. 1970). Fourteen fish species are present in the Chena River watershed (5,130 km^2), including two salmon species: Chinook and chum salmon. The mainstem Chena River is approximately 140 km in length and has five major tributaries: the North, West, South, and East Fork Chena rivers and Little Chena River. Chinook salmon telemetry studies from 2002-2005 (Eiler et al. 2004) and historic run surveys by the ADF&G (Evenson 2002) have shown that the majority of spawning occurs in the mainstem reaches. The upstream extent of this project study site was located at an old mining camp on the East Fork Chena River known as Van Curler's bar (233 river kilometer [rkm]) and extended downstream to the confluence with the Tanana River (Figure 1). The Moose Creek Flood Control Project (FCP; Army Corps of Engineers) was established at 77 rkm due to historical floods of Fairbanks; it also marks the escapement point for the downstream fisheries and delineates a rather abrupt change in substrate condition. The substrate in the river below the FCP is primarily fine sediment (silt and loess) unsuitable for spawning salmon and is accepted as the lower limit of Chinook salmon spawning habitat (Mundy 1998). Upstream of the FCP, the substrate is composed of mixed gravel/cobble.

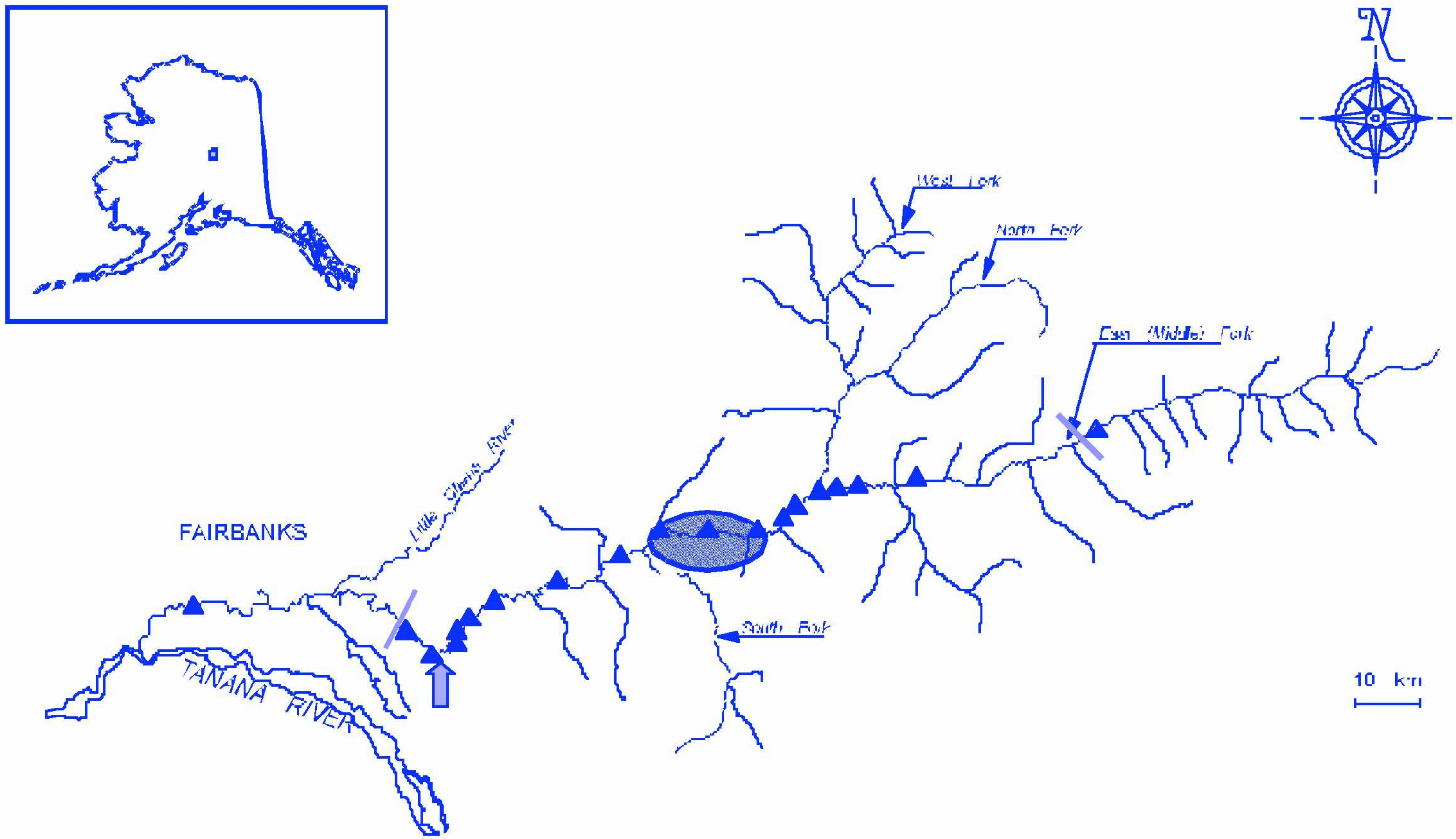

Figure 1. Map of the Chena River, Alaska. Solid triangles demarcate locations of 21 sampling stations (between 11 rkm and 233 rkm) where water temperatures were measured in 2006 and 2007. The gray bars demarcate the extent of observed spawning. Grey arrow demarcates the Moose Creek Flood Control Project (FCP). The shaded oval demarcates highest density spawning habitat (46% of redds between 130-150 rkm).

Sampling Design and Data Collection

The study was designed to collect water temperature data at sampling stations encompassing the area of the river known to contain spawning Chinook salmon, and then extending both downstream and upstream. Sampling stations were selected first by obtaining satellite photos of the Chena River; using ArcView version 9.0 geographic information system software (GIS; Environmental Systems Research Institute, Incorporated [ESRI, Inc.], Redlands, California) to delineate rkm. The first sampling location was selected by adding a random number between 1 and 20 to 77 rkm (the escapement point location at the FCP). The next six upstream sampling stations were systematically spaced 12 rkm apart to evenly cover the primary spawning habitat. An additional seven stations were established at expanding intervals (2, 2, 2, 4, 6, 10, and 50 km) for the purpose of detecting rapid thermal changes at the upstream and downstream edges of the spawning habitat. Three stations were adjusted to more accessible and secure locations (16 rkm became 11 rkm, 116 rkm became 114 rkm, and 240 rkm became 233 rkm). Thus, twenty-one stations were established between 11 and 233 rkm as early in the spring as possible after ice-out. The stations were monitored throughout the summers of 2006 and 2007 and retrieved before freeze up.

Automatic temperature loggers (Hobo Pro V2 by Onset Computer Corporation, Bourne, Massachusetts) were installed at each station and accessed by foot, helicopter, and outboard motorboat, and station locations were marked with a handheld global positioning system (GPS; Map 76, Garmin, Olathe, Kansas). The loggers were placed as close to the thalweg as safety allowed and hourly water temperatures were recorded to the nearest 0.02°C. Loggers were secured to the substrate with a small duckbill anchor, 45 centimeters of steel cable, and 1.5 meters of nylon twine. Loggers were weighted with metal washers to prevent floating to the surface. Downloads of data from loggers were periodically conducted throughout the summer, and retrieval was attempted prior to freeze-up to prevent data loss if loggers were lost during spring ice-out. Data extracted from loggers were exported for review and analysis.

The frequency of logger monitoring depended upon river conditions. Frequent floods during the spawning season caused the loss of multiple loggers. While double anchors of parachute cord used in 2006 appeared to save two loggers (they were found free of the steel cable, but still attached to the parachute cord), the cords also caught snags and broke, resulting in two loggers found attached to the steel cable without the secondary anchor. In addition, two loggers were lost when both anchors broke. In 2007, double anchors were not used, and more temperature loggers were recovered, but this was probably due to better judgment of placement.

Aerial redd surveys were used to determine the extent and density of the spawning areas; one end-of-spawning-season aerial redd survey was conducted in 2005; the survey planned for 2006 was canceled due to inclement weather; and, in 2007, three surveys (early, middle and end-of-season) were conducted. Redd locations and additional observations (e.g., number of redds, if active spawning was observed, number of fish in the vicinity, and number of white tails indicating female salmon with tails injured during redd construction) were marked with a handheld GPS. GIS software was used to create map layers to display redds and to extract the number of redds per river kilometer for the length of the river sampled.

Data Analysis

Lethal thermal limits for juvenile and adult Chinook salmon in the Chena River were identified by comparing summer maxima to reported upper incipient lethal limits (Table 1) and the freeze-up date to the lower incipient lethal limits (LILL). Chinook salmon spawning season on the Chena River is typically between July 1 and August 4 therefore this study used a broader time span (25 June through 15 August) for accumulating thermal units and broader still (15 June through 15 August) for the warming scenario to encompass all potential spawners. Absolute thermal boundaries were investigated by calculating the spawning season ATUs for all potential spawning days (25 June-15 August) through the freeze-up date to detect the minimum of 450 dd. Temporal boundaries could be caused by warm or cold waters, although, at this latitude, a warm water boundary was not anticipated. However, the number of hours above water temperatures optimal for egg development (15°C; Table 1) were calculated for each station to investigate the potential for warm water boundaries. Downstream temperatures were compared against known adult avoidance temperatures to investigate the potential for run-timing alteration caused by warm waters downstream. ATUs were calculated by averaging hourly temperature measurements to create a mean daily temperature for each sampling station. To investigate the compression of thermally suitable habitat, we summed the mean daily temperature across the possible spawning dates at each rkm.

Incomplete data sets limited the extent of analyses possible. Ideally, three full years of temperature data would have been collected and multiple redd surveys would have been completed. The natural fluctuations of flow in this rainwater-fed river caused some temperature loggers to become dry or encounter very shallow water (only several cm in depth) and others froze into the ice; all of these conditions resulted in measurement errors and gaps in data relevant to the study. Loggers found dry were noted and moved into the thalweg. The minimum temperature detection of the logger is - 2°C; readings below 0°C were assumed to be from loggers that were frozen in the ice, and, in these cases, data were excluded from analyses. The most complete data set was collected in 2007; water temperatures were retrieved from 16 of 21 deployed temperature loggers and three aerial redd surveys (2 July, 16 July, and 2 Aug) were conducted. During the 2006 season, 11 of 21 deployed temperature loggers were successfully retrieved, with no aerial redd survey (due to inclement weather). In 2005, only five data loggers were deployed as a pilot study, and locations did not coincide with the later sampling stations. Only one helicopter redd survey was conducted at the end of the spawning season in 2005.

To investigate river water temperatures in a biologically meaningful way, spawning dates were rendered into successful or unsuccessful at achieving the ATUs needed for egg development to hatching prior to freeze up. A range of threshold levels of ATUs (400, 450, 500) were set to account for variability of development rates with water temperature (as water temperatures increase, development rates vary; Quinn 2005) and for local adaptation to cold water. The probability of achieving the threshold ATUs by rkm was modeled using the logit procedure in SAS (SAS Institute Incorporated, Cary, North Carolina). Separate analyses were conducted at regular intervals throughout the spawning season (7 July, 15 July, 22 July, 31 July, and 7 August). A similar set of analyses were conducted under a warming scenario; a comparison of 2006 and 2007 data suggested possible interannual variation of 2°C for average and maximum temperatures. The 2006 daily mean temperature at each station was increased 4°C and ATUs recalculated by potential spawning date at each sampling station to investigate the potential for range expansion under a more dramatic warming scenario. We examined Deviance and Pearson Goodness-of-Fit statistics for all analyses.

Results

River temperatures fluctuated diurnally and exhibited a longitudinal gradient, with the coolest temperatures upriver and gradual warming downstream (Figures 1 and 2). Interannual temperature variability was also evident; mean temperature (18°C) from all sampling stations in 2007 was 2°C warmer than in 2006, as was maximum summertime temperature (16°C in 2006; Figure 2). Five temperature loggers (66 rkm, 76 rkm, 82 rkm, 92 rkm, 104 rkm) were left in the river over winter (2006-2007) and recorded water temperature reaching 0°C between 26 October and 1 November and reaching positive temperatures again between 14-28 April 2007.

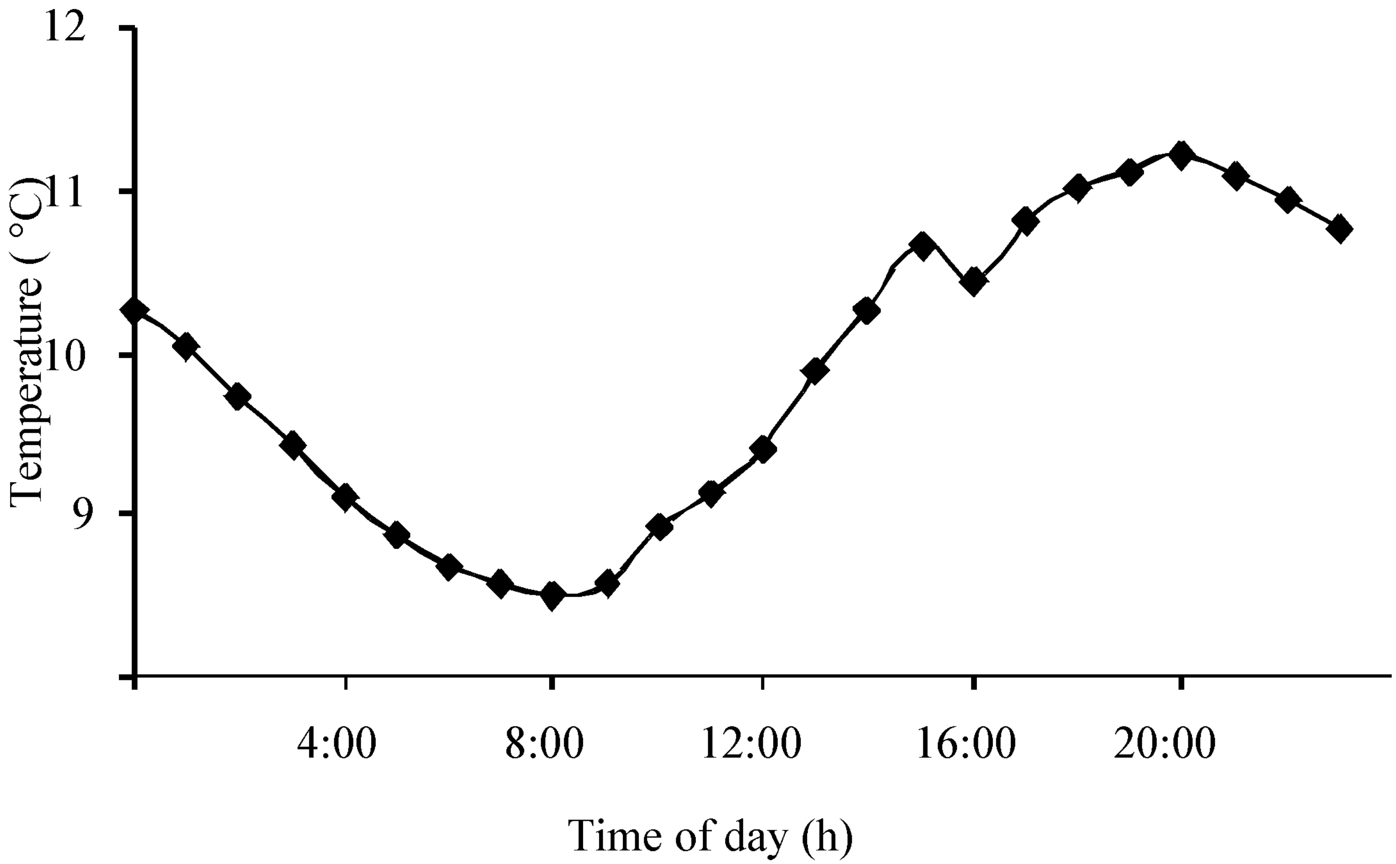

Figure 2. Diurnal temperature fluctuations at 152 rkm on July 22, 2007 in the Chena River, Alaska.

The uppermost sampling location at Van Curler's Bar (233 rkm) achieved more than 400 ATUs within the Chinook salmon spawning season in both years (623 ATU in 2006 and 624 ATU in 2007). Therefore, no *absolute* thermal boundary to potential spawning habitat was discovered within the study area. However, a temporal compression of thermally viable habitat was evident, as the probability of exceeding 400, 450 and 500 ATUs over the spawning season decreased over the spawning season (Figures 4, 5 and 6, respectively).

Summer high temperatures recorded in 2006 and 2007 (16°C and 18°C, respectively) were within the tolerances of adult Chinook salmon, not exceeding either avoidance temperatures or upper incipient lethal limits (20-21°C and 22-25°C; Table 1). However, temperatures did exceed recorded optimal egg development temperatures (15°C; Table 1) with the lower river sites exceeding 15°C more often than upriver sites, as would be expected (Figure 7). While the uppermost sites (190 rkm and 233 rkm) also exceeded 15°C, they did so prior to the arrival of the spawners (1-7 July 2007; Figure 7). Chinook salmon concentrated in locations with a high number of days at optimal egg survival temperatures (6-14°C; Table 1), rather than at locations optimal for adult salmon (4-11°C, Table 1 and Figure 8).

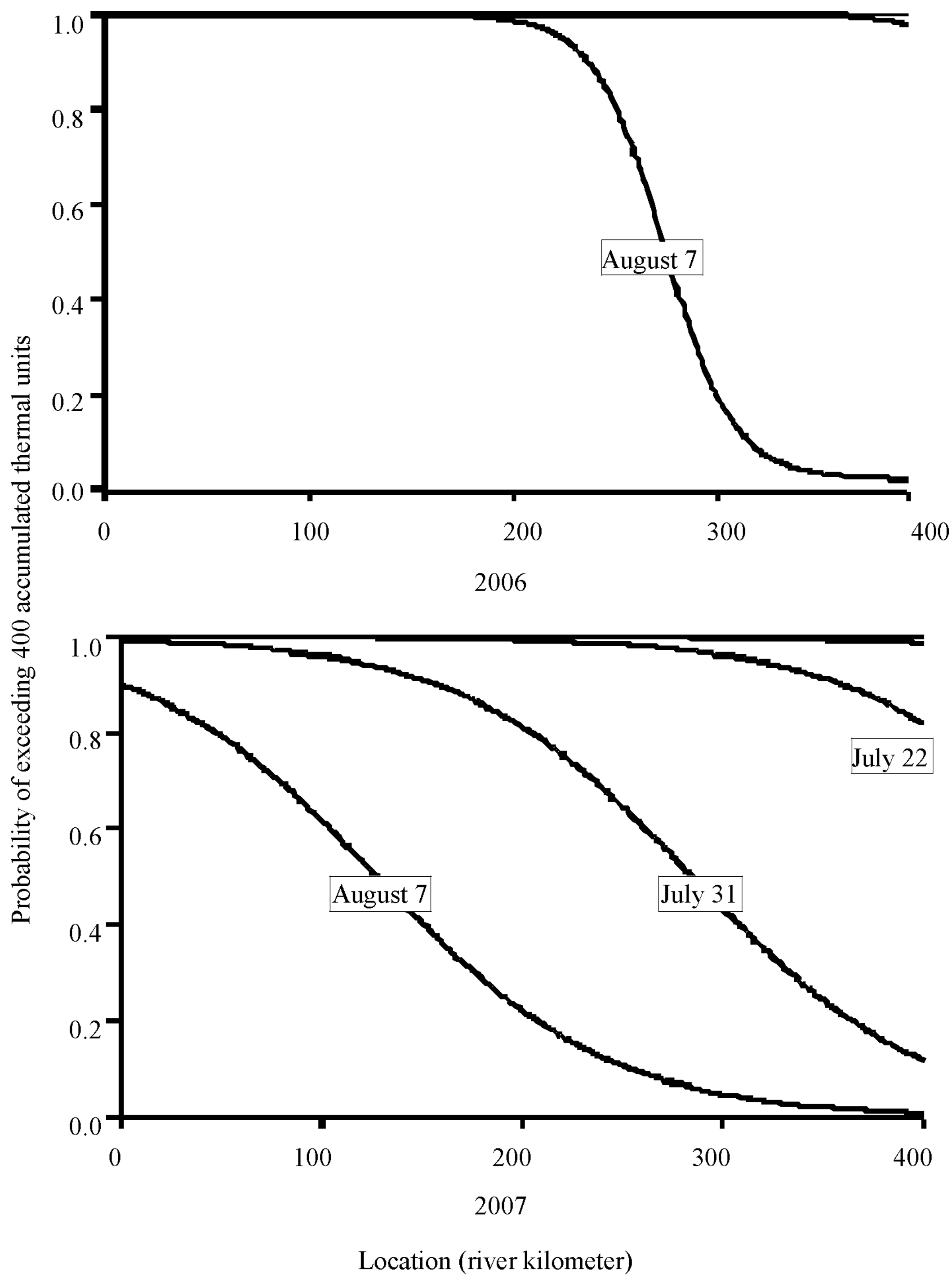

Figure 4. Probability of exceeding 400 accumulated thermal units for Chinook salmon egg development to hatching by Chena River kilometer on selected spawning dates for the Chena River, Alaska, in 2006 and 2007 based on logistic regression.

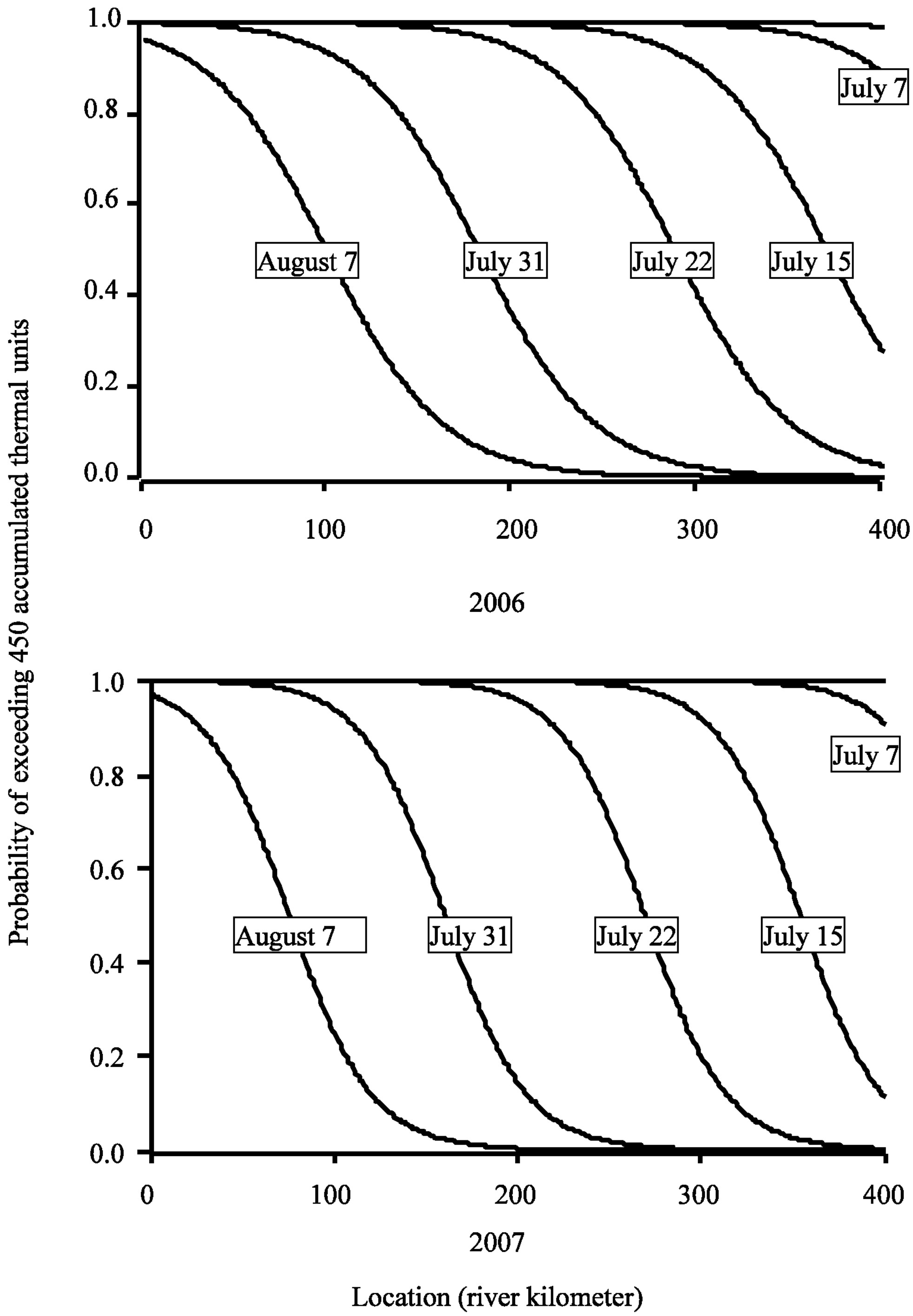

Figure 5. Probability of exceeding 450 accumulated thermal units by Chena River kilometer for Chinook salmon egg development to hatching on selected spawning dates for the Chena River, Alaska, in 2006 and 2007 based on logistic regression.

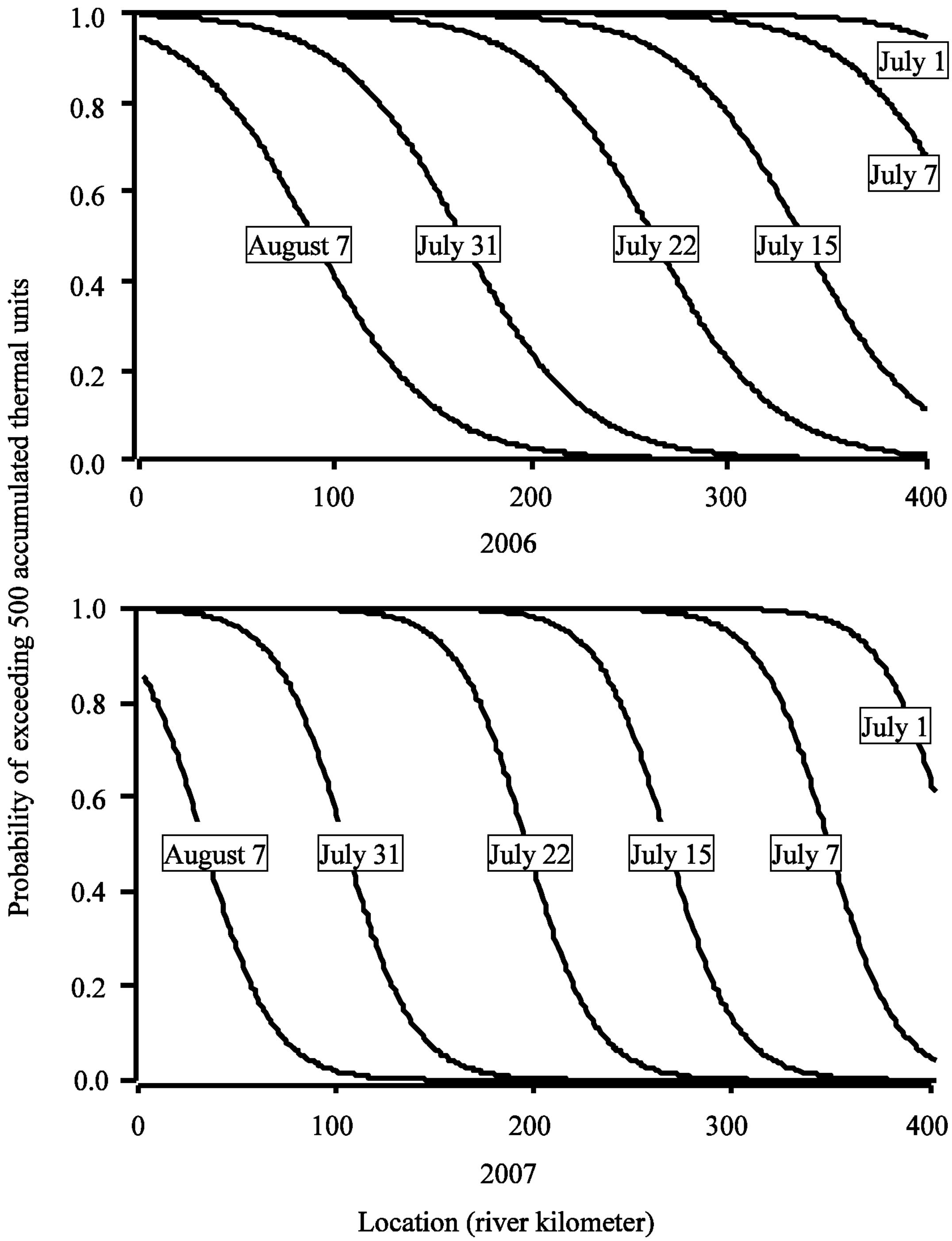

Figure 6. Probability of exceeding 500 accumulated thermal units for Chinook salmon egg development by Chena River kilometer to hatching on selected spawning dates for the Chena River, Alaska, in 2006 and 2007 based on logistic regression.

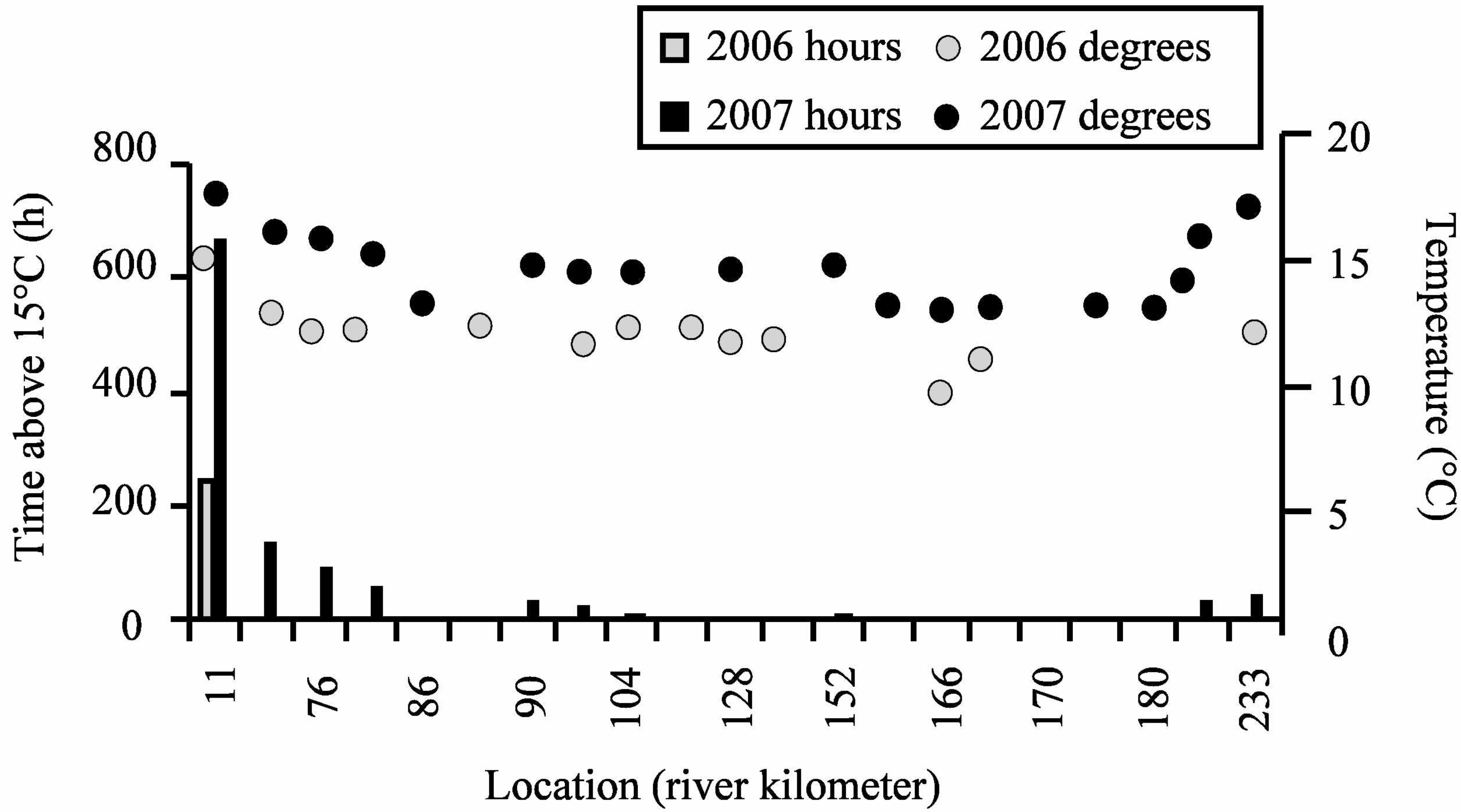

Figure 7. Number of hours water temperatures exceeded the recorded optimal for Chinook salmon egg development (15°C) by Chena River kilometer and the summer maximum water temperature at 21 sampling stations between 11 rkm and 233 rkm during the spawning season 1 July –10 August, 2006 and 2007.

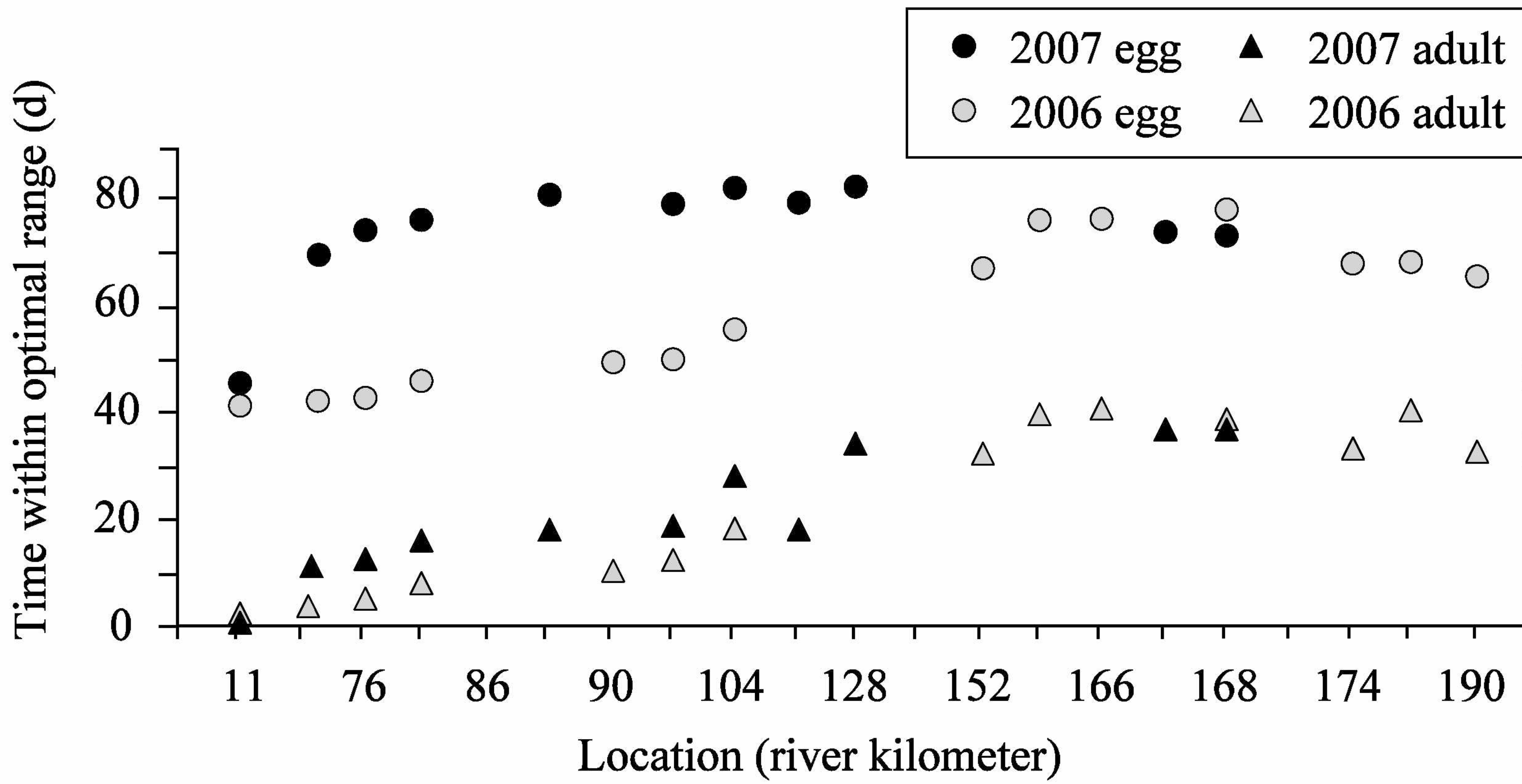

Figure 8. Number of days within optimal range of 4-11°C for adult Chinook salmon (triangles) between 1 July and 10 August, and 6-12° C for egg-development time (dots) 1 July-freeze up by Chena River kilometer.

The Alaska Department of Fish and Game 2007 Chinook salmon run enumeration documented spawners arriving at the FCP between 2 July and 2 August, with 20% (696 fish) of the run arriving in the 48-hour period between 17 and 18 July and 35% of the run arriving between 17 and 20 July (1,236 fish; Figure 9; Savereide In prep). Aerial surveys in 2007 (2 July, 16 July, 2 August) revealed redd densities to be highest between 130 and 150 rkm, where 38% of all redds were documented (Figure 10). Spawning was observed at 232 rkm, 30 rkm farther upstream than previously documented in the Anadromous Waters Catalog (64.958 N, 145.823 W; Johnson and Weiss 2007).

Interannual thermal variation affected the probability of exceeding the selected ATU thresholds necessary for egg development (400, 450 and 500 ATUs); temporal compression of thermally suitable spawning habitat took place along the river that was consistent in both years and for all assumed development rates (Table 2; Figures 4, 5 and 6). The peak of the 2007 run (35%) took place at a time (17-20 July) when the river reach with the highest density of redds (130-150 rkm) was still thermally available (i.e., had high probability of accumulating the necessary ATUs before freeze up) under all egg-development scenarios. In fact, logistic regression models predicted that 98.5% of redds spawned on or before the peak of the run had a 90% probability of accumulating 450 ATUs before freeze up (Figure 11).

Table 2. Deviance and Pearson goodness-of-fit tests for the logit analysis models (variables: date, location (rkm)) separated by year.

Criterion	Value	Degrees of Freedom	Pr > ChiSq
2006 Deviance	70.2799	497	1.0000
2006 Pearson	84.3497	497	1.0000
2007 Deviance	239.6337	814	1.0000
2007 Pearson	293.4292	814	1.0000

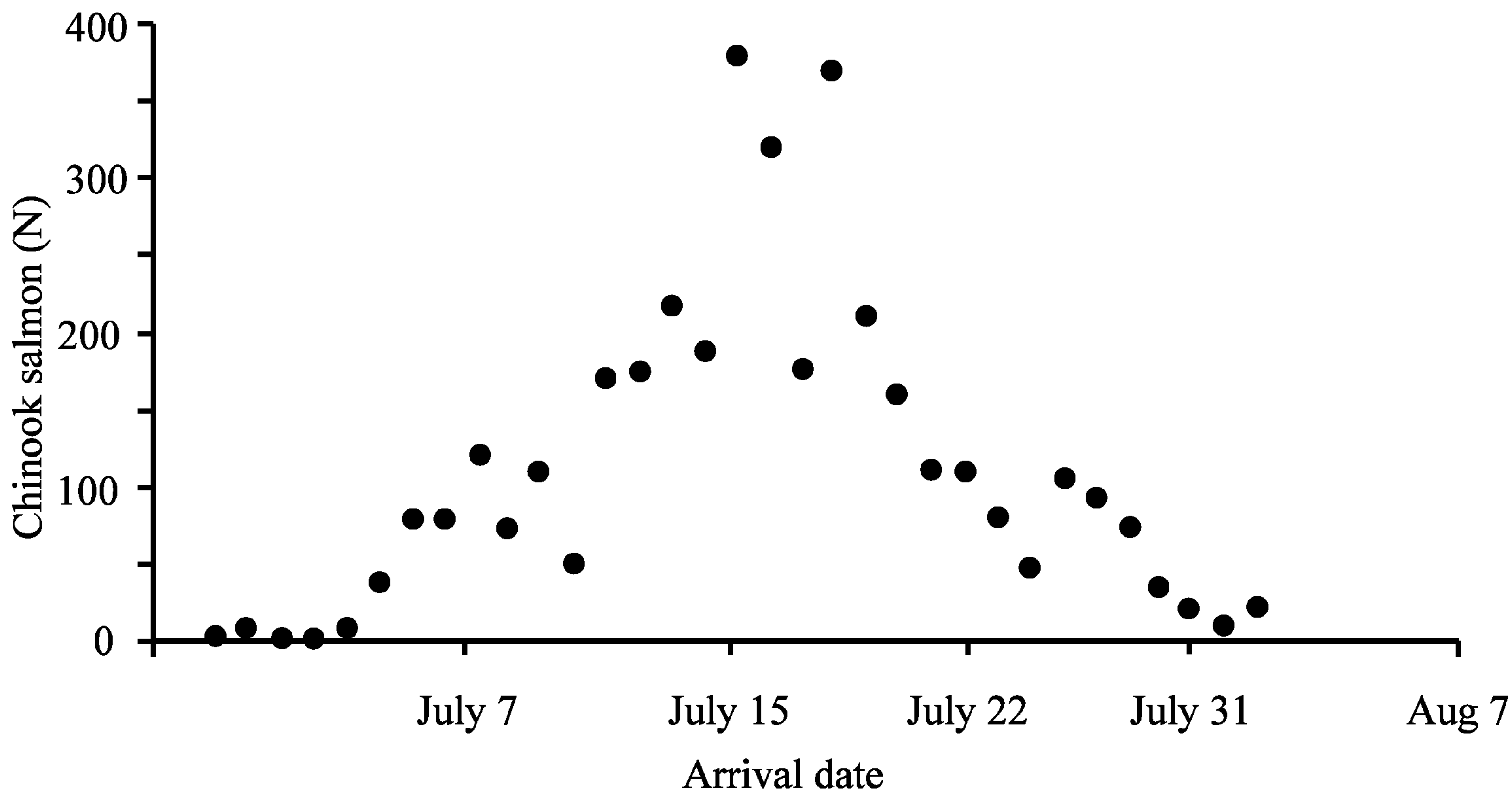

Figure 9. Number of Chinook salmon counted by date passing the Moose Creek Flood Control Project (77 river kilometer) on the Chena River by the Alaska Department of Fish and Game in the summer of 2007.

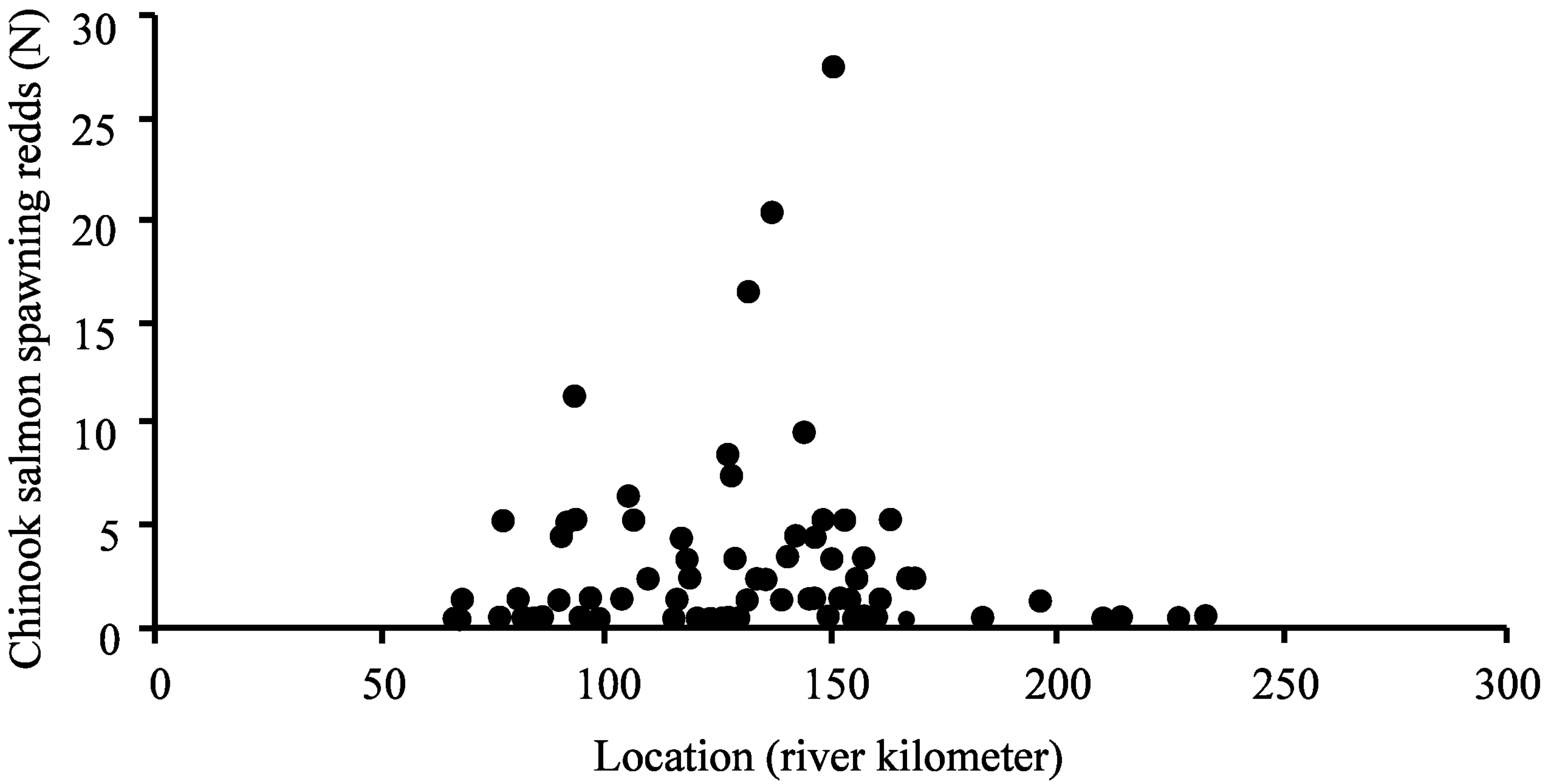

Figure 10. Combined counts of Chinook salmon spawning redds per river kilometer on the Chena River, Alaska, counted during helicopter surveys on 16 July and 2 August 2007.

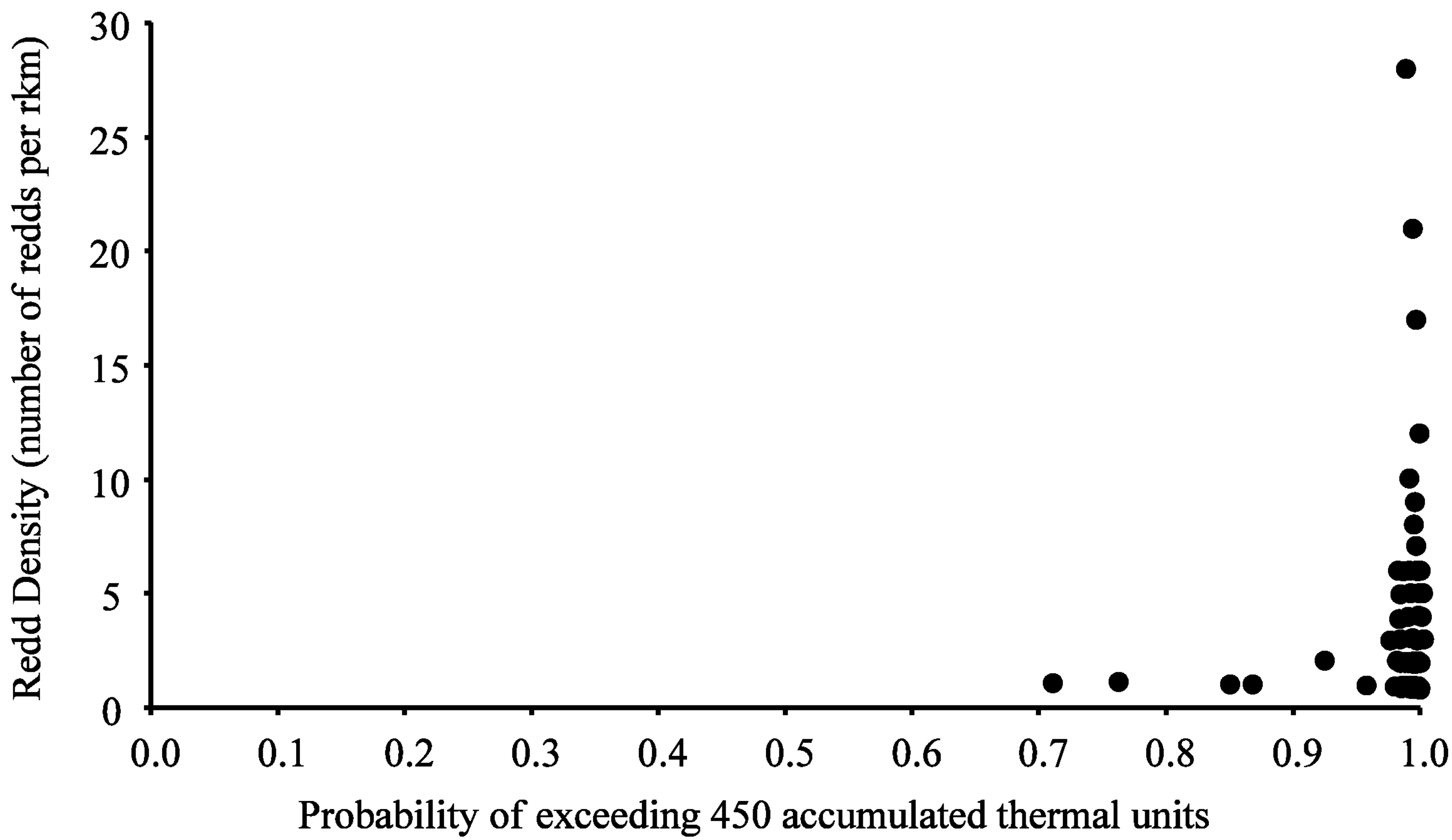

Figure 11. Density of Chinook salmon redds compared with the probability of exceeding sufficient accumulated thermal units (450 dd; Quinn 2005) for incubation (calculated from logistic regression analysis) at the most dense spawning habitat (130-150 rkm, where 38% of the redds were located) during the peak of the spawning run.

The warming temperature model predicted an expansion in the temporal availability of the current spawning habitat by 33-35 d for the 400 dd developmental scenario and 27-34 d for the 500 dd scenario (Table 3). The modeled increase also exposed the salmon to higher temperatures in downstream areas, resulting in extended periods above the optimal egg development temperature and nearing the upper incipient lethal limits (Figure 12).

Table 3. The last date (ISO) when a Chinook salmon can spawn on the Chena River, Alaska, and still accumulate the thermal units necessary to achieve egg development to hatching before freeze up (400 dd and 500 dd), based on daily mean temperatures in 2006 and in a warming regime scenario that was 4° C warmer on average than 2006 temperatures.

	2006		2006 + 4? C	
	66rkm	104 rkm	66rkm	104 rkm
400 dd	227	225	262	258
500 dd	218	215	252	242

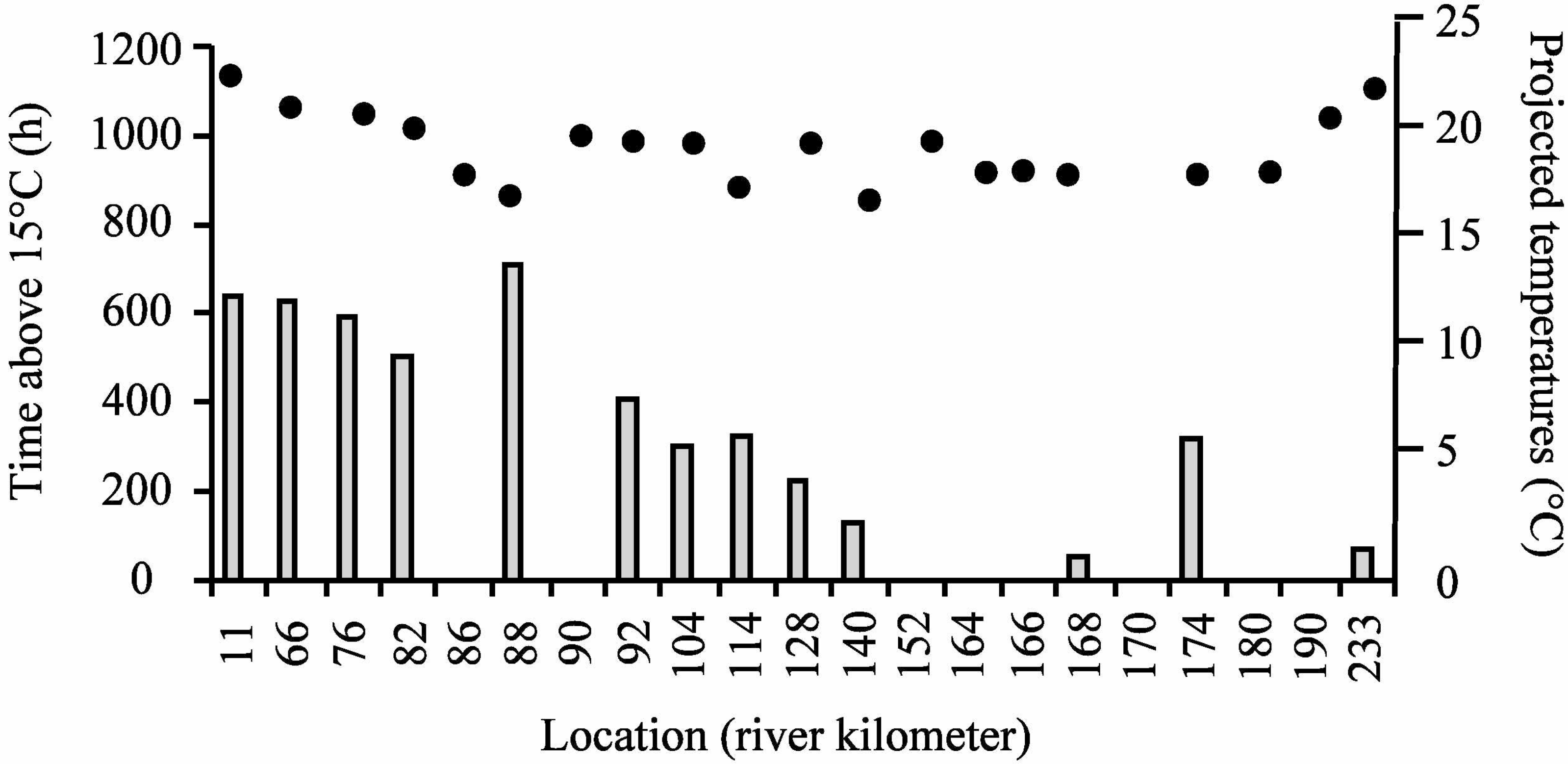

Figure 12. The number of hours above 15˚C (vertical bars) with a projection of 4˚C warming above measured 2006 water temperatures (closed symbols) at 21 sampling stations along the Chena River, Alaska.

Discussion

Current research in thermal limits of Chinook salmon caused an inherent gap in knowledge by not testing survival and development at water temperatures commonly experienced by wild Alaskan fish. This study addresses the concern that the majority of published thermal developmental requirements and limits for Chinook salmon should not be applied to Alaskan populations. The reported thermal bounds for egg survival and optimal development (3°C and 15°C, Myrick and Cech 2004)) are most likely unrealistic for Alaskan Chinook salmon; the successful and persistent Chena River population routinely experiences water temperatures outside those limits for extended periods.

Due to it's proximity to Fairbanks, the Chena River has a history of human use (e.g., travel, food, and leisure), which has led to a number of studies on geology, hydrology, water chemistry, and ecology of the system. However much is still unknown. The information gathered from this study has confirmed the documented spawning habitat and expanded the upstream range. As expected, Chinook salmon spawning habitat and run timing were strongly linked to the geographically and temporally available hydrothermal habitat on the Chena River. Results of this study support the notion that water temperature is limiting range expansion and habitat use at the northward limit of their range. As the spawning season progressed, the area of river thermally suitable to the survival of salmon offspring was dramatically reduced. Further, run timing and areas of high redd density fall spatially and temporally within the thermally suitable habitat.

The Chena River is typical of freshwater streams in interior Alaska as evidenced by the observed daily temperature fluctuations, downstream warming and interannual variation in water temperatures. The Chena River is well mixed river (Frey et al. 1970) and it is likely that our riverbed measurements approximated interstitial water temperatures. A high degree of overlap in areas containing high densities of redds for the two years surveyed (2005 and 2007) indicated consistency in habitat selection and river conditions. Interannual variability in the upstream thermal boundary for spawning habitat was evident; 2007 had more fish spawning upstream than 2005, potentially due to the larger run and warmer water temperatures in 2007. Water temperatures did not exceed the thermal tolerances of Chinook salmon and therefore did not delineate a downstream boundary. The downstream boundary is more likely dictated by other physical features such as substrate size and hyporheic flow associated with lower gradient (Soulsby et al. 2001).

An absolute upstream thermal boundary to spawning habitat was not discovered; the upper most sampling station at Van Curler's bar (233 rkm) achieved over 600 ATUs during the spawning season in both 2005 and 2007. However, limitations in salmon migration timing include freshwater entry timing, distance to spawning site, swimming speed during migration and residence time in the spawning grounds constrain the spawning season. The first Chinook salmon entered the Chena River spawning grounds in 2007 on 2 July (by passing the counting tower, at 77 rkm). After that date, it would take approximately 3.5 d to reach the most upstream end of our study reach (assuming swimming speeds of 45-49 km/day; Eiler et al. 2004). Accounting for a mean additional

7.5 d for site selection, courting, and redd preparation (Morbey 2003), and 450 ATUs for embryo development before freezing, the viable spawning window compresses to only 10 d in 2007 (10 – 19 July). In a cooler year, such as 2005, the spawning window at Van Curler's Bar is even shorter at only 6 d (10- 15 July). In the current climate regime the upstream area has limited use as spawning habitat with successful offspring survival.

A strong correspondence in the range of Chinook salmon spawning locations in the Chena River with measures of ATUs imply that colder water temperatures are limiting potential spawning habitat for Chinook salmon on the Chena River. However, potential for local adaptive shifts, strong inter-annual variability in water temperature, warming due to climate change, and the presence of suitable spawning gravel outside of thermally limited areas implies that potential for upstream and northern range expansion in spawning habitat is high. Although our focus is primarily on cold-temperature limitations, water temperatures at the downstream end of our study area also have potential to reach suboptimally high temperatures for adult passage and egg development (over 20-21°C, and 15.5°C; Alderdice and Velsen 1978). This suggests that upstream expansion of Chinook salmon with warming would not necessarily translate into increased spawning capacity of the river. However, several high latitude effects also work to moderate the warmer temperatures: the nightly cooling of water temperature, access to pools, discontinuous permafrost, and a healthy riparian zone, which, coupled with the low angle of the sun at this latitude, resulted in shadows that cast completely across the river for most of the day (personal observation during aerial surveys). Potential for thermal refugia increase the adult salmon's ability to tolerate occasional extremes (Marine and Cech 2004; Richter and Kolmes 2005), and, with the opportunity for acclimation inherent in natural systems, Chinook salmon have tolerated temperatures as high as 24°C (Marine and Cech 2004).

Limitations to this study include a gap in temperature data caused by the spacing of loggers and the discovery of new upstream spawning habitat. While aerial surveys confirmed prior knowledge of core spawning habitat (76 rkm and 152 rkm), the upriver extent expanded an additional 30 rkm based on new surveys (2007). Loggers did not extend far enough upriver, nor with necessary proximity to the four redds observed between 190 and 232 rkms to understand the upstream hydrothermal patterns. We recognize the simplifications inherent in this project. There are many other habitat factors that significantly influence fish carrying capacity (150 habitat characteristics; Fausch et al. 1988), however, one of the goals of this project was to conduct an efficient large scale sampling design specifically for the northern extent of Chinook salmon range. Due to the macro-scale of this project, we could not detect the micro-scale differences in stream temperature associated with measurements such as groundwater upwelling that is also recognized as a critical influence in redd site selection and egg survival (Maclean 2002).

It is likely that Chinook salmon at the northern extent of their range have lower thermal tolerance limits than their southern counterparts, and egg development may continue at lower temperatures; further research on the details of thermal tolerances of northern range Chinook salmon could provide insight. A study into finer-scale variation in water temperature would also be useful in understanding redd selection and offspring survival, particularly on the upstream reaches (between 180 rkm and 230 rkm) where spawning was newly documented. Further explorations could also include examination of local thermal adaptations, run timing confirmation through mortality-sensing radio tags or archival tags (e.g., used by Eiler et al. 2004), and egg survival and development under different thermal regimes (e.g., Maclean 2002). This would entail a higher degree of investment, but could provide more definitive results to the questions of local adaptation, thermal spawning habitat preferences and offspring survival. Future attempts to monitor water temperature on the large scale could be aided by the USGS water monitoring network, which already measure many aspects of rivers across the nation and could also collect water temperatures.

A strong temporal component was evident in the extent of suitable spawning habitat in the Chena River; as the spawning season progressed, the area of river thermally suitable for sufficient redd development to promote survival of offspring contracted. The Chinook salmon run timing and high redd densities fell spatially and temporally within the thermally suitable habitat. The combined thermal and temporal analysis suggest that spawning location along the study reach is key to achieving the degree days needed for egg development to hatching before the river freezes and is therefore likely the key to survival. As the spawning season progressed, the probability of exceeding the selected threshold for egg development decreased over the length of the Chena River, closing off the upper sections of the river as potential spawning habitat. The relatively short developmental window for successful spawning at 233 rkm (5 d in 2006 and 9 d in 2007) implies that, in a particularly cool year, no viable spawning window exists at this location. In contrast, evidence suggests fish are selecting spawning habitat based on the probability of egg survival and development (here measured as the probability of accumulating 450 ATUs before freezing); in fact, 90% of the 2007 spawning (246 redds) occurred in locations with a 90% probability of accumulating 450 ATUs or more.

Conclusions

This study contributed to thermal research on Chinook salmon by investigating wild fish near the northern extent of their range where such data are limited. While spawning was recorded farther upstream than previously documented, Chinook salmon responded predictably to limitations in water temperatures suitable for the growth and survival of their eggs. This research established a baseline for more advanced study of Chinook salmon habitat preferences, river carrying capacity, and predictive modeling of abundance by mechanistically establishing thermal boundaries for egg development, which could represent the fundamental niche of this species on rivers at the northern extent of their range (Pearson and Dawson 2003; Soberón and Peterson 2005). It is often assumed that fish will shift northward and upstream in response to warming water temperatures. This project tested the underlying premise of this assumption; that fish species at the northern edge of their habitat are thermally limited. Should climate warming continue as predicted and affect thermal regimes of Alaskan rivers, this work could be used to predict Chinook salmon range shifts northward or upstream and to investigate how soon habitat will be limited by increased water temperatures. While a broad range of habitat characteristics have proven important for detecting spawning habitat and calculating carrying capacity of stream fishes (150 characteristics; Fausch et al. 1988) in the central part of their range, a single factor may limit accessibility of habitat at the range extremes. On the regional scale, habitat accessibility is particularly important for understanding ecological niches and species distribution (Soberón and Peterson 2005), and this study documented that water temperature limits accessibility of Chinook salmon to viable spawning habitat at the extreme edges of their range.

Literature Cited

AAC (Alaska Administrative Code). 2000. 5 AAC 39.222 and 5 AAC 39.223. In Alaska Fish and Game Laws and Regulations Annotated 2000-2001 edition. Lexis Publishing, New York.

Alderdice, D. F., and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of Chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of Canada 35:69-75.

Beer, W. N., and J. J. Anderson. 2001. Effect of spawning day and temperature on salmon emergence: interpretations of a growth model for Methow River Chinook. Canadian Journal of Fisheries and Aquatic Sciences 58:943-949.

Brannon, E. L., M. S. Powell, T. P. Quinn and A. Talbot. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science 12:99-232.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9:265-323.

Brett, J. R. 1956. Some principles in the thermal requirements of fishes. The Quarterly Review of Biology 31:75-87.

Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times for two runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the

Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693-700.

Eiler, J.H., T. R. Spencer, J. J. Pella, M. M. Masuda, and R. R. Holder. 2004. Distribution and movement patterns of Chinook salmon returning to the Yukon River basin I 2000-2002. U. S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-148.

Evenson, M. J. 2002. Optimal production of Chinook salmon from the Chena and Salcha rivers. Alaska Department of Fish and Game, Fishery Manuscript Series No. 02-01, Anchorage.

Fausch, K. D., C. L. Hawkes and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. General Technical Report PNW-GTR-213. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, Oregon.

Frey, P. J., E. W. Mueller, and E. C. Berry. 1970. The Chena River: the study of a subarctic stream. Federal Water Quality Administration Project number 1610-10/70. Available from National Technical Information Service (NTIS) as PB-197 857. Washington, D.C.

Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Heming, T. A. 1982. Effect of temperature on utilization of yolk by Chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. Canadian Journal of Fisheries and Aquatic Sciences 39:184-190.

Johnson, J., and E. Weiss. 2007. Catalog of waters important for spawning, rearing, or migration of anadromous fishes – Interior Region. Alaska Department of Fish and Game, Special Publication No. 07-04, Anchorage.

Maclean, S. H. 2002. Influence of hydrological processes on the spatial and temporal variation in spawning habitat quality for two chum salmon stocks in interior Alaska. Master's thesis. University of Alaska Fairbanks.

Marine, K. R., and J. J. Cech, Jr. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. North American Journal of Fisheries Management 24:198-210.

Morbey, Y. E. 2003. Pair formation, pre-spawning waiting, and protandry in kokanee, *Oncorhynchus nerka*. Behavioral Ecology and Sociobiology 54:127-135.

Mundy, P. R. 1998. Principles and criteria for sustainable salmon management: a contribution to the development of a salmon fishery evaluation framework for the state of Alaska. Alaska Department of Fish and Game, IHP-98-045, Juneau, Alaska.

Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266-273.

Myrick, C. A., and J. J. Cech, Jr. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know? Reviews in Fish Biology and Fisheries 14:113-123.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361-371.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and Steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23-49.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191. Ottawa, Ontario.

Savereide, J.W.. In prep. Salmon studies in the Chena, Delta Clearwater, Goodpaster and Salcha rivers, 2006. Alaska Department of Fish and Game, Fishery Data Series, Anchorage.

Seymour, A. 1959. Effects of temperature upon the formation of vertebrae and fin rays in young Chinook salmon. Transactions of the American Fisheries Society 88: 58-69.

Snieszko, S. F. 1974. The effects of environmental stress on outbreaks of infectious diseases of fishes. Journal of Fish Biology 6:197-208.

Soberón, J., and A.T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1-10.

Soulsby, C., A. F. Youngson, H. J. Moir, and I. A. Malcolm. 2001. Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. The Science of the Total Environment 265:295-307.

Zaugg, W. S., and L. R. McLain. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). Comparative Biochemistry Physiology 54A:419-421.