THERMAL TOLERANCE OF PACIFIC SALMON (*ONCORHYNCHUS SPP.*): METHODOLOGICAL AND INHERENT VARIABILITY IN UPPER THERMAL TOLERANCE LIMITS AND THEIR USE IN ASSESSING VULNERABILITY TO CLIMATE CHANGE

by

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Abstract

Aquatic systems are warming and exceeding upper thermal limits (UTL) of Pacific salmon (*Oncorhynchus spp*), yet quantifying UTL and understanding how they inform resilience to climate change is challenging. This thesis focuses on quantifying upper thermal tolerance limits in Pacific salmon with specific reference to Kokanee salmon (*O. nerka*).

I conducted a systematic review involving 168 papers investigating UTL in five Pacific salmon species and found considerable variation among species, within species, and across life stages - largely due to different methodological approaches (e.g. CT_{max}/UILT, Aerobic/Cardiac Scope, Thermal Migration Barriers, Rearing Mortality, Thermal Preference/Avoidance). Each method displayed strengths and weaknesses owing to logistics, time scale, and ecological realism, I recommend reporting an 'UTL range' instead of single UTL values, to reflect inherent and methodology-based variation. Comparing studies with similar experimental design showed that within species, UTL was higher for populations that historically encountered higher temperatures suggesting local thermal adaptation. Within populations, UTL differed across the lifecycle - highest in fry for some populations and in migrating adults for others. UTL has not been assessed for spawning fish and few studies examined estuarine and marine stages, limiting life history perspectives. My analysis suggests pink salmon are most resilient to warming due to their exceptional aerobic capacity, high straying rates, short generation time and limited exposure to high temperatures.

In an additional experiment, I conducted thermal tolerance trials using two commonly employed methodologies: The Critical Thermal Maximum (CT_{max}) and Thermal Performance Curves for Aerobic Scope (AS). Juvenile and spawning adult fish were held overnight at a range of experimental temperatures (12°, 17°, 20°, 22° and 24°C).. In CT_{max} trials water temperatures

were increased at a constant temperature ($0.3°Cmin^{-1}$) until fish lost equilibrium. CT_{max} values ranged on average from 28.7°C – 29.7°C and differed significantly between life stages. Absolute AS – the difference between maximal and standard metabolic rates – were found to differ significantly between male and female adults, however Optimal (T_{opt}) and functional temperature limits (T_{pejus}) occurred at similar temperatures (Topt: ~15°C, T_{pejus}: ~20°C). The large degree of variation in upper thermal tolerance metrics highlights the need for careful selection of values when conducting vulnerability assessments.

Lay Summary

Aquatic ecosystems are increasingly threatened by climate change-induced increases in air temperatures, receding glaciers and earlier snow-melt timing. Such changes pose a major threat to the future persistence of aquatic species. Pacific salmon, a species of high cultural, economic, recreational, and ecological value, are particularly vulnerable given the limited thermal range in which they can thrive. This thesis aims to quantify Upper Thermal Tolerance (UTL) in Pacific salmon and offer a comprehensive framework for assessing their vulnerability to warming. UTL was assessed through a systematic literature review. To further, understand nuances in upper thermal tolerance at the population-level, I also assessed differences in thermal tolerance across the lifecycle and between sexes for a single population of Pacific salmonid native to southeastern British Columbia. This thesis provides compelling evidence for the need to incorporate species and population-specific thermal tolerance nuances into fisheries management.

Preface

This research was carried out as a component of a broader research program investigating the effects of climate change on Kokanee salmon. I held primary responsibility for research design and experimental protocols, collection and analysis of data, and preparation of manuscripts. I received considerable logistical and analytical support from my colleagues and guidance from my supervisors Scott G. Hinch and Erika Eliason. Collaborators on this project who were instrumental to the development, experimentation and/or manuscript preparation will be listed as co authors on manuscripts when they are submitted for publication. All experimental procedures were conducted with approval from the University of British Columbia Animal Care Committee (#A12-0142) and in accordance with guidelines set forth by the Canadian Committee on Animal Care.

Chapter 2: Thermal tolerance in Pacific salmon: A systematic review of species, populations, life stages, and methodologies

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Comments: This review was conducted and written by NBM with the assistance of EJE under the supervision and guidance of SGH, who helped to conceptualize the review and contributed to preparation of the manuscript.

Chapter 3: Life-stage and sex-specific differences in the upper thermal tolerance of

Kokanee Salmon (*Oncorhynchus nerka*)

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      Birnie-Gauvin, Jacey Van Wert and Brian J. Hendricks, who either helped to

      conceptualize the study and/or contributed to preparation of the manuscript.

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List of Abbreviations

AAS – Absolute Aerobic Scope (The difference between maximal and resting metabolic rates)

ABT – Arrehnius Break Test

AS – Aerobic Scope

CTM – Critical Thermal Method

CT_{max} – thermal tolerance metric derived from CTM studies, measured as the temperature at which fish lose equilibrium (unable to right itself in the water colum)

FAS – Factorial Aerobic Scope (the ratio of maximal and resting metabolic rates)

LOE – Loss of Equilibrium

MMR – Maximal Metabolic Rate

RMR – Resting Metabolic Rate

T_{AB} or T_{ABT} – Arrhenius Break Temperature (the temperature above which maximum heart rate becomes limited with increasing temperature)

T_{arr} – Arrhythmic Temperature (Temperature at which heart rate becomes arrhythmic)

T_{crit} - Critical Temperature for Aerobic Scope (temperature where there is no difference between maximal and resting metabolic rates)

T_{pejus} – temperature that corresponds with the amount of aerobic scope necessary for fish to carry out activities necessary to thrive (e.g. swim, forage, digest, reproduce)

TPC – Thermal Performance Curve

TSM – Thermal Safety Margin

T_{opt} – Optimal Temperature for Aerobic Scope (temperature where difference between maximal and resting metabolic rates is greatest)

UILT – Upper Incipient Lethal Temperature

UTL – Upper Thermal Tolerance Limits

UTTR – Upper Thermal Tolerance Range

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I would like to express my sincere gratitude to my supervisors, Scott Hinch and Erika Eliason, for their incredible mentorship. I attribute so much of my success in carrying out this project to their guidance and support throughout my steep learning curve as a scientist as well as some personal challenges I have encountered. They have both created outstanding research programs that have contributed greatly to the field, and it has been an honour to work under these excellent researchers. I would also like to thank my other supervisory committee member, Michael Russello for his input and guidance in bringing this thesis together and for leading a research project that has come to mean so much to me.

Special acknowledgement is owed to Jacey Van Wert, Kim-Birnie Gauvin, and Brian Hendricks, who provided field experiment guidance and coached me through protocol development, scheduling, and building of experimental equipment. Each of these researchers possess incredible skills in conducting field-based experiments and I benefited greatly from working alongside them.

I am also especially grateful to my lab mates Krista Kraskura, Stephanie Lingard and Paige Roper who have brought my feet back to the ground in the moments where I doubted my abilities to complete this project. Special acknowledgement must be made to Krista for her guidance in analyzing respirometry data – it was instrumental to my ability to complete the third chapter of this thesis and words cannot sufficiently express my gratitude to her.

Chapter 1: Introduction

The synergistic effects of climate change induced warming air temperatures, earlier snow melt timing and receding glaciers have caused dramatic increases of temperatures in freshwater systems (Mote *et al.* 2003, Battin *et al.* 2007, Martins *et al.* 2011). Such temperature changes threaten many aquatic species that are adapted to narrow thermal regimes (Barbarossa *et al.* 2021). These effects are exacerbated by a reduction in snowfall leading to increased streamflow synchronization and further reductions in summer runoff and, subsequently, higher stream temperatures and a higher risk of drought in the summer months (VeyWey et al. 2018). As a result, a major challenge in ecological research is to quantify the extent to which species are impacted by climate change (Mathes *et al.* 2021). The vulnerability to rising temperatures is a product of three factors: thermal tolerance (the range of temperatures in which a species can persist), thermal exposure (temperatures experienced by a species throughout its lifecycle), and adaptive capacity (the ability for a species to adapt to changes in environmental conditions through evolution and phenotypic plasticity) (Williams *et al.* 2008). Pacific salmon (*Oncorhynchus spp.)* are especially vulnerable given their narrow optimal temperature range (Farrell *et al.* 2009), exposure to high temperatures during rearing and migration periods, and limited capacity to extend their upper thermal tolerance (Muñoz *et al.* 2014, 2015). With time, natal homing and localised selective pressures have given rise to fine-tuned local adaptations that increase fitness in native environments. Such local adaptations have contributed to the development of thousands of genetically distinct populations of Pacific salmon throughout their geographic range (Taylor *et al.* 1991, Adkison 1995, Fraser *et al.* 2011).

One phenotypic trait with high intraspecific variation is upper thermal tolerance, which has been found to be correlated with historic temperature experiences (Farrell *et al.* 2008, Eliason et al. 2011). These findings suggest that fish possess some adaptive potential to warming. However, many populations of Pacific salmon are already imperiled and the potential for these species to adapt their thermal tolerance to match the pace at which water temperatures are rising remains unknown (Zillig *et al.* 2021, Zhang *et al.* 2019, Crozier *et al*. 2019). Therefore, quantifying the extent of intraspecific variation in upper thermal tolerance and identifying populations that possess traits that may allow them to better cope with rising temperatures is imperative to the development of effective management regimes in the climate change era.

The effects of freshwater warming on individual populations of Pacific salmon depends on a multitude of environmental factors including the region and idiosyncratic nature of the hydrology of a given watershed. Biological factors also play a role through life-history strategy, proclivity for natal homing, and the extent of standing genetic variation in thermal tolerance traits that selection can act upon (Grant et al. 2019, Chen et al. 2018). Current trends in climate change have resulted in widespread declines in Pacific salmon populations (Peterman and Dorner 2012, Ward *et al*. 2015, Crozier *et al*. 2021). However, changes in productivity are not homogenous across the native range. Broadly, warming in more southern latitudes has been linked to decreases in productivity and survival, whereas populations of Pacific salmon that reside on the northwestern end of the range have experienced increased productivity over the last few decades (Connors *et al.* 2020). At the watershed level, the extent to which warming will affect stream temperatures depends largely on the hydro climatology. For example, in snow-dominated watersheds, a moderate increase in air temperatures can lead to a dramatic reduction

in the proportion of winter precipitation that falls as snow (VeyWey et al. 2018). This shift will lead to a reduced spring snowpack and further increases in summer stream temperatures (VeyWey et al. 2018). The hydrologic variation within a watershed (i.e. snow-dominated, rain-dominated, rain-on-snow, glaciers) adds to the variability in the mosaic of habitat available to salmon and is a major component of understanding how vulnerable a given population is to current and future warming.

In addition to latitudinal and watershed-specific variation in freshwater warming, elements such as migration timing and distance as well as life-history strategy (i.e. anadromous vs. resident) are critical to understanding how certain species and populations of Pacific salmon will respond to a warming climate. Further, sex and life stage have also been found to play a role in an individual's capacity to cope with high water temperatures. A recent literature review of sex-specific mortality in adult Pacific salmon revealed that females perish at over twice the rate of males when migration conditions are difficult, and in particular when rivers are warm (Hinch *et al*. 2021). The causes of these high levels of female migration mortality are numerous including energy depletion, cardiac collapse, physiological stress, and immune issues, and there is evidence that spawning ground sex ratios are being affected by this phenomenon (Hinch *et al*. 2021). Given these findings, it is imperative that future thermal tolerance research examine the effects of sex, and life-stage on upper thermal tolerance.

The overarching goal of this thesis was to address the paucity of information surrounding the causes and extent of the variability in reported upper thermal limits for Pacific salmon. Further, I aimed to demonstrate how various thermal metrics can be used in concert to develop a robust understanding of a population or species vulnerability to climate warming. My primary objectives were four-fold: i) review the existing literature on upper thermal tolerance in Pacific

salmon in order to understand how these limits were being quantified and identify sources of variation in these estimates (Chapter 2), ii) make recommendations for how thermal tolerance limits can best be used in assessing vulnerability to warming (Chapter 2), iii) apply the main results from Chapter 2 to assess the upper thermal tolerance of Kokanee salmon, using two commonly employed approaches in thermal tolerance research; the Critical Thermal Maximum (CTmax) and the Thermal performance curves for Aerobic Scope (AS) (Chapter 3), and, iv) investigate within population variability in thermal tolerance by examining differences in CTmax and AS across the lifecycle and between sexes (Chapter 3).

Chapter 2 is a review of existing literature on the upper thermal tolerance limits of the five North American anadromous and semelparous species of Pacific salmon in all life stages. This chapter outlines the link between these thermal limits and a populations' potential exposure based on latitude, migration timing and spawning location to develop a more comprehensive understanding of the variable impacts of climate change on Pacific salmon.

Chapter 3 aims to identify optimal and critical temperatures in Kokanee salmon - a resident life-history of sockeye salmon (*Oncorhycnhus nerka)*. While information on intraspecific variation in thermal tolerance and temperature-induced migration mortality in sockeye salmon has been obtained (Eliason *et al.* 2011, Whitney *et al.* 2013, Chen *et al.* 2013, Hinch et al. 2012), no equivalent research has been conducted on Kokanee salmon, despite their high cultural, economic, ecological, and recreational value. Research into the genetic structure and phenotypic specialization within and among populations of Kokanee salmon can provide key insights regarding the persistence and recovery of declining populations of both anadromous and resident *O. nerka* in the climate change era. Therefore, this chapter of my thesis will focus on

quantifying life stage- and sex-specific differences in optimal and critical temperatures for a single population of Kokanee salmon, an area where limited research has been conducted.

My concluding chapter (Chapter 4), synthesizes the findings from my review and thermal tolerance experiments, with specific focus on the nuances in thermal tolerance of Pacific salmon and highlights the importance of considering how thermal tolerance varies across levels of biological organization (individual, population, species) and methodological approaches when utilizing thermal tolerance research to inform conservation and management. To my knowledge, the thermal tolerance studies describe herein are the first to quantify upper thermal limits of Kokanee salmon and examine potential life-stage and sex-specific differences in the thermal tolerance of this species.

Chapter 2: Thermal tolerance in Pacific salmon: A systematic review of species, populations, life stages, and methodologies[1]

2.1 Introduction

Temperature has long been considered the 'ecological master factor' due to its profound effects on the ecology, behaviour, biochemistry, and physiology of salmonids (Fry 1971). As a result, a large body of literature has developed with the aim of qualifying and quantifying thermal criteria, in particular, the upper thermal limits of Pacific salmon (Brett 1952, Beacham and Murray 1988, Caudill et al. 2007, Clark et al. 2011, Abe et al. 2013). Several reviews on thermal metrics for salmonids have been conducted in the past to try and synthesize data on this topic. McCullough et al. (1999) reviewed numerous temperature metrics assessed in the literature including thermal stress, temperature limits on distribution, and the impacts of temperature on rearing, growth and production. They also synthesized this information to develop distributional limits for coho salmon (*Oncorhynchus kisutch)* and rainbow trout *(O. mykiss)*. Two years later, an additional review on temperature-related incubation requirements, swimming speed and variation in thermal responses among different species of salmonids was conducted (McCullough 2001). Myrick and Cech (2004) summarized the existing information on thermal requirements related to incubation, rearing, growth and smoltification for Chinook salmon (*O. tshawytscha)* and steelhead trout (*O. mykiss)* in the Sacramento-San Joaquin River system. Richter and Kolmes (2005) synthesized numerical values reported on thermal tolerance of Chinook, coho and chum salmon (*O. keta)* and steelhead trout throughout the Pacific Northwest and compared these values with existing Environmental Protection Agency guidelines. Most recently, Zillig *et al.* (2021), reviewed the evidence of intraspecific variation in thermal

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[1] A version of chapter 2 has been accepted to the journal *Fish and Fisheries* with revisions. Mayer, N.B.[1], S.G. Hinch,[2] E.J. Eliason[3]. (Accepted with revisions 08/2021). Thermal tolerance in Pacific salmon: A systematic review of species, populations, life stages, and methodologies. Fish and Fisheries. 40p.

physiology among populations of Chinook salmon native to California and emphasized the need for incorporating population-specific thermal metrics into future management schemes.

Due to the dramatic declines in Pacific salmon survival in basins with historically high productivity, understanding their responses to rising temperatures is becoming increasingly important (Crozier *et al.* 2008a). However, reported upper thermal limits (UTL) can vary quite extensively. The extent of the variation in reported UTL and the amount that can be attributed to natural variability in thermal tolerance versus variability introduced by the methodological details remains unknown (Baird *et al.* 2018, Clark *et al*. 2011, Poletto *et al*. 2017). Further, the variation in UTL that may emerge from research using different methods, life stages or populations will make it challenging for decision-makers to apply this information to management or conservation actions. Therefore, our ability to assess the vulnerability and predict how Pacific salmon may respond to continued warming will be highly dependent on the UTL selected for any given analysis. Further, the variation in UTL that may emerge from research using different methods, life stages or populations will make it challenging for decision-makers to apply this information to management or conservation actions. Despite the presence of several reviews on the governing effects of temperature on the growth, production and survival of Pacific salmon, further analysis and a more comprehensive framework is needed to outline how thermal metrics can be better used in predicting the response of Pacific salmonids to climate change. Based on these knowledge gaps, the objectives of this review are to (1) categorize the different methodologies employed to define UTL in Pacific salmon, (2) assess how research into the governing effects of temperature on these species has changed over time, (3) classify the extent and sources of variation in UTL, (4) examine how life stages, populations and species vary in UTL and identify where research is limited, and (5) discuss how UTL can be used to

develop a thermal framework to assist in predicting future persistence and survival of Pacific salmon in a warming world.

2.2 Methods
2.2.1 Data collection

To comprehensively collect studies that report UTL metrics for Pacific salmon, I conducted a systematic literature search in two databases: Web of Science and Aquatic Sciences and Fisheries Abstracts. The search included all papers published from January 1900- June 2020 and relevant papers published after that point were added to the review manually. I used a keyword-based search with the following query combinations:

1. Focal Species: sockeye salmon OR chinook salmon OR coho salmon OR pink salmon OR chum salmon

2. Temperature synonyms: thermal* OR temperature OR warming OR climate OR heat OR thermoregulat*

3. Keywords to encompass the diverse approaches used to assess thermal tolerance in ecological and physiological research: tolerance OR threshold OR limit OR resistance OR resilience OR stress* OR surviv* OR lethal OR sublethal OR optim* OR maxim* OR behavior OR infection OR disease OR recovery OR distribution OR migrat* OR exercise

The keywords were formatted to include all relevant iterations of a root word using an asterix (e.g. migrat* to encompass migratory, migration, migrating. migrate). I also scanned the reference sections of all relevant studies to check for additional publications (peer-reviewed or grey literature) that had not been captured through my initial keyword-based literature search.

2.2.2 Data organization and Analysis

The scope of this review was limited to the five anadromous and semelparous North American species of Pacific salmon (sockeye salmon *(O. nerka),* Chinook salmon, coho salmon, chum salmon, pink salmon *(O. gorbuscha*)). However, I believe these recommendations on thermal limits will be applicable for making predictions about future persistence and survival of all salmonids, and our conclusions about how thermal tolerance varies with methodology should be applicable to all fish species. Only papers that reported novel numerical thermal metrics for these species of Pacific salmon were included in this review. I excluded papers that looked at the relationship between temperature and growth unless a scope curve for growth was developed and a temperature at which growth could no longer occur was identified. Studies that assessed the cumulative effects of temperature and chemical exposure were excluded and research on the interaction between temperature and disease were only kept if they looked at how temperature reduced the resilience of the fish to the infection or pathogen. I read through the abstract, methods, results and discussion sections of all relevant papers.

Each study was classified by species, life stage, stock, study type, decade, methodology and corresponding temperature metric. Temperature metrics were reported as the mean value (with standard deviation if reported by the authors). I identified 7 major study types (Swimming/Physiology, Incubation and Rearing, Capture/Count, Holding, Capture Simulation, Tagging, Model; study types are defined in Table 1) that have been used to assess the effects of temperature on salmon function and behavior.

In addition to categorizing by broad study type, I identified seven distinct methodologies (Table 2) that have been used to assess upper thermal limits for Pacific salmon stemming from both

physiological and ecological fields of research. My goal in classifying each methodology is to identify sources of variation in thermal limits reported and provide insight on how these values can be used when making projections about the impacts of climate change on Pacific salmon. I also made comparisons among different methodologies based on their relative ecological realism. For the purpose of this review, I defined ecological realism as: representative of a realistic scenario for what the test fish experience in nature and reflective of the temperatures at which fitness promoting activities can no longer be performed. When making these comparisons, I focused on the following methodologies (described in detail in section 3.2): Critical Thermal Maximums (CT$_{max}$), Upper Incipient Lethal Temperatures (UILT), Preference/Avoidance, Thermal Migration Barriers, Scope for Activity/Aerobic Scope and Cardiac Function. I selected these methodologies for further analysis as they are most commonly employed in the literature when quantifying thermal optimums and upper limits of Pacific salmon across species and life stages. Finally, in order to further illustrate how reported UTL differ due to intraspecific variation (i.e. species, population, life stage) and methodology-based variation (both within and among methodologies), I also draw upon five case studies where I compare reported temperature limits from a number of studies collected in this review.

2.3 Results and Discussion

2.3.1 General Trends in the Literature

There was a total of 168 peer-reviewed studies and technical reports included in this review that spanned across all life stages and species of Pacific salmon (Appendix 1, Table 1). Of these studies, 19 were not found in our literature search but were included as additional relevant sources. The majority of studies were focused on the freshwater juvenile life stage (57%), followed by freshwater adult migrants at various stages of maturity (38%), and then smolts (3%)

and lastly immature fish in the ocean (1.8%) (Appendix 1, Table 1). The limited attention given to marine portion of the lifecycle is not unexpected given that during the marine phase, salmonids do not experience temperatures near their known upper thermal limits (Morita et al. 2010). Freshwater life stages are of greater concern with respect to the impact of climate induced warming, especially for adults, as they possess a finite amount of endogenous resources with which to complete their spawning migrations (Cooke *et al.* 2008). Further, reproductive life stages (spawning and embryonic) have been identified as a critical thermal bottleneck in the lifecycle of fishes (Dahlke *et al*. 2020). In terms of the relative attention that each of the five anadromous Pacific salmon species has received (Appendix 1; Table 1), Chinook (39%) and sockeye (38%) salmon were the most commonly studied species followed by coho (28%), pink (10%) and chum salmon (7%). Pacific salmon that spend the most time in freshwater (i.e. stream-type Chinook, lake-type sockeye and coho) had previously been identified as more vulnerable to climate change compared to those that migrate to the ocean more immediately after emergence (i.e. pink, chum and ocean-type Chinook salmon; Grant *et al.* 2019). The higher potential vulnerability to climate change of sockeye, coho and stream-type Chinook salmon may partially explain why these species have historically received greater attention in the literature in terms of assessing UTL metrics. Pink and chum salmon exhibit higher rates of straying than the other species which may reduce their vulnerability to freshwater habitat changes because greater flexibility in spawning location may allow for higher rates of reproduction in years where conditions in natal streams are not ideal (Gilk *et al.* 2004, Quinn 1993, Keefer and Caudill 2014). Given that abundances of pink and chum salmon are at all-time highs in the North Pacific Ocean, (Ruggerone and Irvine 2018), and their commercial fisheries value now surpasses the other species of Pacific salmon (Gislasan et al. 2017), it is more important than ever to conduct further

research into the UTL of the various life stages of pink and chum salmon. This information will be essential for effective management of species and populations which possess qualities that reduce potential vulnerability to the adverse effects of anthropogenic climate change.

When assessing how research examining the thermal tolerance of Pacific salmon has evolved over time, several trends were identified (Figure 2.1). The earliest source included in this review was published in 1941 by Donaldson and Foster and employed both Critical Thermal Maximum (CT$_{max}$) and preference approaches (Table 2.1) on juvenile sockeye salmon. Unlike more modern CT$_{max}$ studies, the author set the endpoint as "temperatures where fish refused to eat and respiration became excessive" with a warming period that occurred very gradually over the course of one week. In the following decades, research in this area remained fairly limited (but see Brett et al. 1952, Olson and Foster 1955, Davis *et al.* 1963, Major and Mighell 1967). However, in the 1980s there was increase in studies corresponding with the desire to understand thermal limits in order to discourage fish from entering nuclear development facilities and to aid in attaining desirable yields for commercial and recreational fisheries (Coutant 1987). Throughout the 1980s and 1990s research into thermal criteria remained fairly consistent. From the 2000s to 2010s there was a two-fold increase in published papers and reports and nearly a three-fold increase in the following decade. The majority (56%) of all papers assessing thermal metrics in adults were published within the last decade which corresponds with the development in our understanding that migrating and spawning adults represent critical life stages where warming river temperatures are associated with high mortality in numerous stocks of Pacific salmon (Naughton *et al.* 2005, Crossin *et al.* 2008, Mathes *et al.* 2010).

2.3.2 Identification and comparison of methodologies

Physiological and ecological-based research into the thermal tolerance of Pacific salmon has given rise to numerous temperature metrics with varying definitions and endpoints (Bates and Morely 2020). However, the thermal limits proposed vary extensively depending on the experimental design and represent a range of responses that are relevant over varying time scales such as thermal resistance, acclimation, and evolutionary adaptation (Bates and Morely 2020). Therefore, the variation in methodological details and the thermal responses of these appraoches must be considered when using such metrics to improve management designs and predict future vulnerability to climate change. The following section reviews the four primary methodological approaches that have been employed to assess upper thermal tolerance and discusses their benefits and potential limitations especially in regard to their ecological realism. I believed that comparing the methodologies in this manner would situate them within in the broader ecological context of thermal performance and limitations since in nature, from diurnal to seasonal fluctuations as well as across the lifecycle. For example, spring and summer-run Chinook in the Columbia River experience diel fluctuations of ~2-5°C (Keefer *et al*. 2019). Further, during the migratory adult life stage of Koeye river sockeye salmon, average temperatures have been found fluctuate from 12-18°C (Atlas *et al.* 2021). These natural fluctuations can serve to either mediate or exacerbate threats posed by climate induced changes in the hydro climatology of salmon producing watersheds.

CT_{max}/UILT

Background

Both the CT_{max} and the UILT are identified through acclimating/acclimatizing organisms to a given temperature and involve time and temperature as primary test variables (Becker and

Genoway 1979, Beitinger *et al.* 2000). However, these approaches were developed

independently and possess two critical differences. CT_{max} involves a continuous warming from

the acclimation to exposure temperature with loss of equilibrium as the endpoint (Baird *et al.*

2018, Abe *et al.* 2019). Whereas the UILT method involves a rapid transfer from the acclimation

to exposure temperature and with death as the endpoint (Brett 1952, Becker and Genoway 1979).

Ecological realism

Traditional CT_{max} and UILT studies generate consistently high thermal limits compared to other

methodologies and possess the least ecological realism (Figure 2). This is primarily due to three

main factors. First the rapid changes in temperature that occur in CT_{max} studies, and the abrupt

changes used to develop estimates for UILT do not reflect a realistic scenario for the thermal

experience of Pacific salmon in nature (Becker and Genoway 1979). Second, for CT_{max}, the

lethal limit obtained is highly influenced by the acclimation temperature and rate of warming and

does not necessarily reflect any genetic or adaptive characteristics of the test subjects

(Terblanche *et al.* 2007, Kingsolver and Umbanhowar 2018, McKenzie *et al.* 2021). During

continuous warming, a lag between body temperature and ambient water temperature can occur

if the rate of warming is too rapid and there is a risk of partial acclimation to higher temperatures

than intended when warming too slowly (Becker and Genoway 1979). Further, the mechanisms

that lead to loss of equilibrium remain unknown and may not be ubiquitous across species or

warming rates which makes it challenging to determine the cause of variation in CT_{max} among

species or explain why the resulting values are modified by acclimation temperature (Lefevre *et*

al. 2021). Third, organ systems central to fitness promoting activities often decline far before

either the CT_{max} or UILT is reached. This mismatch between tissue function and loss of righting

response or death calls into question both the functional utility and ecological realism of these approaches and limits their use beyond being a simple relative measure of thermal tolerance across populations, species or organisms (Muñoz *et al*. 2014). Even then, comparing across studies is challenging as UTL can be altered by the methodological details of any given experiment (Terblanche et al. 2007). Comparing studies that employ the CT_{max} methodology, in particular, is difficult if no standardized rate of warming has been established. Additionally, a recent study on upper thermal tolerance in brown trout (*Salmo trutta)* found that intraspecific variation in CT_{max} did not have any clear relationship with migration timing or strategy, growth or predation vulnerability (Desforges *et al*. 2021). Their results provide further evidence that CT_{max} values are not indicative of how temperature affects a fish's ability to perform fitness promoting activities. However, this metric is widely used across a broad range of fish species and is repeatable, easy and relatively low cost to perform (Beitinger *et al*. 2000). Therefore, I do not discourage use of this metric, rather I encourage careful interpretation when integrating these values into future management schemes.

Preference/Avoidance

Background

Fish have evolved to be thermally selective based on temperatures that optimize physiological, ecological and reproductive performance (Brett 1971). As a result, identifying temperatures that fish actively avoid or prefer became popular throughout the 1970s and 1980s as understanding this temperature-based selective process was integral to incentivizing fish to move towards or away from certain areas (Coutant 1987). This was especially beneficial for attaining more desirable yields in fisheries (Coutant 1987). These studies can be performed in both lab and

field-based settings. Field-based experiments often utilize tagging technologies to identify areas where fish congregate more densely as well as areas where fish are unlikely to be found, and correlate these movements with water temperatures in those areas (Armstrong et al. 2016). Vertical gill netting and trawl surveys have also been employed to define temperature preferences for Pacific salmonids (Crowder and Magnuson 1982). Lab-based experiments are performed in tanks where an artificial thermal gradient is created and the movement and congregation of fish in the water column is observed over some set time period (see Christensen et al. 2021 for details).

Ecological realism

The preference/avoidance approach consistently reports some of the lowest UTL among the various methodologies compared in this review (Figure 2.2). This may be partially due to the fact that temperatures that fish actively avoid only suggests a preference for lower temperatures. While temperature preferences can indicate a behavioural manifestation of an individual's physiological response to its surrounding environment (Huey 1991, Chirstensen *et al.* 2021), they do not indicate whether fish are capable of tolerating higher temperatures. Furthermore, the majority of these studies are lab-based which creates further complications for relating the experimental observations to the experience of the test species in the wild. In reality, there are numerous environmental factors aside from temperature (e.g. predators, food, salinity, dissolved oxygen levels) that can incentivize fish to select one area over another (Eliason and Farrell 2016).

Thermal Migration Barriers

Background

Studies that aim to identify temperature limits to up and downstream migration are largely field-based and dominated by tagging studies (Hallock *et al.* 1970, Keefer *et al*. 2008 a&b, MacDonald *et al.* 2010). Another common experimental design uses fish counts at dams and weirs to link slower passage rates or limited passage with a thermal barrier for migration (Goniea *et al.* 2006). Multiple limiting effects of temperature on migration have been assessed in the literature including delayed migration or slowing of migration rates (Hodgson and Quinn 2002, Hyatt *et al*. 2003, Goniea *et al*. 2006, Caudill *et al*. 2007, Keefer *et al*. 2008a), inability to reach natal spawning grounds (Keefer *et al*. 2008b, Connor *et al*. 2019), and cessation of migration (Hallock *et al.* 1970, MacDonald *et al*. 2010).

Ecological Realism

The thermal migration barrier methodology reports similar thermal limits to avoidance studies (Figure 2.2). This approach demonstrates a correlation between temperature and the ability for fish to migrate upstream and only applies in the smolt and adult migrant life stages. However, there are numerous other factors that reduce an individual's capacity to migrate successfully (e.g. accelerated loss of endogenous resources, pathogen virulence) that can operate independently or interactively with temperature (Martins *et al*. 2011). There is also a large degree of variation in upper thermal limits reported using this approach. This may be due to there being three general definitions for upper thermal limits to migration in the literature:

1. Temperatures at which successful migration declines significantly

2. Temperatures at which migration ceases or becomes limited

3. Temperatures at which passage rates slow significantly

This is problematic as the variation in reported thermal limits may be less a function of inherent variation in thermal tolerance between species, populations or regions and more a product of how the thermal limit is defined.

Temperature dependence of the Scope for Activity/Aerobic scope

<u>Background</u>

For aquatic ectotherms like Pacific salmon, it has been suggested that thermal limits are set by insufficient aerobic capacity to support essential activities (Pörtner and Farrell 2008). This theory developed when Fry (1947) demonstrated the controlling influence of temperature on a fish's 'scope for activity'. Scope for activity is also commonly referred to as aerobic scope which is defined as the difference between maximum metabolic rate (MMR, the peak metabolism possible) and standard metabolic rate (SMR, the minimum metabolism required to sustain life). Aerobic scope represents the amount of energy available to the fish to perform any activities beyond basic body maintenance (e.g. swim, digest a meal, compete for mates or territory, escape a predator). Since this seminal study was conducted, research into the temperature dependence of aerobic scope has been built upon and used to determine both optimal ($T_{opt(AS)}$ – the temperature where aerobic scope is greatest) and critical temperatures ($T_{crit(AS)}$ – temperature where aerobic scope is zero) for many species and populations of fish. However, the mechanisms that triggers the decline in maximum oxygen consumption and thus, in aerobic scope, above the $T_{opt(AS)}$ remains a contentious topic. Pörtner (2001) hypothesized that aerobic scope becomes limited with increasing temperature due to limitations of organ systems to deliver oxygen to tissues (termed the oxygen and capacity limited thermal tolerance hypothesis, OCLTT). Data

from migrating adult sockeye salmon support this hypothesis (Eliason *et al*. 2011; but see counter arguments from other fish species Clark *et al*. 2013, Lefevre *et al*., 2021). In sockeye salmon, the decrease in aerobic scope at high temperatures was associated with a collapse in cardiac performance (Eliason *et al*., 2011; Eliason *et al* 2013). As a result, recent research into the limiting effects of temperature on cardiac performance has given rise to cardiac based optimal (T_{ABT} – the temperature above which maximum heart rate becomes limited with increasing temperature) and critical temperatures (T_{arr} – the temperature at which heart rate becomes arrhythmic). These values tend to yield temperatures that parallel the $T_{opt(AS)}$ and $T_{crit(AS)}$ (Muñoz *et al*. 2015).

In addition to optimal and critical temperatures for aerobic and cardiac scope, there have been a few studies over the past two decades that aim to determine the highest temperatures where Pacific salmon can maintain sufficient aerobic scope to successfully carry out spawning migrations (Farrell *et al.* 2008, Eliason *et al*. 2011). These studies assume that a functional temperature limit for successful upriver migration lies somewhere between the $T_{opt(AS)}$ and the $T_{crit(AS)}$, however, the precise temperature will vary depending on the difficulty of the spawning migration and on the individual's maximum aerobic capacity (Farrell *et al*. 2008). Eliason *et al*. (2011), referred to such a temperature as the Pejus Temperature (T_P) value and suggests that the amount of aerobic scope required for adult migrants to complete spawning migrations is 80-90% of total aerobic capacity. However, data on temperature dependence of aerobic scope in Pacific salmon is limited (absent for many species and populations) making it very difficult to discern how much aerobic scope is actually required for adults to reach spawning grounds.

Ecological Realism

The estimates for optimal and critical temperatures for aerobic and cardiac scope offer a more

mechanistic understanding of the controlling effects of temperature on an organism's ability to

function than other methodologies employed in the literature. However, similarly to CT_{max} and

UILT thresholds (Figure 2.2), fitness-promoting activities such as predator avoidance and

upriver migrations are impossible to perform at the temperatures where these critical limits occur

(i.e. $T_{crit(AS)}$). Additionally, most studies on the temperature dependence of cardiac and aerobic

scope are conducted in controlled laboratory settings and prove difficult to relate to an

individual's experience in nature. There are also several methodological issues that must be

considered when comparing across studies (Lefevre *et al.* 2021). Specifically, the duration of

thermal exposure and the range of acclimation temperatures varies across studies, which can

influence the shape of the aerobic scope curve (Lefevre *et al*. 2021). Therefore, comparisons

across studies should be made with caution. Lastly, when investigating the temperature

dependence of aerobic scope, RMR and MMR is measured and calculated at several

experimental temperatures. Since, AS is not evaluated over a continuous temperature gradient,

$T_{opt(AS)}$ and $T_{crit(AS)}$ must be estimated by fitting a polynomial regression onto the data.

For adult migrants, T_p estimates are more ecologically realistic (Figure 2.2) because they reflect

the fact that upriver migrations require more than a minimum amount of aerobic capacity. If

upriver migrants require 80-90% of their total aerobic scope to migrate upstream (Eliason *et al.*

2011), that would correspond to lower temperatures than those at which complete aerobic

collapse ($T_{crit(AS)}$) or whole animal incapacitation (CT_{max}) occurs. However, it is important to

recognize that not all species or life stages utilize the full extent of their aerobic capacity (Lowe

and Davidson 2006, Kunz *et al.* 2018). It is unknown how much absolute aerobic scope is necessary for juvenile life stages to thrive (e.g. to swim, digest, grow, compete for space, forage). Therefore, while this approach may be useful for migrating adult salmonids, it may not be the best tool for assessing how temperature affects fitness in juvenile life stages where less of their total aerobic capacity is required to carry out activities essential to survival. Due to the potential non-uniformity of the use of full aerobic capacity across life stages and among species it can be difficult to relate reductions in aerobic scope to overall fitness in the wild (Lefevre *et al.* 2021).

2.3.3 Case studies: natural variability and variability within- and among-UTL approaches

There is some degree of natural variability in temperature tolerance among species, populations and life stages which can partially be attributed to different historic thermal experiences (Angilletta 2008) and the length and difficulty of spawning migrations (Crossin *et al.* 2004, Farrell *et al.* 2008, Eliason *et al.* 2011). Our analysis also indicates a high degree of variation in thermal limits reported depending on the methodology employed and the differences in experimental details within a given methodology. In the following section, I explore five case studies to demonstrate the inherent and methodological sources of variability in estimates of optimal temperatures for performance and UTL.

Interspecific variation in UTL metrics: Comparing $T_{opt(AS)}$ across different species of anadromous Pacific salmon

The data extracted for this case study comes from select research that analyzed the impacts of temperatures on optimal metabolic performance using the Scope for Activity/Aerobic Scope methodology (Table 2.3). These studies present the only published data identified in this review

that assesses $T_{opt(AS)}$ in adult Pacific salmon. Clark *et al.* (2011) investigated the thermal physiological performance of Lower Fraser River pink salmon in British Columbia and suggested that their exceptional aerobic scope may partially explain why this population was exhibiting relatively higher spawner recruitment than other anadromous Pacific salmonids in that region. Abe *et al.* (2019) developed $T_{opt(AS)}$ estimates for one early- and one late-run population of chum salmon from the Sanriku Coast (Japan). In addition to being the only study to employ the Scope for Activity/Aerobic scope methodology on chum salmon, their research suggests that considerable intraspecific variation in thermal performance may also be related to run-timing. I pooled data from four studies (Lee *et al.* 2003a, Farrell *et al.* 2008, Eliason *et al.* 2011, 2013a) to assess how the average $T_{opt(AS)}$ for multiple populations of sockeye salmon may differ from other species of Pacific salmon. Table 2.4 illustrates how the $T_{opt(AS)}$ varies considerably between these four species with an ~12°C difference in optimal temperatures when comparing a coastal winter-run population of coho salmon and a coastal fall-run population of pink salmon. Interestingly, the $T_{opt(AS)}$ for sockeye, coho and chum salmon coincide with the historical average temperature experiences during upriver migration (Lee *et al.* 2003a, Farrell *et al.* 2008, Eliason *et al.* 2011, Abe *et al.* 2019). However, for pink salmon, the same metric seems to be more reflective of historical maximum temperatures (Clark *et al.* 2011). It is possible that these differences may be caused by variation in life-history strategies yet, evidence is lacking to provide concrete reasoning for the differences in $T_{opt(AS)}$ among species of Pacific salmonids.

Intraspecific variation in UTL: Comparing $T_{crit(AS)}$ for adult migrants in seven populations of Fraser River sockeye salmon

Eliason *et al.* (2011, 2013a) were selected for demonstrating the possible extent of intraspecific variation among populations of Pacific salmon from the same region as they are the only studies published to date that develop optimal and critical temperatures for the greatest number of populations from a Pacific salmon species using the same experimental design across populations. These papers developed aerobic scope curves for seven populations of Fraser River sockeye salmon in British Columbia, Canada under the expectation that intraspecific variation in $T_{crit(AS)}$ is associated with the difficulty of the upriver migration and historical environmental temperatures. Fraser River sockeye salmon populations co-migrate and thus can be divided into broad run timings based on when they re-enter the river (Early Stuart, Summer Run, Fall Run). Early Stuart enter the Fraser River in early July, encountering high river flows, and warming temperatures as they approach distant spawning grounds. Summer Run populations (Chilko, Quesnel, Gates, Nechako) encounter peak temperatures when they enter the Fraser and moderate river flows. Fall Run populations (Weaver and Harrison) encounter cool temperatures, low flows and have the shortest, least difficult migration. Figure 2.4 illustrates the correlation between a migration difficulty index (migration slope = migration elevation/migration distance) and the $T_{crit(AS)}$ and $T_{opt(AS)}$ estimates for the populations assessed in these two studies. $T_{crit(AS)}$ is more variable (range: 20.8°C – 29.4°C) than $T_{opt(AS)}$ (range: 14.5°C – 17.2°C) among populations and $T_{crit(AS)}$ is more strongly correlated with migration slope. As such, these studies suggest that populations with less challenging, cooler migrations may be less thermally tolerant and thus, more vulnerable to climate-induced increases in freshwater temperatures. The intraspecific variation in thermal tolerance observed in these studies calls for a more nuanced approach to salmonid conservation and management that reflects population specific thermal physiology (Zillig *et al.* 2021).

Life-stage specific UTL: Comparisons among embryo, fry and adult migrants in sockeye salmon

In addition to both inter- and intraspecific variation, research also suggests that thermal metrics differ depending on life stage. To demonstrate this third source of inherent variation in thermal tolerance, Figure 2.4 illustrates the differences in *relative* thermal tolerance for nine populations of sockeye salmon native to the Fraser River Basin and highlights the finely tuned local adaptations in thermal tolerance during freshwater life stages. Embryo data were extracted from a study by Whitney et al. (2013) assessing thermal tolerance of nine populations during embryonic development. Among the populations used in their research, Chilko and Gates sockeye had the most dramatic declines in embryonic survival when incubated at 16°C relative to 14°C and 10°C groups. They suggested that the stark reduction in survival may be due the historically cool spawning and incubation temperatures experienced by these populations, while the Scotch and Adams populations, with the superior thermal tolerance, incubate in the warmest environments. Chen *et al.* (2013) developed CT_{max} values for the same nine populations of sockeye salmon in the fry life stage after incubation under three different thermal regimes (10°C, 14 °C and 16°C). Populations did differ in CT_{max}, though this was strongly related to body size. In general, the absolute differences in CT_{max} across populations were minimal at this life stage, particularly when compared at a common body size. $T_{opt(AS)}$ and $T_{crit(AS)}$ values for migrating adult fish were estimated by Eliason *et al.* (2011) who discovered that the Chilko population (Summer migrant) had exceptionally high upper thermal tolerance and are more resilient to warming whereas, the Weaver population (Fall migrant) had the lowest thermal tolerance and appeared to be the most vulnerable population to warming during this life stage.

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Taken together, these studies suggest that populations are strongly locally adapted to their environmental conditions at both the embryo and adult stage. They also demonstrate that there is considerable intraspecific variation in thermal tolerance and that relative thermal tolerance differs across the lifecycle. For example, the Chilko population had the lowest thermal tolerance at the embryo stage but the highest thermal tolerance at the adult stage. As such, fisheries managers and other decision-makers should avoid extrapolating thermal tolerance metrics across populations or across the life cycle.

I also compared *absolute* thermal tolerance across the lifecycles of three populations of sockeye salmon, to identify potential thermal bottlenecks (Dalhke et al 2020; Portner and Farrell 2008) using data extracted from Whitney et al. (2013), Chen et al. (2013), and Eliason et al. (2011, 2013). The current paradigm suggests that thermal windows are narrowest for embryos and spawners and widest during the juvenile life stage (Portner and Farrell 2008; Dahlke *et a*l 2020). In this case study, absolute thermal tolerance increased as salmon age from embryos to fry, as predicted. However, three different trends were observed between the transition from fry to adult. Populations displayed a decrease (Weaver), minimal change (Gates), and increase (Chilko) in thermal tolerance from the fry stage to the migrating, sexually maturing adult stage. Chilko sockeye, in particular, provide an interesting case where the thermal tolerance window is widest for migrating adults contrary to this existing paradigm. This highlights how bottlenecks in thermal tolerance may differ across populations. Therefore, trends in the way thermal tolerance may change across the lifecycle cannot be generalized. While the degree of life stage-specific variation shown in this case study might be somewhat confounded by the differences in

experimental details between studies, the data compiled in Figure 2.5 is the most detailed

information available on life-stage specific UTL across populations. All of these methodologies

(Tcrit(AS), CTmax,, embryo survival) reflect temperatures where death is imminent and were

performed in controlled lab environments. While it would be ideal to only compare across

studies that employ the same methodologies, studies that look directly at life-stage differences in

thermal tolerance are largely absent from the literature. A recent alternative proposed by

FitzGerald et al. (2021) employs a modelling approach where life-stage specific thermal

tolerance is standardized by assessing the likelihood of survival to the succeeding life stage at a

given temperature.

I found extremely limited data on the upper thermal tolerance of alevin, smolt and marine

life stages or the fully mature spawning life stage (Figure 2.5). There was only one published

study that identified a CT_{max} threshold for Chinook salmon in the alevin life stage (Del Rio *et al*.

2019). Since alevins have limited mobility and therefore are unable to behaviourally

thermoregulate (Myrick and Cech 2004), further research into their upper thermal tolerance is

necessary. Several studies on smolt and marine life stages have developed temperature

preference estimates (Hinke *et al*. 2005, Sauter *et al*. 2001) and distributional limits (Welch *et al.*

1995, Azumaya *et al.* 2007) but only one study has assessed the upper thermal limit in Chinook

smolts (Baker *et al*. 1995). The absence of data on thermal tolerance in mature spawning adults

is also a concern given that warming in spawning streams is expected to cause thermal stress in

spawning adults (FitzGerald *et al.* 2020). Further, there is good evidence that for mature

spawning adults, thermal tolerance is likely to be lower than has been found for less mature adult

migrants. Thermal tolerance is proposed to decrease in reproductively mature adults due to the

increased oxygen demand of gamete production and maintenance (Portner and Farrell 2008).

Hruska *et al*. (2010) assessed physiological changes of individual spawning adults from the Weaver Creek population and found that rapid senescence was associated with increasing concentrations of plasma cortisol and lactate to a point that indicated extremely high levels of anaerobiosis. Relatively high plasma lactate concentrations due to a heightened mismatch in oxygen supply and demand is associated with collapse in thermal tolerance in migrating adult sockeye (Eliason *et al*. 2013a).

Variation in upper thermal tolerance within- and among-methodological approaches

Becker and Genoway (1979) generated CT_{max} values for juvenile coho salmon under two acclimation temperatures and five different heating rates. In their study, upper thermal tolerance varied by ~4.5 °C when comparing CT_{max} values for an individual acclimated to 5°C and heated at a rate of $1°C·h^{-1}$ compared to a fish acclimated to 15°C and heated at a rate of $60°C·h^{-1}$ (Figure 2.6). Further the absolute change in CT_{max} became greater at faster heating rates indicating that in addition to a systematic difference, there may also be a multiplicative effect on the CT_{max} value derived as heating rate increases. Their results provide an excellent illustration of how traditional CT_{max} values can be altered significantly by two primary methodological details: the rate at which the water is heated and the initial acclimation temperature.

On a broader level, variation in upper thermal limits is also prevalent among different methodologies. The variation in upper thermal tolerance values between T_p, $T_{crit(AS)}$ and upriver migration methodologies indicates that some of the variation in reported upper thermal tolerance limits can also be attributed to the differences between approaches. One major reason for this variation is that different methodologies define the upper thermal limit in different ways. The

upper thermal tolerance of adult sockeye salmon from the Early Stuart population has been assessed using two methodological approaches: a 'Thermal Migration Barrier' and 'Scope For Activity/Aerobic Scope' (Table 2.3). MacDonald *et al*. (2010) investigated the impacts of environmental conditions (e.g. temperature and discharge) on spawning migration mortality and determined that 18.5°C represented a temperature threshold that explained some of the discrepancy between lower-river and spawning escapement estimates for Early Stuart sockeye salmon. Eliason *et al*. (2011) employed the Scope for Activity/Aerobic Scope methodology to develop $T_{crit(AS)}$, and T_p estimates for the same population. In this case study, the thermal limit to upriver migration and the T_p estimate correspond closely (18.5 °C and 19°C respectively. However, the $T_{crit(AS)}$ was ~7°C higher than the two other more conservative estimates. This reflects the fact that T_p and Thermal Migration Barrier metrics have both generally set the thermal limit as the temperatures above which successful migration becomes challenging whereas, $T_{crit(AS)}$ defines the upper thermal limit as the temperature where complete aerobic collapse occurs and is not an ecologically relevant metric.

2.3.4 Considerations for the use of UTL metrics in conservation and management

An essential component of successful conservation and management in the current era is to identify species and populations that are most vulnerable to climate change and develop actions to mitigate this threat (Bottrill *et al*. 2008, FitzGerald *et al*. 2021). A comprehensive understanding of thermal criteria for Pacific salmonids is critical to make predictions about survival and persistence in both the short- and long-term. Variation in thermal tolerance exists at the species, population, and life-stage levels, therefore thermal guidelines for Pacific salmonids should be developed to reflect these nuances. Additionally, a recent analysis of thermal

bottlenecks in fish species identifies both spawning adults and embryonic development as the most sensitive life stages for many fish species with respect to climate-induced warming of aquatic environments (Dahlke *et al*. 2021). The authors did not report any thermal ranges for spawning adult Pacific salmon, nor did they account for population specific differences in thermal tolerance which is a potential limitation to their study. However, their work demonstrates that even if some species exhibit high thermal tolerance at one point in their lifecycle this may not be indicative of overall resilience to future warming. For example, Chilko sockeye have displayed considerably higher thermal tolerance than other Fraser River stocks during the adult migrant life stage (Eliason *et al.* 2011) but have the lowest tolerance in the embryonic life stage (Whitney *et al.* 2013). This suggests that despite their superior cardiac and aerobic capacity at high temperatures as adults, Chilko sockeye may still be a population of conservation concern in the climate change era, and thus may not truly have earned the moniker of 'super fish' (Eliason *et al*. 2011). This variation in thermal tolerance during a critical period in the lifecycle provides an excellent example of how policies surrounding conservation and management of Pacific salmon must account for the fact that within a single population, there may be specific life stages where greater vulnerability to warming exists. Management at these more specific levels will promote genetic diversity and allow for greater adaptive and evolutionary potential to future environmental conditions (Zillig *et al.* 2021).

Our review identified numerous approaches for quantifying UTL in behavioural and physiological research. Each of these methodologies has benefits and drawbacks but all contribute to a more robust understanding of how salmonids respond to warming water temperatures. However, the differences in methodological details between studies contributes

additional sources of variation in reported thermal limits and adds to confusion over where UTL truly lie and thus how climate warming will actually affect the long-term sustainability of salmonid populations. Numerous studies have used a single UTL threshold to quantify how climate warming will impact salmonids (Mantua *et al*. 2010, Wade *et al.* 2013, Flictcroft *et al*. 2019). However, this approach does not reflect life-stage and population-specific differences in thermal tolerance and fails to recognize that salmon respond to rising temperatures in a non-linear manner (Zhang *et al.* 2019). Given that UTL are shaped by a variety of physiological and behavioural responses (Bates and Morely 2020), I advocate instead for the use of an 'upper thermal tolerance range' (UTTR), which encompasses and reflects the inherent and methodology-based variation in thermal metrics outlined in this review. This range could be developed through the use of multiple UTL metrics derived from the most appropriate approaches that help to satisfy conservation or management needs. Such ranges should probably involve approaches that are representative of both physiological (i.e. Aerobic Scope, CT_{max}, Scope for Growth) and behavioural (i.e. thermal migration barrier, predator avoidance) thermal responses for a given life stage (Figure 2.2). Further these ranges should incorporate metrics that reflect thermal responses across various timescales from acute to chronic temperature exposures. For example, drawing a single value from the literature for adult migrant Chinook salmon would set the UTL at 26.5°C using a CT_{max} estimate (Muñoz *et al*. 2014) or at 18°C using a thermal migration barrier metric (Caudill et al. 2007). In reality, these are two opposite ends of range of proposed upper thermal tolerance values that are reflective of different thermal responses. Using a UTTR for adult migrant Chinook salmon of 18-26.5°C would encompass all of the mid-range values that reflect additional physiological thermal responses including critical temperatures for cardiac function (21.2°C; Muñoz *et al*. 2014) and behavioural responses such as a temperature-based

distributional limit (22°C; Wurster *et al.* 2005). Additionally, this range encompasses the differences in upper thermal tolerance among different populations within a species. While UTTR from this example is quite broad, it would be the most accurate reflection for adults within this species – a narrower UTTR could be obtained if all the UTL research methods were deployed just on a single population, a key take-away from our review. However, employing the complete range of UTL research methods for each population from all species of Pacific salmonids is not realistic recommendation. Therefore, this review advocates for the best possible use of all available information when incorporating thermal tolerance research into management regimes. In cases where only one UTL has been examined or reported, information from other populations can be extrapolated to infer what the UTTR might be. For example, if one population only possess a CT_{max} estimate, it would still be necessary to recognize that more "functional" thermal limits are likely to be substantially lower and incorporate that understanding into management. In instances where no information is available, consideration of all the factors that contribute to variation in thermal tolerance such as historical temperature exposure throughout the life cycle and migration difficulty can be used to infer where the UTTR of one population may lie in relation to others with more robust data.

It is important to note that estimating the impacts of climate change based solely on UTL can lead to an underestimation of the negative influences of warming. Throughout their lifecycles, Pacific salmonids will encounter a multitude of biotic and abiotic stressors that may cumulatively affect survival. For example, resilience to pathogens and fisheries capture is higher when salmon are migrating through cooler water, however, significant increases in pathogen susceptibility and inability to recover from capture events have been observed when fish are

faced with higher temperatures (Raby *et al*. 2015, Teffer *et al*. 2019). Therefore, the interactive effects of these cumulative stressors should be considered alongside reported upper thermal limits when developing thermal guidelines for management and conservation of these species.

While quantifying upper temperature limits is an important component to understanding how cold-water fishes may respond to climate warming, thermal tolerance alone does not determine vulnerability to climate warming. Effective conservation and management of Pacific salmon will also require estimates of current and future thermal exposure at the population and life stage levels. Estimates of water temperatures in rivers across space and time, an understanding of how these species move through river networks, and quantifying potential thermal exposure are all required in order to develop an understanding of current and future vulnerability to warming (FitzGerald *et al.* 2020). Migratory salmonids complete phases of their lifecycles in different habitats and the thermal tolerance of a specific population in any given life-stage can vary extensively (Figures 4 and 5). Moreover, thermal exposure differs depending on which part of the lifecycle and individual is in. Therefore, a thorough understanding of how thermal exposure compares to the UTTR proposed for a population at any point in their lifecycle is another essential component of designing effective management schemes and determining the potential for Pacific salmonids to withstand future warming.

There have been several attempts to relate UTL to current and potential future exposure through the development of concepts such as Thermal Safety Margins (TSM). TSM is an index of the relative proximity of an organism's current thermal experience to its upper thermal limit and can be used to compare vulnerability across populations and species (Pinsky *et al*. 2019). This is

usually done by subtracting the known CT_{max} for a population from the highest current temperatures experienced (Sunday *et al*. 2014, Vinagre *et al*. 2019). However, there are limits to the use of TSM in making predictions about how populations may fare under future warming as sublethal temperatures are major drivers of mortality and extirpation before TSM's reach zero (Pinsky *et al*. 2019). Further, CT_{max} reflects a maximum tolerance level and does not possess the same ecological realism as other metrics (e.g. Tp, thermal migration barriers). Therefore, developing TSM's that utilize a more functional range of upper thermal limits (e.g. Tp, thermal migration barriers, temperature when growth ceases) may provide a more realistic understanding of a populations' vulnerability to warming.

While there is clear evidence of population and life-stage specific differences in thermal tolerance (Figure 2.5 and 2.6), very limited research has been conducted into how sex and size affect UTL. Some studies have demonstrated that smaller individuals, within a life stage, may be better able to withstand high temperature exposures than larger individuals (Daufresne *et al*. 2009, Clark *et al*. 2012). Additionally, a recent and comprehensive literature review of sex-specific mortality in adult Pacific salmon revealed disproportionately higher female mortality (over 2 times greater than in males) when migration conditions are difficult, and in particular when rivers are warm (Hinch *et al*. 2021). The potential causes of these high levels of female migration mortality range from energy depletion and cardiac collapse to immune issues, and there is evidence that spawning ground sex ratios are being affected by this phenomenon (Hinch *et al*. 2021). Given these findings, it is imperative that future thermal tolerance research examine the effects of sex, and size on all life stages.

Beyond developing a knowledgebase on the UTTR and the thermal exposure of Pacific salmonids, an understanding of the potential for thermal adaptation is another key component in predicting the consequences of climate change for these species. Given the current scenarios for future warming in the Pacific Northwest, non-genetic responses such as phenotypic plasticity are unlikely to be sufficient to withstand climate warming for many populations (Crozier et al. 2008). Therefore, evolutionary adaption of thermal tolerance should be considered when making predictions about long-term resilience in native environments (Chen et al. 2018a). As temperatures continue to rise, it is probable that selection will act in favour of thermally tolerant phenotypes as long as there is heritable variation in these traits. However, whether thermal adaptation within in a population of Pacific salmonids can occur at a rate that allows these fish to withstand climate induced warming is unknown (Angilletta 2008). Traits (and the thermal metrics derived from them) related to thermal tolerance and performance have been found to be heritable in salmonids. However, the genomic basis of thermal tolerance is highly complex and research into microevolution towards increased thermal tolerance is extremely limited (Chen *et al*. 2018). As research into population and life stage specific thermal tolerance develops, an understanding of how species upper thermal tolerance has evolved over time is a critical component in understanding how they may continue to adapt to future temperature conditions (Bennett *et al.* 2019). There are many behavioural and physiological mechanisms (i.e. behavioural thermo-regulation and aerobic scope) that may act synergistically to limit or promote the potential for adaptive evolution to warmer environmental conditions. Therefore, a consideration of the range in upper thermal tolerance metrics that reflect these mechanisms will be central in making accurate predictions about the potential for adaptive evolution of thermal tolerance traits as water temperatures continue to increase.

Successful evolutionary adaptation to new environmental conditions depends largely on how the rate of environmental change compares to the generation time of the species or population. Previous studies indicate that climate-induced freshwater warming acts as a relatively strong selective pressure on genes controlling migration timing and suggests that the rate of evolution towards earlier migration can be as short as two generations (Kovach *et al*. 2012, Reed et al. 2011). For traits related to thermal tolerance, there is evidence of intraspecific variation (Eliason *et al*. 2011,2013a, Chen *et al*. 2013; see Figure 2.3). However, in the research I reviewed, individual variation within a population appears to be limited (Muñoz *et al*. 2015, Chen *et al*. 2018). This lack of variation can be partially attributed to the small size of some populations of Pacific salmonids and their proclivity for natal homing which has allowed for evolution of thousands of populations that are finely tuned to local conditions. These findings suggest that a single population may not possess sufficient genetic variation to evolve their thermal tolerance rapidly enough to withstand expected future warming. In these cases, consideration of the heritable intraspecific variation in upper thermal tolerance is essential to determining whether adaptation could occur through the transfer of thermally tolerant traits from one population to another.

In wild populations, straying acts as a crucial evolutionary feature that can allow for adaptation over relatively short ecological time frames (Keefer and Caudill 2014). Introduction of novel genetic diversity into a population can increase the probability of genetic rescue and allow for a population to adapt to new environmental conditions more quickly (Carlson *et al*. 2014). However, the transfer of traits that are maladaptive to local conditions is also a possibility especially given the highly specific local adaptions that these populations have developed (Fraser *et al.* 2011). The potential for straying to impact the genetic structure of recipient populations

depends on the relative size of the donor and recipient population and the frequency of straying from the donor population (Bett *et al*. 2016). Research into the extent and causes of straying suggests that straying becomes more common with increasing temperatures as fish are more likely to enter non-natal tributaries when main-stem temperatures reach stressful levels (Keefer *et al.* 2008a, Westley *et al*. 2015). Therefore, as freshwater temperatures continue to rise in response to climate change, increased rates of straying between wild populations may occur. With respect to climate warming and thermal tolerance, strays have the potential to either hinder or enable evolution in thermal tolerance traits. For example, high rates of straying by the Chilko sockeye salmon population to the Gates Creek spawning area was observed in 2012 (Bett *et al*. 2016). Gates Creek is a relatively small population and interbreeding with Chilko sockeye salmon could allow for the transfer of exceptional cardiac adaptations that individuals from this donor population possess (Eliason *et al*. 2011, Anttila *et al*. 2019). Conversely, less favourable traits like lower fecundity, smaller eggs and low thermal tolerance during the embryonic life stage could also be transferred (Bett *et al*. 2016, Whitney *et al.* 2013). Therefore, building upon research into the extent and rate of straying in Pacific salmonids and relating this work to our current understanding of population and life stage specific UTTR will be an important component in determining the potential for Pacific salmon to successfully adapt to changing environmental conditions.

2.3.5 Future Persistence and Survival

Climate warming presents numerous challenges for successful management and conservation of Pacific salmonids and calls into question whether these species have the potential to persist under climate change. Global climate models project a 4.8°C increase in air temperature by the end of the 21st century (IPCC 2013). Such increases in temperature will continue to drive marked

changes in both ocean and freshwater temperatures among other environmental factors like food

availability and oxygen concentration (Ficke *et al.* 2007, IPCC 2019). Many of the most

productive freshwater basins for Pacific salmon have and will continue to see increases in water

temperatures that exceed known tolerances limits (Patterson *et al.* 2007, Ferrari *et al.* 2007,

Mantua *et al.* 2010). Over the coming decades, maximum average summer stream temperatures

are projected to increase to ~ 21°C in northern latitudes (e.g. Alaska; Mauger *et al.* 2017), ~ 22-

27°C in mid-latitudes (e.g. British Columbia, Washington, Oregon; Hague *et al.* 2011, Ficklin *et*

al. 2014), and ~ 30 °C in southern latitudes (e.g. California, Ficklin *et al*. 2013). Considering the

imminent threat that climate change poses to the survival and persistence of Pacific salmon

throughout their range, in the following section I consider the UTTRs for the five species in

relation to expected warming. I developed these UTTRs based on data extracted from this

literature review, to make general assessments regarding long-term persistence of these species

in a warming world. However, these proposed UTTRs have limitations arising from data

deficiencies for UTL from Pacific salmon in certain regions (i.e. Alaska), species (i.e. chum and

pink salmon) and life stages (i.e. ocean rearing or spawning). Further, given the substantial and

compelling evidence that thermal tolerance is highly population-specific, managers should aim to

develop thermal guidelines at population, rather than species-wide level (please refer to section

2.3.4 for more details).

Sockeye salmon

More region-, population- and life-stage specific UTL research has been conducted on sockeye

salmon than any of the other species of Pacific salmon. Therefore, they provide the best model

for developing life stage-specific UTTRs. Sockeye salmon display a high degree of intraspecific

(i.e. among population) variation in thermal tolerance across life stages. In contrasting seven to nine populations of Fraser River sockeye, the UTTR for: embryos is ~15 to 17°C, juveniles is ~23-25°C, and adults is ~18-29°C (Appendix 1, Table 2). Considering just the adult migrant life stage, water temperatures have routinely exceeded 18°C for several days to weeks in the summer, with several days exceeding 20°C, therefore all adult migrants are currently experiencing temperatures that are within their UTTR - this has led to massive *en route* migration mortality events in some populations (Hinch and Martens 2011). As summer temperatures are predicted to routinely reach 22°C in the Fraser River in the near future (Patterson *et al.* 2007, Department of Fisheries and Oceans, Canada 2020), the UTTR will be exceeded for adults in additional populations (Eliason *et al.* 2011).

In applying a UTTR framework, it is important to consider regional (e.g. latitudinal) differences. For example, summer temperatures in the Columbia River already exceed 22°C (Hinrichsen et al. 2011) and are expected to increase by a further 3-5°C (Ficklin *et al.* 2014, Crozier *et al.* 2020). The UTTR for migrating adult sockeye salmon in this region is 21°C - 24°C (Appendix 1, Table 1), which is lower than the expected temperature levels in the coming years. Therefore, we might expect to see future high levels of migration mortality in these populations similar to Fraser River populations. The one caveat is that this UTTR does not include upper thermal limits derived from physiological-based approaches like with the Fraser populations, so this UTTR may reflect a conservative range.

Chinook salmon

Proposed UTL estimates for Chinook salmon suggest that withstanding warming conditions will become increasingly difficult and potentially impossible for some populations. Based on all proposed UTL estimates identified in this review the UTTR for: embryos is ~12-17°C, juveniles is ~20-29°C, adult migrants is ~18-26°C. (Appendix 1, Table 3), Given that water temperatures in major Chinook salmon producing basins are expected to reach average temperatures up to 21°C in their northern range, and 30°C in their southern range in the coming decades (Ficklin e*t al.* 2013, Mauger *et al*. 2017), withstanding projected warming will be incredibly challenging for this species as summer river temperatures approach (northern latitudes) and exceed (southern latitudes) the current UTTR for both juvenile and adult migrant life stages. These UTTRs do not necessarily encompass the extent to which thermal tolerance may vary by population. Previous research indicates some degree of intraspecific differences in thermal tolerance, however, unlike with sockeye salmon, little work has been undertaken to quantify the extent of this variation (Zillig *et al.* 2021). A study conducted on a hatchery population of juvenile Chinook salmon native to California found that the full extent of absolute aerobic scope could be maintained at temperatures up to 23°C (Poletto *et al.* 2017). This superior aerobic capacity at high temperatures suggests that some populations may possess thermal tolerance traits that will allow them to adapt to future thermal conditions. Further investigation should be undertaken to determine whether traits associated with this thermal insensitivity in absolute aerobic capacity are present in other populations as they may provide a critical source for genetic rescue, especially in southern latitudes where thermal exposure is particularly high.

Coho salmon

Limited research on the thermal requirements for embryonic development has been conducted

for coho salmon. However, 14°C has been identified as a critical temperature for incubation

(Tang *et al*. 1987, Murray and McPhail 1988). The UTTR in juvenile coho salmon appears to be

higher than both Chinook and sockeye salmon with reported limits ranging from ~24-29°C

(Appendix 1, Table 4). Additionally, optimal temperatures for swimming performance in

juvenile coho salmon occur at 20°C (Brett *et al.* 1958), a relatively high temperature indicating

their aerobic capacity at this life stage may be robust to expected warming conditions. For

migrating adults, it was not possible to derive a UTTR; however, the UTL was low for a winter-

run population (~17°C; Appendix 1, Table 4). A recent study found that maximum aerobic scope

in migrating adults from a coastal population did not differ over a broad thermal range (9-18°C)

suggesting that, like with juveniles, their aerobic scope is thermally insensitive at temperatures

approaching 20°C (Kraskura *et al.* 2021). Despite high aerobic capacity under relatively warm

temperatures for both juveniles and adults, cumulative effects of climate change and reduction in

habitat quality is a major threat to survival and future persistence of coho salmon, particularly in

the southern extent of their range where many populations are endangered (Grant *et al*. 2019,

Stenhouse et al. 2012). Maximum summer daily temperatures in southern and mid latitude

regions regularly exceed 21°C and are expected to reach ~24 °C within the next four decades

(Crozier *et al*. 2020). Therefore while, future warming will not reach the juvenile UTTR for this

species, and is only a few degrees above physiological optimum temperatures for adults, the

combined impacts of habitat degradation and further increases in temperature above current

optimums is a major concern for this species. Due to their extended rearing period in small

streams, juveniles also experience higher exposure to rapidly rising stream temperatures during

the summer before migrating downstream to the ocean. Further investigation into potential

intraspecific variation in adult and embryonic thermal tolerance in coho salmon is recommended to determine whether some populations possess favourable traits for selection to act upon as temperatures continue to rise.

Chum salmon

Chum salmon are the most data deficient of the five Pacific salmon species with respect to defining upper thermal tolerance limits. The embryonic temperature limit for a chum salmon population from Vancouver Island, B.C. was 14°C (Murray and McPhail 1988). Maximum temperature tolerance was found to be 23.9°C in a juvenile hatchery population in British Columbia (Brett 1952) and 27.8°C for an adult migrant population from the Sanriku coast in Japan (Abe *et al.* 2019). Temperature-based distributional limits in the ocean range from 10.4-13°C (Appendix 1, Table 5). Since very few studies have been conducted, I was unable to propose life-stage specific UTTR's for this species. However, the combination of a life-history where this species spends limited time in freshwater and the peak migration time occurs in the late-fall allows the majority of chum salmon populations to avoid lethal temperature exposures. Based on these behaviours, it is expected that chum salmon will be better able to withstand future climate warming than species which have greater rates of migration during the summer and early fall and who spend more time in freshwater as both juveniles and adults.

Pink salmon

Pink salmon have also received limited attention in thermal tolerance research, however, the data that exist suggests that some populations are highly thermally tolerant and are overall less vulnerable to rising freshwater temperatures and declining habitat quality. Like chum and coho

salmon, the critical temperature for incubation is 14°C for a coastal population of pink salmon in the Fraser River. The maximum temperature limit in the juvenile life stage has been identified as 25°C (Brett 1952) and marine temperature limits have been estimated to range from 10.4-16.6°C (Appendix 1, Table 6). To date no studies have attempted to quantity upper critical thermal tolerance in the adult life stage, and limited studies have been conducted on embryo and juvenile phases, preventing the development of life-stage specific UTTRs for this species. However, a study by Clark $et\ al.$ (2011) indicates that some populations may have the capacity to maintain a high degree of aerobic scope at temperatures exceeding 20°C. Though it is important to note that the rate of decline in aerobic scope above $T_{opt(AS)}$ is unknown and there is a possibility that it could drop off dramatically beyond this point. Additionally, pink salmon have been found to have a higher propensity to stray than other populations of Pacific salmon which allows them to avoid adverse environmental conditions in native spawning areas (Keefer and Caudill 2014). This may also allow for greater transfer of thermally tolerant traits among populations within the same river systems. Further, the relatively short generation time for these species (two years) may allow for more rapid evolution of thermally tolerant traits relative to other species like Chinook salmon where generation times can extend up to seven years. Pink salmon also spend most of their lifecycle in the marine environment and migrate towards the ocean almost immediately after emergence. This substantially reduces their potential exposure to water temperatures that exceed juvenile tolerance thresholds (Grant $et\ al$. 2019). Their superior aerobic capacity in combination with their high rates of straying, short generation time, and low thermal exposure as juveniles indicates that this species may emerge as a front-runner with respect to withstanding climate-induced warming.

2.4 Conclusion

In this review, I have outlined the importance of considering the potential sources of variation in reported upper thermal limits (UTL) for Pacific salmon. More specifically, I have demonstrated how the use of a species- and life stage-specific 'upper thermal tolerance range' (UTTR) can provide a more accurate depiction of how these species may respond to future warming as such ranges encompass numerous methodologies and various thermal responses. This is especially important since both behavioural and physiological thermal responses will play significant roles in potential evolutionary adaptation to warmer temperatures. However, the UTTRs proposed in this paper are meant to demonstrate a new framework for comparing thermal tolerance to thermal exposure, and thus aid in determining vulnerability to warming. Major data deficiencies exist at region/latitude, species, population, and life stage levels for all species reviewed. Therefore, continued research into Pacific salmonid UTLs should continue to be conducted across the native range in additional life stages to develop comprehensive UTTRs that more completely reflect the full extent of the variability in thermal tolerance. Another caveat is that other factors can drive reductions in functional thermal limits (e.g. oxygen content, disease, fisheries capture, flow) and therefore, UTTRs may be a liberal estimate of overall tolerance to warming given the impacts of cumulative stressors. Thermal tolerance research is dominated by studies that assess UTL in Chinook, sockeye and coho salmon. I were unable to develop species-level UTTRs for pink and chum salmon due to data deficiencies in multiple life-stages. However, their life-history strategies (e.g., limited rearing in freshwater, high rates of straying) may allow for greater resilience to future warming, and, given their relatively high abundances and high fisheries value, further investigation into their UTTR is strongly recommended.

I identified seven methodological approaches that have been employed to quantify UTL for Pacific salmon. Some of these approaches possess more ecological relevance than others and, in certain cases, their use may be limited to specific life stages. Further, our findings demonstrate that both inherent (species, population, life-stage) and methodological (with in and among) variation contribute to the considerable differences observed in proposed UTL for Pacific salmon. These results highlight that vulnerability to warming is both population- and life stage-specific and future fisheries management and conservation actions should be developed with careful consideration of these nuances. However, all of the approaches I reviewed possess some limitations owing to logistics and/or ecological realism and there is certainly room for the development of novel approaches that fill gaps in our understanding of the overall thermal response of Pacific salmonids to rising temperatures. Recent studies that have examined thermal stress through cellular stress responses (e.g. heat shock protein induction, transcriptomics), represent another promising methodological tool for identifying UTLs in Pacific salmon (Jeffries et al. 2012, Anttila *et al.* 2014, Carey *et al*. 2019, von Biela *et al.* 2021). These molecular approaches could be integrated with other whole animal physiological methods like aerobic scope to provide a more 'mechanistic' perspective in creating UTTRs. Lastly, there is a dearth of information on the role of life stage and sex in relation to thermal tolerance and is an area where future research should be directed.

Overall, I advocate for careful interpretation of UTL estimates and consideration of a range of values from diverse methodologies that possess that most ecological realism for a given life-stage, species, or population to develop effective management strategies and make meaningful predictions about future persistence and survival of Pacific salmon in a warming world.

Table 2.1 - Study types used to assess thermal tolerance in Pacific salmon

Study Type	Description	References
Swimming/Physiology	Primarily used in this context to assess the relationship between temperature and scope for activity	Brett *et al.* (1958), Davis *et al.* (1963), Brett (1964), Brett (1967), Griffiths and Alderdice (1972), Glova and McInerney (1977), Gray *et al.* (1977), Brett (1982), Lee *et al.* (2003 a,b), Tierney and Farrell (2004), MacNutt *et al.* (2006), Steinhausen *et al.* (2008), Clark *et al.* 2011, Eliason *et al.* (2011), Burt *et al.* (2012b), Casselman *et al.* 2012, Eliason *et al.* (2013 a,b), Anttila *et al.* (2013, 2014),), Raby *et al.* (2016), Eliason *et al.* (2017), Polletto et al. (2017), Abe *et al.* (2019),
Incubation and Rearing	Studies that incubate and rear individuals under different thermal regimes and may assess survival and growth and behavior during alevins and fry	Olson and Foster (1955), Heming (1982), Kwain (1982), Garling and Masterson (1985), Beacham and Murray (1986a,b), Tang *et al.* (1987), Beacham (1988), Murray and McPhail (1988), Beacham and Murray (1988), 1989, 1990), Murray and Beacham (1990), Beacham and Varnavskaya (1991), Sauter *et al.* (1996), Marine and Cech (2004), Geist *et al.* 2006, Burt *et al.* (2012a,b), Whitney *et al.* (2013), Muñoz *et al.* (2014, 2015), Chen *et al.* (2015, a,b), Del Rio *et al.* (2019), Muñoz *et al.* (2018),
Capture/ Count	Involves trawl surveys in the ocean to determine distributional temperature limits , as well as counting as fish pass dams and weirs to establish thermal migration barriers (Quinn et al. 1997, Stiff et al. 2019)	Fish and Hanavan (1948), Coutant (1973), Lindsay *et al.* (1986), Alabaster (1988), Pearcy et al. (1989), MacDonald *et al.* (2000), Hodgson and Quinn (2002), Madej *et al.* (2006), Nagat *et al.* (2007), Morita (2015), Chiaramonte *et al.* (2016), Bowerman *et al.* (2018), Carey *et al.* (2019),

Holding	Held at acclimation and test temperatures and then exposed to test temperatures (e.g. CTmax, UILT) to determine lethal (Geist et al. 2010) and sublethal (Jeffries et al. 2012) responses to high temperatures, temperature preferences and the effects of temperature on susceptibility to infection (Gray et al. 1977, Groberg et al. 1973).	Donaldson and Foster (1941), Brett (1952), Sylvester (1972), Becker (1973), Coutant (1973),Wedemeyer (1973), Fryer and Pilcher (1974), DeHart (1975), Holt *et al.* (1975), Udey *et al.* (1975), Fryer *et al.* (1976), Groberg *et al.* (1978), Becker and Genoway (1979), Groberg *et al.* (1983), Neitzel and Baker (1985), Thomas *et al.* (1986), Barton and Schreck (1987), Berman (1990), McGeer *et al.* (1991), Franklin *et al.* (1992), Varnavsky *et al.* (1993), Konecki *et al.* (1995a, 1995b), Glova and McInerney (1997), Servizi and Jensen (1997), Palmisano *et al.* (2000), Sauter *et al.* (2001), Mesa *et al.* (2002), Birtwell *et al*. (2003), Zenke *et al.* (2005), Quigley and Hinch (2006), Arkush *et al.* 2008, Clark et al. (2008), Crossin *et al.* (2008), Steinhausen *et al.* (2008), Bellgraph *et al.* (2010), Geist *et al.* (2010), Clark *et al.* (2011,2012), Jeffries *et al.* (2012a, 2012b) Antilla et al. (2013), Ray et al. (2012), Chen *et al*. (2013), Jeffires *et al*. (2014), Ray *et al.* (2014), Muñoz *et al.* (2014, 2015), Tomalty *et al.* (2015), Chiaramonte *et al.* (2016), Prystay *et al.* (2017), Baird *et al*. (2018), Teffer *et al*. (2018, 2019), Muñoz *et al.* (2018), Abe *et al*. (2019), Carey *et al.* (2019), Elsner and Shrimpton 2019,
Capture Simulation	Capture simulations: mimic a capture experience (recreational or commercial) at various temperatures to assess the interactive effects of these two stressors (Gale et al. 2011, Clark et al. 2012, Teffer et al. 2018)	Barton and Schreck (1987), Kreiberg and Blackburn (1994), Gale *et al*. (2011), Clark *et al*. (2012), Robinson *et al*. (2013), Gale *et al*. (2014), Raby *et al*. (2015), Prystay *et al*. (2017), Teffer *et al*. (2018. 2019)
Tagging	Includes sonic tags, archival tags, radio telemetry, PIT tags and acoustic telemetry – this study type began to be used in thermal tolerance research in the 1970s as a way to determine thermal barriers that arose from anthropogenic flow alteration in the San Joaquin Delta (Hallock 1970) and increased in prominence from the 2000s onwards primarily for identifying a threshold for the onset of temperatures that impact the ability to successfully migrate upstream (Caudill et al. 2007, 2013, Hyatt et al. 2003, Farrell et al. 2008)	Major and Mighell (1967), Hallock (1970), Baker *et al*. (1995), Connor *et al*. (2003), Hinke *et al*. (2005), Naughton *et al*. (2005), Newell and Quinn (2005), Goniea *et al*. (2006), Salinger and Anderson (2006), Caudill *et al*. (2007), Keefer *et al*. (2007, 2008), Crossin *et al*. (2008), Farrell *et al*. (2008), Chesney *et al*. (2009), Tiffan *et al*. (2009), Bellgraph *et al*. (2010), MacDonald *et al*. (2010), Mathes *et al*. (2010), Pon *et al*. (2010), Roscoe *et al*. (2010),Strange (2010), Martins *et al*. (2011, 2012), Hayes *et al*. (2012), Sutton and Soto (2012), Caudill *et al*. (2013), Antilla *et al*. (2014), Elde*r et al*. (2016),Mann and Snow (2018), Minke-Martin *et al*. (2018), Teffer *et al*. (2018), Courtney *et al*. (2019), Drenner *et al*. (2019),
Model	Modelling techniques have been utilized for thermal tolerance research in for a range of purposes including:	

- characterizing thermal regimes historically tolerated by salmon to predict likely effects of forest practices on adult migrant survival (Berman 1990), - developing predictions about the combined effects of temperature and flow on successful up river migration (MacDonald et al. 2010), - determining the potential effects of water temperature on parasite induced mortality (Fujiwara et al.2014), and exploring the joint effects of fixed temperatures on net energy gain and growth (Huey and Kingslover 2019)	

Table 2.2 - Methodologies employed to quantify upper thermal tolerance in Pacific salmon

Behavioural	Methodologies	
	Preference/Avoidance	Temperature based observations on areas where fish most densely congregate and/or actively avoid.
	Thermal Migration Barrier	Temperatures at which migrating up or downstream becomes challenging (e.g. slower passage rates, cessation of migration, decreased survival)
	Temperature Limits to Distribution	Presence or absence surveys linked to temperature profiles to determine temperature-based limits to distribution
	Temperature Driven Changes in Behaviour	Determining temperatures at which obvious changes in behaviour occur (e.g. increased used of off-channel thermal refugia, decreased ability to avoid predation)
Physiological	**Methodologies**	
	Scope for Activity ($T_{opt(AS)}$, $T_{crit(AS)}$, T_p, T_{ABT}, T_{arr})	Quantification of optimal and critical temperatures for performing activities beyond basic maintenance
	Scope for Growth	Quantification of optimal and critical temperatures for growth

		through the development of a temperature-dependent scope for growth curve.
	Upper Incipient Lethal Temperature (UILT)	Abrupt transfer from acclimation to exposure temperature. Resistance times to an acute temperature increase is assessed.
	Critical Thermal Maximum (CT_{max})	Gradual heating from acclimation temperature to the temperature at which test fish lose equilibrium.
	Incubation and Rearing Optimums and Limits	Quantification of optimal and critical temperatures for embryonic and early juvenile life stages through incubating at a range of temperatures and observing differences in survival between groups.
	Critical Temperature (T_{crit})	Temperature below which no mortality occurs.
	Cellular/Tissue Response	Molecular approach to identifying critical temperature thresholds in fish (e.g. induction of heat shock proteins, transcriptomics)

Table 2.3 - $T_{opt(AS)}$ estimates for sockeye, coho, pink and chum salmon (Lee et al. 2003, Farrell et al. 2008. Eliason et al. 2011, 2013, Clark et al. 2011, Abe et al. 2019). Ranges are given when optimal temperatures for aerobic scope has been assessed in more than one study: sockeye N=9 (six populations), coho N=2 (one population, chum N=2 (two populations).

Species	Sockeye	Coho	Chum	Pink
$T_{opt(AS)}$ average (°C)	15.89	8.75	15.80	21.00
$T_{opt(AS)}$ range (°C)	14.50-17.20	8.50-9.00	14.00-17.60	--
Mean Migration Temperature (°C)	~16.2	~7.1	~11.1	~16.9
Maximum Migration Temperature (°C)	~22	~12	~19	~21
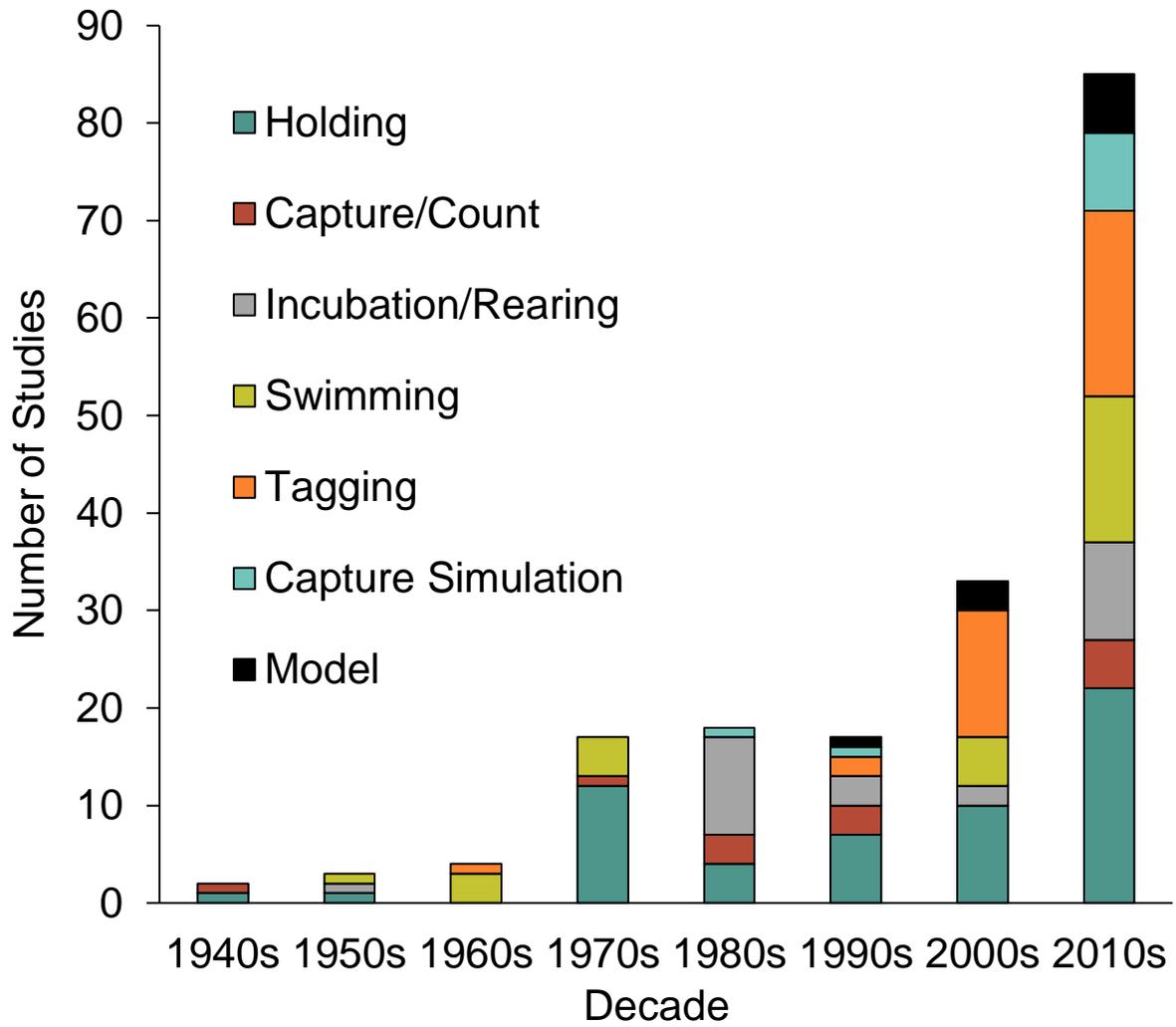
Figure 2.1- Number of studies by decade and by study type. See Table 2.2 for more details about each study type
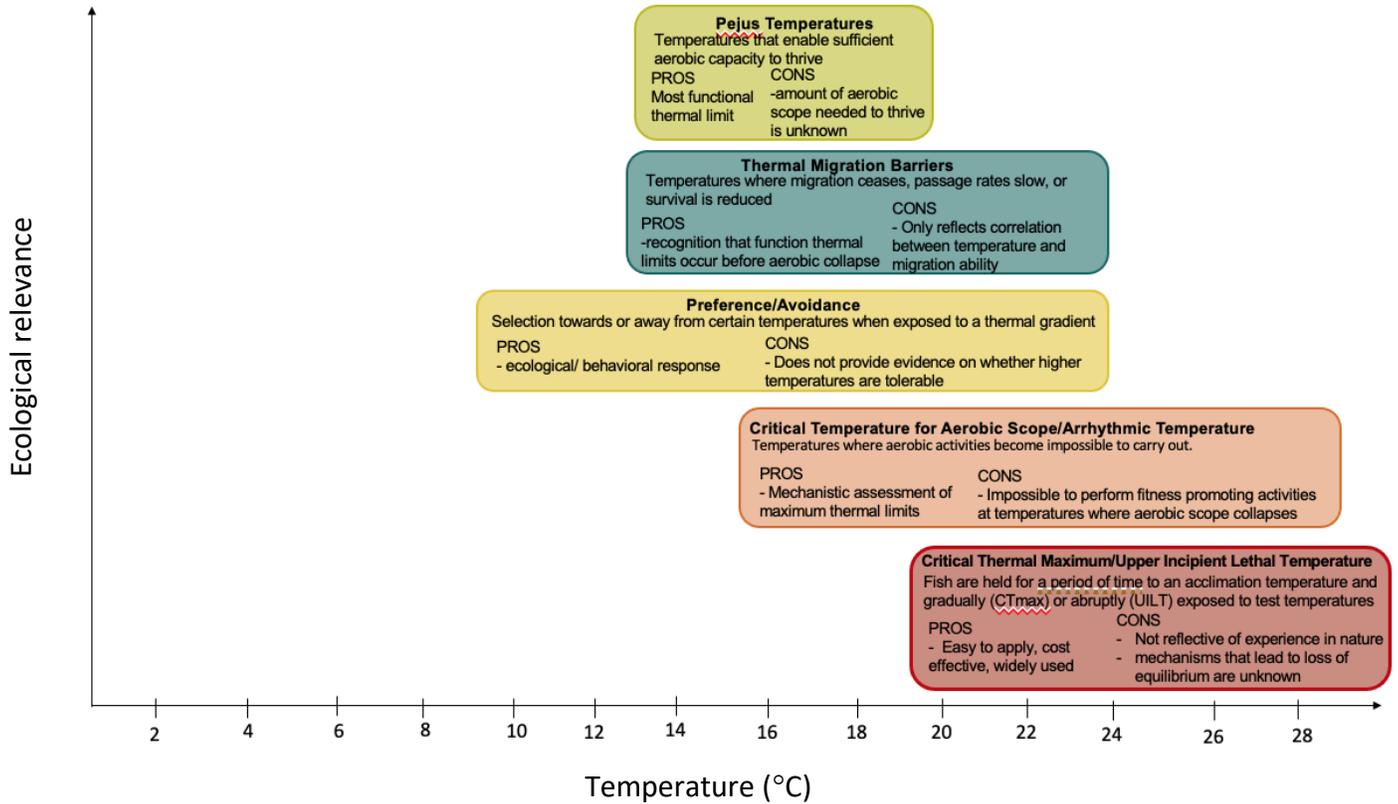
Figure 2.2 - Conceptual Figure illustrating the relative ecological realism of the Critical Thermal Maximum (CT$_{max}$), Upper Incipient Lethal Temperature (UILT), Critical Temperature for Aerobic Scope (T$_{crit(AS)}$), Arrhythmic Temperature (T$_{arr}$), Avoidance, Thermal Migration Barrier, and Pejus Temperatures (Tp) methodologies for quantifying thermal limits of Pacific salmon.
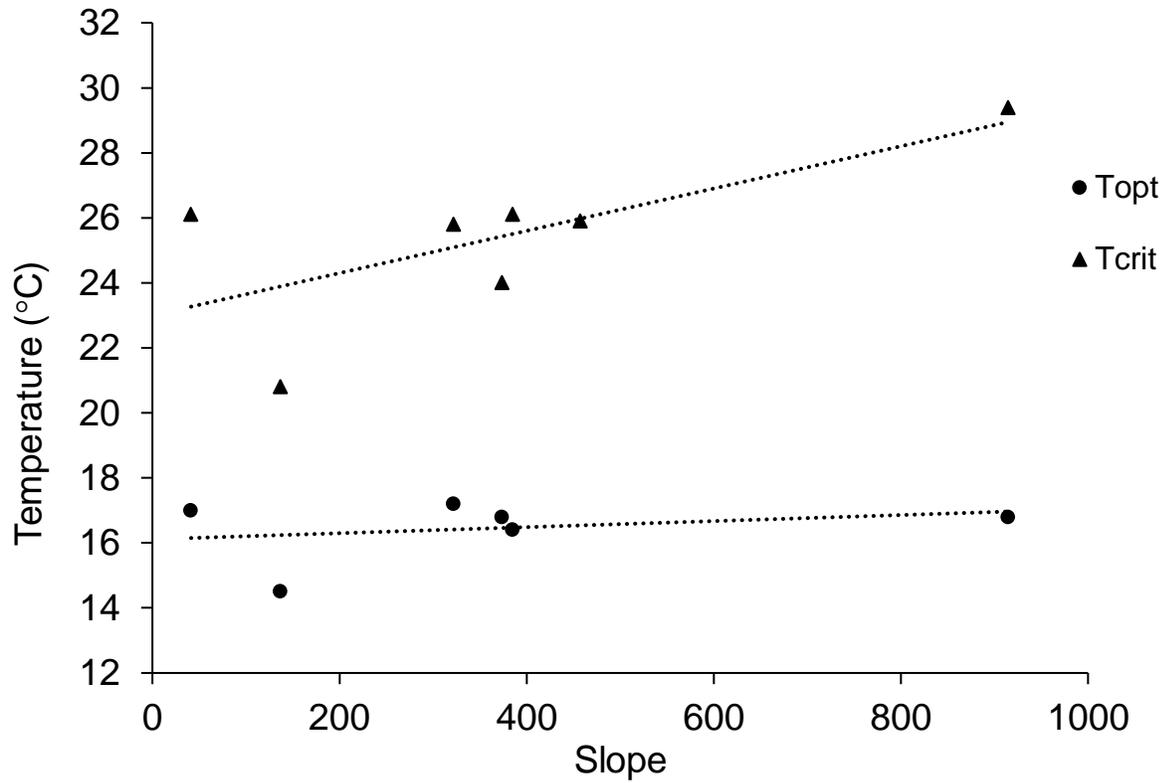
Figure 2.3 - Correlation between migration slope (Migration Elevation/Migration Distance) and Critical (Tcrit) and Optimal (Topt) for Aerobic scope for Fraser River adult migrating sockeye salmon populations (data from Eliason et al. 2011, 2013).
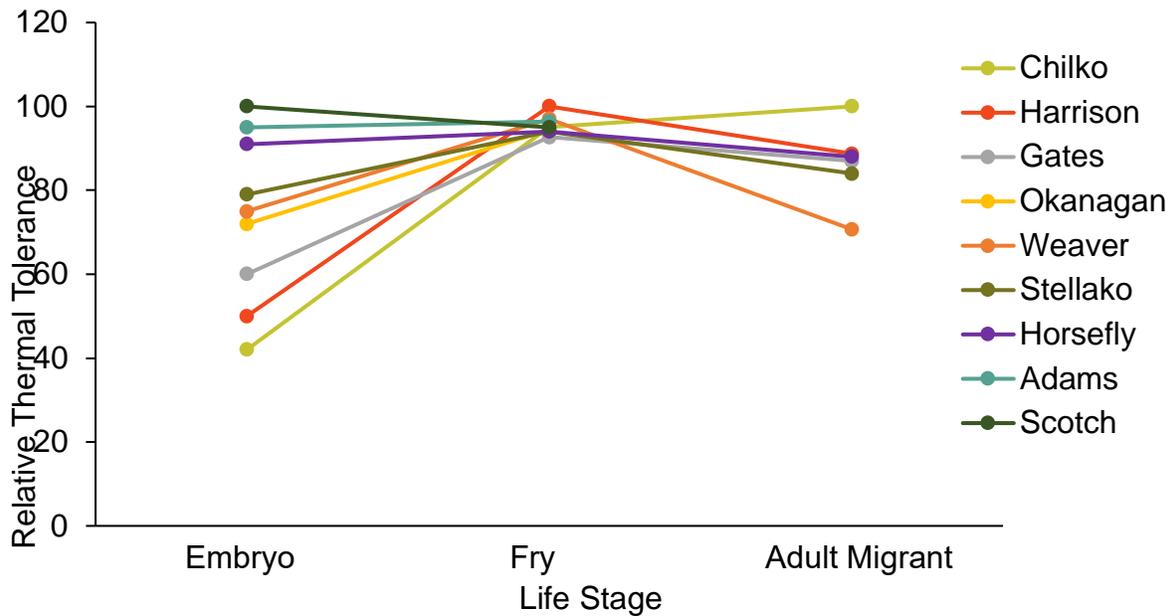
Figure 2.4 - Intraspecific variation in relative upper thermal tolerance across the sockeye salmon life cycle. Relative thermal tolerance adapted from critical temperatures for aerobic scope ($T_{crit(AS)}$) in adults (Eliason et al. 2011), fry (1 g) reared at 10°C, critical thermal maximums (CT_{max}) for fry (1g) reared at 10°C, (Chen et al 2013) and estimates of 60% survival (derived from survival curves for embryos incubated at 10°C, 14°C, and 16°C) for embryos (Whitney et al 2013) were compared. Relative thermal tolerance for each life stage was generated by relating each population to the population with the highest upper thermal limit (UTL): 100 - (population max UTL – population X UTL)/population max UTL.
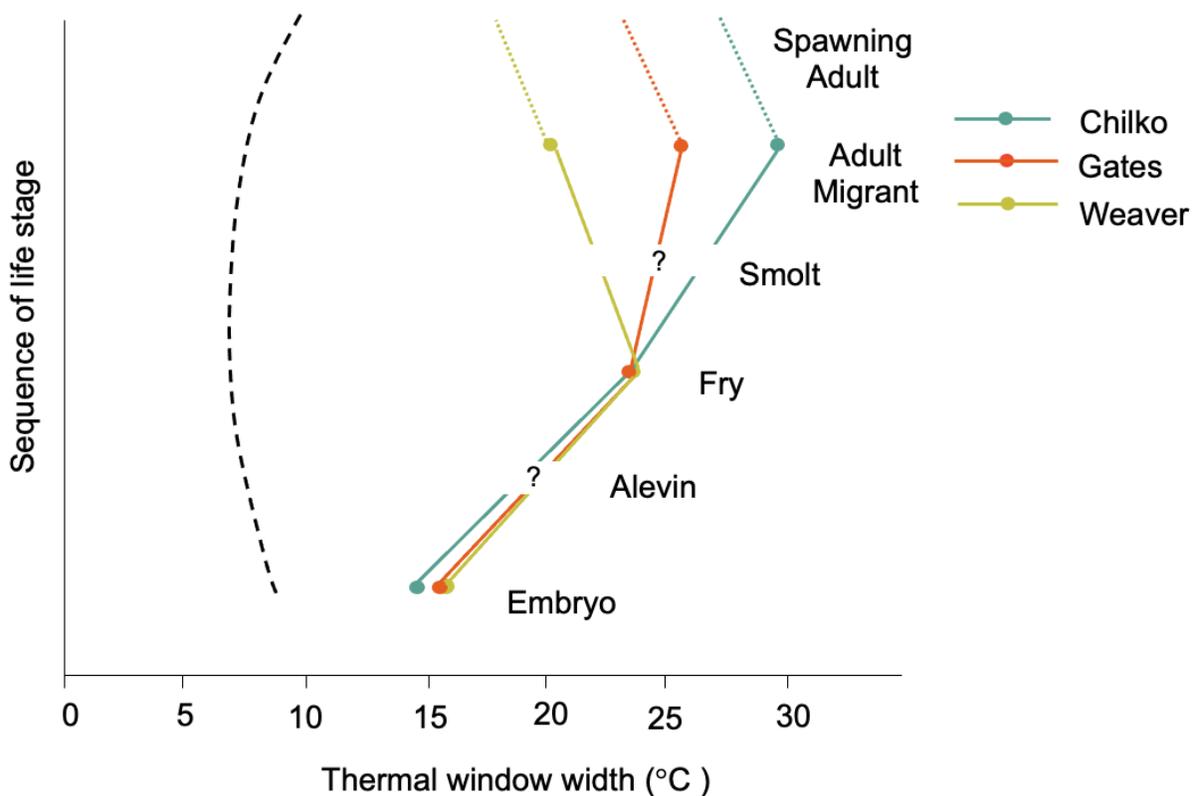
Figure 2.5 - Life stage specific variation in absolute upper thermal tolerance for Fraser River sockeye salmon populations Weaver, Gates, and Chilko based on comparable critical temperatures: critical temperatures for aerobic scope ($T_{crit(AS)}$) in adults (Eliason et al. 2011), critical thermal maximums (CT_{max}) for fry (1g) reared at 10°C (Chen et al 2013), and estimates of 60% survival in embryos (from survival curves for embryos incubated at 10°C, 14°C, and 16°C; Whitney et al 2013). Dotted lines illustrate hypothetical upper thermal tolerance in mature spawning adults and the grey dashed line represents a hypothetical lower temperature tolerance limit. (unp). The range of temperatures between the upper and lower tolerance limits represents the thermal window width for a given life stage. The embryo and reproductive adult life stages are predicted to have the narrowest thermal window widths (Portner and Farrell 2008; Dahlke et al 2020), which is likely true for Weaver, though not for Chilko. Despite considerable research attention on thermal tolerance in sockeye salmon, gaps in knowledge remain.
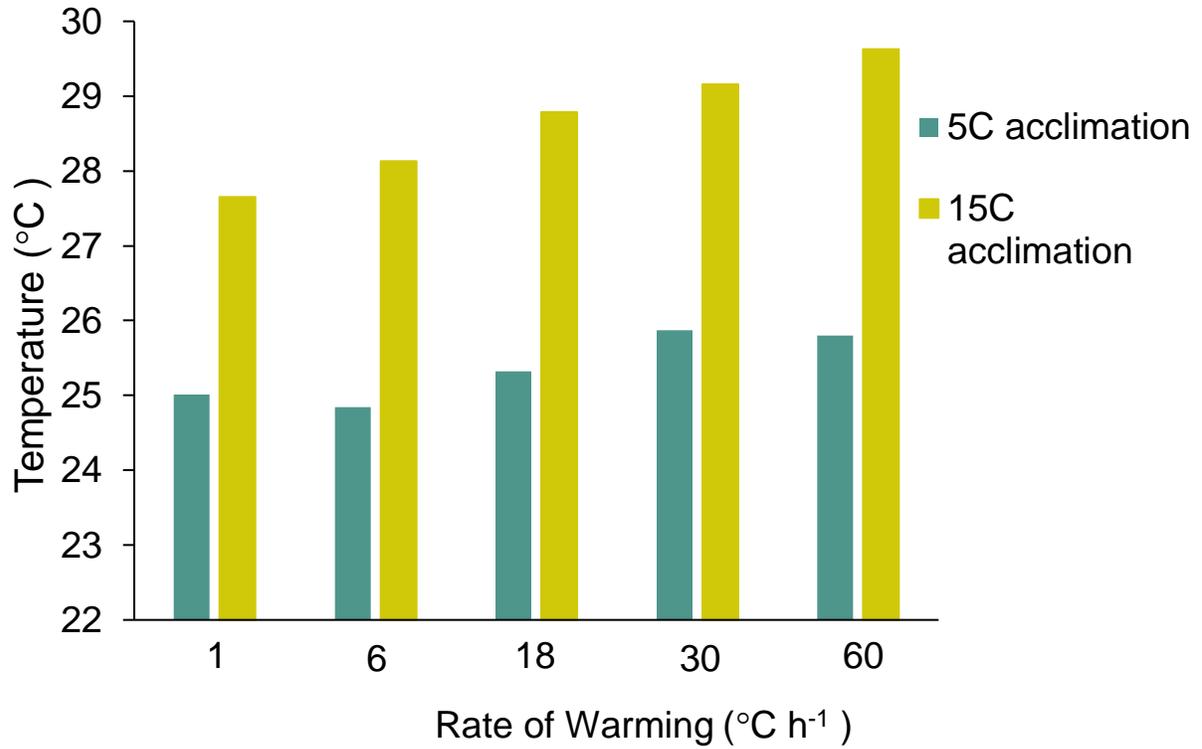
Figure 2.6 - Critical thermal maximum (CT_{max}) values obtained for coho salmon when using different acclimation temperatures and heating rates (adapted from Becker and Genoway 1979).

Chapter 3: Life-stage and sex-specific differences in the upper thermal tolerance of Kokanee Salmon (*Oncorhynchus nerka*)

3.1 Introduction

High proclivity for natal homing, distinct run timing and strong localized selective pressures have contributed to the evolution of hundreds of genetically distinct populations of both resident and anadromous *Oncorhynchus nerka* with fine-tuned local adaptations (Varnavskaya *et al.* 1994, Taylor *et al.* 1996, Chang *et al.* 2021) As such, a high degree of variability in thermal tolerance has been found among and within populations of sockeye salmon (Eliason *et al.* 2011, 2013). Within populations, thermal tolerance has been hypothesized to vary across the lifecycle, with the narrowest thermal windows occurring during embryonic and spawning life stages and becoming widest in the juvenile life stage (Pörtner and Farrell 2008, Dhalke *et al.* 2020). A handful of studies have also begun to examine potential sex-specific differences in the temperature dependence of aerobic and cardiac scope (Sandblom *et al.* 2009, Clark et *al.* 2011, Kraskura *et al.* 2021). Further a recent review of mortality in migrating sockeye salmon, identified disproportionately higher rates of mortality in females, attributing this difference to a wide range of mechanisms including energy depletion, cardiac collapse, physiological stress, and immune issues (Hinch *et al.* 2021).

One recurring criticism directed at papers that aim to identify patterns and quantify variation in thermal tolerance across the lifecycle, is that these assessments may be confounded by variation in the methods used to investigate thermal tolerance at different life-stages (Pottier *et al.* 2022). In Chapter 2, I provided an assessment of life-stage specific differences in sockeye salmon thermal tolerance. However, a limitation of this case-study was that thermal tolerance at each life stage was assessed using a different methodological approach. Therefore, some of the

variation in upper thermal tolerance may be attributed to differences in experimental design as well to the fact that different methodologies assess different thermal responses (i.e. loss of equilibrium, survival at high temperatures, collapse of aerobic scope). As a result, a major knowledge gap identified in Chapter 2, is the lack of thermal tolerance studies focused on assessing life-stage specific differences in upper thermal tolerance using identical experimental procedures.

The experiments performed in this study employ two commonly used approaches for evaluating thermal tolerance in Pacific salmon (the Critical Thermal Method, CTM, and temperature dependence of Aerobic Scope, AS) to investigate ontogenetic and sex-specific differences in the thermal tolerance of Kokanee salmon (*Oncorhynchus nerka)*. Kokanee salmon are a vastly understudied life form of *O. nerka*, with little known about its general ecology, behaviour and physiology. Across their native range, *O. nerka* exhibit a spectrum of life-history strategies (Quinn and Myers, 2004) and there is evidence that all ecotypes possess the ability to adopt either resident or anadromous migration tactics (Dodson *et al.* 2013). In British Columbia, sockeye salmon populations have repeatedly given rise to sympatric Kokanee since the last glaciation (Lemay and Russello 2015). However, divergent reproductive behaviors are often displayed with respect to spawning habitat and timing (Lemay and Russello 2015). As a result, persistent genetic differences have been found between co-occurring populations of sockeye and Kokanee salmon (Taylor *et al.* 1996). While anadromous life forms of *O. nerka* are in dramatic decline, resident populations are abundant and may be better able to withstand climate change induced warming than anadromous forms. Research into the genetic structure and phenotypic specialization within and among populations of Kokanee salmon can provide key insights regarding the persistence and recovery of declining populations of both anadromous and resident

O. nerka in the climate change era. Therefore, the third chapter of this thesis focuses on

quantifying life stage- and sex-specific differences in optimal and critical temperatures for a

single population of Kokanee salmon, an area where limited research has been conducted.

The CTM and temperature dependence of AS were selected as the thermal performance

experiments for this study since they are both commonly used methods throughout the literature

on Pacific salmon thermal tolerance (Farrell *et al*. 2008, Eliason *et al*. 2011, Poletto *et al.* 2017,

Kraskura *et al*. 2021). CTM is one of the most widely used approaches for quantifying upper

thermal limits in ectotherms (Beitinger *et al.* 2000). It is used to develop an estimate of CT_{max} by

acclimating organisms to a given temperature and then increasing the temperature at a constant

rate until the test fish exhibit a loss of equilibrium (Beitinger *et al.* 2000). This method is

repeatable, easy to perform, and relatively low cost compared to other approaches. Results

yielded from CTM studies provide information about the overall thermal response to climate

warming that are not evident in AS studies, such as, the plasticity of upper thermal tolerance with

acclimation temperature (Becker and Genoway 1979). The CT_{max} (the upper thermal tolerance

metric obtained from CTM studies) is also a useful relative measure of thermal tolerance and has

been used to compare vulnerability to warming across species and populations (Pinsky *et al.*

2019). In addition to CTM studies, estimating metabolic rates in fish has long been a major

pursuit in the field of comparative physiology (Steffensen *et al.* 1984, Svedson *et al.* 2016,

Killen *et al*. 2021). AS, the difference between maximal and standard metabolic rates, has been

used to examine a broad range of ecological phenomena (Killen *et al*. 2021, Klieber *et al.* 1947,

Hatton *et al*. 2019). More recently, AS has been applied in the context of investigating the

capacity of fish to cope with warming in aquatic ecosystems (Lee et *al.* 2003a, Clark *et al*. 2011,

Eliason *et al.* 2011, 2013, Abe *et al.* 2013, Kraskura *et al.* 2021). The temperature dependence of AS can be expressed in the form of a thermal performance curve (TPC) that can provide valuable predictions about the theoretical capacity of fish to preform aerobic activities as temperatures increase (Eliason et al. 2022).

Given the paucity of information on Kokanee salmon thermal tolerance and sex-specific differences in Pacific salmon thermal tolerance in general, as well as the absence of studies focused on evaluating ontogenetic variability in upper thermal limits (UTL), there were two primary objectives for this study: 1) determine the upper thermal tolerance limits of Kokanee salmon and 2) characterize potential life-stage and sex-specific differences in thermal tolerance limits. To that end, a stream-spawning population of Kokanee salmon native to southeastern British Columbia, Canada, were briefly exposed to one of five treatment temperatures ranging from ambient to 24°C. Following an overnight temperature exposure, both juvenile and adult fish were used in either the CTM or AS trials to evaluate the upper thermal tolerance limits. I expected that female mortality at high temperatures would be higher than in male fish, and that this discrepancy would be largely driven by reduced AS in females compared to males. Second, I hypothesized that juvenile thermal tolerance would exceed that of spawning adults as this would be consistent with the prevailing theory about how the thermal window of Pacific salmonids expands and contracts across the lifecycle.

3.2 Methods

3.2.1 Study Population

The Norbury creek population of Kokanee salmon were used in this study. This is a non-native population that was inadvertently introduced to Lake Kookanusca (a reservoir of the Libby Dam

in Montana). Lake Kookanusca is a transboundary reservoir located in northwestern Montana and British Columbia and has a total volume of 7.16 km^3 and total length of 148 km (Schmidt, Mebane and Schaar 2020). Between 1969 and 1978, nearly 1.5 million Kokanee salmon were discharged into Norbury Creek by the Kootenay Trout hatchery (Ericksen et al. 2009). These fish originated from a mix of stocks including Meadow Creek, Okanagan River and Chilliwack River Kokanee salmon (Ericksen et al. 2009). Upon release in to Norbury Creek, these fish were thought to be moribund but some survived and rapidly expanded into the newly created reservoir of the Libby Dam (Ericksen et al. 2009). By 1987 the abundance of Kokanee salmon in Lake Kookanusca had reached 5.7 million (Skaar et al. 1996). Kokanee salmon that rear in Lake Kookanusca now spawn in two distinct tributaries, Norbury Creek and the Lussier River. Straying between the two populations is thought to be limited, though no genetic testing has been conducted to confirm this belief. Adult Kokanee salmon from Norbury creek carry out a short migration (maximum of ~ 150 km) from Lake Kookanusca and historically reach spawning grounds between early-to-mid September. At present, the Norbury Creek Kokanee salmon population is a partially-hatchery reared stock, managed by the Kootenay Trout Hatchery. Each year a subset of the returning spawners is collected and brought back to the hatchery. The rest of returning fish spawn naturally in Norbury Creek.

3.2.2 Fish Collection and Holding

Juvenile hatchery-reared Kokanee salmon (N =102) were provided by the Kootenay Trout Hatchery and held in a circular groundwater-fed tank from August 17 – 29, 2021. Groundwater temperature fluctuated between 8-11°C over the course of the study. Juvenile fish were fed a maintenance ration of 50 g/day. Natural photoperiod conditions were mimicked by LED

lightbulb in the center of the room set to turn on at 6:00 and off at 20:30. Sexually mature

Kokanee females (F; N= 91), and males (M; N= 105) returning to spawning grounds in Norbury

Creek were collected at a fish fence, operated by the Kootenay Trout Hatchery, transported by

truck to the experimental site and immediately placed in oval-shaped outdoor holding tanks. The

fish fence was located just below the confluence of the Kootenay River and Norbury Creek

(Figure 3.1). Fish collection and adult thermal tolerance trials trials occurred between September

8-17, 2021. During this period, water temperatures in Norbury creek fluctuated between 7-15°C.

For both juvenile and adult trials, fish were haphazardly assigned to Ambient/12°C, 17°C, 20°C,

22°C, and 24°C treatment groups (N = 20-24 per temperature treatment). The lowest temperature

treatment for juvenile trails was a constant 12 °C, however, due to the wide fluctuation in stream

temperatures, the lowest treatment for adults was an ambient thermal experience where

temperatures were left to fluctuate with the stream. Fish were transferred from the holding tank

to treatment tank (~100 L for juveniles and ~300 L for adults) where water temperature was

increased from ambient to the treatment temperature at a rate of 3°C per h ($\pm$ 0.6°C for juveniles

and $\pm$ 0.7°C for adults). Once the treatment temperature was reached, fish were exposed for 20-

21hr before beginning any experimental trials. This relatively brief holding period offers a more

ecologically relevant exposure to elevated temperatures compared to studies that acclimate fish

over the course of days-weeks. This temperature exposure prior to conducting thermal tolerance

trails, was intended to mimic an acute heat event which is more reflective of what these fish

would experience in the wild, as stream temperatures in this system heavily depend on

fluctuation in air temperatue. It is important to note that with such a brief exposure, acclimation

processes are still in progress. Previous studies have demonstrated the ability for oxygen

consumptions rates (MO_2) to rapidly acclimate over the course of a few days (Anlauf-Dunn et al.

2022). However, fish experience rapid and short-lived (e.g. hours) increases in temperature and will need to be able to cope with these exposures as temperatures continue to rise (Osler et al. 2014). Therefore, investigating the potential for salmon to display plasticity in upper thermal tolerance without complete acclimation is critical to understanding their resistance to acute heat stress.

Each individual was only used once during the study, either for intermittent flow respirometry or CTM experiments. All experimental protocols were approved by the Animal Care Committee at the University of British Columbia in accordance with the Canadian Council of Animal Care (Protocol #A12-0142).

3.2.3 CT_{max} Trials

Upper thermal tolerance limits were determined using the CTM (Fangue *et al.* 2006). The CTM test tank consisted of two coolers (150L and 75L). The smaller cooler contained two Eheim Universal (600 L $^{h-1}$ Eheim universal Aquarium Pump, Eheim, Germany) pumps (one pulling water out of the main cooler and one pushing water into the main cooler), and a single 1700 Watt SmartOne EasyPlug Metal Axial Bottom Heater. The main cooler contained a single Eheim Universal pump used to ensure proper mixing and create surface disruption. A stainless-steel metal coil was also used in adult trials to aid in maintaining the desired warming rate. Fish were transferred from acclimation tanks to the main cooler and allowed to acclimate to the new tank for 10 minutes prior to beginning the trial. Water was heated at a rate of 0.3°C/min from exposure temperature to the endpoint temperature. The endpoint for the trial occurred when fish displayed a loss of equilibrium (inability to right themselves within the water column).

3.2.4 Intermittent Flow Respirometry Trials

Intermittent flow respirometry is routinely used to measure oxygen uptake in aquatic organisms (Killen *et al.* 2021). Test subjects are placed in gas-impermeable chambers with oxygen sensors and exposed to alternating 'flush' and 'measurement' phases. During the measurement phase, chambers are sealed and dissolved oxygen content of the water in the chamber begins to decline as the oxygen is consumed by the fish. Flush phases prevent oxygen levels from falling to the point where hypoxia ensues and the accumulation of metabolic waste occurs (Killen et al. 2021). These alternating phases allow for real-time measurements of oxygen consumption over extended periods of time without disturbing the animals, thereby allowing for estimates of standard or resting metabolic rates (RMR) to be acquired. By allowing for measurements to take place over longer time period, estimates can account for changes in oxygen uptake due to initial handling stress and circadian rhythms.

Respirometers were constructed from clear acrylic containers with an airtight seal and locking mechanisms on all four sides of the lid (volumes of 3.85-4.2 L for adults and 435-450 ml for juveniles). Lids were removable to allow for loading fish. Water was recirculated continuously through each respirometer using an inline water pump (300 L h^{-1} Eheim universal Aquarium Pump, Eheim Germany). Water was flushed from the surrounding tank through each respirometer after an MO_2 measurement cycle was completed to replace water inside the chamber. Four respirometers were placed in each of three 170 L temperature-controlled flow-through tanks, thus 12 fish could be measured simultaneously. Dissolved oxygen content was measured continuously (every 1-2 seconds) in each respirometer with a robust fiber optic oxygen probe and Firesting oxygen optical oxygen meter (Pyroscience, Germany). Each probe was placed along the recirculation line at the exit of the chamber and before the in-line pump. To

measure RMR, fish were transferred directly from treatment tanks to individual respirometers after the temperature exposure period was completed (13:00- 13:30). RMR measurements were taken first over a period of 19-20 h and shade cloths were placed over tanks to minimize potential disturbance. Measurements were taken repeatedly (4-5 minute measurement, 5-6 minute flush; 6 measurements h^{-1} for adults, 7-9 minute measurement, 6-8 minute flush; 4 measurements h^{-1} for juveniles) over the 19-20 h period to account for dynamic changes in oxygen consumption caused by factors such as handling stress and circadian rhythm (Jourdan-Pineau et al. 2010).

Upon completion of RMR measurements, fish were removed from the chambers and introduced to a chase tank where one person manually motivated the fish to burst swim continuously for 3 minutes, to elicit maximal metabolic rate (MMR). Fish were forced to swim by making quick hand movements under water, splashing and lightly touching the caudal fin. After chasing, fish were air exposed for one minute. This chase protocol has been identified as one of the most effective methods for obtaining MMR in salmon during respirometry trials (Little *et al.* 2020), though additional findings suggest that post-exercise respirometry may underestimate maximum metabolic rates in juveniles (Raby et al. 2020). Chases occurred between 9:00-10:00 from September 9-17, 2021 for adults and 10:00 -11:30 from August 20-29 for juveniles. Two fish were chased in separate tanks simultaneously. Dissolved oxygen recordings were initiated as soon as the respirometer was sealed. Immediately after the fish was placed in the chamber, MO2 was recorded for 4 minutes followed by a 6 min flush period. As peak MO2 subsided, measurement cycles were automated (Adults: 4-5 min closed measurement, 5-6 minute flush; 6 measurements h^{-1}, Juveniles: 5-7 min closed measurement, 5-8 minute flush, 4-6 measurements h^{-1}) to measure oxygen consumption over a one hour recovery period. Upon

completion of recovery measurements, fish were removed from respirometers and euthanized via cerebral concussion and mass and length measurements were recorded. Further details of the methods and materials are in Appendix 2, Tables 1-5.

3.2.5 Data and Statistical Analysis

The minimum oxygen uptake rate, measured during a post-absorptive, non-reproductive, quiescent state, is commonly used to measure Standard Metabolic Rate, SMR (Chabot et al. 201). However, since adult fish used in this study were sexually mature, I applied the term resting metabolic rate (RMR) to the average lowest 10% of MO_2 values measured over a 19-20 h period. This RMR calculation was used in estimating Absolute and Factorial Aerobic Scope (AAS = MMR-RMR; FAS = MMR/RMR). MMR was estimated from the slope of the steepest 120 s windows across all measurement cycles. While the chase protocol was intended to induce MMR, >90% of the steepest slope measurements were found during the RMR measurement period in both adult and juvenile trials, indicating that these fish remained relatively active (See Appendix 2; Figure 2 and 3) throughout the respirometry trial. AAS was calculated for each individual and reflects the absolute energetic capacity for activity. Additionally, FAS (the ratio of MMR to RMR) was calculated to identify temperatures where a metabolic constraint might arise under rising temperatures.

In fish, metabolism has been found to scale allometrically with body size (Glazier et al. 2005, da Silva et al. 2006, White et al. 2006, Killen et al. 2010). Consequently, I checked for body mass effects on oxygen consumption rates (MMR and RMR) using a linear regression between natural log transformed raw oxygen consumptions rates and the natural log transformed

body mass of each individual. Regression values confirmed that no scaling factor was necessary (i.e., MMR and RMR scaled isometrically with body mass; Appendix 2, Figure 1).

All data were statistically analyzed using RStudio version 1.4.1717 (2021). A significance level of $\alpha = 0.05$ was applied for all statistical tests. Where necessary, residuals were evaluated for normality using quantile-quantile plots and Shapiro-Wilks test. CT_{max}, MMR, RMR, and AAS were analyzed using two-way ANOVAs and Tukey's post-hoc tests (R package 'caret', Haynes, 2013, Kuhn, 2021). A linear model was developed to assess the relationship between temperature treatment and CT_{max}. I ran additional models with mass, length and Fulton's Condition Factor as random effects; however, these body size metrics did not improve model fit (explained an additional ~2% of the variance). Therefore, the original simple linear regression was used in the analysis. To test my hypothesis that AAS would vary across the life cycle and between sexes, I included the interaction between temperature and group (male, female, juvenile) in all ANOVAs (Type III). For all measurements, the interaction was not significant, therefore, sex and temperature were later assessed independently (Type II ANOVA). To assess differences in RMR across groups, I developed a log-normal linear model fit with RMR as the response variable and two fixed effect factors (temperature and group). To evaluate differences in MMR across groups, a linear model was fit to MMR as the response variable with the same fixed factors as were used in the log linear RMR model. To estimate AAS, second order polynomial models were applied to both juvenile and adult respirometry data. For FAS data, a linear model was developed. Regressions were fit with AAS or FAS as the response variable and treatment temperature and group as fixed effect factors. To investigate a potential cause for sex-specific differences in AS, I looked at differences in relative ventricular mass (RVM) between males and female fish. I also assessed potential differences in additional

morphometrics including: hepatosomatic index (HSI), and total body mass (g). I conducted a two-sample t-test to determine whether RVM, body mass, and HSI was significantly different between sexes.

3.2.6 Evaluating Vulnerability to Warming

Metabolic rate reflects a temperature-dependence performance trait that can influence how vulnerable a given population or species is to warming (Eliason and Farrell 2016). Therefore, in addition to CT_{max} values, functional thermal limits can be extracted from respirometry data. These functional limits are referred to as the Upper Pejus Temperature (T_{pejus}) (Farrell et al. 2008, Eliason et al. 2011). For adults, the upper T_{pejus} was calculated as 80% of total aerobic scope. Previous research suggests that mature adults require ~80-90% of their total aerobic capacity to successfully complete their spawning migration (Farrell et al. 2008, Eliason et al. 2011). I selected the lower end of this range due to the shorter and less hydraulically challenging migration Norbury Creek Kokanee salmon engage in relative to many anadromous sockeye populations. In the juvenile life stage, the full extent of an individual's aerobic capacity is rarely needed to carry out activities essential to survival (Farrell et al. 2016, Adams et al. 2022). As such, the juvenile T_{pejus} was calculated from a FAS threshold rather than as a percentage of total aerobic capacity. As a measure of the proportional amount of scope available to perform aerobic functions that scale with SMR (i.e. digestion), FAS can be indicative of temperatures where a metabolic constraint develops and is therefore a more useful metric to identify temperatures where activities essential to survival in the juvenile life stage, can no longer be performed. (Eliason et al. 2022). Previous studies found that a FAS of 2 (a doubling of metabolic rate above SMR) is the minimum amount of metabolism required for a salmonid to digest a small meal

(Eliason et al. 2008. Adams et al. 2022). However, at this level of metabolism, there would be no energy available to engage in activity beyond maintenance and digestion. Therefore, a FAS of 3 has been proposed as a threshold that would allow for sufficient energy to both digest a meal and support minimal additional activity (i.e. foraging, locomotion), reflecting the amount of aerobic capacity required for juvenile salmonid to grow, recover from stressful events and behave normally (Anlauf-Dunn et al., 2022; Eliason et al. 2022). As such, I selected temperatures where FAS=3 as the T_{pejus} for juvenile fish in this study.

3.3 Results

During juvenile trials, ambient temperatures of the groundwater source ranged from 8-10°C (mean: 9.3 ± 0.16 °C). Body mass ranged from 2.26-8.45g (4.92 ± 0.21 g) and fork length ranged from 6.4-9.3 cm (7.98 ± 0.01 cm). During adult trials ambient temperatures in Norbury Creek ranged from 7.68-14.52°C (mean: 11.32 ± 0.11°C). Body mass ranged from 79.27-140.80 g (105.81 ± 2.17 g) in male fish and $75.52 - 175.70$ g (103.70 ± 2.95 g) in female fish. Fork length ranged from $19.7 - 24.5$ cm (21.73 ± 0.15 cm) in male fish and 19.6-25.7 cm (21.50 ± 0.43 cm) in females. Adult fish could be a mix of 3- and 4-year-old age classes. RVM was found to be significantly different between adult male and female fish (F: $0,14 \pm 0.004$, (M: 0.17 ± 0.003; P<0.0001). HSI was also found to differ significantly between sexes (F: 0.94 ± 0.04, M: 1.19 ± 0.02 ;P<0.0001). Body mass did not vary significantly between sexes (F: 104.01 ± 3.00g, M: 105.81 ± 2.17g). Mean gonadosomatic index (GSI) was 14.10 (± 0.54) in females and 2.26 (± 0.13) in males.

3.3.1 Survival

All fish survived the ambient/12°C temperature treatments; however, survival during

respirometry trials declined at higher treatment temperatures (22 and 24 °C). Females exhibited

the highest survival at the warmest temperatures (22°C: 80%; 24°C: 67% survival), followed by

males (22°C: 71%; 24°C: 25%) and juveniles respectively (22°C: 83%, 24°C: 0% survival)

(Table 3.1). For juveniles, between 22°C and 24°C temperature treatments, I observed a dramatic

decline in survival, whereas adult fish survival declined more gradually across higher treatment

temperatures.

3.3.2 Critical Thermal Maxima

Adult fish displayed significantly higher mean CT_{max} temperatures (F: 29.7 ± 0.13°C; M: 29.5 ±

0.12°C) than juvenile fish (28.7 ± 0.11°C). CT_{max} values were found to increase significantly

with treatment temperature in all groups (P<0.0001). Across treatment temperatures juvenile fish

had lower CT_{max} values (P > 0.0001, See Appendix, Table 6 for details) than adults of both

sexes, however, no significant differences were found between adult male and female fish

(Figure 3.2). Of note in the adult trails for the 22°C treatment temperature, one fish (a silver

female) lost equilibrium at 26.9°C, approximately 3.5-4.5°C before any of the other fish from

that trial. The remaining fish lost equilibrium between 29.2-31.3 °C. Perhaps the most important

finding from these trials is the plasticity in CT_{max} under a rapid (~20 h) thermal exposure period.

While most CT_{max} studies acclimate fish over longer timeframes (i.e. weeks, Baird et al. 2018,

Desforges et al. 2021), to achieve complete acclimation to treatment temperatures, our study is

the first to find compelling evidence of the ability for salmonids to extend their upper thermal

tolerance after only 20 hours of exposure. These results arguably possess greater ecological

relevance than previous studies with much longer acclimation periods in cases where the population being studied does not experience extended periods of stable temperatures under natural conditions.

3.3.3 Resting and maximal metabolic rates

Resting metabolic rate (RMR) increased exponentially with temperature in both life stages and sexes (Figure 3.3). RMR was significantly higher in adult male fish across treatment temperatures, followed by female and juvenile fish respectively (P<0.0001; see Appendix ,Table 6 for details). In all groups, RMR was lowest in the ambient (12°C) treatment (Figure 3.3). Maximum metabolic rates (MMR) exhibited a slight linear increase with temperature, a pattern that repeated across groups (Figure 3.4). MMR values were significantly different between temperature treatments (P = 0.0032) and between groups (P<0.0001; see Appendix Table 6 for more details). It is important to note that at the 24°C male and females RMR values are represented by 1 and 3 fish respectively, that survived the acclimation trials so trends at that temperature may be limited by low sample sizes.

3.3.4 Aerobic Scope

All groups showed a significant increase in AAS with temperature until intermediate temperatures were reached (Female T_{opt}: 15.25 °C; Male T_{opt} ; 14.50°C, Juvenile T_{opt} : 15.25°C), at which point AAS began to decline (Figure 3.5). Peak AAS was significantly higher in adult male fish but did not differ between juvenile and adult female fish (F: 9.75 $\pm$ 0.52 mg O_2 kg^{-1} min^{-1} , M: 11.99 $\pm$ 0.49 mg O_2 kg^{-1} min^{-1}, J: 10.34$\pm$ 0.34 mg O_2 kg^{-1} min^{-1}; P=0.0008). FAS decreased in a linear manner with increasing temperature (Figure 3.6), however, no significant

differences were found between groups (see Appendix 2 Table 6 for details). AAS = 80% of maximum at 19.6°C for females and 20.05°C for males.

3.4 Discussion

In this study I identified intra-population variation in metabolic performance and thermal tolerance in a steam-spawning population of Kokanee salmon. Adults had higher CT_{max} values than juveniles across all temperature treatments, however for AAS male adults differed significantly from both female adult and juvenile fish, whereas, no difference was found between female adult and juvenile fish. Across groups, 24°C represented a temperature threshold beyond which high mortality occurred, particularly in the juvenile fish, where completion of the ~20 h temperature exposure treatment was not possible. This 24°C threshold has been observed in juvenile sockeye salmon as well, where difficulty holding fish at this temperature was observed and classified as a "near-lethal" temperature (Brett 1964). Further, optimal temperatures and functional limits for performance occurred at ~15°C (T_{opt}) and ~ 20 °C (T_{pejus}) in all groups. 15°C is an optimal temperature also formally identified for juvenile sockeye salmon (Brett 1964). This T_{opt} is also consistent with previous findings for adult sockeye with relatively short, cool fall spawning migrations (Eliason *et al.* 2011). The ~5°C difference between T_{opt} and T_{pejus} represents a thermal window in which Norbury Creek Kokanee salmon maintain sufficient aerobic scope to thrive beyond their physiological optimum.

The results from this study indicate that fish physiological performance and thermal tolerance vary across the lifecycle and between sexes. While temperature thresholds (T_{opt} an T_{pejus}) were similar across groups, the absolute amount of aerobic scope available for activity at

these temperatures varied significantly between the Adult fish and the female and juvenile fish. Additionally, adult fish had higher CT_{max} (~1°C higher at all temperature treatments) compared to juveniles. AAS was also highest in adult males (~2.24 mg O_2 kg^{-1} min^{-1} higher than females, and ~1.65 mg O_2 kg^{-1} min^{-1} higher than in juveniles). Consistent with previous findings for coho and pink salmon, females had lower RMR (Kraskura et al. 2021), MMR and AAS than males (Clark et al. 2011). The lower RMR in female fish suggests that they are more energetically conservative than male fish and that the cost of gonadal maintenance does not present a loading factor when compared to males during the spawning life stage (Kraskura et al. 2021). It is possible that the higher AAS exhibited by adult male fish reflects a fitness advantage on the spawning grounds as males need to outcompete one another to ensure reproductive success. Higher activity levels and heart rates have been observed in male Atlantic salmon on the spawning grounds relative to females, indicating that maintaining greater AS during this final life stage may provide a fitness advantage that has been selected for over generations (Altimiras *et al*. 1996). One potential partial explanation for the higher AAS observed in male fish is their higher RVM; larger hearts allow for greater cardiac stroke volume, allowing for greater oxygen transport to periphery tissues and, thus, a higher capacity to meet the oxygen demands of the tissues (Farrell 1991).

While AAS was statistically different between groups, FAS did not differ significantly, indicating that while absolute increases in metabolism above RMR differed, proportional increases were equal. AAS is the most commonly employed index of aerobic capacity, however, the ratio between these rates (FAS) is often also calculated to provide additional information about AS, that is not captured through analysis as absolute value (Halsey et al. 2018). AAS provides a tangible estimate of the total aerobic capacity for oxygen transport that can be

achieved by an individual above baseline, whereas, FAS evaluates AS as a proportion of aerobic scope available to carry out aerobic activity (Eliason et al. 2022). When plotted against temperature AAS and FAS can yield vastly different results that lead to opposing interpretations of a single dataset (Halsey et al. 2018). My results suggest different relationships between AS with temperature when comparing FAS and AAS of the study population. FAS decreases with temperature across all temperature treatments from this experiment, whereas, AAS increases from the ambient treatment group until intermediate temperatures (~14-15 °C) before declining again. However, this difference is largely driven by the 12 °C treatment group and at higher temperatures treatments both AAS and FAS provide the same message: aerobic capacity declines substantially at high temperatures.

Consistent with my findings from the literature review performed in Chapter 2, upper thermal tolerance is highly dependent on the methodological approach selected to measure it. In this study I assessed both CT_{max} and the T_{pejus} in juvenile and adult kokanee salmon and found a ~8-9 °C difference in these metrics. CT_{max} values were higher than T_{pejus} as they indicate a temperature where whole animal incapacitation occurs. However, organ systems essential to survival are known to fail far before the CT_{max} is reached (Chen et al. 2013, Muñoz et al. 2015). T_{pejus} temperatures are set even lower than those at which aerobic collapse occurs to provide the most functional estimate of upper thermal tolerance. Across groups in this study, T_{pejus} occurred at ~20°C in all three groups, a temperature that is consistent with the survival data from this study (noticeable declines in survival occurred at temperatures above 20°C). The discrepancy between CT_{max} and T_{pejus} highlight a very important aspect of assessing vulnerability to warming; how vulnerable a species is believed to be, depends greatly on the thermal metric used in the assessment. While CT_{max} is a much more common metric than T_{pejus}, use of this metric in

vulnerability assessments runs the risk of vastly underestimating actual vulnerability to warming. This research suggests that T_{pejus} provides a much more realistic threshold for upper thermal tolerance and should be used where possible in place of more extreme estimates like CT_{max}.

A prevailing hypothesis surrounding the inability for salmonids to persist at high temperatures is that ventilatory systems are unable to meet the increasing oxygen demands of the tissues as temperature increases (Pörtner et al. 2001, Pörtner and Laning 2009). As such, I had hypothesized that the onset of a collapse in aerobic capacity would disproportionality affect females as their AS was found to be lower than males in a previous study on pink salmon, *O. gorbuscha* (Clark et al. 2011). However, while indeed male AS was higher than female AS, male survival was substantially lower at the higher temperature treatments (22°C and 24°C), suggesting that the collapse in AS was not a driver of thermal mortality in this study. Numerous studies looking at migrating and spawning sockeye salmon found higher mortality in females than in males (see Hinch et al. 2021). However, the studies reviewed in Hinch et al. (2021) all focused on the adult migratory life stage, not spawning state, therefore there are potentially different sex-specific factors driving mortality on spawning grounds. It is possible that in my study, females which were thermally intolerant perished during their migration, resulting in more thermally tolerant females left to arrive on the spawning grounds. Nonetheless, the discrepancies in sex-specific survival rates between anadromous sockeye and the resident Kokanee population used in this study is a topic that would benefit from further research to investigate the opposing results and identify the mechanisms driving differential mortality.

In addition to life stage and sex-specific differences in upper thermal tolerance, previous research has confirmed that extensive variation in thermal tolerance among populations exists,

particularly in sockeye salmon (Whitney et al. 2013, Eliason et al. 2011, Zillig et al. 2020). Therefore, to further our understanding of the thermal tolerance of Kokanee salmon and evaluate the capacity for this species to persist in a warming world, investigating the degree of intraspecific variability in upper thermal tolerance is a crucial step-forward for this research. Further, while thermal tolerance and thermal exposure are essential components in understanding climate vulnerability, further research into the adaptive capacity of this species will also be essential to developing a robust assessment of overall vulnerability.

3.5 Conclusions

This study provides compelling evidence that upper thermal tolerance varies across the lifecycle and between sexes in Kokanee salmon (*Oncorhynchus nerka*). To my knowledge, this study is the first account of the plastic capacity in CT_{max} in a salmonid following a brief thermal exposure, demonstrating rapid acclimation, and suggesting that fish may benefit from short term exposures to warm temperatures in order to increase resistance to acute high temperature exposure. While thermal thresholds (T_{opt} and Tpejus) were fairly similar in juveniles and adults and between adults of both sexes, I found that aerobic capacity at these temperature thresholds was highest in adult male fish and lowest in adult female and juvenile fish. Results from aerobic scope trails suggest a ~5°C thermal window in which Norbury Creek Kokanee salmon possess the sufficient aerobic capacity to thrive above their physiological optimum (T_{opt}). This study also demonstrates the variation in thermal tolerance depending on metric/method selection. CT_{max} values were consistently higher (~8-9 °C) than functional temperature limits obtained in respirometry data in all groups (female adults, male adults, juveniles). These results indicate the need for careful metric selection in vulnerability assessments and an understanding of the

limitations and advantages of the thermal tolerance estimates available for use in such

assessments.

Table 3.1 - Survival data from respirometry trials. Survival measurements were taken as any mortalities from the start of acclimation to the end of the 1 h recovery period. Data is displayed for each treatment temperature.

Group	Percent Survival									
	Ambient	**n**	**17**	**n**	**20**	**n**	**22**	**n**	**24**	**n**
Female	100	12	100	10	83	12	80	10	67	6
Male	100	12	100	14	96	12	71	14	25	8
Juvenile	100	12	100	12	92	12	83	12	0	22
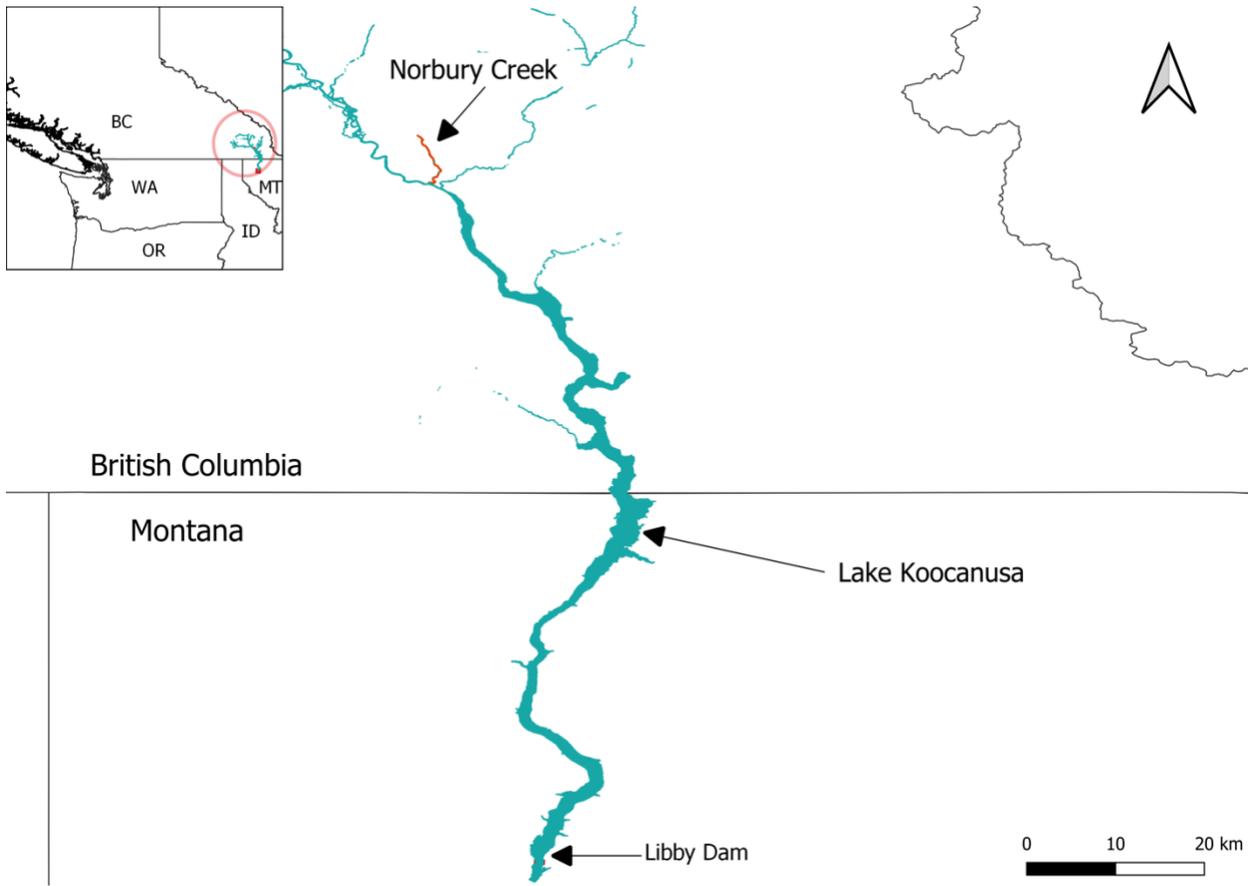
Figure 3.1 - Map of study Area
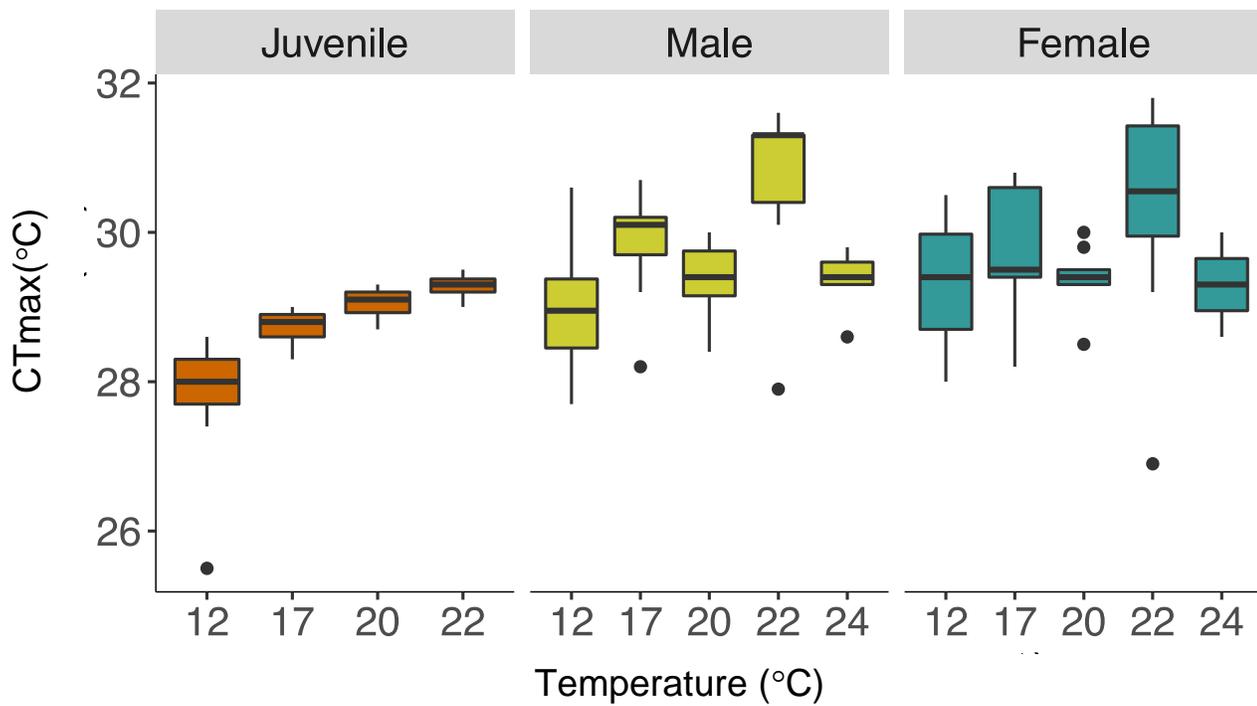
Figure 3.2 - CT$_{max}$ data across treatment temperatures and group. Boxplots represent means and Standard error of the Means. Significant differences were observed between the adult fish and the juvenile fish (P <0.0001), while male and female groups did not differ statistically.
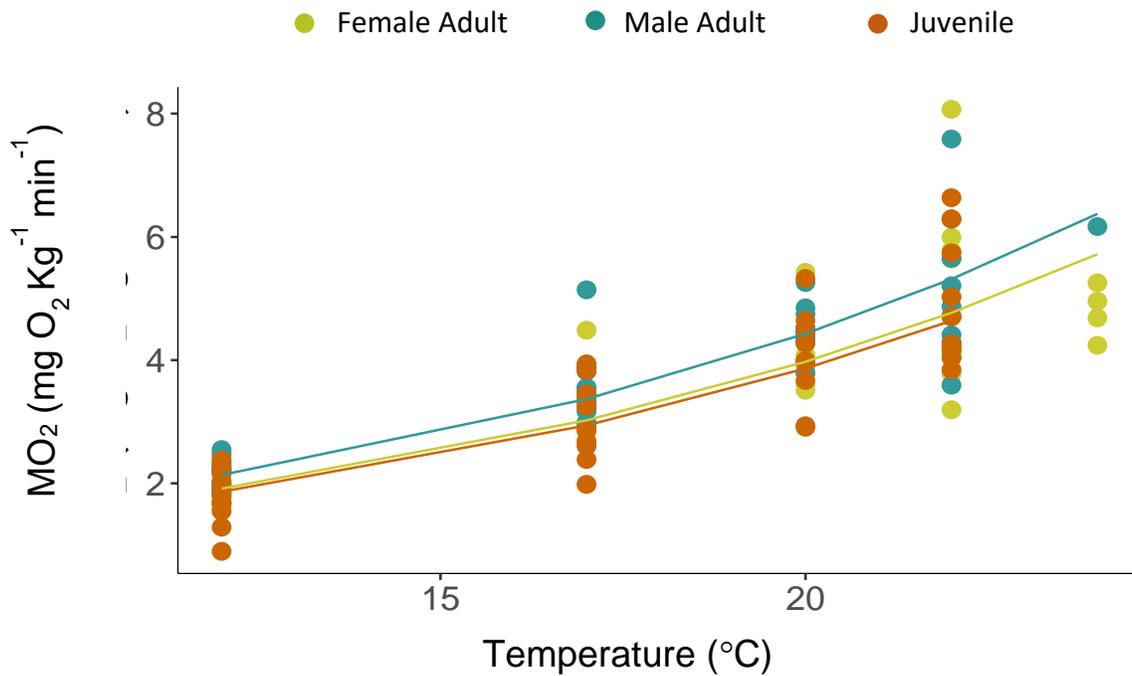
Figure 3.3 - Log normal linear regression model with RMR as response variable and Treatment Temperature and Group (juvenile, adult female, adult male) as a fixed effect variable. There were significant differences between adult male fish and the adult female and juvenile fish ($P = 0.0189$). No significant differences were observed between adult female and juvenile fish.
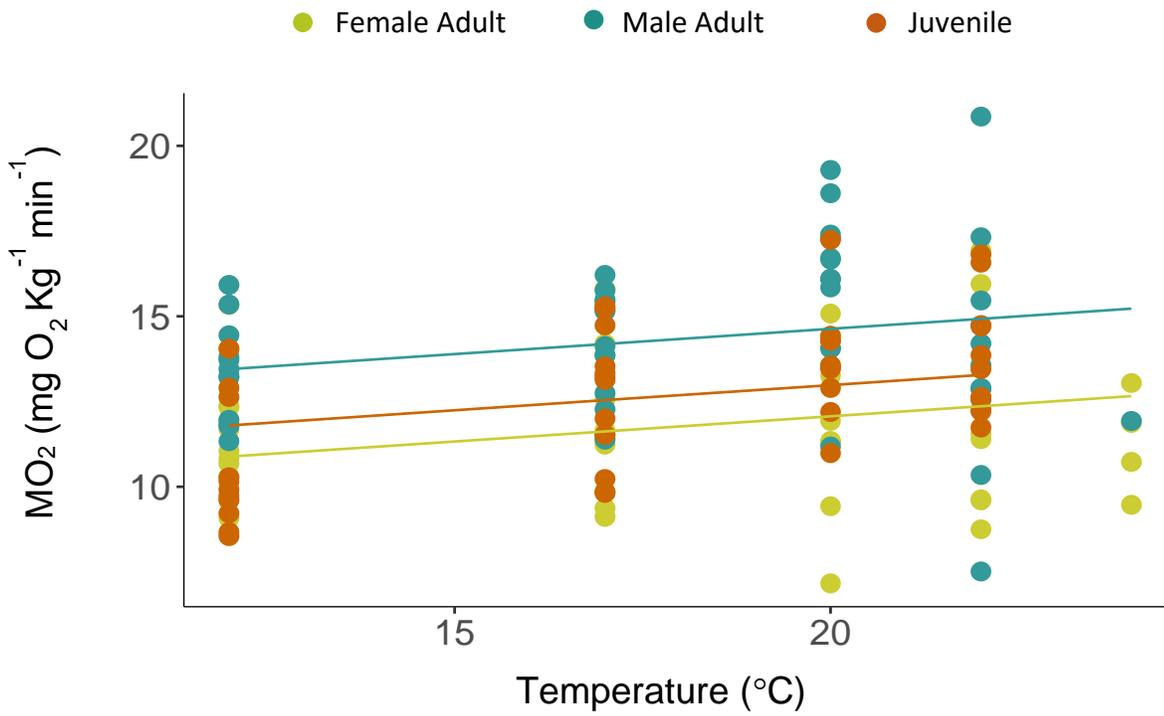
Figure 3.4 - Linear regression model with MMR as response variable and Treatment Temperature Group (juvenile female, , male) as a fixed effect variable. There were significant differences between adult male fish and the adult female and juvenile fish (P < 0.0001). No significant differences were observed between adult female and juvenile fish.
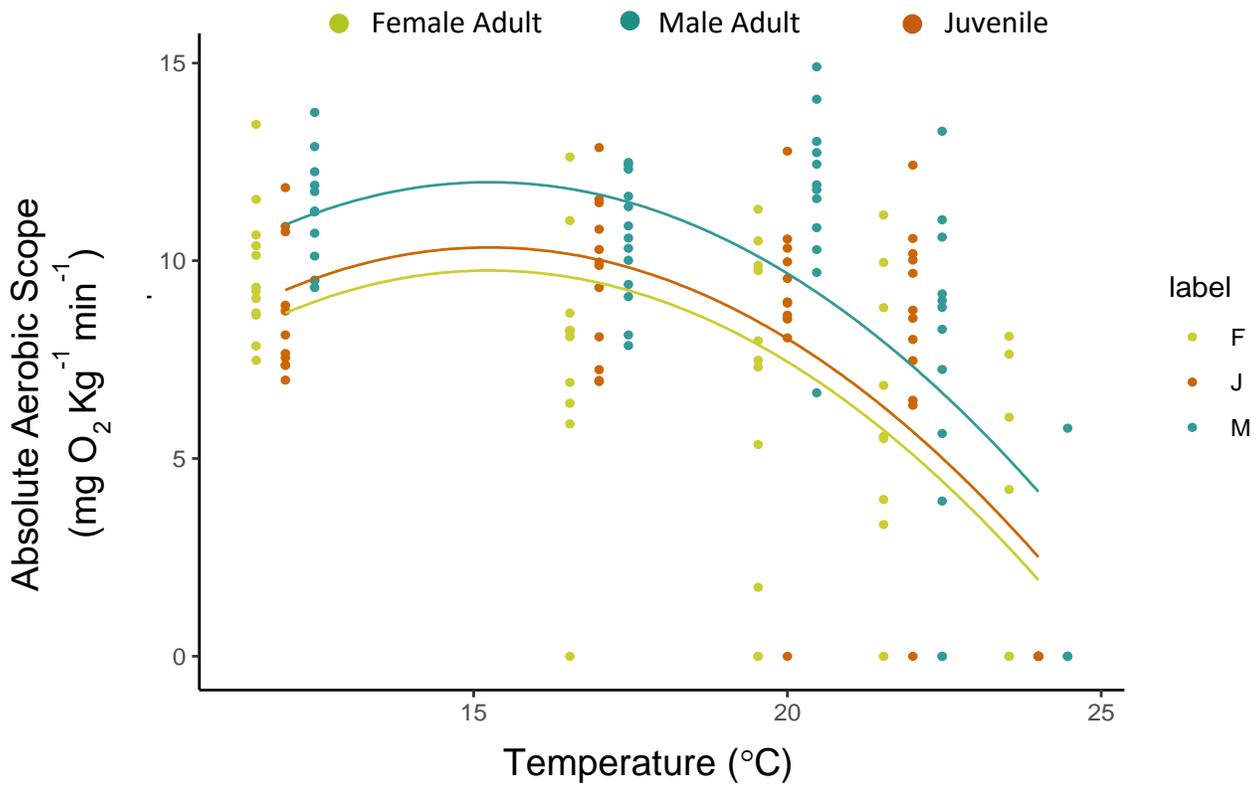
Figure 3.5 - Thermal performance curves for Absolute Aerobic Scope (AAS) for each group (AAS estimates were fit to a quadratic regression model with AAS as response variable and Treatment Temperature and Group as fixed effect variable. If a fish died during the 20 h temperature acclimation or during the RMR trial, it was included as a zero on the AAS estimate. Male fish differed significantly from both female and juvenile fish ($P<0.0001$), whereas, no statistical differences were found between female and juvenile fish.
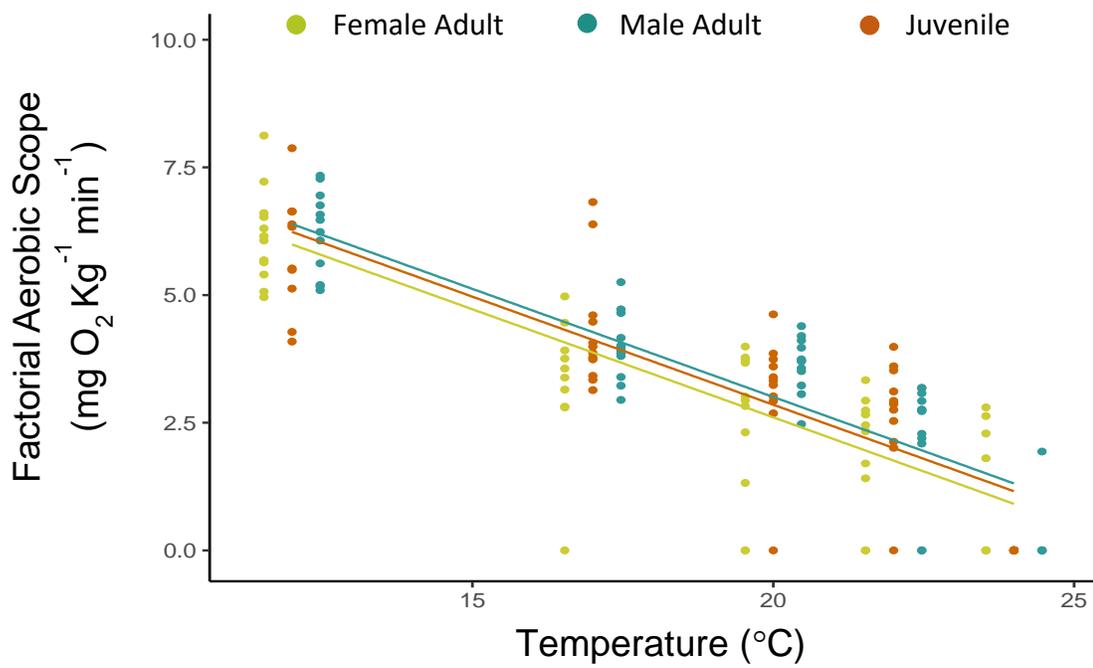
Figure 3.6 - Factorial Aerobic Scope Curve. Linear regression model with FAS as response variable and treatment temperature and group as fixed effect variables. No significant differences were found between groups.
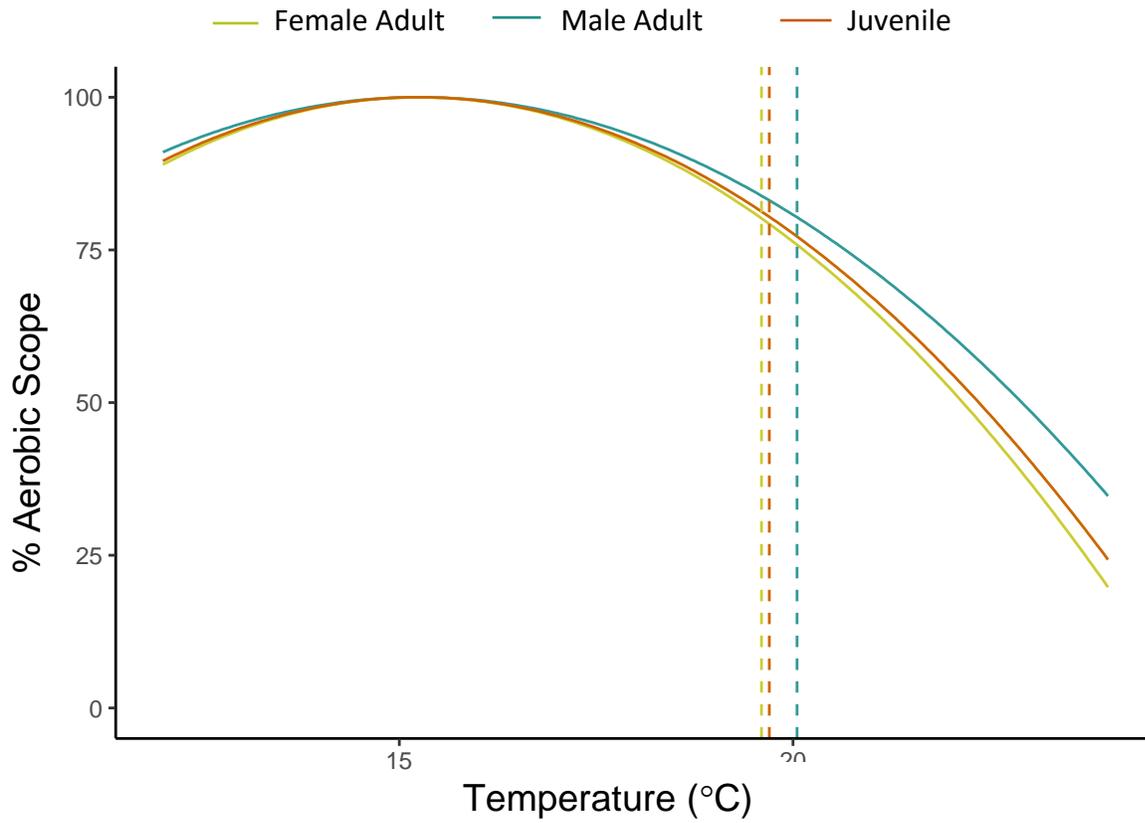
Figure 3.7 - Percent Aerobic Scope (max AAS value designated as 100% of total scope and all other values relative to the max value). Vertical dashed lines indicate point where AS is at 80%.

Chapter 4: Conclusion

Climate change induced increases in freshwater temperature pose a major threat to the survival and persistence of many fish species (Martins *et al*. 2011, Cheung *et al.* 2021). This is particularly true for Pacific salmon, which display fine-tuned local adaptions and high variability in their upper thermal tolerance limits across various levels of biological organization (Crozier *et al*. 2008, Muñoz *et al.* 2014, 2015). The widespread decline in Pacific salmon populations throughout much of their native ranges has incited the development of a vast body of literature on the thermal tolerance of these species. Due to the controlling influence of temperature on all aspects of the physiology and behavior of Pacific salmon, several methodological approaches have been developed to quantify their upper thermal limits (Caudill *et al*. 2007, Martins *et al.* 2011, Eliason *et al.* 2011, Muñoz *et al.* 2014, Baird *et al*. 2018). I identified several methodological approaches that are most commonly employed in the literature: the critical thermal method, upper incipient lethal temperature, scope for activity/aerobic scope, temperature preference and avoidance, and thermal migration barriers. More recent research also aims to investigate the impacts of thermal stress at the cellular level (e.g.. production of various protein isoforms such as heat shock proteins, gene expression profiles) (Jeffries et al. 2012, Anttila et al. 2014, von Biela et al. 2021). Each of these approaches provides meaningful information on the overall thermal response that fish will have as water temperatures continue to rise (Bates and Morely 2020). However, the results from these different approaches cannot be used interchangeably and applying these values to projections on future persistence and survival must be done with an understanding of what information each of these approaches offers. For example, the CT_{max} provides insights about upper thermal limits on acute timescale and thus, CT_{max} values should not be used to investigate tolerance to chronic high temperature exposures.

However, plasticity in the thermal response with acclimation or acclimatization that is seen in CTM studies can provide useful information on the non-evolutionary adaptive capacity of a given population or species. Further using results from various approaches in concert is critical to developing a more robust understanding of both the numeric temperature limits and the mechanisms governing them. For example, new molecular approaches can be integrated with other whole animal or organ-level physiological methods (i.e. aerobic or cardiac scope) to provide further insights into the mechanisms driving thermal mortality. My literature review (Chapter 2) illustrates the extent and sources of variation in upper thermal limits and highlights the importance of selecting thermal tolerance limits that recognize inter-specific, life stage-specific, and methodology-based nuances in reported Upper thermal limits (UTLs). This review also highlighted the paucity of information on the role of life stage and sex on thermal tolerance.

In the second and final data chapter (Chapter 3), I aimed to address the research gaps surrounding potential differences in thermal tolerance across the life cycle and between sexes as well as demonstrate how the use of multiple approaches to quantify thermal tolerance allows for a more robust understanding of a populations' vulnerability to warming. This chapter focused on a resident life form of *Oncorhynchus nerka* – Kokanee salmon. This study was the first to employ the CT_{max} and Aerobic Scope (AS) approaches to quantify UTL in Kokanee salmon and reports novel findings on the ability for a salmonid to adjust its UTL under rapid acclimation (~20 h). This study provided compelling evidence that thermal tolerance varies between sexes and across the lifecycle in salmon. Absolute aerobic capacity was significantly higher in adult male than adult female and juvenile fish ($P = 0.0008$) across treatment temperatures ($P < 0.0001$; see Appendix 2 Table 6 for more details). Further relative ventricular mass (RVM) was ~21%

higher in male fish than female fish, suggesting that higher AAS could be partially driven by greater cardiac output. While AAS varied across groups, optimal temperatures (~15°C) and functional thermal limits (~20°C) were similar across groups and suggest a ~5°C thermal window in which this population of Kokanee salmon maintain sufficient aerobic capacity to thrive beyond their physiological optimum. The disparity between CT_{max} and T_{pejus} estiamtes (~10°C difference) further illustrates my findings from Chapter 2 that UTL is highly dependent on the methodological approach selected. While the CT_{max} results provide information on the resistance to acute exposure and potential for rapid acclimation, these results have a tendency to underestimate a populations true vulnerability to warming. The T_{pejus} estimates provide a more functional and ecologically relevant thermal threshold and were also much more consistent with the temperatures at which we began to see substantial declines in survival.

Overall, my results suggest that there is a high degree of variation in in the upper thermal tolerance of Pacific salmon that ranges from the individual to species scale. My use of two methodological approaches to assess thermal tolerance in a single population of Kokanee salmon highlight the importance of careful metric selection when assessing the current and future vulnerability of Pacific salmon to warming. My research emphasizes the importance of accounting for nuances in thermal tolerance at the population level where possible, and contributes to the growing body of literature demonstrating that Pacific salmon are becoming increasingly vulnerable to warming river temperatures. A greater understanding of the variation in upper thermal tolerance of Pacific salmon will allow managers to develop more relevant thermal guidelines, facilitate the development of ecologically relevant vulnerability assessments, and identify populations that possess greater resiliency to warming in the climate change era.

An area that would benefit from further research is the adaptive potential of Pacific salmon to

increase their thermal tolerance. Previous research has shown that thermal tolerance is heritable

in salmonids however, the genomic basis of thermal tolerance is not well understood and the

microevolution towards increased thermally tolerance in salmonids is a vastly understudied area

of research (Chen *et al*. 2018). Since adaptive capacity is an essential component of vulnerability

to warming, it is vital that future research attempts to address the dearth of information on this

subject. Without a more thorough understanding of the adaptive potential in thermal tolerance

traits a robust investigation of a populations vulnerability to warming will remain incomplete.

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Appendix A

Table A.1 - List of studies included in this review

Reference		Species Used				
Author	*Year*	*Sockeye*	*Chinook*	*Pink*	*Chum*	*Coho*
Donaldson	1941	1				
Fish and Hanavan	1948		1			
Brett	1952	1	1	1	1	1
Olson and Foster	1957					
Brett et al.	1958	1				1
Davis et al.	1963		1			1
Brett	1964	1				
Brett	1967	1				
Major and Mighell	1967	1				
Hallock et al.	1970		1			
Griffiths and Alderdice	1972					1
Sylvester	1972	1				
Becker	1973		1			1
Brett and Glass	1973	1				
Coutant	1973		1			
Wedemeyer	1973					1
Fryer and Pilcher	1974		1			1
DeHart	1975					1
Holt et al.	1975		1			1
Udey et al.	1975					1
Servizi and Jensen	1997	1				
Fryer et al.	1976		1			1
Glova and McInerney	1977	`				1
Gray et al.	1977		1			
Groberg et al.	1978		1			1
Becker and Genoway	1979					1
Brett	1982			1		
Heming	1982		1			
Kwain	1982			1		
Groberg et al.	1983					1
Garling and Masterson	1985		1			
Neitzel and Baker	1985		1			
Beacham and Murray	1986				1	
Beacham and Murray	1986			1		

Author	Year					
Lindsay et al.	1986		1			
Thomas et al.	1986					1
Barton and Schreck	1987		1			
Tang et al.	1987					1
Alabaster	1988		1			
Beacham	1988			1	1	
Beacham and Murray	1988			1		
Murray and McPhail	1988	1	1	1	1	1
Beacham and Murray	1989	1	1			
Pearcy et al.	1989				1	
Beacham and Murray	1990	1	1	1	1	1
Berman	1990		1			
Murray and Beacham	1990					1
Armour et al.	1991		1			
Beacham and Varnavskaya	1991			1		
McGeer et al.	1991					1
Franklin et al.	1992	1	1			
Henderson et al.	1992	1				
Varnavsky et al.	1993			1		
Kreiberg and Blackburn	1994	1				
Baker et al.	1995		1			
Konecki et al.	1995					1
Konecki et al.	1995					1
Welch et al.	1995	1		1	1	1
Sauter et al.	1996		1			
Quinn et al.	1997	1				
Welch et al.	1998	1				
McCullough	1999		1			
MacDonald et al.	2000	1				
Palmisano et al.	2000		1			
Sauter et al.	2001		1			
Sullivan et al.	2001					1
Welsh et al.	2001					1
Hodgson and Quinn	2002	1				
Mesa et al.	2002		1			
Birtwell et al.	2003				1	
Connor et al.	2003		1			
Hyatt et al.	2003	1				
Lee et al.	2003	1				
Lee et al.	2003	1				1

Marine and Cech	2004		1			
Tierney and Farrell	2004	1				
Hinke et al.	2005		1			
Naughton	2005	1				
Newell and Quinn	2005	1				
Wurster et al.	2005		1			
Zenke at al.	2005	1				
Geist et al.	2006		1			
Goniea et al.	2006		1			
MacNutt et al.	2006	1		1		
Madej et al.	2006					1
Quigley and Hinch	2006		1			
Salinger and Anderson	2006		1			
Azumaya et al.	2007	1	1	1	1	1
Caudill et al.	2007		1			
Keefer et al.	2007	1				
Nagata et al.	2007				1	
Arksuh et al.	2008					1
Clark et al.	2008		1			
Crossin et al.	2008	1				
Farrell et al.	2008	1				1
Keefer et al.	2008		1			
Steinhausen et al.	2008	1				
Chesney et al.	2009					1
Stewart and Bowlby	2009		1			
Tiffan et al.	2009		1			
Bellgraph et al.	2010		1			
Geist et al.	2010		1			
Macdonald et al.	2010	1				
Mathes et al.	2010	1				
Pon et al.	2010	1				
Roscoe et al.	2010	1				
Strange	2010		1			
Clark et al.	2011			1		
Eliason et al.	2011	1				
Gale et al.	2011	1				
Martins et al.	2011	1				
Burt et al.	2012	1				
Burt et al.	2012	1				
Casselman et al.	2012					1

Clark et al.	2012					1
Hayes et al.	2012					1
Jeffries et al.	2012	1		1		
Jeffries et al.	2012	1				
Martins et al.	2012	1				
Ray et al.	2012		1			1
Stenhouse et al.	2012					1
Sutton and Soto	2012					1
Anttila et al.	2013				1	
Caudill et al.	2013		1			
Chen et al.	2013	1				
Eliason et al.	2013	1				
Eliason et al.	2013	1				
Robinson et al.	2013	1				
Whitney et al.	2013	1				
Anttila et al.	2014	1				
Drenner et al.	2014	1				
Fujiwara	2014		1			
Gale et al.	2014	1				
Jeffries et al.	2014	1		1		
Munoz et al.	2014		1			
Ray et al.	2014		1			1
Chen et al	2015					1
Morita	2015				1	
Munoz et al.	2015		1			
Raby et al.	2015					1
Tomalty et al.	2015		1			
Armstrong et al.	2016	1				
Chiaramonte et al.	2016		1			1
Elder et al.	2016		1			
Raby et al.	2016					1
Eliason et al.	2017	1				
Martin et al.	2017		1			
Poletto et al	2017		1			
Prystay et al.	2017	1				
Baird et al.	2018		1			
Bowerman et al.	2018		1			
Mann and Snow	2018		1			
Minke-Martin et al.	2018	1				
Munoz et al.	2018		1			

Reference	Year				
Teffer et al.	2018		1		
Abe et al.	2019			1	
Anttila et al.	2019	1			
Carey et al.	2019	1			
Connor et al.	2019		1		
Courtney et al.	2019		1		
Del Rio et al.	2019		1		
Elsner and Shrimpton	2019				1
Huey and Kingslover	2019				
Stiff et al.	2019	1			
Teffer et al.	2019				1
Whitney et al.	2014	1			
von Biela et al.	2020		1		
Karuska et al.	2021				1

Table A.2 Reported upper thermal tolerance values for sockeye salmon in all life stages

Reference	Methodology	Population	Life stage	Value
Beacham and Murray (1989)	Incubation Optimum	Weaver, adams	Embryo-alevin	15°C
Burt et al. (2012)	Critical Temperature for Incubation	Weaver	Embryo-alevin	16°C
Murray and McPhail (1988)	Incubation Optimum	Weaver Creek	Embryo-alevin	14°C
Whitney et al. (2013)	Incubation optimum and critical temperature	Stellako, Chilko, Horsefly, Okanagan, Weaver, Harrison	Embryo	Optimum: 10°C Critical: 16°C

Chen et al. (2013)	CT_{max}	Harrison, Weaver, Gates, Scotch, Adams, Chilko, Horsefly, Stellako, Okanagan	Juvenile	Harrison – incubated at 10C: 25.6C, 14C: 24.8C, 23.8C, Weaver – 10C: 25.9C, 14C: 24.1C, 16C: 23.1C, Gates – 10C: 24.3C, 14C: 24.1C, Scotch – 10C: 24.2C, 14C: 23.5C, Adams – 10C: 25.4C, 14C: 23.9C, 16C: 22.8C, Chilko – 10C: 24.4C, 14C: 23.5C, Horsefly – 10C: 24.5C, 14C: 23.2C, Stellako – 10C: 24.6C, 14C: 23.3C, Okanagan – 10c: 25.6C, 14C: 23.4C, 16C: 22.8C
Donaldson and Foster (1941)	CT_{max}	Unknown	Juvenile	25.5°C
Brett (1952)	UILT	Issaquah Hatchery	Juvenile	24.8°C
Brett (1964)	Scope for Activity	unknown	Juvenile (Parr)	$T_{opt(AS)}$: 15°C
Chen et al. (2013)	Cardiac Function	Weaver, Gates, Chilko, Okanagan	Juvenile	T_{ar}: Incubated at 10°C Weaver: 24.1°C Gates: 24.0° C Chilko: 24.2°C Okanagan: 23.0°C Incubated at 14°C: Weaver: 23.2°C Gates: 24.4°C Chilko: 23.1°C Okanagan: 24.5°C
Sylvester (1972)	Change in Behaviour	Unknown	Juvenile	Increased predation with temperatures above 22°C

Azumaya et al. (2007)	Distributional limits	unknown	Immature	13.3°C
Welch et al. (1995)	Distributional limits	Unknown	Immature	8.9°C
Keefer et al. (2007)	Thermal Migration Barrier	Snake River Hatchery	Adult	21-24°C
Martins et al. (2011)	Thermal Migration Barrier	Chilko, Quesnel, Stellako, Adams	Adult	19°C
Martins et al. (2012)	Thermal Migration Barrier	Stellako	Adult	20°C
Naughton et al. (2005)	Thermal Migration Barrier	unknown	Adult	21-23°C
Hogdson and Quinn (2002)	Thermal Migration Barrier	129 populations (see paper for details)	Adult	19°C
MacDonald et al. (2000)	Thermal Migration Barrier	All fraser stocks	Adult	18-22°C
MacDoanld et al. (2010)	Thermal Migration Barrier	Early Stuart	Adult	18.5°C
Major and Mighell (1967)	Thermal Migration Barrier	Wenatchee, Okanagan	Adult	21°C
Quinn et al. (1997)	Thermal Migration Barrier	Columbia	Adult	22°C

Armstrong et al. (2016)	Avoidance	Wood River	Adult	15°C
Eliason et al. (2011)	Scope for Activity	Weaver, Gates, Chilko, Nechako, Early Stuart, Quesnel	Adult	$T_{opt(AS)}$: Weaver:14.5°C Gates: 16.4°C Chilko:16.8°C Nechako: 16.8°C Early Stuart: 17.2°C T_p: Weaver: 16.4°C Gates: 19.5°C Chilko: 20.7°C Quesnel:18.5°C Nechako: 19°C Early Stuart: 19.9°C $T_{crit(AS)}$: Weaver: 20.8°C Gates: 26.1°C Chilko: 29.4°C Quesnel: 25.9°C Nechako: 24.0°C Early Stuart: 25.8°C
Eliason et al. (2013b)	Scope for Activity	Harrison	Adult	$T_{crit(AS)}$: 17.0° Harrison - 26.1°C
Farrell et al.	Scope for Activity	Weaver, Gates	Adult	$T_{opt(AS)}$: Weaver: 14.3°C Gates: 16.3°C Tcrit(AS): Weaver: 20.4 °C Tp: 19.6°C
Lee et al. (2003a)	Scope for Activity	Weaver, Gates Chehalis	Adult	$T_{opt(AS)}$: Weaver: 15C Gates: 17.5C Chehalis: 8.5C
Prystay et al. (2017)	Cardiac function	Chilko, Quesnel	Adult	Factorial heart rate and scope for heart rate were greatest at 21°C

Table A.3 Reported upper thermal tolerance values for Chinook salmon in all life stages

Reference	Methodology	Population	Life stage	Value
Garling and Masterson (1985)	Incubation Limit	Lake Michigan	Embryo	15.1°C
Geist et al. (2006)	Incubation Limit	Snake River (Hatchery)	Embryo-alevin	17.0°C
Martin et al. (2017)	T_{crit}	Sacramento	Embryo	Lab: 15.4°C Field: 12°C
Murray and McPhail (1988)	Incubation Optimum	Babine River	Embryo-alevin	14°C
Baird et al. (2018)	CT_{max}	Nimbus Fish Hatchery	Juvenile	28.6°C
Del Rio et al. (2019)	CT_{max}	Coleman National Fish Hatchery	Embryo-Juvenile	Embryo: 30.65°C Alevin: 28-29°C
Geist et al. (2010)	CT_{max}	Snake River	Juvenile	27°C
Brett (1952)	UILT	Dungeness Hatchery	Juvenile	25.1°C
Connor et al. (2003)	Thermal Migration Barrier	Snake River	Juvenile	20C
Elder et al. (2016)	Thermal Migration Barrier	Columbia	Juvenile	12C
Poletto et al. (2017)	Scope for Activity	Mokelumne River Hatchery	Juvenile	$T_{opt(AS)}$: 23°C
Muñoz et al.(2014)	Cardiac Function	Big Qualicum River	Adult	T_{AB}: 15.0 ±1.1 °C T_{arr}: 22.4± 2.5°C $T_{peak fH}$: 21.2±2.4°C

Muñoz et al. (2015)	Cardaic Function	Quinsam River	Juvenile	T_{arr}: 24.2±2.6°C - 24.5±2.2°C (depending on acclimation temperature) T_{AB}: 14.0±1.1 °C- 16.1±0.9°C (depending on acclimation temperature) $T_{peak fH}$: 20.8±2.3°C – 22.8±1.9°C (depending on acclimation temperature) *all values reported as ±1 standard deviation of the mean
Baird et al. (2003)	Avoidance	Nimbus Fish Hatchery	Juvenile	20.2°C
McCullough et al. (1991)	Distributional limits	Multiple stocks (data from review of existing literature)	Juvenile	22-24°C
Hinke	Preference	Unknown	Smolt	9-12 °C
Azumaya et al. (2007)	Distributional limits	Unknown	Immature	13.4°C
Courtney et al. (2019)	Distributional limits	Unknown	Immature	8-12°C
Muñoz et al. (2014)	CT_{max}	Big Qualicum River	Adult	26.5°C
Becker (1973)	UILT	Columbia	Adult	22°C
Alabaster (1988)	Thermal Migration Barrier	Lower Williamette	Adult	21-23°C

Caudill et al. (2007)	Thermal Migration Barrier	Upriver Bright	Adult	18°C
Fish and Hanavan (1948)	Thermal Migration Barrier	Unknown	Adult	21.7-23.9°C
Hallock et al. (1970)	Thermal Migration Barrier	Sacramento	Adult	19-21°C
Keefer et al. (2008)	Thermal Migration Barrier	19 stocks (see paper for details)	Adult	19°C
Mann and Snow (2018)	Thermal Migration Barrier	Okanagan	Adult	20°C
Strange (2010)	Thermal Migration Barrier	Trinity River Hatchery, Iron Gate Hatchery, Trinity Gate Hatchery	Juvenile	23°C
Gray et al. (1977)	Avoidance	Unknown	Adult	Avoidance of heated plumes when change in temperature from bottom to top was >9-11
Wurster et al. (2005)	Distributional limits	Unknown	Adult	22°C

Table A.4 Reported upper thermal tolerance values for coho salmon in all life stages

Reference	Methodology	Population	Life stage	Value
Murray and McPhail (1988)	Critical Temperature for Incubation	Rosewall Creek	Embryo-alevin	14°C
Tang (1987)	Critical Temperature for Incubation	University of Washington Hatchery Dungeness River	Embryo-alevin	14°C
Becker and Genoway (1979)	CT$_{max}$	Unknown	Juvenile	24.8°C-29.63°C
Brett et al. (1958)	Scope for Acvtivity	Unknown	Juvenile	Optimal swimming performance: 20°C
Casselman et al. (2012)	Scope for Activity	Seymour River Hatchery	Juvenile	T$_{opt(AS)}$: 17C
Chen et al. (2015)	CT$_{max}$	Chehalis	Juvenile	26.9°C
Konecki et al. (1995a)	CT$_{max}$	Bignham	Juvenile	28.21
		Bockman		29.13
		Snow		29.23C
McGeer et al. (1991)	CT$_{max}$	Chilliwack	Juvenile	23.8°C
		Eagle River		24.4°C
Arkush et al. (2008)	UILT	Unknown	Juvenile	27°C
Brett (1952)	UILT	Nile Creek Hatchery	Juvenile	25°C

Reference	Methodology	Population	Life stage	Value
Sullivan et al. (2001)	T_{crit}	Unknown	Juvenile	26°C
Chen et al. (2015)	Cardiac Function	Chehalis	Juvenile	T_{ABT}: Chehalis: 17.3°C
Sutton and Soto	Change in Behaviour	Beaver creek, Tom Martin creek, Cade Creek, Sandy Bar Creek	Juvenile	Dramatic increase in use of off channel habitat when mainstem approaches 22-23°C
Azumaya et al. (2007)	Distributional limits	Unknown	Immature	15.7°C
Welch et al. (1995)	Distributional limits	Unknown	Immature	9.4°C
Farrell et al. (2008)	Scope for Activity	Chehalis	Adult	$T_{opt(AS)}$: 9°C $T_{crit(AS)}$: 17°C
Lee et al. (2003a)	Scope for Activity	Chehalis	Adult	$T_{opt(AS)}$: 8.5°C

Table A.5 Reported upper thermal tolerance values for chum salmon in all life stages

Reference	Methodology	Population	Life stage	Value
Beacham (1988)	Incubation Optimum	Bella Coola Kshwan	Embryo-alevin	8°C
Beacham and Murray (1986)	Incubation Optimum	Jones, Alouette, Vedder, Chehalis	Embryo-Alevin	4°C for Vedder, 8°C for others
Murray and McPhail (1988)	Critical temperature for incubation	Rosewall Creek	Embryo-alevin	14°C
Brett (1952)	UILT	Issaquah Hatchery	Juvenile	23.9°C
Birtwell et al. (2003)	Avoidance	Hatchery – North Vancouver	Juvenile	20.2°C
Pearcy et al. (1989)	Distributional limits		Juvenile	14-16°C

Azumaya et al. (2007)	Distributional limits	Unknown	Immature	15.6°C
Nagata et al. (2007)	Distributional limits	Abashiri River Hatchery	Immature	13°C
Welch et al. (1995)	Distributional limits	Unknown	Immature	10.4°C
Abe et al. (2019)	CT_{max}	Kitakami River Kasshi River	Adult	27.8°C
Abe et al. (2019)	Scope for Activity	Kitakami River Kasshi River	Adult	$T_{opt(AS):}$ 17.6C 14.0C

Table A.6 Upper thermal tolerance values for pink salmon in all life stages

Reference	Methodology	Population	Life stage	Value
Beacham (1988)	Incubation Optimum	Quinsam Harrison	Embryo-Alevin	8°C
Beacham and Murray (1986)	Incubation Optimum	Jones, Coquihalla, Puntledge, Quinsam, Keogh	Embryo-Alevin	8°C
Beacham et al. (1988)	Incubation Optimum	19 stocks – see paper for details	Embryo-alevin	8°C
Beacham and Varnavskaya (1991)	Incubation Optimum	Chilliwack	Embryo-alevin	8°C
Murray and McPhail (1988)	Critical Temperature for Incubation	Weaver Creek	Embryo-alevin	14°C
Brett (1952)	UILT	Nile Creek Hatchery	Juvenile	25°C
Azumaya et al. (2007)	Distributional limits	Unknown	Immature	16.6°C
Welch et al. (1995)	Distributional limits	Unknown	Immature	10.4°C
Clark et al. (2011)	Scope for Activity	Harrison	Adult	$T_{opt(AS)}$: 20C

Appendix B

Table B.1 Additional details on equipment, materials and set up for respirometry trials.

Criteria	Details for Trials in this Study	Additional Comments
Body mass of fish used in respirometry trials	Adult: 104.45 ±1.08g Juvenile: 4.80 ± 0.21g	
Respirometer volume	Adult: 3 L Juvenile: 0.36 L	
Respirometer material	Acrylic	
Method of chamber mixing	External in-line pump	
Ratio of net respirometer volume to animal body mass	Adults -1:30 Juveniles - 1:75	Recognize that juvenile respirometers were large for the actual size of the fish, but due to time constraints and misinformation about fish size this was our only option.
Tubing material	Tygon	
Tubing volume	65-100 ml	
Sampling frequency of water-dissolved oxygen	1 reading per 1-2 seconds	
Placement of oxygen probe	Along tubing once water exits chamber and before re-entering the recirculation pump	
Flow rate	Adults: flush – 3L/min Juveniles: flush 1L/min, recirculation	Dissolved oxygen content returned to at least 95% during flushing
Timing of flush/measurement cycles	Adults: 5-6 minute flush and 4-5 minute measure or 6 minute flush and 4 minute measure Juveniles: 4-5 minute flush and 10-11 at lower temperatures, 4 minute flush, 6 minute measure at higher temperatures	Altered flush/measure cycles based on size of fish and temperature treatment
Software temperature compensation used	Yes	
Volume of tubing in any mixing circuit was included in calculations of oxygen uptake rates	Yes	
Oxygen probe	Fiber optic robust oxygen probe Measurements recorded every 1-2 seconds	4m cable with optical isolation, stainless steel tip (3mm)
Probe placement	Placed in the inline circuit directly after water exited chamber and prior to water being pulled back through recirculation pump	
Chamber returned to normoxic conditions before commencing new measurement cycle?	Yes	Oxygen levels were always returned to ≥95% air saturation.

Probe calibration	Preformed at beginning of adult trial (9 day trial) and juvenile trial (10 day trial)	
	Probes were calibrated by being placed in experimental water with 100% air saturation (ensured using bubblers) followed by ___ sodium sulfite	

Table B.2 Additional details on measurement conditions for respirometry trials.

Criteria	Details for Trials in this Study	Additional Comments
Temperature during respirometry		
How was temperature controlled	Temperature was controlled using a reservoir of water heated by 3 1700W SmartOne Easy Plug heaters (adult trials), a cold-water reservoir and 1-2 800W finger heaters placed in each of the ambient tanks holding the chambers. Water from both hot and cold-water reservoirs flowed directly into ambient tanks with valve attachments to control the amount of cold and hot water inputs to maintain temperature targets.	
Ambient water bath cleaning and aeration	Due to short duration of trials and the lack of build up of bacteria (confirmed through measuring background respiration) water quality was ensured by using a complete flow through system of 1 tank turnover/h and airlines with bubblers were run to each tank.	
Minimum O_2 levels reached during trial	72% air saturation	In most cases air saturation did not drop below 80% during measurement cycles.
Were tanks visually shielded from visual disturbance	Yes.	
# of animals being measured during a single trial	n = 12	4 fish were placed in individual respirometers held in one of 3 ambient tanks. Fish could visually see others in the same ambient tank.
Animal fasting duration	Juvenile fish were fasted for 24 h prior to conducting trials Spawning adults were not fed. (does this go without saying?)	
Time since capture	Juvenile fish were provided by Kootenay trout hatchery and had been in the holding tank for ~6 months (confirm with marika) Adult fish were captured 26-27 hours before conducting trials.	

Table B.3 Details on methods for accounting for background respiration during respirometry trials

Criteria	Details for Trials in this Study	Additional Comments
Was background respiration measured?	Yes	For at least 30 minutes pre- and post trial (at least 3 slopes used in calculating background respiration)
Tank cleaning	Due to short duration of trials and conduction of trials in freshwater build of bacteria was very low. Tanks were cleaning with 10% virkon if bacterial respiration measurements indicated that levels had increased over the previous trial.	

Table B.4 Additional details about measurements of RMR in respirometry trials

Criteria	Details for Trials in this Study	Additional Comments
Time to first measurement after placement in Chamber	Measurements began immediately after fish were placed in chambers. For resting metabolic rate measurements were taken over 19-20 hours to account for variation in oxygen consumption due to handling effects and circadian rhythms.	
RMR calculation	Calculated as the lowest 10 quantile. (4-6 slopes/hr over 19-20 hours – 76-120 slopes). Measurement cycles were longer for juvenile fish due to chambers being slightly oversized and measurement cycles were reduced for both juveniles and adults at higher temperatures to ensure that oxygen levels did not drop below 70% air saturation.	
RMR measurements removed?	Yes, measurements needed to have an R^2 of 97% (under a linear regression between time and oxygen level) to be included.	

Table B.5 Details on the MMR in respirometry trials

Criteria	Details for Trials in this Study	Additional Comments
MMR measurement in relation to RMR	MMR was measured after RMR – however, highest levels of MO_2 during RMR were also identified and used in place of original MMR	

|	measurements if MO_2 consumption was higher (referred to as MMR overall)
Method for calculating AAS and FAS	MMR overall was treated identically to MMR in data analyses (r^2 threshold of 97%, sliding window of 120 seconds). Using RMR lowest 10 quantile etimates and either MMR or MMR overall depending on which possessed a higher MO_2 value.

Table B.6 Summary of thermal performances in Norbury Creek Kokanee salmon (*O. nerka*). Values are expressed as mean ± SEM and are set to a common body mass of 1 kg with no metabolic scaling coefficient for RMR and MMR, AAS as MMR-RMR (mg O_2 kg^{-1}min^{-1}), FAS as MMR/RMR (unit-less). ($P < 0.05$); significant p-values are bolded for emphasis. Letters (a,b,c,d,e) indicate significant differences between groups, and (v,w,x,y,z) is used to indicate where temperatures are significantly different within a single group.

Performance Metric	Temperature (°C)	N Female Adult	N Male Adult	N Juvenile	Mean ± SEM Female Adult	Mean ± SEM Male Adult	Mean ± SEM Juvenile	Group F_{df}	Group P-value	Temp F_{df}	Temp P-value
CT$_{max}$ (°C)	12	10	10	21	29.1 ± 0.16^{aw}	29.0 + 0.16^{aw}	28.1 ± 0.14^{bw}	2	**<0.0001**	4	**<0.0001**
	17	9	11	11	29.8 ± 0.17^{ax}	29.8 ± 0.16^{ax}	28.8 ± 0.16^{bx}				
	20	9	11	10	29.6 ± 0.17^{awx}	29.6 ± 0.16^{awx}	28.6 ± 0.17^{bwx}				
	22	12	6	10	30.4 ± 0.16^{ay}	30.3 ± 0.181^{ay}	29.4 ± 0.17^{by}				
	24	2	5	NA	29.4 ± 0.31^{axy}	29.3 ± 0.29^{axy}	28.4 ± 0.32^{bxy}				
Resting Metabolic Rate (mg O_2kg^{-1}min^{-1})	12	12	12	11	1.89 ± 0.15^{av}	2.18 ± 0.15^{av}	1.77 ± 0.15^{av}	2	**0.019**	4	**< 0.0001**
	17	13	9	12	3.23 ± 0.16^{bw}	3.52 ± 0.14^{bw}	3.11 ± 0.15^{bw}				
	20	12	9	10	4.13 ± 0.16^{cx}	4.42 ± 0.15^{cx}	4.01 ± 0.15^{cx}				
	22	10	8	11	4.95 ± 0.16^{dy}	5.24 ± 0.15^{dy}	4.83 ± 0.15^{dy}				
	24	1	4	NA	5.00 ± 0.32^{ez}	5.29 ± 0.34^{ez}	4.88 ± 0.35^{ez}				
Maximum Metabolic Rate 1h (mg O_2 kg^{-1}min^{-1})	12	12	12	11	10.80 ± 0.46^{aw}	13.2±0.45^{bw}	11.50 ± 0.46^{aw}	2	**<0.0001**	4	**0.0007**
	17	13	9	12	11.80 ± 0.49^{awx}	14.20 ± 0.45^{bwx}	12.50 ± 0.46^{awx}				
	20	12	9	10	13.00 ± 0.49^{axy}	15.30 ± 0.46^{bxy}	13.70 ± 0.48^{axy}				
	22	10	8	11	12.20 ± 0.50^{ay}	14.6 ± 0.48^{by}	12.90 ± 0.48^{ay}				
	24	1	4	NA	10.9 ± 0.98^{az}	13.3 ± 1.05^{bz}	11.7 ± 1.07^{az}				
Absolute Aerobic Scope (mg O_2 kg^{-1}min^{-1}) [with 0's for mortalities if died to this point]	12	12	12	11	8.95 ± 0.60^{aw}	11.12 ± 0.60^{bw}	9.62± 0.60^{aw}	2	**0.0008**	4	**< 0.0001**
	17	13	10	12	8.33 ± 0.61^{aw}	10.50 ± 0.59^{bw}	9.01 ± 0.59^{aw}				
	20	12	11	11	8.06 ± 0.61^{awx}	10.23 ± 0.60^{bwx}	8.73 ± 0.60^{awx}				
	22	12	10	12	6.07 ± 0.62^{ay}	8.25 ± 0.60^{by}	6.75 ± 0.60^{ay}				
	24	4	7	12	0.709 ± 0.72^{z}	2.886 ± 0.75^{z}	1.386 ± 0.68^{z}				
	12	12	12	11	5.97 ± 0.22^{w}	6.33 ± 0.22^{w}	6.25 ± 0.23^{w}	16.4 30$_1$	0.224	34.5 87$_3$	**< 0.0001**

|											
Factorial Aerobic Scope mg O_2 kg^{-1}min^{-1}) [with 0's for mortalities if died to this point]	17	13	10	12	3.66 ± 0.23^x	4.02 ± 0.22^x	3.95 ± 0.22^x				
	20	12	11	11	2.89 ± 0.23^{xy}	3.25 ± 0.22^{xy}	3.17 ± 0.23^{xy}				
	22	12	10	12	2.10 ± 0.23^y	2.46 ± 0.22^y	2.38 ± 0.22^y				
	24	4	7	12	0.314 ± 0.27^z	0.67 ± 0.28^z	0.67 ± 0.28^z				
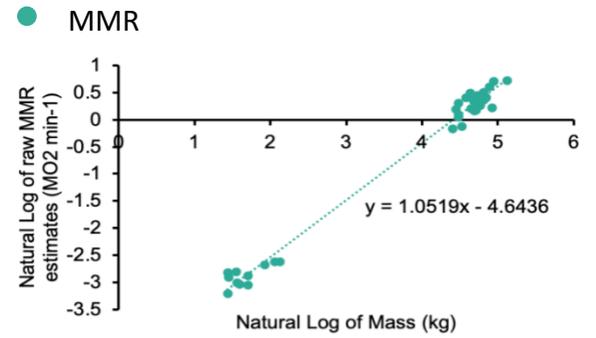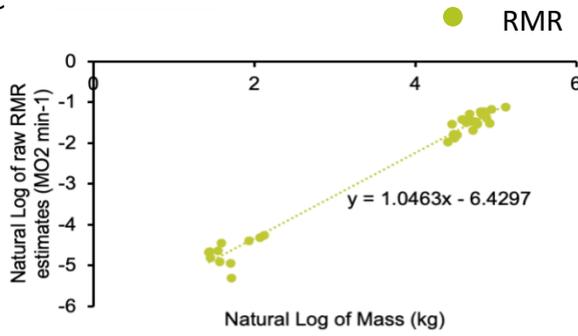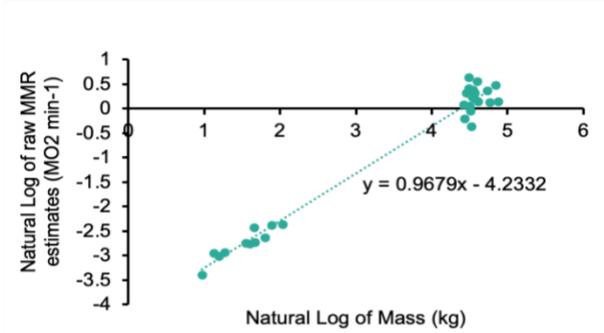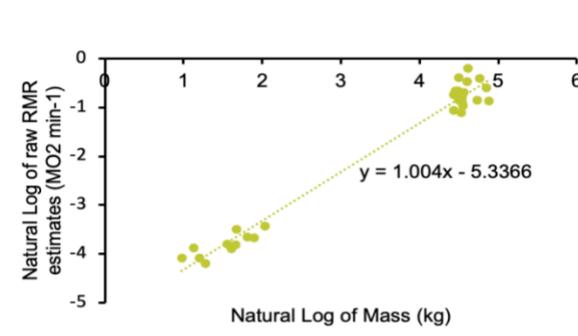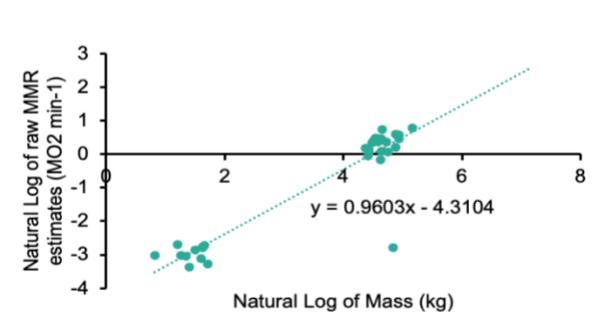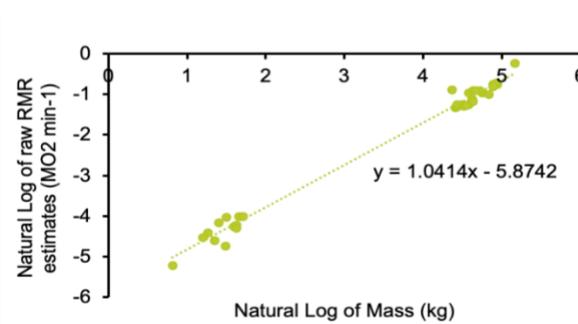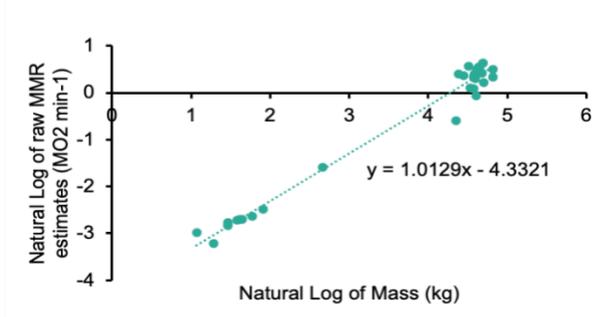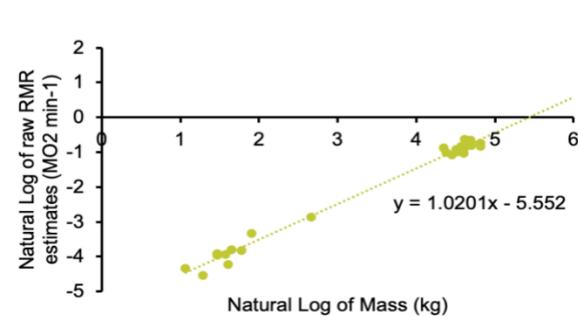
Figure B.1- Log normal Body Mass and Oxygen consumption scaling relationships for Resting (green) and Maximal (blue) resting metabolic rates.
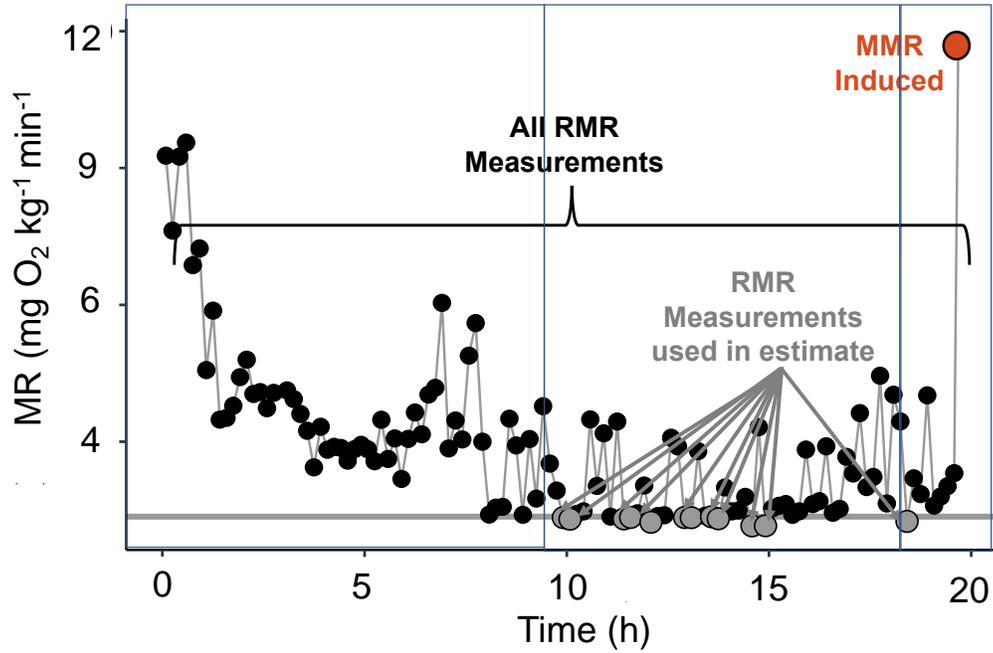
Figure B.2 - representative example of a trace plot for an individual fish displaying a full overnight measurement period (~21h) showing all recorded oxygen consumption rates (MO_2). In this case the Maximal Metabolic Rate (MMR) induced from the chase protocol was the highest MO_2 measurement recorded. Grey points indicate the measurements used in the estimation of Resting Metabolic Rate (RMR) for this fish. Yellow and blue sections are used to distinguish between daylight and nightime hours.
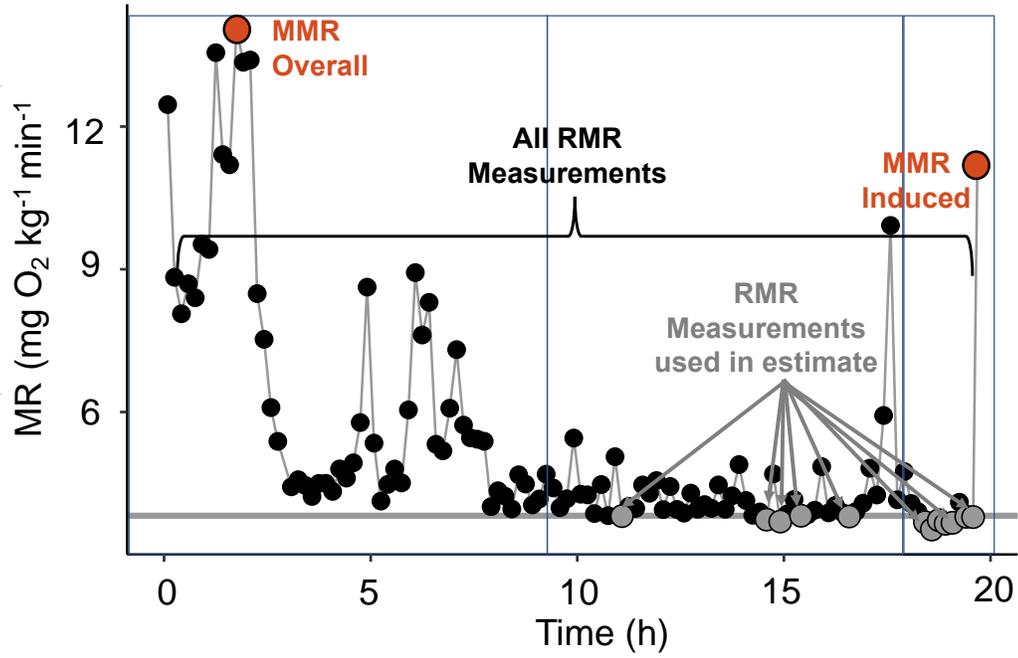
Figure B.3 - representative example of a trace plot for an individual fish displaying a full overnight measurement period (~21h) showing all recorded oxygen consumption rates (MO_2). In this case there was a recorded MO_2 measurement (Maximal Metabolic Rate, MMR, overall) that was higher than the MMR induced from the chase protocol. This phenomenon was observed in <90% of fish used in this study. The Grey points indicate the measurements used in the estimation of Resting Metabolic Rate (RMR) for this fish. Yellow and blue sections are used to distinguish between daylight and nightime hours.