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

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Abstract

Aquatic systems are warming and exceeding upper thermal limits (UTLs) for many fish species, yet understanding how they inform resilience to climate change is challenging. Using Pacific salmon (*Oncorhynchus* spp.) as a model, we conducted a systematic review involving 168 papers investigating UTL in five species. We found considerable variation in UTL among species, within species and across life stages; largely attributed to methodological approaches (e.g. CT_{max}/UILT, Aerobic/Cardiac Scope, Thermal Migration Barriers, Rearing Mortality, Thermal Preference/Avoidance). Given that each method has strengths and weaknesses owing to logistics, time scale and ecological realism, we offer a new framework for assessing vulnerability to warming that stresses the importance of considering UTL metrics in the context of intended use (i.e. the development of management guidelines, projections of future persistence and survival) and what aspect (physiological or behavioural) of thermal response a metric investigates. Comparing studies with identical UTL approaches revealed that within species, UTL was higher for populations historically encountering higher temperatures—suggesting local thermal adaptation. Within populations, UTL differed across the lifecycle, being highest in fry and lowest in embryo and migrating adults, but this was not universal. For spawning Pacific salmon, UTL has not been assessed and few studies have examined estuarine and marine stages. Ultimately, this data gap limits the life-history thermal perspectives that can be drawn and may indicate a broader gap for all fishes, given that Pacific salmon are among the most well-studied species. Our framework illustrates the inherent and methodological inconsistencies in UTL and offers a guide for how thermal limits can best be used to assess the warming tolerance and vulnerability of fishes.

KEYWORDS
behaviour, climate change, methodology, mortality, *Oncorhynchus*, upper thermal limits

1 | INTRODUCTION

Vulnerability of fish to high temperatures is primarily a product of three main factors: thermal tolerance (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). Yet a scheme for assessing thermal tolerance that incorporates these elements is lacking. In this paper, we describe a new framework for assessing thermal tolerance that focuses on the three primary elements of a species' vulnerability to warming and outlines how current thermal limits can best be used for assessing climate warming vulnerability in fish.

Few groups of species have been studied thoroughly enough in a thermal tolerance context to develop such a framework, with the exception of the Pacific salmon (*Oncorhynchus* spp., Salmonidae). As a model system, this group of species is ideal for this task as they possess a narrow optimal temperature range (Farrell, 2009), they have a limited ability to extend upper thermal tolerance (Muñoz et al., 2014, 2018) and are exposed to a wide range of climate change impacts due to their anadromous migratory behaviours (Flemming & Jensen, 2002). Natal homing and localized selective pressures have facilitated the development of finely tuned local adaptations that allow for higher fitness in native environments and have given rise to thousands of genetically distinct populations of Pacific salmon (Adkison, 1995; Fraser et al., 2011; Taylor, 1991). Specifically, intraspecific variation in thermal tolerance has been found to correlate with historical temperature experiences (Farrell et al., 2008) and suggests that these fish possess some adaptive potential to warming (Zillig et al., 2021). However, many populations are already imperilled throughout their historical range, and it remains unknown whether Pacific salmon can adapt their thermal tolerance to match the pace at which temperatures have and will continue to increase (Crozier et al., 2019; Zhang et al., 2019).

The reported upper thermal limits (UTLs) for Pacific salmon 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). As a result, assessing vulnerability and predicting how Pacific salmon may respond to continued warming will be highly dependent on the temperature threshold 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 (McCullough, 1999; McCullough et al., 2001; Myrick & Chech, 2004; Richter & Kolmes, 2005; Zillig et al., 2021), 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, and our intention is that this framework can be broadly adopted by researchers examining thermal tolerance in other species.

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 fish in a warming world.

2 | METHODS

2.1 | Data collection

To comprehensively collect studies that report UTL metrics for Pacific salmon, we 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 to June 2020 and relevant papers published after that point were added to the review manually. We used a keyword-based search using 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). We 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 our initial keyword-based literature search.

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 [*Oncorhynchus nerka*], Chinook salmon [*Oncorhynchus tshawytscha*], coho salmon [*Oncorhynchus kisutch*], chum salmon [*Oncorhynchus keta*], pink salmon [*Oncorhynchus gorbuscha*]). Only papers that reported novel numerical thermal metrics for these species of Pacific salmon were included in this review. We 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. We 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 or standard error of the mean if reported by the authors). Distributional studies were reported as the maximum value recorded during the study. We identified seven major study types (Swimming/Physiology, Incubation and Rearing, Capture/Count, Holding, Capture Simulation, Tagging and Model) that have been used to assess the effects of temperature on salmon function and behaviour (see Table S1).

We further identified seven distinct methodologies (Table 1) that have been used to assess UTL for Pacific salmon stemming from both physiological and ecological fields of research. Our 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. We also made comparisons among different methodologies based on their relative ecological relevance which we defined 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. We 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. We 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), we also draw upon four case studies where we compare reported temperature limits from a number of studies collected in this review.

3 | RESULTS AND DISCUSSION

3.1 | General trends in the literature

There were 168 peer-reviewed studies and technical reports included in this review that spanned across life stages and species of Pacific salmon (see Table S1). Of these, 20 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%), smolts (3%) and lastly immature ocean fish (1.8%) (see Table S1). 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 UTLs (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 finite endogenous energy with which to complete spawning migrations (Cooke et al., 2008). Further, reproductive life stages (spawning and embryonic) are identified as a critical thermal bottleneck in lifecycle of fishes (Dahlke et al., 2020). 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) are believed to be 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; Keefer & Caudill, 2014; Quinn, 1993). Given that abundances of pink and chum salmon are at all-time highs in the North Pacific Ocean, (Ruggerone & Irvine, 2018), and their commercial fisheries value now surpasses the other species of Pacific salmon (Gislason 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. Upper thermal tolerance metrics obtained from the literature, by species and life stage, are included in Tables S2–S5.

3.2 | Identification and comparison of methodologies

Physiological and ecological research into thermal tolerance of Pacific salmon has given rise to numerous temperature metrics with varying definitions and endpoints (Bates & Morley, 2020). However, the thermal limits proposed vary extensively depending on the experimental design and represent a range of responses such as thermal resistance, acclimation and evolutionary adaptation (Bates & Morley, 2020). Therefore, the variation in methodological details and the thermal responses that various approaches reflect 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 relevance. We felt that comparing the methodologies in this manner would situate them within in the broader ecological context of thermal performance and limitations since, in nature, fish can experience temperature variations at multiple temporal scales from diurnal to seasonal fluctuations as well as across the lifecycle. For example, Spring and summer-run Chinook in the Columbia naturally experience diel fluctuation 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 to fluctuate from 12 to 18°C (Atlas et al., 2021). These natural fluctuations can either mediate or exacerbate threats posed by changes in the hydro climatology of salmon-producing watersheds. Such changes refer to both shifts in climate trajectories (presses) and extreme events (pulses) (Harris et al., 2018). Therefore, long-term changes in temperature and flow must be considered in combination with shifts in the frequency and intensity of extreme events to improve the detection of climate change impacts on biological systems (Harris et al., 2018).

TABLE 1 Behavioural and physiological methodologies employed to quantify upper thermal tolerance in Pacific salmon.

	Methodologies	Description
Behavioural	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	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)

3.2.1 | CT_{max}/UILT

Background

CT_{max} and UILT are identified through acclimating/acclimatizing organisms to a given temperature and involve time and temperature as primary test variables (Becker & 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 (Abe et al., 2019; Baird et al., 2018). UILT involves a rapid transfer from acclimation to exposure temperature with death as the endpoint (Becker & Genoway, 1979; Brett, 1952).

Ecological relevance

Traditional CT_{max} and UILT studies generate consistently high thermal limits compared to other methodologies and possess the least ecological relevance (Figure 1). 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 & Genoway, 1979). Second, for CT_{max} in particular, 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 (Kingslover & Umbanhowar, 2018; McKenzie et al., 2020; Terblanche et al., 2007). During continuous warming, a lag between body temperature and ambient water temperature can occur if rate of warming is too rapid and there is a risk of partial acclimation to higher temperatures than intended when warming too slowly (Becker & Genoway, 1979; Desforges et al., 2023). 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 at far lower temperatures than those quantified by the CT_{max} or UILT approaches. 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). However, efforts to develop models that allow for comparison across CT_{max} and UILT trials with varying warming protocols are being undertaken (Jørgensen et al., 2021; Ørsted et al., 2022). This research offers a promising framework for improving comparative assessments of thermal tolerance across populations where critical thermal limits have been obtained. 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, we do not discourage use of this metric, rather we encourage both careful interpretation and combined use of metrics to improve the ecological relevance of the thermal thresholds used in future management schemes. CT_{max} values may be the only thermal metric available for a population, and when this is the case, these values should be considered in proper context—are there CT_{max} and T_{crit} values for other populations that exhibit similar life histories and exist in similar climates? This information could then be used to infer that ecologically relevant thermal thresholds are 'x' degrees lower than what the CT_{max} suggests.

3.2.2 | 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 laboratory- 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 & Magnuson, 1982). Laboratory-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 period of time (see Christensen et al., 2021 for details).

Ecological relevance

The preference/avoidance approach consistently reports some of the lowest UTL among the various methodologies compared in this review (Figure 1). 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 (Christensen et al., 2021; Huey, 1991), they do not indicate whether fish are capable of tolerating higher temperatures.

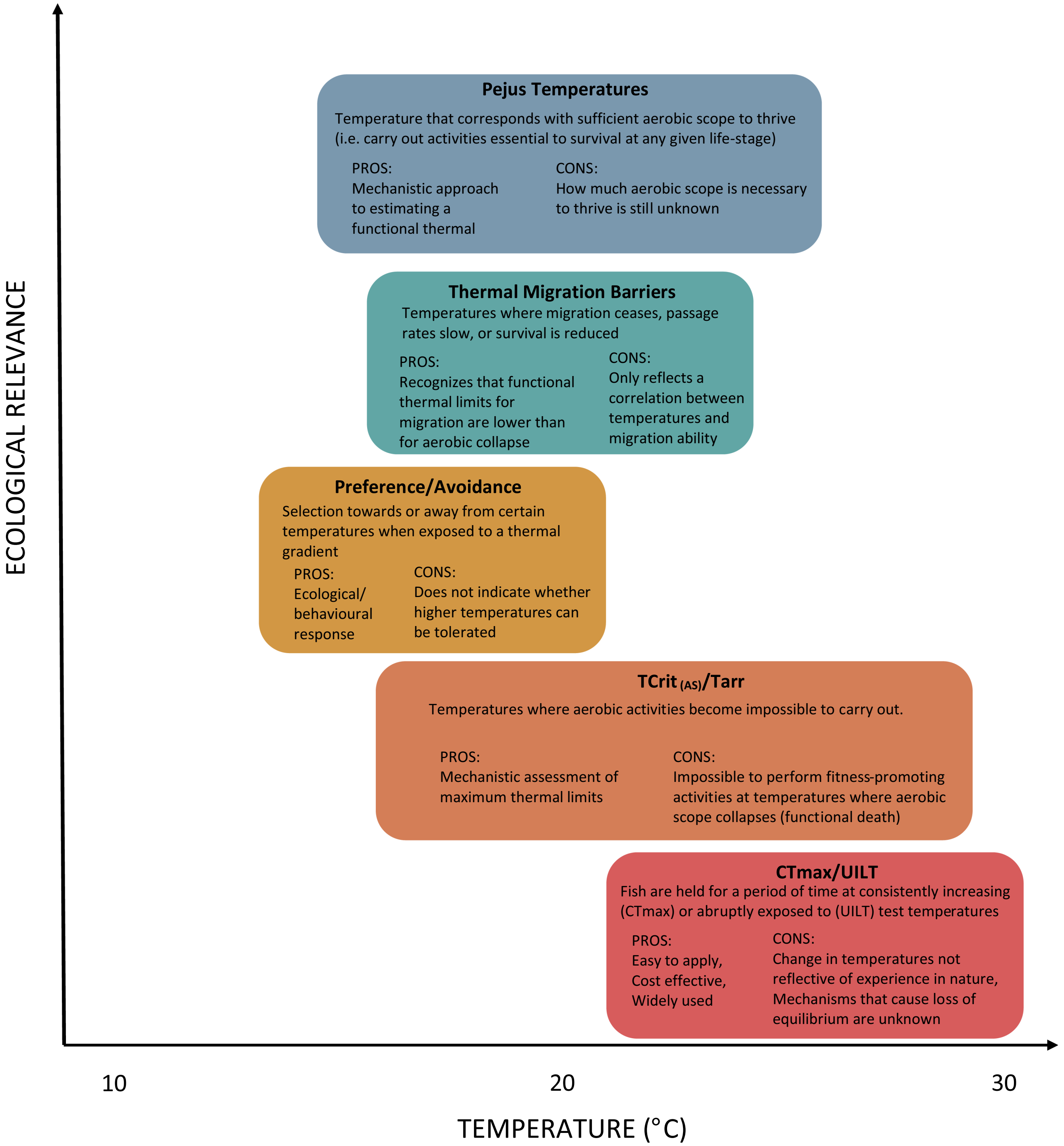


FIGURE 1 Conceptual Figure illustrating the relative ecological relevance of the critical thermal maximum (CT_{max}), upper incipient lethal temperature (UILT), critical temperature for aerobic scope ($T_{crit(AS)}$), arrhythmic temperature (T_{arr}), avoidance, thermal migration barrier and Pejus temperatures (T_p) methodologies for quantifying thermal limits of Pacific salmon. Widths and placement of the boxes reflect the breadth of temperatures for each category.

Furthermore, the majority of these studies are laboratory-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 & Farrell, 2016).

3.2.3 | 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, Caudill, et al., 2008; Keefer, Peery, & Heinrich, 2008; 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 (Caudill et al., 2007; Crossin et al., 2008; Goniea et al., 2006; Hodgson & Quinn, 2002; Hyatt et al., 2003; Keefer, Caudill, et al., 2008), inability to reach natal spawning grounds (Connor et al., 2019; Keefer, Peery, & Heinrich, 2008) and cessation of migration (Hallock et al., 1970; MacDonald et al., 2010).

Ecological relevance

The thermal migration barrier methodology reports similar thermal limits to avoidance studies (Figure 1). 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 UTLs reported using this approach likely due to different definitions for upper thermal migratory limits: temperatures when (i) successful migration declines (% of fish that no longer reach spawning grounds, this % threshold varies across studies), (ii) migration ceases (little to no fish detected at receivers further upstream or observed at fish fences), (iii) passage rates slow significantly (time between detections at receivers or fish fences along the migration route increases). This is problematic as variation in reported thermal limits may be less a function of inherent variation in thermal tolerance and more a product of how the thermal limit is defined.

3.2.4 | Scope for activity/aerobic scope

Background

For aquatic ectotherms like Pacific salmon, thermal limits can be determined by insufficient aerobic capacity to support essential activities (Pörtner & Farrell, 2008). This theory developed when Fry (1947) demonstrated the controlling influence of temperature on a fish's 'scope for activity'. Scope for activity (aka aerobic scope) is 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 is the amount of energy available to fish to perform any activities beyond basic body maintenance (e.g. swim, digest a meal, compete for mates or territory and 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; Lefevre et al., 2021). In sockeye salmon, the decrease in aerobic scope at high temperatures (MacNutt et al., 2006) was associated with a collapse in cardiac performance (Eliason et al., 2011; Eliason, Clark, et al., 2013; Eliason, Wilson, 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 $T_{crit(AS)}$ (Casselman et al., 2012; 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 (Eliason et al., 2011; Farrell et al., 2008). 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 are 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 relevance

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 1), 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). When assessing cardiac capacity in relation to temperature, T_{ABT} and T_{arr}, experiments are typically performed on anaesthetized and pharmacologically stimulated fish (to ensure they reach max heart rate), which may impact the results in ways that are irrespective of temperature. Further heating rates across aerobic and cardiac scope studies also vary which can impact the acclimation response. Therefore, comparisons across studies should be made with caution. Further, an inability to assess excess post-exercise oxygen consumption and its effects on acclimation means that only aerobic processes are being considered when assessing thermal tolerance (Lee, Farrell, Lotto, Hinch, & Healey, 2003). Lastly, when investigating the temperature dependence of aerobic scope, RMR and MMR are measured and calculated at several experimental temperatures. Since AS is not evaluated over a continuous temperature gradient, $T_{opt(AS)}$ and $T_{crit(AS)}$ are typically estimated by fitting a polynomial regression onto the data.

For adult migrants, T_p estimates are more ecologically relevant (Figure 1) 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 (Kunz et al., 2018; Lowe & Davison, 2006). It remains 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).

3.2.5 | 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 historical thermal experiences (Angilletta et al., 2008) and the length and difficulty of spawning migrations (Crossin et al., 2004; Eliason et al., 2011; Farrell et al., 2008). 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, we explore four 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 analysed the impacts of temperatures on optimal metabolic performance using the Scope for Activity/Aerobic Scope methodology (Table 2). We pooled data from four studies (Eliason et al., 2011; Eliason, Wilson, et al., 2013; Farrell et al., 2008; Lee, Farrell, Lotto, MacNutt, et al., 2003) to assess how the average $T_{opt(AS)}$ for multiple populations of sockeye salmon may differ from other species of Pacific salmon. Table 2 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 (Abe et al., 2019; Eliason et al., 2011; Farrell et al., 2008; Lee, Farrell, Lotto, MacNutt, et al., 2003). 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) and Eliason, Wilson, et al. (2013) were selected to demonstrate 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 at the same life stage, 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 sockeye 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 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: 20.8–29.4°C) than $T_{opt(AS)}$ (range: 14.5–17.2°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. Additional studies on chum salmon (Abe et al., 2019), Chinook salmon (Zillig et al., 2021), sockeye salmon fry (Chen et al., 2013) similarly have discovered that salmon populations differ in thermal tolerance. Collectively, these data suggest that Pacific salmon have a remarkable capacity to respond to their environment via genetic adaptation and/or phenotypic plasticity.

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 3 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 and 10°C groups. They suggested that the stark reduction in survival may be due to 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 $\mathrm{CT}_{\mathrm{max}}$ values for the same nine populations of sockeye salmon in the fry life stage after incubation under three different thermal regimes (10, 14 and 16°C). Populations did differ in $\mathrm{CT}_{\mathrm{max}}$, although this was strongly related to body size. In general, the absolute differences in $\mathrm{CT}_{\mathrm{max}}$ across populations were minimal at this life stage, particularly when compared to a common body size. $T_{\mathrm{opt(AS)}}$ and $T_{\mathrm{crit(AS)}}$ 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.

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.

We also compared *absolute* thermal tolerance across the lifecycles of three populations of sockeye salmon, to identify potential thermal bottlenecks (Dahlke et al., 2020; Pörtner & Farrell, 2008) using data extracted from Whitney et al. (2013), Chen et al. (2013), Eliason et al. (2011) and Eliason, Wilson, et al. (2013). The current paradigm suggests that thermal windows are narrowest for embryos and spawners and widest during the juvenile life stage (Dahlke et al., 2020; Pörtner & Farrell, 2008). 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 transitions 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 4 is the most detailed information available on life stage-specific UTL across populations. All these methodologies (embryo survival, CT_{max}, $T_{\mathrm{crit(AS)}}$) reflect temperatures where death is imminent and were performed in controlled laboratory 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. Therefore, the examples provided here represent the best life stage comparison available in the literature on thermal tolerance in Pacific salmon. A recent alternative proposed by FitzGerald et al. (2020) 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.

We found extremely limited data on the upper thermal tolerance of alevin, smolt and marine life stages or the fully mature spawning life stage (Figure 4). There was only one published study that identified a $\mathrm{CT}_{\mathrm{max}}$ 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 & Chech, 2004),

TABLE 2 $T_{\mathrm{opt(AS)}}$ estimates for sockeye, coho, pink and chum salmon (Abe et al., 2019; Clark et al., 2011; Eliason et al., 2011; Eliason, Clark, et al., 2013; Farrell et al., 2008; Kraskura et al., 2020; Lee, Farrell, Lotto, MacNutt, et al., 2003).

Species	Sockeye	Coho	Chum	Pink
$T_{\mathrm{opt(AS)}}$ average (°C)	15.89	12.35	15.80	21.00
$T_{\mathrm{opt(AS)}}$ range (°C)	14.50–17.20	8.50–18.00	14.00–17.60	–
Mean migration Temperature (°C)	~16.2	~7.1	~11.1	~16.9
Maximum migration temperature (°C)	~22	~12	~19	~21

Note: Ranges are given when optimal temperatures for aerobic scope have been assessed in more than one study: sockeye $N=9$ (six populations), coho $N=2$ (one population), chum $N=2$ (two populations).

further research into their upper thermal tolerance is necessary. Several studies on smolt and marine life stages have developed temperature preference estimates (Eliason et al., 2017; Hinke et al., 2005) and distributional limits (Azumaya et al., 2007; Welch et al., 1995) but only one study has assessed the UTL 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 (Pörtner & 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, Wilson, et al., 2013).

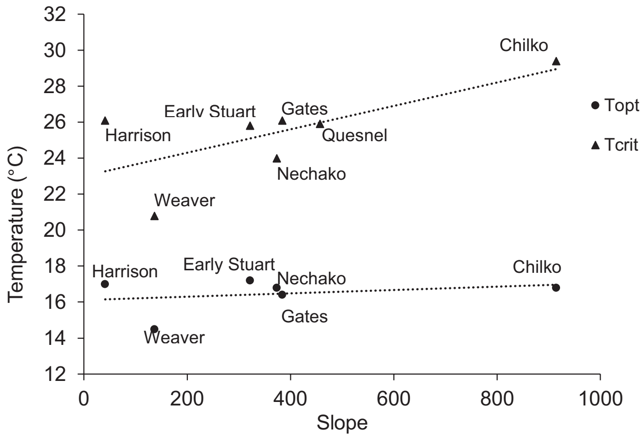


FIGURE 2 Correlation between migration slope (migration elevation/migration distance) and critical (T_{crit}) and optimal (T_{opt}) for Aerobic scope for Fraser River adult migrating sockeye salmon populations (T_{crit} correlation: $y = 0.0065x + 22.99$, $R^2 = 0.49$, $p = .08$; T_{opt} correlation: $y = 0.0009x + 16.11$, $R^2 = 0.08$, $p = .81$; data from Eliason et al., 2011; Eliason, Wilson, et al., 2013).

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 a test group acclimated to 5°C and heated at a rate of 1°Ch^{-1} compared to a fish acclimated to 15°C and heated at a rate of 60°Ch^{-1} (Figure 5). 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 components of the CT_{max} methodology: the rate at which the water is heated and the initial acclimation temperature. Variation across studies in one or both of these components makes comparison extremely difficult due to the variable impacts that acclimation treatments and heating rates can have on CT_{max} estimates.

On a broader level, variation in UTLs 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

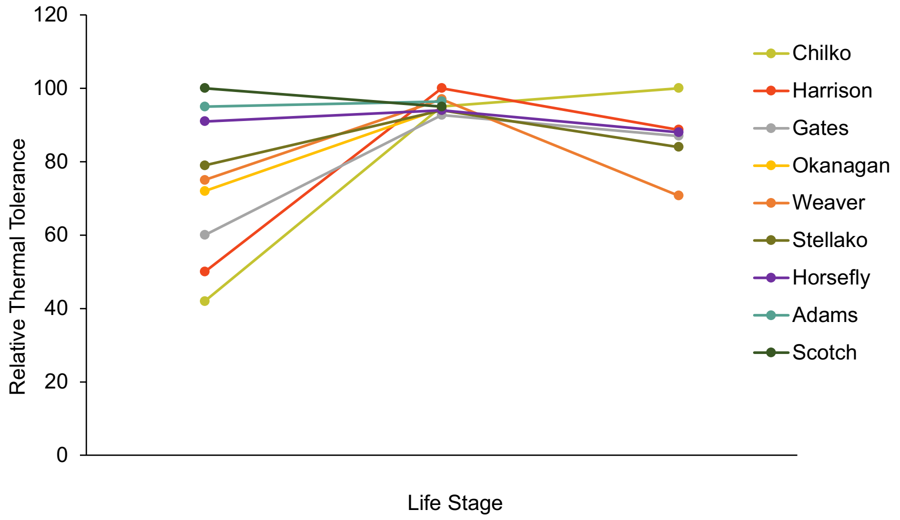


FIGURE 3 Intraspecific variation in relative upper thermal tolerance across the sockeye salmon life cycle. Relative thermal tolerance adapted from critical temperatures for aerobic scope ($T_{crit(AS)}$) in adults (Eliason et al., 2011), critical thermal maximums (CT_{max}) for fry (1 g) reared at 10°C, (Chen et al., 2013) and estimates of 60% survival (derived from survival curves for embryos incubated at 10, 14 and 16°C) for embryos (Whitney et al., 2013). 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 × UTL)/population max UTL.

major reason for this variation is that different methodologies define the UTL 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). 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 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 UTL as the temperature where complete aerobic collapse occurs and is not an ecologically relevant metric.

3.3 | A framework for assessing vulnerability to warming in the climate change era

An essential component of successful conservation and management in the climate change 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., 2020). In order to comprehensively determine a fish species' vulnerability to warming, there are three main factors to consider: The thermal tolerance (temperature range in which a species can thrive), the thermal exposure (the temperatures that a species experiences through its lifetime) and the adaptative capacity (ability for a population or species to extend their upper thermal tolerance through phenotypic plasticity and/or adaptive evolution) and the pace at which that adaptation occurs (Figure 6).

As researchers begin to recognize the extensive differences in both thermal tolerance and exposure at different life stages in fishes, another major question arises: at which life stages are fish most vulnerable to climate warming? An 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., 2020). 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. Our investigation into the UTL for Chilko sockeye indicates low thermal tolerance during the juvenile life stage despite superior aerobic and cardiac capacity at high temperatures during the adult migrant life stage. These differences in thermal tolerance

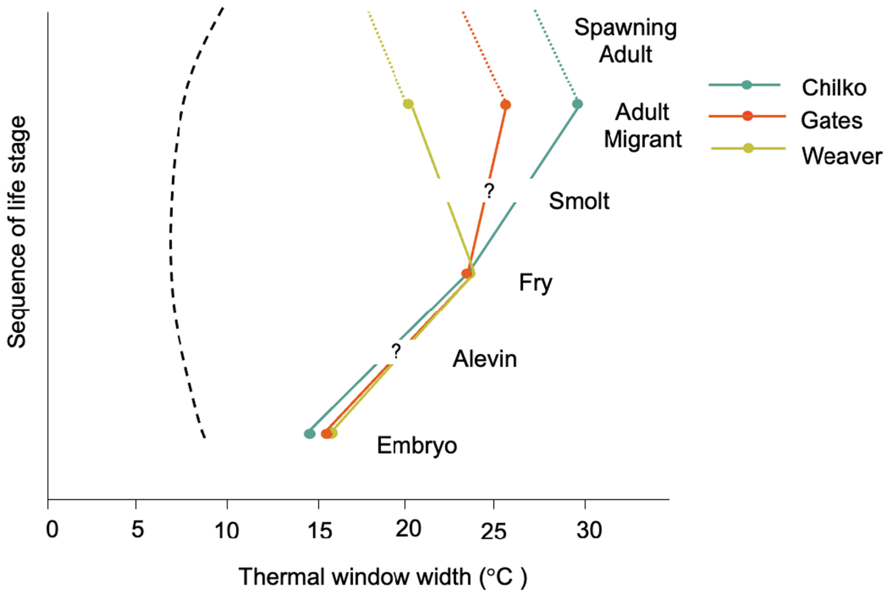


FIGURE 4 Life stage-specific variation in absolute upper thermal tolerance for Fraser River sockeye salmon populations Weaver, Gates and Chilko based on comparable critical temperatures: critical temperatures for aerobic scope ($T_{crit(AS)}$) in adults (Eliason et al., 2011), critical thermal maximums (CT_{max}) for fry (1 g) reared at 10°C (Chen et al., 2013) and estimates of 60% survival in embryos (from survival curves for embryos incubated at 10, 14 and 16°C; Whitney et al., 2013). Dotted lines illustrate hypothetical upper thermal tolerance in mature spawning adults and the black dashed line represents a hypothetical lower temperature tolerance limit. 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 (Dahlke et al., 2020; Pörtner & Farrell, 2008), which is likely true for Weaver, though not for Chilko. Despite considerable research attention on thermal tolerance in sockeye salmon, gaps in knowledge remain.

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 lower levels of biological organization (population and life stage) will promote genetic diversity and allow for greater adaptive and evolutionary potential to future environmental conditions (Zillig et al., 2021).

While there is clear evidence of population and life stage-specific differences in thermal tolerance (Figures 3 and 4), 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 (Clark et al., 2012; Daufresne et al., 2009). Additionally, a recent and comprehensive 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 size on all life stages.

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, significant increases in pathogen susceptibility and inability to recover from capture events have been observed when fish are faced with higher temperatures (Gale et al., 2011, 2014; Raby et al., 2015, 2016; Teffer et al., 2018, 2019). Therefore, the interactive effects of these cumulative stressors should be considered alongside reported UTLs 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 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 3 and 4). Moreover, thermal exposure differs depending on which part of the lifecycle an individual is in and can be modulated by shifts in behaviour (e.g. changes in run-timing). Therefore, a thorough understanding of how thermal exposure compares to the UTL 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 (Figure 6).

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 UTL 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 relevance as other metrics (e.g. T_p, thermal migration barriers). Therefore, developing TSM's that utilize a more functional range of UTLs (e.g. T_p, thermal migration barriers, temperature where growth is limited) may provide a more realistic understanding of a populations' vulnerability to warming. For example, a recent study on the population-specific thermal tolerance of juvenile rainbow trout suggests using the T_p rather than the CT_{max} provides a more ecologically relevant estimate of a population's warming tolerance (Anlauf-Dunn et al., 2022).

Beyond developing a knowledge based on the UTL 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. Both developmental and intergenerational plasticity can play a major role in an individuals' survival and fitness as well as population persistence (Figure 6). For example, Burt et al. (2012a, 2012b), found that, parental identity had a significant influence on embryonic survival, particularly under a high-temperature incubation treatment (16°C). Further, fry incubated at higher temperatures have been shown to maintain higher maximum upper thermal tolerance limits in the subsequent life stage (Chen et al., 2013).

In response to warming, fish populations can (a) alter behaviour to avoid unfavourable conditions (e.g. Minke-Martin et al., 2018; Roscoe et al., 2010), (b) acclimate through phenotypic plasticity to withstand high temperatures over short time periods (minutes, hours, days) or (c) adapt through natural selection to increase thermal tolerance at the gene level (Anttila et al.,2014). However, 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, Hendry, et al., 2008; Crozier, Zabel, & Hamlet, 2008). Therefore, evolutionary adaption of thermal tolerance should be considered when making predictions about long-term resilience in native environments (Chen et al., 2017). 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 remains unknown (Angilletta et al., 2008). Traits (and the thermal metrics derived from them) related to thermal tolerance and performance have been found to be heritable in salmonids. Research into the genomic underpinnings for thermal tolerance in salmonids is underway; however, the genomic basis of thermal tolerance is highly complex and research into microevolution towards increased thermal tolerance is extremely limited (Chen et al., 2017). Muñoz et al. (2015) quantified the heritability of cardiac thermal performance. Chen et al. (2017) and demonstrated genomic patterns of evolutionary adaptation to extreme climates among populations of redband trout (*Oncorhynchus mykiss*) and identified potential candidate genes related to the thermal sensitivity of cardiac function (including IRX5, CASQI, CACID and TITIN). However, thermal performance is a polygenic phenotype that will likely require whole genome sequencing to identify genomic regions that are associated with thermal limits (Chen et al., 2015). 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., 2021). 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 various UTL metrics that reflect these mechanisms will be central in making accurate predictions about the potential for adaptive evolution of thermal tolerance under future warming.

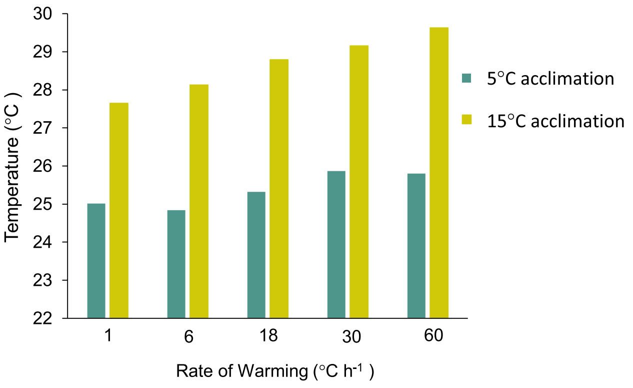
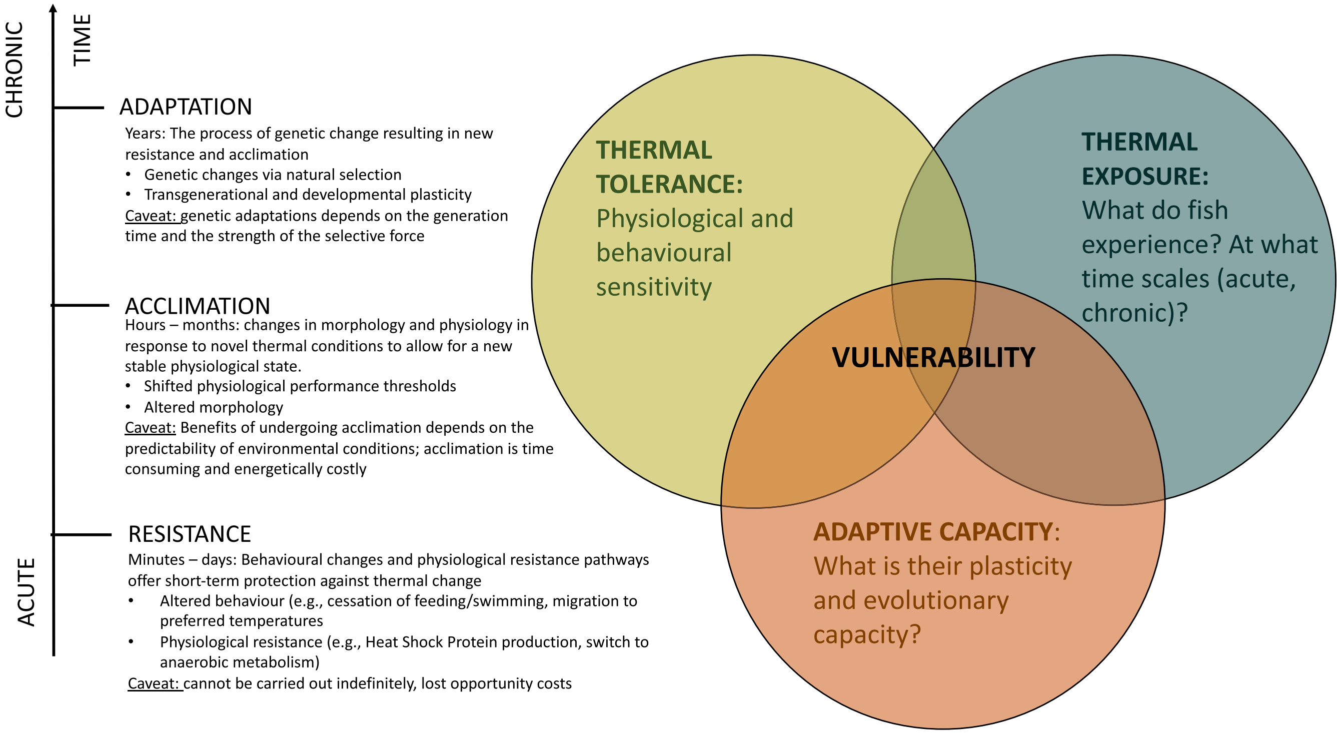


FIGURE 5 Critical thermal maximum (CT$_{max}$) values obtained for coho salmon (n = 16 for all test groups) when using different acclimation temperatures and heating rates (adapted from Becker & Genoway, 1979).

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 (Chen et al., 2013; Eliason et al., 2011; Eliason, Wilson,



ADAPTATION
Years: The process of genetic change resulting in new resistance and acclimation
- Genetic changes via natural selection
- Transgenerational and developmental plasticity

Caveat: genetic adaptations depends on the generation time and the strength of the selective force

ACCLIMATION
Hours – months: changes in morphology and physiology in response to novel thermal conditions to allow for a new stable physiological state.
- Shifted physiological performance thresholds
- Altered morphology

Caveat: Benefits of undergoing acclimation depends on the predictability of environmental conditions; acclimation is time consuming and energetically costly

RESISTANCE
Minutes – days: Behavioural changes and physiological resistance pathways offer short-term protection against thermal change
- Altered behaviour (e.g., cessation of feeding/swimming, migration to preferred temperatures
- Physiological resistance (e.g., Heat Shock Protein production, switch to anaerobic metabolism)

Caveat: cannot be carried out indefinitely, lost opportunity costs

THERMAL TOLERANCE: Physiological and behavioural sensitivity

THERMAL EXPOSURE: What do fish experience? At what time scales (acute, chronic)?

VULNERABILITY

ADAPTIVE CAPACITY: What is their plasticity and evolutionary capacity?

FIGURE 6 Framework for assessing vulnerability to warming in fishes. The three components of vulnerability are depicted in the Venn diagram. Represented along the vertical axis are definitions and temporal scales over which the components of thermal tolerance are most relevant.

et al., 2013; see Figure 3). However, in the research we reviewed, individual variation within a population appears to be limited (Chen et al., 2017; Muñoz et al., 2015). 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 & Caudill, 2014). Introduction of novel genetic diversity into a population can increase the probability of genetic rescue and allow for a population to more quickly adapt to new environmental conditions (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 as well as 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, Caudill, et al., 2008; 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 were 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 (Anttila et al., 2019; Eliason et al., 2011). 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 UTL will be an important component in determining the potential for Pacific salmon to successfully adapt to changing environmental conditions.

When endeavouring to assess vulnerability to warming temperatures, the range of responses (behavioural, physiological, biochemical, morphological, phenological) must be considered. Further, these responses have varying temporal importance (acute, chronic, intergenerational; Figure 6). This review has identified several approaches that aim to quantify thermal tolerance at the physiological (CT_{max}, Aerobic and Cardiac Scope, biochemical responses) and behavioural (thermal migration barriers, preference/avoidance) levels. Each of these approaches provides meaningful information on the overall thermal response that fish will have as water temperatures rise (Bates & Morley, 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. When selecting a UTL estimate to use in the development of thermal management guidelines, we must consider the UTL metrics in context; both the intended use (informing management tactics like fish quotas or fisheries closures, modelling future persistence) and limitations of what information each metric provides must be taken into account to avoid over- or underestimating vulnerability. For example, CT_{max} provides insights about UTLs on acute timescale and thus, CT_{max} values should not be used to investigate tolerance to chronic high temperature exposures, when other metrics are available. However, plasticity in the thermal response with acclimation or acclimatization that is seen in CT_{max} studies can provide useful information on the non-evolutionary adaptive capacity (plasticity) of a given population or species. Further, physiological resistance pathways, such as the production of heat shock proteins or a shift to anaerobic metabolism are important mechanisms for surviving acute thermal stress (Bates & Morley, 2020). With respect to more chronic temperature exposures, the ability to acclimate and extend thermal tolerance is more critical to survival. In these cases, using results from multiple approaches can provide meaningful insights regarding 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 (Jeffries, Hinch, Martins, et al., 2012; von Biela et al., 2019). Given that UTL are shaped by a variety of physiological and behavioural responses there are instances where using a combination of metrics may be most appropriate and allow for a more robust representation of the overall thermal response to warming. Using multiple metrics in concert can also aid in determining whether a metric is either physiologically or ecologically relevant or both (two concepts that are often used interchangeably in the literature). When metrics assessing various behavioural or physiological aspects of the thermal response to warming yield consistent results, such metrics are extremely powerful in their possessing both ecological relevance (are indicative of how individuals may respond to warming temperatures) and physiological relevance (provide a physiological thermal limit beyond which a species can no longer survive and persist). Though sparse, consistent behavioural and physiological metrics are present in the literature in the form of thermal migration barriers and Pejus temperatures (T_p). For example, thermal migration barriers have been identified for adult sockeye salmon from the Chilko, Quesnel and Stellako/Early Stuart populations at ~19°C (MacDonald et al., 2010; Martins et al., 2011). T_p estimates for these same populations are within a similar range (Chilko: 20.7°C, Quesnel: 18.5°C, Stellako/Early Stuart: 19.9; Eliason et al., 2011). Alternative efforts for reconciling UTLs derived from experiments with differing protocols have recently been proposed by

Ørsted et al. (2022) in which ecological and physiological evaluation of thermal stress is based off the net sum of two biological processes; thermal injury (disruption of homeostatic regulation) and thermal repair (temperatures where homeostatic regulation can be carried out).

4 | CONCLUSIONS

We outlined the importance of considering the potential sources of variation in reported UTL for Pacific salmon and demonstrated how the use of species- and life stage-specific UTLs can provide a more accurate depiction of how these species may respond to future warming. In instances where complimentary metrics are available (i.e. thermal performance curves for aerobic scope and cellular responses to thermal stress) they can and should be used in concert to develop a more robust understanding of UTL. Furthermore, metrics that are consistent across both physiological and behavioural studies are most powerful and possess high ecological relevance as they are rooted in a mechanistic understanding of why fish can no longer thrive at high temperatures and reflective of the thermal experience and energetic requirements of the fish in nature. Major data deficiencies exist at region/latitude, species, population and life stage levels for all species reviewed, however pink and chum salmon are vastly underrepresented in the literature.

We identified seven methodological approaches employed to quantify UTL, some of which possess more ecological relevance than others and, in certain cases, their use may be limited to specific life stages. Further, our findings demonstrated that both inherent (species, population, life stage) and methodological (within and among approaches) variation contribute to the considerable differences observed in proposed UTL—a finding that would be universally applicable to most fish species. Further, all of the approaches we reviewed possess specific limitations owing to logistics and/or ecological relevance 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 (Carey et al., 2019; Jeffries et al., 2014; Jeffries, Hinch, Sierocinski, et al., 2012; von Biela et al., 2020). Lastly, there is a dearth of information on the role of body size and sex in relation to thermal tolerance and is an area where future research should be directed. This finding is likely not just limited to Pacific salmonids and would be relevant to most fish species. Overall, future fisheries management and conservation actions should be developed with careful consideration of the nuances we identified in how thermal tolerance is assessed.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data are available in a supplemental file attached to this paper.

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REFERENCES

Abe, T. K., Kitagawa, T., Makiguchi, Y., & Sato, K. (2019). Chum salmon migrating upriver adjust to environmental temperatures through metabolic compensation. *Journal of Experimental Biology*, *222*(3), jeb186189. https://doi.org/10.1242/jeb.186189

Adkison, M. D. (1995). Population differentiation in Pacific salmon: Local adaptation, genetic drift or the environment. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(12), 2762–2777. https://doi.org/10.1139/f95-865

Angilletta, M. J., Ashley Steel, E., Bartz, K. K., Kingsolver, J. G., Scheuerell, M. D., Beckman, B. R., & Crozier, L. G. (2008). Big dams and salmon evolution: Changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications*, *1*(2), 286–299. https://doi.org/10.1111/j.1752-4571.2008.00032.x

Anlauf-Dunn, K., Kraskura, K., & Eliason, E. J. (2022). Intrapsecifc variability in thermal tolerance: A case study with coastal cutthroat trout. Conservation. *Physiology*, *10*(1), coac029. https://doi.org/10.1093/conphys/coac029

Anttila, K., Eliason, E. J., Kaukinen, K. H., Miller, K. M., & Farrell, A. P. (2014). Facing warm temperatures during migration: Cardiac mRNA responses of two adult Oncorhynchus nerka populations to warming and swimming challenges. *Journal of Fish Biology*, *84*(5), 1439–1456. https://doi.org/10.1111/jfb.12367

Anttila, K., Farrell, A. P., Patterson, D. A., Hinch, S. G., & Eliason, E. J. (2019). Cardiac SERCA activity in sockeye salmon populations: An adaptive response to migration conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(1), 1–5. https://doi.org/10.1139/cjfas-2018-0334

Armstrong, J. B., Ward, E. J., Schindler, D. E., & Lisi, P. J. (2016). Adaptive capacity at the northern front: Sockeye salmon behaviourally thermoregulate during novel exposure to warm temperatures. *Conservation Physiology*, *4*(1), 1–10. https://doi.org/10.1093/conphys/cow039

Atlas, W. I., Seitz, K. M., Jørgensen, J. N. W., Millard-Martin, B., Housty, W. G., Ramos-Espinoza, D., Burnett, N. J., Reid, M., & Moore, J. W. (2021). Thermal sensitivity and flow-mediated migratory delays drive climate risk for coastal sockeye salmon. *FACETS*, *6*, 71–89. https://doi.org/10.1139/facets-2020-0027

Azuma, T. (1995). Biological mechanisms enabling sympatry between salmonids with special reference to sockeye and chum salmon in oceanic waters. *Fisheries Research*, *24*(4), 291–300. https://doi.org/10.1016/0165-7836(95)00383-3

Azumaya, T., Nagasawa, T., Temnykh, O. S., & Khen, G. V. (2007). *179-187Azumaya*. *4*, 179–187.

Baird, S. E., Steel, A. E., Cocherell, D. E., Cech, J. J., & Fangue, N. A. (2018). Native Chinook salmon Oncorhynchus tshawytscha and non-native brook trout Salvelinus fontinalis prefer similar water temperatures. *Journal of Fish Biology*, *93*(5), 1000–1004. https://doi.org/10.1111/jfb.13810

Baker, P. F., Terence, P., & Ligen, F. K. (1995). Estimating the influence of temperautre on the survival of Chinook salmon smolts

(Oncorhycnhus tshawytscha) migrating through the Sacramento San Jaoquin River Delta of California. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(4), 855–863.

Bates, A. E., & Morley, S. A. (2020). Interpreting empirical estimates of experimentally derived physiological and biological thermal limits in ectotherms. *Canadian Journal of Zoology*, *98*(4), 237–244. https://doi.org/10.1139/cjz-2018-0276

Becker, C. D., & Genoway, R. G. (1979). Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. *Environmental Biology of Fishes*, *4*(3), 245–256. https://doi.org/10.1007/BF00005481

Beitinger, T. L., Bennett, W. A., & Mccauley, R. W. (2000). Temperature tolerances of north American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes*, *58*, 237–275. https://doi.org/10.1023/A:1007676325825

Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar, A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahnek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., & Olalla-Tárraga, M. (2021). The evolution of critical thermal limits of life on earth. *Nature Communications*, *12*, Article 1198. https://doi.org/10.1038/s41467-021-21263-8

Bett, N. N., Hinch, S. G., Burnett, N. J., & Donaldson, M. (2016). Causes and consequences of straying into small populations of Pacific salmon. *Fisheries*, *42*(2), 220–230. https://doi.org/10.1080/03632415.2017.1276356

Bottrill, M. C., Joseph, L. N., Carwadine, J., Bode, M., Cook, C., Game, E. T., Granthan, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R. L., Walker, S., Wilson, K. A., & Possingham, H. P. (2008). Is conservation triage just smart decision making? *Trends in Ecology and Evolution*, *23*(12), 649–654. https://doi.org/10.1016/j.tree.2008.07.007

Brett, J. R. (1952). Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Research Board of Canada*, *9*(6), 265–323. https://doi.org/10.1139/f52-016

Burt, J. M., Hinch, S. G., & Patterson, D. A. (2012a). Parental identity influences progeny responses to incubation thermal stress in sockeye salmon *Oncorhynchus nerka*. *Journal of Fish Biology*, *80*(2), 444–462. https://doi.org/10.1111/j.1095-8649.2011.03190.x

Burt, J. M., Hinch, S. G., & Patterson, D. A. (2012b). Developmental temperature stress and parental identity shape offspring burst swimming performance in sockeye salmon (*Oncorhynchus nerka*). *Ecology of Freshwater Fish*, *21*(2), 176–188. https://doi.org/10.1111/j.1600-0633.2011.00535.x

Carey, M. P., Keith, K. D., Schelske, M., Lean, C., McCormick, S. D., Regish, A. M., & Zimmerman, C. E. (2019). Energy depletion and stress levels in sockeye salmon migrating at the northern edge of their distribution. *Transactions of the American Fisheries Society*, *148*(4), 785–797. https://doi.org/10.1002/tafs.10172

Carlson, S. M., Cunningham, C. J., & Westley, P. A. H. (2014). Evolutionary rescue in a changing world. *Trends in Ecology and Evolution*, *29*(9), 521–530. https://doi.org/10.1016/j.tree.2014.06.005

Casselman, M. T., Anttila, K., & Farrell, A. P. (2012). Using maximum heart rate as a rapid screening tool to determine optimum temperature for aerobic scope in Pacific salmon *Oncorhynchus* spp. *Journal of Fish Biology*, *80*(2), 358–377. https://doi.org/10.1111/j.1095-8649.2011.03182.x

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., Zabel, R. W., Bjornn, T. C., & Peery, C. A. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(7), 979–995. https://doi.org/10.1139/f07-065

Chen, Z., Anttila, K., Wu, J., Whitney, C. K., Hinch, S. G., & Farrell, A. P. (2013). Optimum and maximum temperatures of sockeye salmon (*Oncorhynchus nerka*) populations hatched at different temperatures. *Canadian Journal of Zoology*, *91*(5), 265–274. https://doi.org/10.1139/cjz-2012-0300

Chen, Z., Devlin, R. H., & Farrell, A. P. (2015). Upper thermal tolerance of wild-type, domesticated and growth hormone-transgenic coho salmon *Oncorhynchus kisutch*. *Journal of Fish Biology*, *87*(3), 763–773. https://doi.org/10.1111/jfb.12736

Chen, Z., Farrell, A. P., Matala, A., & Narum, S. R. (2017). Mechanisms of thermal adaptation and evolutionary potential of conspecific populations to changing environments. *Molecular Ecology*, *27*(3), 659–674. https://doi.org/10.1111/mec.14475

Christensen, E. A. F., Andersen, L. E. J., Bergsson, H., Steffensen, J. F., & Killen, S. S. (2021). Shuttle-box systems for studying preferred environmental ranges by aquatic animals. *Conservation Physiology*, *9*, 1–22. https://doi.org/10.1093/conphys/coab028

Clark, T. D., Donaldson, M. R., Pieperhoff, S., Drenner, S. M., Lotto, A., Cooke, S. J., Hinch, S. G., Patterson, D. A., & Farrell, A. P. (2012). Physiological benefits of being small in a changing world: Responses of coho salmon (*Oncorhycnhus kisutch*) to an acute thermal challenge and a simulated capture event. *PLoS One*, *7*(6), e39079. https://doi.org/10.1371/journal.pone.0039079

Clark, T. D., Jeffries, K. M., Hinch, S. G., & Farrell, A. P. (2011). Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate. *Journal of Experimental Biology*, *214*(18), 3074–3081. https://doi.org/10.1242/jeb.060517

Connor, W. P., Tiffan, K. F., Chandler, J. A., Rondorf, D. W., Arnsberg, B. D., & Anderson, K. C. (2019). Upstream migration and spawning success of Chinook salmon in a highly developed, seasonally warm river system. *Reviews in Fisheries Science and Aquaculture*, *27*(1), 1–50. https://doi.org/10.1080/23308249.2018.1477736

Cooke, S. J., Hinch, S. G., Farrell, A. P., Patterson, D. A., Miller-Saunders, K., Welch, D. W., Donaldson, M. R., Hanson, K. C., Crossin, G. T., Mathes, M. T., Lotto, A. G., Hruska, K. A., Olsson, I. C., Wagner, G. N., Thomson, R., Hourston, R., English, K. K., Larsson, S., Shrimpton, J. M., & Van der Kraak, G. (2008). Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: An interdisciplinary case study on adult Fraser River sockeye salmon. *Fisheries*, *33*(7), 321–339. https://doi.org/10.1577/1548-8446-33.7.321

Coutant, C. C. (1987). Thermal preference: When does and asset become a liability? *Environmental Biology of Fishes*, *18*, 161–172. https://doi.org/10.1007/BF00000356

Crossin, G. T., Hinch, S. G., Cooke, S. J., Wlech, D. W., Patterson, D. A., Jones, S. R. M., Lotto, A. G., Leggatt, R. A., Mathes, M. T., Shrimpton, J. M., Van der Kraak, G., & Farrell, A. P. (2008). Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Canadian Journal of Zoology*, *86*(2), 127–140. https://doi.org/10.1139/Z07-122

Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D., & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: Effects of upriver migratory distance and elevation. *Journal of Fish Biology*, *65*(3), 788–810. https://doi.org/10.1111/j.0022-1112.2004.00486.x

Crowder, L. B., & Magnuson, J. J. (1982). Thermal habitat shifts by fishes at the thermocline in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*(7), 1046–1050. https://doi.org/10.1139/f82-139

Crozier, L. G., Hendry, A. P., Lawson, P. W., Quinn, T. P., Mantua, N. J., Battin, J., Shaw, R. G., & Huey, R. B. (2008). Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications*, *1*(2), 252–270. https://doi.org/10.1111/j.1752-4571.2008.00033.x

Crozier, L. G., McClure, M. M., Beechie, T., Bograd, S. J., Boughton, D. A., Carr, M., Cooney, T. D., Dunham, J. B., Greene, C. M., Haltuch, M. A., Hazen, E. L., Holzer, D. M., Huff, D. D., Johnson, R. C., Jordan, C. E., Kaplan, I. C., Lindley, S. T., Mantua, N. J., Moyle, P. B., … Willis-Norton, E. (2019). Climate vulnerability assessment for Pacific salmon and steelhead in the California current large marine ecosystem. *PLoS One*, *14*(7), e0217711. https://doi.org/10.1371/journal.pone.0217711

Crozier, L. G., Zabel, R. W., & Hamlet, A. F. (2008). Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. *Global Change Biology*, *14*(2), 236–249.

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*(6499), 65–70. https://doi.org/10.1126/science.aaz3658

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106

Del Rio, A. M., Davis, B. E., Fangue, N. A., & Todgham, A. E. (2019). Combined effects of warming and hypoxia on early life stage Chinook salmon physiology and development. *Conservation Physiology*, *7*(1), 1–14. https://doi.org/10.1093/conphys/coy078

Desforges, J. E., Birnie-Gauvin, K., Aarestrup, K., & Cooke, S. J. (2021). Upper thermal tolerance indicated by CT_{max} fails to predict migration strategy and timing, growth, and predation vulnerability in juvenile Brown trout (*Salmo trutta*). *Physiological and Biochemical Zoology: PBZ*, *94*(4), 215–227. https://doi.org/10.1086/714636

Desforges, J. E., Birnie-Gauvin, K., Jutefelt, F., Gilmour, K. M., Eliason, E. J., Dressler, T. L., McKenzie, D. J., Bates, A. E., Lawrence, M. J., Fangue, N., & Cooke, S. J. (2023). The ecological relevance of critical thermal maxima methodology for fishes. *Journal of Fish Biology*, *102*(5), 1000–1016. https://doi.org/10.1111/jfb.15368

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, *332*(6025), 109–112. https://doi.org/10.1126/science.1199158

Eliason, E. J., Clark, T. D., Hinch, S. G., & Farrell, A. P. (2013). Cardiorespiratory collapse at high temperature in swimming adult sockeye salmon. *Conservation Physiology*, *1*(1), 1–19. https://doi.org/10.1093/conphys/cot008

Eliason, E. J., & Farrell, A. P. (2016). Oxygen uptake in Pacific salmon *Oncorhynchus* spp.: When ecology and physiology meet. *Journal of Fish Biology*, *88*(1), 359–388. https://doi.org/10.1111/jfb.12790

Eliason, E. J., Gale, M. K., Whitney, C. K., Lotto, A., & Hinch, S. G. (2017). Intraspecific differences in endurance swim performance and cardiac size in sockeye salmon (*Oncorhynchus nerka*) parr tested at three temperatures. *Canadian Journal of Zoology*, *95*(6), 425–432. https://doi.org/10.1139/cjz-2016-0248

Eliason, E. J., Wilson, S. M., Farrell, A. P., Cooke, S. J., & Hinch, S. G. (2013). Low cardiac and aerobic scope in a coastal population of sockeye salmon *Oncorhynchus nerka* with a short upriver migration. *Journal of Fish Biology*, *82*(6), 2104–2112. https://doi.org/10.1111/jfb.12120

Farrell, A. P. (2009). Environment, antecedents and climate change: Lessons from the study of temperature physiology and river migration of salmonids. *Journal of Experimental Biology*, *212*(23), 3771–3780. https://doi.org/10.1242/jeb.023671

Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M., & Mathes, M. T. (2008). Pacific salmon in hot water: Applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology*, *81*(6), 697–708. https://doi.org/10.1086/592057

FitzGerald, A. M., John, S. N., Apgar, T. M., Mantua, N. J., & Martin, B. J. (2020). Quantifying thermal exposure of migratory riverine species: Phenology of Chinook salmon populations predicts thermal stress. *Global Change Biology*, *27*(2), 536–549. https://doi.org/10.1111/gcb.15450

Flemming, I. A., & Jensen, A. J. (2002). Fisheries: Effect of climate change on the life cycles of salmon. In *Causes and consequences of global environmental change, encyclopedia of global environmental change* (Vol. 3, pp. 309–312). Wiley.

Fraser, D. J., Weir, L. K., Bernatchez, L., Hansen, M. M., & Taylor, E. B. (2011). Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity*, *106*(3), 404–420. https://doi.org/10.1038/hdy.2010.167

Fry, F. E. J. (1947). Effects of the environment on animal activity. *Ontario Fisheries Laboratory Publication*, *68*, 1–62.

Gale, K. M., Hinch, S. G., Cooke, S. J., Donaldson, M. R., Eliason, E. J., Jeffries, K. M., Martins, E. G., & Patterson, D. A. (2014). Observable impairments predict mortality of captured and released sockeye salmon at various temperatures. *Conservation Physiology*, *2*(1), cou029.

Gale, M. K., Hinch, S. G., Eliason, E. J., Cooke, S. J., & Patterson, D. A. (2011). Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures. *Fisheries Research*, *112*(102), 85–95. https://doi.org/10.1016/j.fishres.2011.08.014

Gilk, S. E., Wang, I. A., Hoover, C. L., Smoker, W. W., Taylor, S. G., Gray, A. K., & Gharrett, A. J. (2004). Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: Marine survival, homing ability, and variability in family size. *Environmental Biology of Fishes*, *69*(1–4), 287–297. https://doi.org/10.1023/B:EBFI.0000022888.28218.c1

Gislason, G., Lam, E., Knapp, G., & Guettabi, M. (2017). *Economic impacts of Pacific salmon fisheries*. *July*, 100.

Goniea, T. M., Keefer, M. L., Bjornn, T. C., Peery, C. A., Bennett, D. H., & Stuehrenberg, L. C. (2006). Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Transactions of the American Fisheries Society*, *135*(2), 408–419. https://doi.org/10.1577/t04-113.1

Grant, S. C. H., MacDonald, B. L., & Winston, M. L. (2019). State of the Canadian pacific salmon: Responses to changing climate and habitats. In *Canadian Technical Report of Fisheries and Aquatic Sciences 3332*. https://www.dfo-mpo.gc.ca/species-especes/publications/salmon-saumon/state-etat-2019/abstract-resume/index-eng.html

Hallock, R. J., Elwell, R. F., & Fry, D. H., Jr. (1970). Migrations of adult king salmon Oncorhynchus tshawytscha in the San Joaquin Delta as demonstrated by the use of sonic tags. *Fishery Bulletin*, *151*(3), 1–58.

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remneyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M. S., Keatley, M. R., Woodward, C. A., Qilliamson, G., … Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, *8*, 576–587.

Hinch, S. G., Bett, N. N., Eliason, E. J., Farrell, A. P., Cooke, S. J., & Patterson, D. A. (2021). Exceptionally high mortality of adult female salmon: A large-scale pattern and a conservation concern. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(6), 639–654. https://doi.org/10.1139/cjfas-2020-0385

Hinke, J., Watters, G., Boehlert, G., & Zedonis, P. (2005). Ocean habitat use in autumn by Chinook salmon in coastal waters of Oregon and California. *Marine Ecology Progress Series*, *258*, 181–192. https://doi.org/10.3354/meps285181

Hodgson, S., & Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: Adaptations by populations to prevailing thermal regimes. *Canadian Journal of Zoology*, *80*(3), 542–555. https://doi.org/10.1139/z02-030

Hruska, K. A., Hinch, S. G., Healey, M., & Patterson, D. A. (2010). Influences of sex and activity level on physiological changes in individual adult sockeye salmon during rapid senescence. *Physiological and Biochemical Zoology*, *83*(4), 663–676. https://doi.org/10.1086/652411

Huey, R. B. (1991). Physiological consequences of habitat selection. *The American Naturalist*, *137*, S91–S115. https://doi.org/10.1086/285141

Hyatt, K. D., Stockwell, M. M., & Rankin, D. P. (2003). Impact and adaptation responses of Okanagan River sockeye salmon (*Oncorhynchus nerka*) to climate variation and change effects during freshwater migration: Stock restoration and fisheries management implications. *Canadian Water Resources Journal*, *28*(4), 689–713. https://doi.org/10.4296/cwrj2804689

Jørgensen, L. B., Malte, H., Ørsted, M., Klahn, N. A., & Overgaard, J. (2021). A unifying model to estimate thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to thermal stress. *Scientific resports*, *11*, 12840. https://doi.org/10.1038/s41598-021-92004-6

Jeffries, K. M., Hinch, S. G., Martins, E. G., Clark, T. D., Lotto, A. G., Patterson, D. A., Cooke, S. J., Farrell, A. P., & Miller, K. M. (2012). Sex and proximity to reproductive maturity influence the survival, final maturation, and blood physiology of pacific salmon when exposed to high temperature during a simulated migration. *Physiological and Biochemical Zoology*, *85*(1), 62–73. https://doi.org/10.1086/663770

Jeffries, K. M., Hinch, S. G., Sierocinski, T., Clark, T. D., Eliason, E. J., Donaldson, M. R., Li, S., Pavlidis, P., & Miller, K. M. (2012). Consequences of high temperatures and premature mortality on the transcriptome and blood physiology of wild adult sockeye salmon (*Oncorhynchus nerka*). *Ecology and Evolution*, *2*(7), 1747–1764. https://doi.org/10.1002/ece3.274

Jeffries, K. M., Hinch, S. G., Sierocinski, T., Pavlidis, P., & Miller, K. M. (2014). Transcriptomic responses to high water temperature in two species of Pacific salmon. *Evolutionary Applications*, *7*(2), 286–300. https://doi.org/10.1111/eva.12119

Keefer, M. L., Caudill, C. C., Peery, C. A., & Boggs, C. T. (2008). Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. *Journal of Fish Biology*, *72*(1), 27–44. https://doi.org/10.1111/j.1095-8649.2007.01652.x

Keefer, M. L., Clabough, T. S., Jepson, M. A., Bowerman, T., & Caudill, C. C. (2019). Temperature and depth profiles of Chinook salmon and the energetic costs of their long-distance homing migrations. *Journal of Thermal Biology*, *79*, 155–165.

Keefer, M. L., Peery, C. A., & Heinrich, M. J. (2008). Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecology of Freshwater Fish*, *17*(1), 136–145. https://doi.org/10.1111/j.1600-0633.2007.00267.x

Keefer, M. L., & Caudill, C. C. (2014). Homing and straying by anadromous salmonids: A review of mechanisms and rates. *Reviews in Fish Biology and Fisheries*, *24*(1), 333–368. https://doi.org/10.1007/s11160-013-9334-6

Kingslover, J. G., & Umbanhowar, J. (2018). The analysis and interpretation of critical temperatures. *Journal of Experimental Biology*, *221*(2), jeb167858. https://doi.org/10.1242/jeb.167858

Kovach, R. P., Gharrett, A. J., & Tallmon, D. A. (2012). Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B*, *279*(1743), 3870–3878. https://doi.org/10.1098/rspb.2012.1158

Kraskura, K., Hardison, E. A., Little, A. G., Dressler, T., Prystay, T. S., Hendriks, B., Farrell, A. P., Cooke, S. J., Patterson, D. A., Hinch, S. G., & Eliason, E. J. (2020). Sex-specific differences in swimming, aerobic metabolism and recovery from exercise in adult coho salmon (Oncorhynchus kisutch) across ecologically relevant temperatures. *Conservation Physiology*, *9*(1), 1–22. https://doi.org/10.1093/conphys/coab016

Kunz, K. L., Claireaux, G., Pörtner, H. O., Knust, R., & Mark, F. C. (2018). Aerobic capacities and swimming performance of polar cod (*Boreogadus saida*) under ocean acidification and warming conditions. *Journal of Experimental Biology*, *221*(21), jeb1884473. https://doi.org/10.1242/jeb.184473

Lee, C. G., Farrell, A. P., Lotto, A., Hinch, S. G., & Healey, M. C. (2003). Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *Journal of Experimental Biology*, *206*(18), 3253–3260. https://doi.org/10.1242/jeb.00548

Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hinch, S. G., & Healey, M. C. (2003). The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology*, *206*(18), 3239–3251. https://doi.org/10.1242/jeb.00547

Lefevre, S., Wang, T., & McKenzie, D. J. (2021). The role of mechanistic physiology in investigating impacts of global warming on fishes. *Journal of Experimental Biology*, *224*, jeb238840. https://doi.org/10.1242/jeb.238840

Lowe, C. J., & Davison, W. (2006). Thermal sensitivity of scope for activity in *Pagothenia borchgrevinki*, a cryopelagic Antarctic nototheniid fish. *Polar Biology*, *29*(11), 971–977. https://doi.org/10.1007/s00300-006-0139-0

MacDonald, J. A., Patterson, D. A., Hague, M. J., & Guthrie, I. C. (2010). Modeling the influence of environmental factors on spawning migration mortality for sockeye salmon fisheries management in the Fraser River, British Columbia. *Transactions of the American Fisheries Society*, *139*(3), 768–782. https://doi.org/10.1577/T08-223.1

MacNutt, M. J., Hinch, S. G., Lee, C. G., Phibbs, J. R., Lotto, A. G., Healey, M. C., & Farrell, A. P. (2006). Temperature effects on swimming performance, energetics, and aerobic capacities of mature adult pink salmon (*Oncorhynchus gorbuscha*) compared with those of sockeye salmon (*O. Nerka*). *Canadian Journal of Zoology*, *84*(1), 88–97. https://doi.org/10.1139/Z05-181

Martins, E. G., Hinch, S. G., Patterson, D. A., Hague, M. J., Cooke, S. J., Miller, K. M., Lapointe, M. F., English, K. K., & Farrell, A. P. (2011). Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). *Global Change Biology*, *17*(1), 99–114. https://doi.org/10.1111/j.1365-2486.2010.02241.x

McCullough, D. A. (1999). A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. In: *Water resources assessment*. U.S. EPA 910-R-99-010-291.

McCullough, D. A., Spalding, S., Sturdevant, D., & Hicks, M. (2001). Summary of technical literature examining the physiological effects of temperature on salmonids. In *EPA region 10 temperature water quality criteria and guidance development project*. U.S. EPA 910-D-01-005.

McKenzie, D. J., Zhang, Y., Eliason, E. J., Schulte, P. M., Claireaux, G., Blasco, F. R., Nati, J. J. H., & Farrell, A. P. (2020). Intraspecific variation in tolerance of warming in fishes. *Journal of Fish Biology*, *98*(6), 1–20. https://doi.org/10.1111/jfb.14620

Minke-Martin, V., Hinch, S. G., Braun, D. C., Burnett, N. J., Casselman, M. T., Eliason, E. J., & Middleton, C. T. (2018). Physiological condition and migratory experience affect fitness-related outcomes in adult female sockeye salmon. *Ecology of Freshwater Fish*, *27*(1), 296–309. https://doi.org/10.1111/eff.12347

Morita, K., Fukuwaka, M., & Tanimata, N. (2010). Age-related thermal habitat use by Pacific salmon *Oncorhynchus* spp. *Journal of Fish Biology*, *77*(4), 1024–1029. https://doi.org/10.1111/j.1095-8649.2010.02721.x

Muñoz, N. J., Anttila, K., Chen, Z., Heath, J. W., Farrell, A. P., & Neff, B. D. (2014). Indirect genetic effects underlie oxygen-limited thermal tolerance within a coastal population of Chinook salmon. *Proceedings* *of the Royal Society B: Biological Sciences*, *281*(1789), 20141082. https://doi.org/10.1098/rspb.2014.1082

Muñoz, N. J., Farrell, A. P., Heath, J. W., & Neff, B. D. (2015). Adaptive potential of a Pacific salmon challenged by climate change. *Nature Climate Change*, *5*(2), 163–166. https://doi.org/10.1038/nclimate2473

Muñoz, N. J., Farrell, A. P., Heath, J. W., & Neff, B. D. (2018). Hematocrit is associated with thermal tolerance and modulated by developmental temperature in juvenile Chinook salmon. *Physiological and Biochemical Zoology*, *91*(1), 757–762. https://doi.org/10.1086/695556

Myrick, C. A., & Chech, J. J. (2004). Temperature effects on juvenile anadromous salmonids in California's central valley: What don't we know? *Reviews in Fish Biology and Fisheries*, *14*(1), 113–123. https://doi.org/10.1007/s11160-004-2739-5

Ørsted, M., Jørgensen, L. B., & Overgaard, J. (2022). Finding the right thermal limit: a framework to reconcile ecological, physiological and methodological aspects of CTmax in ectotherms. *Journal of Experimental Biology*, *225*(19), e244514. https://doi.org/10.1242/jeb.244514

Pörtner, H. O. (2001). Climate change and temperature-dependent biogeography: Oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, *88*(4), 137–146. https://doi.org/10.1007/s001140100216

Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, *332*(5902), 690–692. https://doi.org/10.1126/science.1163156

Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L., & Sunday, J. M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, *569*(7754), 108–111. https://doi.org/10.1038/s41586-019-1132-4

Poletto, J. B., Cocherell, D. E., Baird, S. E., Nguyen, T. X., Cabrera-Stagno, V., Farrell, A. P., & Fangue, N. A. (2017). Unusual aerobic performance at high temperatures in juvenile Chinook salmon, *Oncorhynchus ttshawytscha*. *Conservation Physiology*, *5*(1), 1–13. https://doi.org/10.1093/conphys/cow067

Quinn, T. P. (1993). A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research*, *18*(1–2), 29–44. https://doi.org/10.1016/0165-7836(93)90038-9

Raby, G. D., Casselman, M. T., Cooke, S. J., Hinch, S. G., Farrell, A. P., & Clark, T. D. (2016). Aerobic scope increases throughout an ecologically relevant temperature range in coho salmon. *Journal of Experimental Biology*, *219*(12), 1922–1931. https://doi.org/10.1242/jeb.137166

Raby, G. D., Clark, T. D., Farrell, A. P., Patterson, D. A., Bett, N. N., Wilson, S. M., Willmore, W. G., Suski, C. D., Hinch, S. G., & Cooke, S. J. (2015). Facing the river gauntlet: Understanding the effects of fisheries capture and water temperature on the physiology of coho salmon. *PLoS One*, *10*(4), 1–20. https://doi.org/10.1371/journal.pone.0124023

Reed, T. E., Schindler, D. E., Hague, M. J., Patterson, D. A., Meir, E., Waples, R. S., & Hinch, S. G. (2011). Time to evolve? Potential evolutionary responses of Fraser River sockeye salmon to climate change and effects on persistence. *PLoS One*, *6*(6), e20380. https://doi.org/10.1371/journal.pone.0020380

Richter, A., & Kolmes, S. A. (2005). Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific northwest. *Reviews in Fisheries Science*, *13*(1), 23–49. https://doi.org/10.1080/10641260590885861

Roscoe, D. W., Hinch, S. G., Cooke, S. J., & Patterson, D. A. (2010). Behaviour and thermal experience of adult sockeye salmon migrating through stratified lakes near spawning grounds: The roles of reproductive and energetic states. *Ecology of Freshwater Fish*, *19*(1), 51–62. https://doi.org/10.1111/j.1600-0633.2009.00388.x

Ruggerone, G. T., & Irvine, J. R. (2018). Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries*, *10*(2), 152–168. https://doi.org/10.1002/mcf2.10023

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(15), 5610–5615. https://doi.org/10.1073/pnas.1316145111

Taylor, E. B. (1991). Review of local adaptation in Salmonidac, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, *98*(1–3), 185–207. https://doi.org/10.1016/0044-8486(91)90383-I

Teffer, A. K., Bass, A. L., Miller, K. M., Patterson, D. A., Juanes, F., & Hinch, S. G. (2018). Infections, fisheries capture, temperature, and host responses: Multistressor influences on survival and behaviour of adult Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(11), 2069–2083. https://doi.org/10.1139/cjfas-2017-0491

Teffer, A. K., Hinch, S., Miller, K., Jeffries, K., Patterson, D., Cooke, S., Farrell, A., Kaukinen, K. H., Li, S., & Juanes, F. (2019). Cumulative effects of thermal and fisheries stressors reveal sex-specific effects on infection development and early mortality of adult coho salmon (*Oncorhynchus kisutch*). *Physiological and Biochemical Zoology: PBZ*, *92*(5), 505–529. https://doi.org/10.1086/705125

Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits depend on methodological context. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1628), 2935–2942. https://doi.org/10.1098/rspb.2007.0985

Vinagre, C., Dias, M., Cereja, R., Abreu-Afonso, F., Flores, A. A. V., & Mendonça, V. (2019). Upper thermal limits and warming safety margins of coastal marine species – Indicator baseline for future reference. *Ecological Indicators*, *102*(March), 644–649. https://doi.org/10.1016/j.ecolind.2019.03.030

von Biela, V. R., Bowen, L., McCormick, S. D., Carey, M. P., Donnelley, D. S., Waters, S., Regish, A. M., Laske, S. M., Brown, R. J., Larson, S., Zuray, S., & Zimmerman, C. E. (2020). Evidence of prevalent heat stress un Yukon River Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(12), 1878–1892. https://doi.org/10.1139/cjfas-2020-0209

von Biela, V. R., Sergeant, C. J., Carey, M. P., Liller, Z., Russell, C., Quinn-Davidson, S., Rand, P. S., Westley, P. A. H., & Zimmerman, C. E. (2019). Premature mortality observations among Alaska's Pacific salmon during record heat and drought. *Fisheries*, *47*(4), 157–158. https://doi.org/10.1002/fsh.10705

Welch, D. W., Chigirinsky, A. I., & Ishida, Y. (1995). Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(3), 489–503. https://doi.org/10.1139/f95-050

Westley, P. A. H., Dittman, A. H., Ward, E. J., & Quinn, T. P. (2015). Signals of climate conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon. *Ecology*, *96*(10), 2823–2833. https://doi.org/10.1890/14-1630.1

Whitney, C. K., Hinch, S. G., & Patterson, D. A. (2013). Provenance matters: Thermal reaction norms for embryo survival among sockeye salmon *Oncorhynchus nerka* populations. *Journal of Fish Biology*, *82*(4), 1159–1176. https://doi.org/10.1111/jfb.12055

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, *6*(12), 2621–2626. https://doi.org/10.1371/journal.pbio.0060325

Zhang, X., Li, H. Y., Deng, Z. D., Leung, L. R., Skalski, J. R., & Cooke, S. J. (2019). On the variable effects of climate change on Pacific salmon. *Ecological Modelling*, *397*, 95–106. https://doi.org/10.1016/j.ecolmodel.2019.02.002

Zillig, K. W., Lusardi, R. A., Moyle, P. B., & Fangue, N. A. (2021). One size does not fit all: Variation in thermal ecophysiology among salmonids. *Reviews in Fish Biology and Fisheries*, *31*(9), 94–114. https://doi.org/10.1007/s11160-020-09632-w(0123456789().,-volV()0123456789().,-volV)

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