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Thermal exposure risk in different life stages of Chinook salmon in the Nechako River system, British Columbia

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Abstract
Climate change is affecting freshwater systems, leading to increased water temperatures, which is posing a threat to freshwater ecological communities. In the Nechako River, British Columbia, a water management program has been in place since the 1980s to maintain water temperatures at 20 °C during the migration of adult Sockeye salmon. However, the program's effectiveness in mitigating the impacts of climate change on resident species like Chinook salmon's thermal exposure is uncertain. In this study, we utilised the CEQUEAU hydrological model and life stage-specific physiological data to evaluate the consequences of the current program on Chinook salmon's thermal exposure under two contrasting climate change and socio-economic scenarios (SSP2-4.5 and SSP5-8.5). The results indicate that the thermal exposure risk is projected to be above the optimal threshold for parr (intermediate juvenile) and adult life stages under both scenarios relative to the 1980s. Under the SSP5-8.5 scenario, these life stages could experience an increase in thermal exposure ranging from two to five times higher by the 2090s compared to the 1980s. This exposure is projected to occur during the months in which these life stages emerge, including the period when the program is active (July 20th to August 20th). Additionally, our study shows that climate change will result in a substantial rise in cumulative heat degree days, ranging from 1.9 to 5.8 times (2050s) and 2.9 to 12.9 times (2090s) in comparison to the 1980s under SSP5-8.5. Our study highlights the need for a holistic approach to reviewing the current Nechako management plan, ensuring that all species in the Nechako River system are considered especially in the face of climate change.

Keywords Climate change · Freshwater systems · Water temperatures · Chinook salmon · Thermal exposure risk · Management plan

Extended author information available on the last page of the article

1 Introduction

Freshwater systems are being significantly affected as climate change alters water cycles, nutrient content, physio-chemical parameters, and species habitat structures and distributions (Knouft and Ficklin 2017; Vörösmarty et al. 2010), especially seasonal runoff resulting from snowmelt and influenced water flow (Wieder et al. 2022). Freshwater systems are also subject to other stressors such as urbanisation, vegetation removal, dams, and river regulation. While the influences of these stressors predate the modern rate of climate change (Birk et al. 2020; Göthe et al. 2019), they can exacerbate the effects of climate change (Best 2019; Carpenter et al. 2011; Palmer et al. 2009). These stressors can change the river's thermal regime and the ecosystem community (Birk et al. 2020; Pletterbauer et al. 2018). Therefore, it is crucial to understand the impact of both anthropogenic climate change and legacy stressors on aquatic species.

The thermal regime of rivers plays a key role in the overall health of aquatic ecosystems. The thermal regime of a river influences water quality and quantity, biological processes, community structure, species composition, and distribution (Dugdale et al. 2017; Maheu et al. 2016). As most freshwater species are poikilothermic ectotherms, temperature is important in their survival, distribution, growth, and development. Their physiology is also greatly influenced by environmental temperature, including their metabolic rate, which increases with temperature by accelerating biochemical kinetic energy reaction rates (Abram et al. 2017; Alfonso et al. 2021; Schulte 2015). This, in turn, affects organisms' functioning and performance in the ecosystem. However, climate change is transforming the heat budget of streams through changes in atmospheric fluxes including short-wave solar radiation, convection and long-wave atmospheric radiation. Additional factors such as water flow friction, heat gains from precipitation, and groundwater contribution, further contribute to stream temperature warming (Benyahya et al. 2012; Caissie 2006; Evans et al. 1998). This warming can exceed temperature thresholds which can eventually surpass the optimal or even maximum physiological performance of resident fishes (Farrell 2016; Schulte et al. 2011; Zillig et al. 2022). When fish begin to experience temperatures above their optimal level, they experience a reduced aerobic scope (i.e., less energy available for daily behaviours beyond just maintenance, including, swimming, eating, and competition among other traits) (Eliason et al. 2011; Farrell 2016; Zillig et al. 2023). This can impact growth and reproduction, ultimately hindering long-term survival and population success (Mantua et al. 2010).

Climate change impacts on rivers' thermal regimes are not the only challenge that aquatic species face. Anthropogenic activities such as deforestation, urbanisation, agriculture and dams can also impact water temperatures in rivers and negatively affect aquatic ecosystems (Lessard and Hayes 2003; Maheu et al. 2016; Prats et al. 2012). In particular, dam regulation (e.g., mode of operation, size, and depth of water release) can have profound impacts on downstream conditions including temperature, dissolved oxygen, and pollutant concentrations (Weber et al. 2017; Zaidel et al. 2021).

Flow management programs are part of broader strategies aimed at assisting in mitigating the effects of dam rivers on fish populations (Chen and Olden 2017). These programs often rely on targeted water releases to maintain optimal conditions for specific life stages of migratory species. Such programs are implemented in rivers like the Columbia River basin in the United States (Kareiva et al. 2000) and the Yangtze River basin in China (Cheng et al. 2018) to manage water temperatures and flow patterns during important fish migration and spawning periods. However, the focus on maintaining temperature for migrating fish might negatively impact other resident species that require different flow and temperature conditions for their development.

One such program is the Summer Temperature Management Program (STMP), which was implemented in the Nechako River in central British Columbia, Canada, starting in 1981 (Macdonald et al. 2012). The Nechako River is a culturally, ecologically and economically important system to the Indigenous people and the presence of Kenny Dam has altered the flow patterns impacting the fish population and habitats. The STMP was established in the 1980s to maintain a water temperature below or equal to 20 °C at a specific location (Finmoore) between July 20 and August 20 annually during the migration and spawning season of Sockeye salmon (*Oncorhynchus nerka*) (Macdonald et al. 2012). This program is achieved by releasing water discharges of up to 453 m^3/s through the Skins Lake Spillway (Fig. 1A) into the Nechako River (Ouellet-Proulx et al. 2017).

However, the effectiveness of flow management programs like STMP to maintain temperature depends on a range of factors, including the timing and volume of water releases, the size and depth of water, as well as the specific characteristics of the river and its ecosystem (Chandesris et al. 2019; Seyedhashemi et al. 2021). STMP has effectively reduced the negative impacts of dams on the Nechako River adult sockeye salmon by ensuring suitable migration conditions (Macdonald et al. 2012). The implementation of flow management programs such as STMP has shown the potential to mitigate the deleterious effects of dams on riverine ecosystems. Nevertheless, STMP was designed to assist a single species (sockeye salmon) during its upstream migration, and the program's reliance on a predetermined temperature-only assessment poses a potential limitation, as it may not fully account for the complexities of species-specific physiological tolerance. Similar observations have been made in other large rivers where water management programs focus on mitigating dam impact on single species (Ding et al. 2023; Zarri et al. 2019, 2022). It is important to revisit

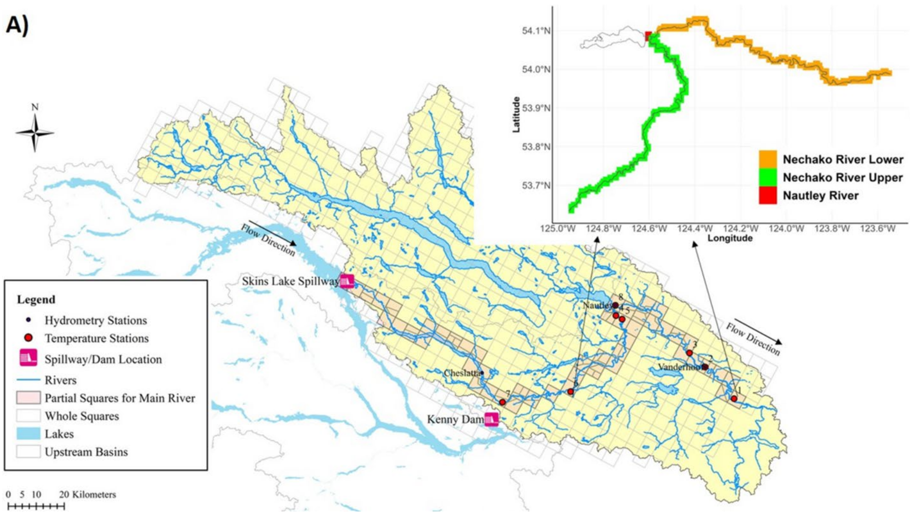

Fig. 1 **A** A map of the Nechako River watershed is shown, featuring the Skins Lake spillway and the Kenny Dam. An inset map displays the classification of the river into three sections based on the distribution of Chinook salmon across the river. **B** Schematic diagram of the framework adopted from Oyinlola et al. (2023) used in this study

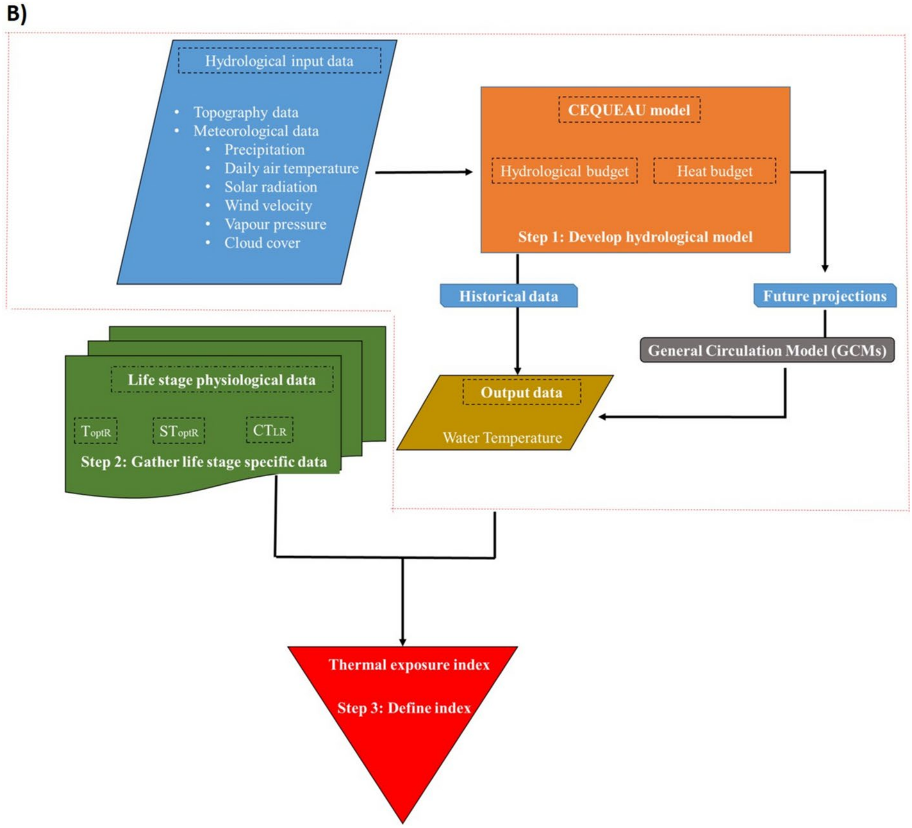

Fig. 1 (continued)

and assess the effectiveness of such programs with a comprehensive approach to promoting the health and sustainability of the entire river ecosystem.

In British Columbia, Pacific salmon are important for Indigenous people's food, culture and spirituality (Jacob et al. 2010), and they are economically important in terms of commercial and recreational fisheries (BCFFS 2013; Gislason et al. 2017). A prominent species in the Nechako River that is not considered in the STMP is the Chinook salmon (*Oncorhynchus tshawytscha*). Chinook salmon are large and long-lived fish species. Juveniles grow in the river before migrating to the ocean to feed and grow, returning to natal areas once mature to spawn and die (Quinn 2018). They are a vital food source for both humans and wildlife (Hinch et al. 2012). The Nechako River historically had one of the largest Chinook salmon runs in the upper Fraser River watershed (Hartman 1996). However, their numbers have declined dramatically over the years (COSEWIC 2018; Jaremovic and Rowland 1988). The Nechako Chinook salmon population is part of the Fraser Chinook population (DFO 1995, 1999). Anthropogenic activities such as habitat alteration, commercial and recreational fishing, changes in river flow regimes and reduced food availability caused by dams have been identified as the primary causes of the population decline (COSEWIC 2018). In addition, climate change including increased temperature and lower oxygen levels could play an important role in the further decline of the Nechako population as well as other Chinook salmon populations by increasing thermal stress (Crozier et al. 2019; Ohlberger et al. 2018; Siegel and Crozier 2018). Given the significance of Chinook salmon in the Nechako River, it is imperative to investigate the potential effects of the Kenny Dam and the STMP management program on this species.

In this study, we utilised a combination of a hydrological model and life stage-specific physiological experimental data to assess the impact of the current Nechako water management program on thermal exposure risk (T_e) to Chinook salmon (Fig. 1B). T_e refers to the likelihood of adverse effects due to temperature extremes, with higher T_e values indicating greater risk and worse physiological performance. Following the framework previously outlined by Oyinlola et al. (2023), we focused on the river system sections where the species are present. First, we employed a semi-distributed hydrological and water temperature model known as CEntre QUébécois des Sciences de l'EAU (CEQUEAU) to simulate the Nechako River's historical daily water temperature between 1980 and 2019. We then developed the thermal exposure index, a quantitative measure of temperature exposure over time for Chinook salmon using physiological data. The index ranges from 0 to 3, where 0 signifies a low risk of thermal exposure, 1 indicates an optimal temperature, and a score greater than 1 indicates an increasing level of exposure risk. Last, we projected the temperature and T_e for the warmest six-month period of the year (May to October), which includes the water release management period (July 20th–August 20th), under two different climate change and socio-economic scenarios: SSP2-4.5 (intermediate scenario) and SSP5-8.5 (high-emission scenario) by mid (the 2050s) and end of the century (the 2090s). We hypothesised that the thermal exposure of Chinook salmon will increase more than the optimal threshold '1' under climate change in most sections of Nechako. In addition, we estimated the cumulative degree-day index, which is a useful tool that measures the amount of accumulated heat above a specific temperature threshold. It has been widely used in various fields, such as agriculture and entomology, to understand the connection between temperature and biological processes (MacDonald et al. 2023; Olaya-Arenas et al. 2024; Soroka et al. 2020).

2 Methodology

2.1 CEQUEAU model: Modelling Nechako River water temperature

We implemented the CEQUEAU (see full model description in supplementary information), a semi-distributed hydrological and water temperature model (Khorsandi et al. 2022; Morin and Couillard 1990; St-Hilaire et al. 2015). CEQUEAU has been used to model the flow and temperature of streams and river watersheds in various regions of the world (Ba et al. 2009; Dugdale et al. 2017; Fniguire et al. 2022; Rahmati et al. 2024). The hydrological module of CEQUEAU includes snowmelt and evapotranspiration formulations as well as conceptual water storage in two soil horizons, while the thermal module calculates the surface heat budget within each model grid cell.

In brief, CEQUEAU requires physiographic data including 10-m resolution land cover from ESRI and ESA (Karra et al. 2021; Zanaga et al. 2022) and 30-m resolution NASA SRTM DEM for topography (Farr et al. 2007). Surface heat fluxes are computed using additional meteorological variables such as daily precipitation and maximum and minimum air temperatures. The watershed is characterised using Elementary Representative Areas (ERA) based on altitude, forest cover, and lake/wetland percentage. ERAs are further divided into partial squares for water routing. The hydrological module output informs the thermal module, computing heat fluxes, including shortwave radiation, latent heat, longwave radiation, convection, and various water inflows.

To implement CEQUEAU for the Nechako watershed, the model's parameters were calibrated using observed streamflow data from Nechako River hydrometric stations and water temperature gauges between the Kenny dam and Vanderhoof. Manual calibration precedes an application of the Covariance Matrix Adaptation Evolution Strategy (CMA-ES) (Hansen 2006) for automation. Additionally, the multi-site temperature calibration method of Khorsandi et al. (2022) is used to adjust the parameters of the water temperature module. For projecting Nechako River's future temperature and flow changes, data from eight General Circulation Models (GCMs) under two Shared Socio-economic Pathways (SSP) scenarios (SSP2-4.5 and SSP5-8.5) from the Coupled Model Intercomparison Project Phase 6 (CMIP6)(O'Neill et al. 2017) are employed (Table 1). These scenarios represent intermediate and high emission trajectories. Each GCM provides meteorological variables through

Table 1 List of General Circulation Models (GCMs) that are part of the Coupled Model Intercomparison Project Phase 6 (CMIP6) used in this study

Model	Full name	Spatial resolution
BCC-CSM2-MR	Beijing Climate Centre Climate System Model	110×110 km (1° Lat×1.4° Lon)
CMCC-CM2-SR5	Euro-Mediterranean Centre on Climate Change coupled climate model	0.9° Lat×1.25° Lon (99.9×98.1 km)
CMCC-ESM2	Second-generation CMCC Earth System Model	0.9° Lat×1.25° Lon (99.9×98.1 km)
EC-Earth3	European Centre Earth3 Model	40×40 km (0.36° Lat×0.51° Lon)
MIROC6	Model for Interdisciplinary Research on Climate	1.4° Lat×1.4° Lon (155.4×109.9 km)
MPI-ESM1-2-HR	Max Planck Institute for Meteorology Earth System Higher-resolution Model	100×100 km (0.9° Lat×1.27° Lon)
MPI-ESM1-2-LR	Max Planck Institute for Meteorology Earth System Lower-resolution Model	200×200 km (1.8° Lat×2.55° Lon
MRI-ESM2-0	Meteorological Research Institute Earth System Model version 2.0	100×100 km (0.9° Lat×1.27° Lon)

SSP forcings, bias-corrected using the N-dimensional Multivariate Bias Correction algorithm (MBCn) (Cannon 2018) based on ERA5 data for the 1981–2010 reference period. The correction improves diurnal cycle representation and daily average precision at 3-h intervals.

2.2 Thermal exposure risk for Nechako Chinook salmon

Nechako River Chinook salmon fry typically emerges in freshwater from March to June and then remains in the river system as parr from July until migrating out to sea as smolts the following Spring. Adults return from July to October, with peak spawning occurring from the end of August to early October (Bradford 1994; NFCP 2015). Thus, our study primarily focuses on the six hottest months (i.e., May to October) when the thermal risk most likely occurs in the Nechako River. Specifically, we examined the thermal risk for different life stages for fish. For fry, we evaluated the risk during May and June, for parr from July to October, and for returning and spawning adults from July to October. Chinook salmon life stage-specific thermal tolerance thresholds were obtained from laboratory studies conducted at the University of British Columbia, Canada and the Cultus Lake Salmon Research Laboratory on Shuswap Chinook salmon, an upper Fraser River population (Table 2). The optimal Temperature Range (T_{optR}), Sub-optimal Temperature Range (ST_{optR}), and Critical Thermal Limit Range (CT_{LR}) were recorded for each early life stage (i.e., fry – newly emerged; parr – larger and older, and adult – freshwater return migrating) using the same approach described in Oyinlola et al. (2023). The T_{optR} was defined as the temperature range

Table 2 Chinook salmon thermal exposure risk applied for this study. The adult life stage temperature is based on the summer run interior Shuswap Population

Life stage	Description	Temperature (°C)	Index	Reference
Fry	Optimal temperature (T_{optR})	15–20	1	(Mayer et al. 2024)
Fry	Sub-optimal temperature (ST_{optR})	>20–23.9	2	(Mayer et al. 2024)
Fry	Critical temperature (CT_{LR})	>23.9	3	(Mayer et al. 2024)
Parr	Optimal temperature (T_{optR})	15–20	1	(Mayer et al. 2024)
Parr	Sub-optimal temperature (ST_{optR})	>20–22.9	2	(Mayer et al. 2024)
Parr	Critical temperature (CT_{LR})	>22.9	3	(Mayer et al. 2024)
Adult	Optimal temperature (T_{optR})	12–20	1	(Van Wert et al. 2023)
Adult	Sub-optimal temperature (ST_{optR})	>20–22	2	(Van Wert et al. 2023)
Adult	Critical temperature (CT_{LR})	>22	3	(Van Wert et al. 2023)

in which fish exhibit their optimal, or highest physiological performance. ST_{optR} is the temperature range coinciding with a loss of some critical function and less than 25% mortality, and CT_{LR} is the temperature range where more than 50% mortality occurred (M. A. Oyinlola et al. 2023). The T_{optR} was also obtained from peer-reviewed literature and government documents when information was missing. Based on T_{optR}, ST_{optR}, and CT_{LR} (Table 2), the thermal exposure risk (T_e) was defined.

$$T_{ei} = 0, if\ [T_a, T_b] < T_{optR} \tag{1}$$

$$T_{ei} = 1, if\ [T_a, T_b] \subset T_{optR} \tag{2}$$

$$T_{ei} = 2, if\ [T_a, T_b] \subset ST_{optR} \tag{3}$$

$$T_{ei} = 3, if\ [T_a, T_b] \subset CT_{LR} \tag{4}$$

where T_{ei} is the daily thermal exposure risk for cell *i*; T_a and T_b are the minimum and maximum physiological temperature ranges, respectively.

2.3 Analysis

2.3.1 Model evaluation

We compared the CEQUEAU model's predicted temperatures with the observed temperatures at the Vanderhoof station using historical temperature https://climate.weather.gc.ca/historical_data/search_historic_data_e.html. Using metrics such as Root Mean Square Error (RMSE), R-squared (R^2) values, and percentage bias, we assessed the model's reliability in predicting Nechako River temperatures.

2.3.2 Current and future thermal exposure risk

We gridded the Nechako River watershed with a resolution of 0.005°×0.005° to analyse the life stage-specific spatio-temporal pattern of T_e for the Nechako River from 1980 to 2099. Our analysis focused on the six warmest months (May to October) of the year, which include the active months of STMP in July and August. For each month, we estimated the daily T_e in each grid cell using the simulated daily temperature data.

To assess the impact of climate change, we performed an analysis to determine the average monthly T_e across all GCMs to account for climate model variability. We calculated the average T_e for the historical period (the 1980s, averaging 1980–1989) and projected future periods in the mid-century (2050s, averaging 2050–2059) and end-century (2090s, averaging 2090–2099) under two emission scenarios: SSP2-4.5 and SSP5-8.5.

To quantify the change in T_e for each life stage relative to the 1980s, we introduced the concept of a T_e multiplier.

$$\text{Multiplier} = \frac{Projected\ Te}{Reference\ period\ Te} \tag{5}$$

This multiplier represents a factor by which T_e has changed compared to the reference period (1980s). This approach allows us to assess and communicate the magnitude of the impact of climate change on thermal exposure risk across various life stages along the Nechako River.

To assess the impact of extended exposure to stressful temperatures and incorporate both temperature and duration in our analysis, we computed the cumulative heat degree-days (CHDD, in units of °C days) for the period when the STMP was active, specifically between July 20th and August 20th. CHDD quantifies the amount of heat accumulation based on the average daily temperature exceeding the upper optimal temperature range threshold. This approach is consistent with prior studies (Neuheimer and Taggart 2007; Oyinlola et al. 2023; Wuenschel et al. 2012) and the threshold calculation is as follows:

$$CHDD = \sum_{d=1}^{n} (T_d - T_{bi}) | (T_d > T_b) \tag{6}$$

where T_b is the upper optimal temperature range, T_d is the mean daily temperature per cell on day *d,* and *n* is the number of days in active STMP months per year.

We calculated the cumulative heat degree-days (CHDD, °C days) for each life stage in the 1980s (average between 1980–1989) and under future scenarios (i.e., SSP2-4.5 and SSP5-8.5) by 2050s (average between 2050–2059) and 2090s (average between 2090–2099). We used the upper optimal temperature for each life stage as the threshold (Table 2). We then divided the Nechako River into three sections based on Chinook salmon distribution across the river (Fig. 1A). We conducted all modelling and analyses using both Matlab (MATLAB and Statistics Toolbox 2018) and R, a statistical programming software (R Core Team 2020).

3 Results

3.1 CEQUEAU model evaluation

We found a strong correlation between the historical temperature data of the primary station, Vanderhoof, and the projected values from the CEQUEAU model (r = 0.90; $p < 0.0001$) showing a significant relationship (Fig. 2). The RMSE value of 1.27 °C indicates good agreement between CEQUEAUprojections and observed values, with slightly underestimate bias of –0.93%.

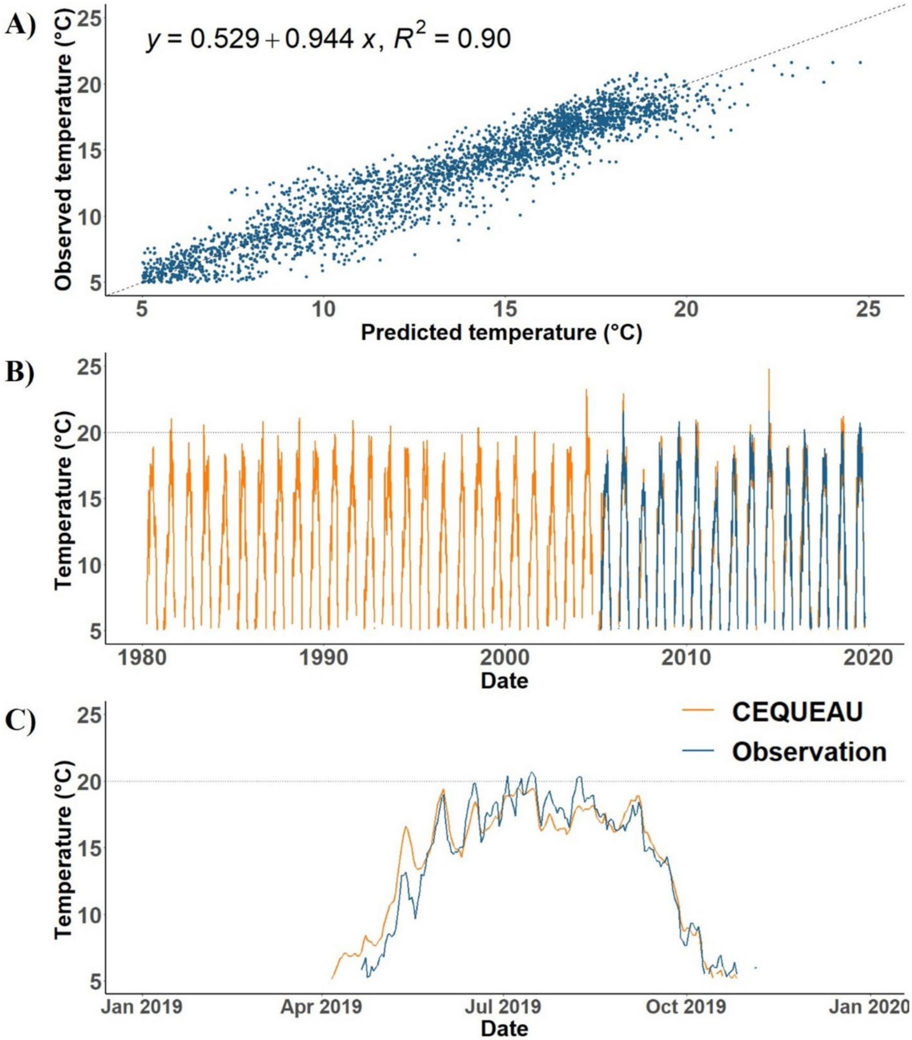

Fig. 2 The relationship between predicted temperature from the CEQUEAU model and the historical temperature data from https://climate.weather.gc.ca/historical_data/search_historic_data_e.html for Vanderhoof station. A) Scatter plots of predicted and observed temperature, with the 1:1 line indicated for comparison. B) Time series of CEQUEAU predicted (orange) and observed (blue) water temperature C) Time series of CEQUEAU predicted (orange) and observed (blue) water temperature data with a 2019 focused plot

3.2 Changes in thermal exposure risk (Te) of Nechako Chinook salmon by the mid and end of the century relative to the 1980s

3.2.1 Changes in thermal exposure risk (T_e) across Nechako River

Our findings indicate that T_e for the fry life stage across the Nechako River (average of all cells throughout the distribution of Chinook salmon in Nechako River) is projected to stay consistently below 1 in each month (i.e. May and June when the life stage is present) by the 2050s relative to the 1980s regardless of the emission scenarios (SSP2-4.5 and SSP5-8.5) (Table 3). On the other hand, the parr life stage T_e is expected to exceed the value of 1 in August, with multipliers of 1.1 and 1.3 by the 2050s relative to the 1980s under SSP2-4.5 and SSP5-8.5, respectively (Table 3). For the adult life stage, T_e is predicted to rise above 1 during July and August under SSP2-4.5 by the 2050s relative to the 1980s. However, under SSP5-8.5 in the same timeframe, T_e values are projected to be above 1, with multipliers of 1.1, 1.3, and 1.4 times higher for July, August, and September compared to the 1980s. It is worth noting that in the 1980s, T_e only exceeded the value of 1 in August and, importantly, the predicted SD for T_e was below 1.

We projected the changes in the fry, parr, and adult life stages of fish in the Nechako River in the 2090s as compared to the 1980s under two different scenarios—SSP2-4.5 and SSP5-8.5. The SSP5-8.5 scenario predicted warmer days and a larger increase in Te compared to SSP2-4.5. According to our findings, the T_e value for the fry life stage will be below 1 in May and June under both scenarios (Table 3). For the parr life stage, we predicted that the T_e value will surpass 1 in July and August under SSP2-4.5. As compared to the 1980s, the T_e value during these months will increase by 1.8 and 1.3 times, respectively (Table 3). On the other hand, under SSP5-8.5, the T_e value is expected to exceed

Table 3 The thermal exposure risk (Mean and Standard deviation) of Nechako Chinook salmon between May and October during the 1980s (average between 1980–1989) and under climate change scenarios: SSP2-4.5 and SSP5-8.5 by 2050s (average between 2050–2059) and the 2090s (average between 2090–2099). The multiplier in the bracket when thermal exposure risk is above 1

		SSP2-4.5		SSP5-8.5		
Month	1980s	2050s	2090s	2050s	2090s	Lifestage
May	0.04 ± 0.03	0.06 ± 0.05	0.12 ± 0.08	0.07 ± 0.06	0.19 ± 0.14	Fry
June	0.24 ± 0.14	0.47 ± 0.17	0.59 ± 0.32	0.59 ± 0.19	0.83 ± 0.29	Fry
July	0.63 ± 0.3	0.95 ± 0.14	**1.17 ± 0.58 (1.9)**	**1.07 ± 0.17 (1.7)**	**1.75 ± 0.32 (2.7)**	Parr
August	0.95 ± 0.05	**1.08 ± 0.12 (1.1)**	**1.2 ± 0.64 (1.3)**	**1.26 ± 0.21 (1.3)**	**2.11 ± 0.24 (2.2)**	Parr
September	0.32 ± 0.03	0.63 ± 0.04	0.43 ± 0.23	0.77 ± 0.06	**1.46 ± 0.04 (4.6)**	Parr
October	0	0	0.01 ± 0.01	0.03 ± 0.01	0.17 ± 0.07	Parr
July	1.00 ± 0.03	**1.09 ± 0.1 (1.1)**	**1.36 ± 0.49 (1.4)**	**1.14 ± 0.16 (1.1)**	**1.86 ± 0.34 (1.9)**	Adult
August	1.02 ± 0.04	**1.11 ± 0.13 (1.1)**	**1.39 ± 0.56 (1.4)**	**1.29 ± 0.24 (1.3)**	**2.31 ± 0.23 (2.3)**	Adult
September	0.75 ± 0.09	0.99 ± 0.02	0.7 ± 0.28	**1.04 ± 0.02 (1.4)**	**1.57 ± 0.04 (2.1)**	Adult
October	0.13 ± 0.02	0.17 ± 0.08	0.1 ± 0.04	0.25 ± 0.09	0.5 ± 0.13	Adult

1 in July, August, and September, with multipliers of 2.8, 2.2, and 4.5, respectively, as compared to the 1980s. For the adult life stage, we predicted that the T_e values would exceed 1 and increase by 1.4 times during July and August under SSP2-4.5, as compared to the same months in the 1980s (Table 3). Under SSP5-8.5, the T_e values are expected to rise 1.9, 2.3, and 2.1 times in July, August, and September, respectively, as compared to the 1980s.

3.2.2 Changes in thermal exposure risk (T_e) Nechako River sections

Our study shows that the T_e values for fry in all sections of the Nechako River (Fig. 1A) during May and June will be below 1 by the 2050s relative to the 1980s, under both SSP2-4.5 and SSP5-8.5 (Fig. S1 and Fig. S2). In the 1980s, for the parr life stage, T_e was only above 1 in Nautley River in August (Fig. 3). However, our projections indicate that by the 2050s, in July, T_e will be above 1 in Nautley River and Nechako River Lower, while in August, all sections will experience this trend under both scenarios (Fig. 4A, Fig. S4A). Finally, for the adult life stage, we projected a T_e above the value of 1 in July, August, and September in all Nechako River sections under both scenarios by the 2050s (Fig. 4B, Fig S4). This is a substantial change from the 1980s, where we estimated above the value of 1 only in Nautley River and Nechako River Lower in July and all Nechako River sections in August (Fig. 3).

According to our projections, in the 2090s, the T_e value below 1 is expected to be under the SSP2-4.5 scenario for the fry life stage (Fig. S1B, Fig. S3) in all sections. However, under the SSP5-8.5 scenario, we projected a T_e value in the Nautley River and Nechako River Lower that will exceed the value of 1 in June (Fig. S1B). For the parr life stage, our projections show that T_e levels in Nautley River and Nechako River Lower will exceed 1 in July and August under the SSP2-4.5 scenario. However, under the SSP5-8.5 scenario, our projections suggest that T_e levels will exceed 1 in all Nechako River sections during the parr life stage duration months (i.e., July, August, and September) (Fig. 4C, Fig. S5). As for the adult life stage, our analysis predicts that T_e levels will exceed the threshold in July and August in the Nautley River and Nechako River Lower sections under the SSP2-4.5 scenario, and in September in Nautley River (Fig. 4D, Fig S5). Under the SSP5-8.5 scenario, our projections reveal that T_e levels will surpass 1 in all Nechako sections in July, August, and September relative to the 1980s.

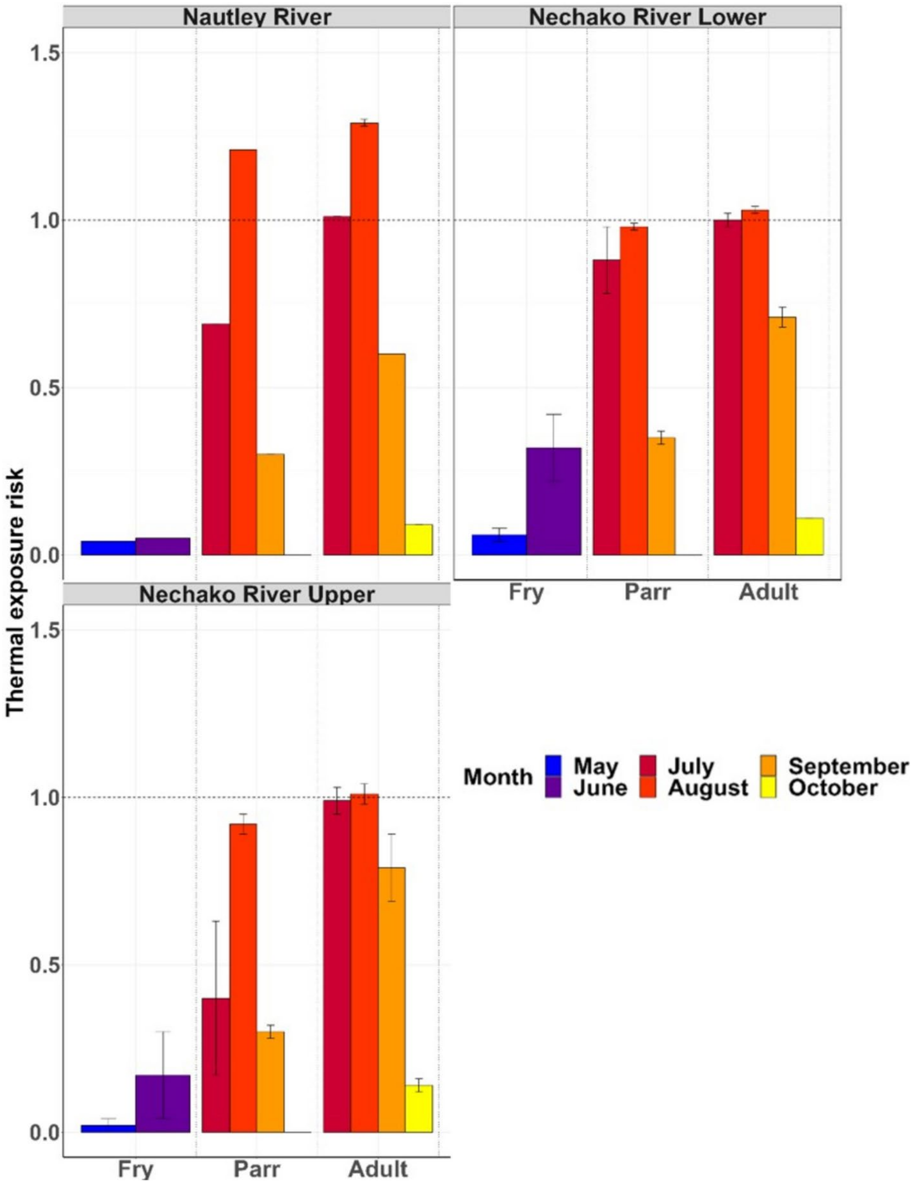

Fig. 3 The thermal exposure risk for Nechako River Chinook salmon life stages (fry, parr and adult) in Nechako River sections in the 1980s (average 1980–1989) for May to October. The dotted line indicates a thermal exposure risk of 1

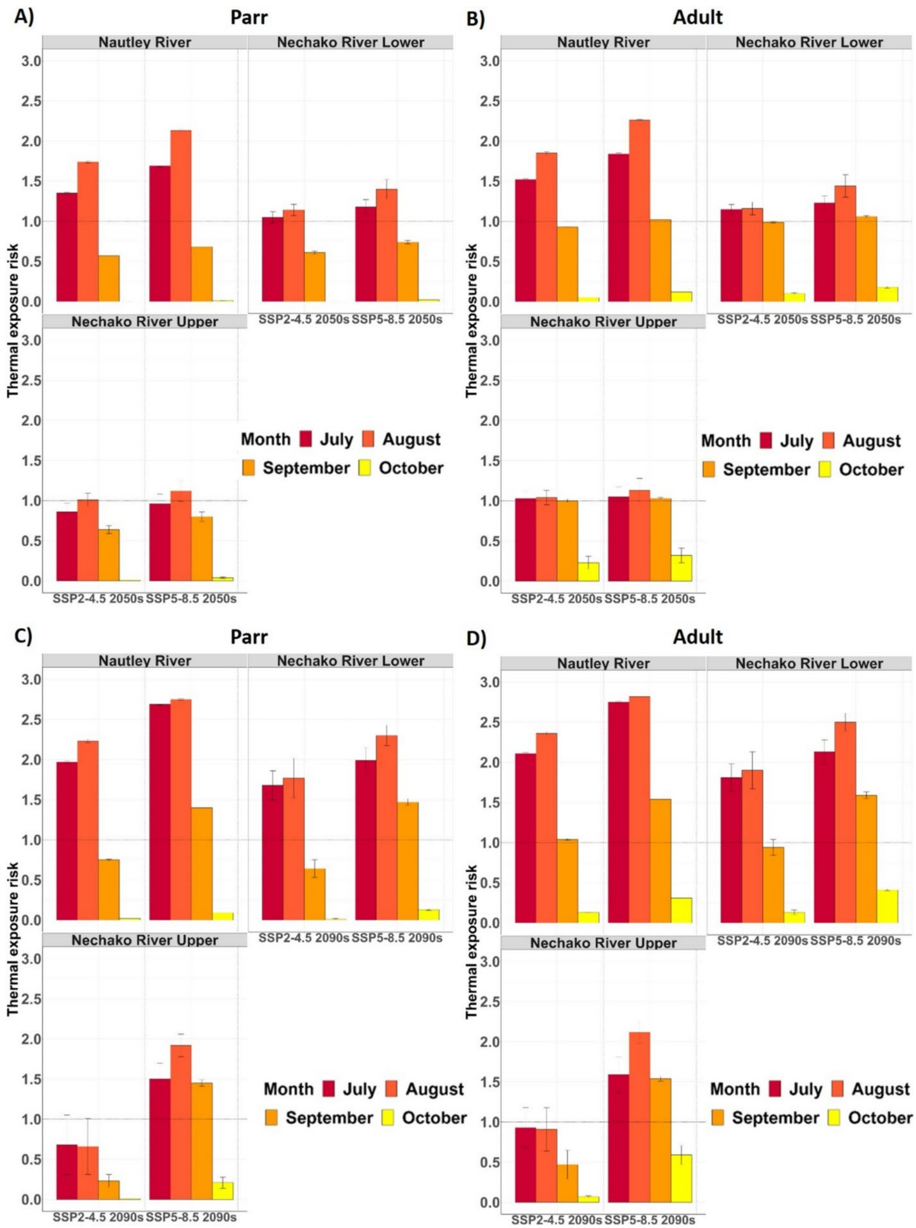

Fig. 4 The thermal exposure risk for Nechako River Chinook salmon life stages under SSP2-4.5 and SSP5-8.5 scenarios. **A** Thermal exposure risk for the Parr life stage in the 2050s (average between 2050–2059), **B** Thermal exposure risk for Adult life stage in the 2050s, **C** Thermal exposure risk for the Parr life stage in the 2090s (average between 2090–2099), **D** Thermal exposure risk for the Adult life stage in the 2090s. The dotted line indicates a thermal exposure risk of 1. Cool to warm colours represent the months included in this study- July to October

3.3 Cumulative heat degree-days above optimal temperatures for Chinook salmon in Nechako River sections

Our research findings present the degree-days data for various sections of the Nechako River during the 1980s and under different climate change scenarios (Fig. 5). According to our results, the Upper Nechako River experienced the highest degree-days of 200 °C-days, while the Nechako River Lower had the lowest degree-days of 61 °C-days during the 1980s. Meanwhile, the Nautley River had 130 °C-days.

Based on our projections for the SSP2-4.5 scenario in the 2050s, the Nautley River will experience the highest increase in °C-day relative to the 1980s of 3.4 times (448 °C-day), while the Nechako River Upper and Lower will experience an increase in °C-days of 1.5 (305 °C-day) and 2.5 (152 °C-day) times, respectively. Under the SSP5-8.5 scenario for the 2050s, the increase in °C-days relative to the 1980s is even greater, with the Nautley River,

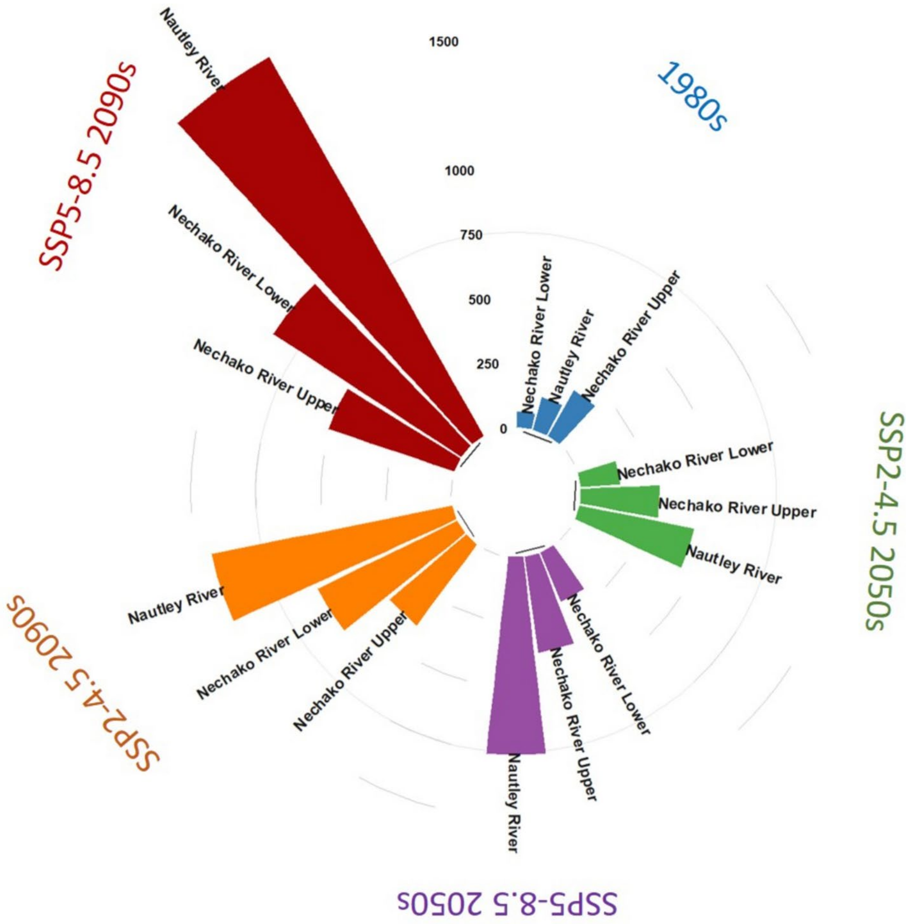

Fig. 5 Cumulative heat degree-days above optimal temperature for Nechako Chinook salmon life stages in Nechako River sections in the 1980s and under SSP2-4.5 and SSP5-8.5 scenarios

Nechako River Upper and Nechako River Lower projected to be 5.8 times (760 °C-days), 1.9 times (373 °C-days) and 3.4 times (205 °C-days) greater, respectively.

In the 2090s, under the SSP2-4.5 scenario, the Nautley River is expected to increase by 7.2 times (942 °C-days) relative to the 1980s, while the Nechako River Upper and the Nechako River Lower are projected to increase by 1.9 times (388 °C-days) and 9.8 times (597 °C-days) relative to the 1980s respectively. Under the SSP5-8.5 scenario, the Nautley River is projected to increase by 12.9 times (1673 °C-days) relative to the 1980s. The Nechako River Upper and the Nechako River Lower are projected to increase by 2.9 times (510 °C-days) and 14.2 times (864 °C-days) relative to the 1980s respectively.

4 Discussion

Our study used a combination of hydrological modelling and physiological data to evaluate how thermal conditions, in the months of the year for which the Nechako STMP was implemented, affected the thermal exposure of Chinook salmon with projections to the future under different climatic and socio-economic scenarios. The STMP regulate water release to maintain river temperatures below 20 °C during the sockeye salmon spawning migration (Macdonald et al. 2012). According to our findings, the current water management program is unlikely to mitigate climate change impacts in intermediate or high emission scenarios, for the short (2050s) or long term (2090s).

Our study found that while the STMP was not designed specifically for Chinook salmon, the thermal exposure risk (T_e) across the Nechako River in the 1980s (average between 1980 and 1989) aligned with the program's goal of addressing the impact of rising temperatures (Macdonald et al. 2012), inadvertently providing benefits to Chinook salmon as well, especially for the fry and parr life stages. The fry and parr life stages did not experience thermal exposure risk during the period the life stages occurred in the Nechako River. However, the adult life stage showed T_e values exceeding 1 in July and August, which points to a potential risk of thermal stress for migrating and spawning adults (DFO 2020), despite the STMP program's implementation.

When comparing the Nechako River sections, distinct patterns and similarities of thermal exposure emerged. In the Nautley River, an important feeding and migration pathway for Chinook salmon, all life stages except fry were projected to have experienced a significant amount of thermal exposure that surpassed the value of 1 in July of the 1980s. Furthermore, in the Upper and Lower sections of Nechako River, adult Chinook salmon have been subjected to an elevated risk of exposure to thermal stress during the STMP months (i.e. July and August). Although the study encompassed a diverse range of habitats in the Nechako River's Lower and Upper sections, these areas include several vital creeks and inlets that are essential for the conservation of Chinook salmon (Bradford 1994). In addition, the areas identified as the Upper Nechako River include the spawning areas of Chinook salmon in the Nechako River (Bradford 2022). Since Pacific salmon are semelparous, spawning behaviours (e.g., digging redds, competing for mates) in these areas are important for reproductive success (Healey et al. 2003) and straying or impaired behaviours due to high temperatures would hinder spawning success.

Our study emphasizes the need to enhance the current STMP program that incorporates physiological considerations for all species' life stages and climate change to ensure the robust resilience of Nechako species. Our study highlighted that climate change may pose an additional threat to the Chinook salmon population across the Nechako watershed, especially during the summer months. Under the intermediate and high emission scenarios (i.e., SSP2-4.5 and SSP5-8.5), the T_e will increase substantially compared to the 1980s when the STMP program began. This is particularly evident for parr in July and August and for adults in July, August, and September by the mid-century. This risk will be aggravated by the end of the century in June, July, August and September for parr and adult life stages, especially under the high emissions scenario. These months coincide with the migration months for the upper Fraser Chinook salmon population including the Nechako population (Bradford and Taylor 2023; DFO 1999).

Our research found that specific sections of the Nechako River may be especially at risk of thermal exposure during the STMP months under both SSP2-4.5 and SSP5-8.5 scenarios. The Nautley River and Nechako River Lower sections are consistently projected to have the highest T_e for both the parr and adult life stages during July and August by the 2050s. By the end of the century, all sections of the Nechako River are projected to have a T_e greater than 1 in some months. This includes early summer months such as June when the fry life stages emerge in the Nechako River (Alcan 2010; Bradford and Taylor 2023). This highlights the need for action to manage the impact of climate change on the Nechako Chinook salmon population beyond the STMP period (July 20th to August 20th) and the review of the current STMP program to include other Nechako resident species (Oyinlola et al. 2023). It is especially important to address this issue given that temperatures in BC are expected to rise significantly in the early Fall season relative to historical observations (Whitfield 2001).

Overall, our study suggests that the Nechako River Chinook salmon freshwater adult life stage will be subjected to high T_e by the middle and end of the century in all Nechako River sections compared to the 1980s under both projected climate scenarios despite the STMP being active. Nevertheless, the risk level is much lower under the intermediate scenario (i.e., SSP2-4.5) than the high-emission scenario (i.e., SSP5-8.5). In addition to the STMP months, T_e is expected to increase in September under the high emission scenario by the end of the century. With peak adult migration typically occurring during these months in the upper Fraser (Bradford and Taylor 2023; DFO 1999), the increased T_e during September could have significant implications for the survival and reproductive success of Nechako River Chinook salmon. The increase in thermal exposure risk observed in the study represents the threat faced by Chinook salmon populations throughout North America (Crozier et al. 2021; FitzGerald et al. 2021; Keefer et al. 2018). These findings highlight the urgency of implementing effective conservation and management strategies to mitigate the impact of rising temperatures on migrating Chinook salmon populations.

The degree-day index has been applied to describe the relationship between temperature and physiology in fish (Chezik et al. 2014; Neuheimer and Taggart 2007; Oyinlola et al. 2023; Steele and Neuheimer 2022). Our study focused on the cumulative heat degree days (CHDD) above optimal temperatures for Chinook salmon in the Nechako River as a relative indicator of predicted thermal stress in the Nechako River system. Our projections indicate a substantial rise in CHDD because of climate change, with values between 1.9 to 5.8 times by the 2050s and 2.9 to 12.9 times by the 2090s compared to the 1980s. These substantial increases are most prominent during the summer months (i.e. July and August), coinciding with the parr and adult life stages of Chinook salmon, which are particularly vulnerable to heat stress (Butler 2024; Keefer et al. 2018; von Biela et al. 2020). Increasing water temperature during the salmon parr stage could lead to salmon parr moving towards cold-water refuges to mitigate heat stress (Dugdale et al. 2016). Increasing temperatures and reduced access to thermal refuges because of climate change can impact salmon parr growth, development and overall survival (Siegel and Crozier 2018).

While the current STMP program aims to reduce water temperatures between July 20th to August 20th, our findings suggest that this program will be insufficient to reduce the thermal stress on Chinook salmon under both intermediate or high emission scenarios or in the short (2050s) and long term (2090s). However, if we consider the intermediate scenario (SSP2-4.5), the CHDD value only slightly increases compared to the high emission scenario (SSP5-8.5), where there is a substantial increase. Hence, the water management system must be re-evaluated with a focus on reducing temperatures to be within the optimal temperature ranges for the different Nechako species that inhabit the river. This study highlights the urgency of the matter and the need for immediate action.

The projected increases in CHDD are consistent across different sections of the Nechako River. However, the projections indicate that the Nautley and Lower Nechako Rivers will experience the most substantial increases in thermal stress. The lower reaches of rivers are often the warmest (Caissie 2006), and under future climate scenarios, these sections are projected to become even more impacted. By the 2090s, the Lower Nechako River could experience a 14.2-fold increase in CHDD under the high-emission SSP5-8.5 scenario, this indicated prolonged periods of extreme heat that could make this section nearly uninhabitable for Chinook salmon. Such thermal conditions could lead to a reduction in available habitat, further concentrating Chinook salmon populations in shrinking cool-water refuges and increasing competition for resources.

4.1 OuStudy limitations

R study integrates a spatially explicit hydrological model with the physiological limits of different life stages of Chinook salmon, providing insights into how changes in water temperatures may influence this species across the Nechako River. This approach surpasses the limitations of traditional single river point analyses, allowing for a comprehensive evaluation of Chinook salmon's thermal vulnerability within the reach of the Nechako River. However, limitations exist. The accuracy of our temperature prediction model may be underestimated due to various factors, such as the reliability of the input meteorological data, observed water temperature data, potential heat budget variations and the resolution of the physical catchment properties and their aggregation or disaggregation processes (Khorsandi et al. 2022; Markhali et al. 2022; Yoshida et al. 2022). Mismatches between the data resolution of the physical catchment properties and the model resolution can introduce additional uncertainties in the results (Shrestha et al. 2006), requiring careful consideration during the data preparation step. Although our approach has yielded valuable insights into the thermal vulnerability of Chinook salmon, the limitations of our modelling methods underscore the need for continuous refinement and improvement. Future research efforts should prioritise the enhancement of observed data reliability and resolution for calibration, as well as the refinement of model mechanisms and parameters to improve their accuracy in simulating extreme temperatures and accounting for the complexities of the Nechako River ecosystem.

One limitation of our study pertains to the thermal metrics at a large scale. We have not factored in the precise local cooling patterns that may arise from groundwater or hyporheic exchange (Kurylyk et al. 2015; Sullivan et al. 2021), offering potential thermal refuges for parr and adults in the Nechako River. To address this limitation, future research should focus on measuring the unique ground features and determining the specific areas where these life stages reside within the Nechako River. This could involve a longitudinal study monitoring different Chinook salmon life stages, and comparing empirical data of these stages growth rates and survival across various thermal conditions predicted by our model.

Relying solely on laboratory thermal limits data may not accurately predict the thermal exposure risk (Childress and Letcher 2017; Martin et al. 2017; Payne et al. 2021) for Chinook salmon in their natural habitat. The complexity of ecosystems and the potential interactions between species and their environment are not completely accounted for in the data, which can affect species' distributions, population dynamics, and community structure. Thus, it is important to consider these ecological interactions when studying the effects of temperature on Chinook salmon. Moreover, some of the physiological data used here was collected across the life stages of Shuswap Chinook salmon. This upper Fraser River population continues to have strong returns whereas the Nechako River Chinook population because of population declines and sustainability concerns. Pacific salmon populations are known to be locally adapted to their specific environmental conditions (Abe et al. 2019; Eliason et al. 2011; Hecht et al. 2015), thus differences in thermal risk could exist between these populations. However, Shuswap and Nechako River Chinook salmon migrate at the same time and experience similar thermal conditions. Additionally, the thermal limit metrics may overlook the adaptive capacity of Chinook salmon species. Organisms can exhibit phenotypic plasticity or undergo evolutionary adaptations in response to changing environmental conditions and our study does not address acclimation or future adaptation (Burton et al. 2022; Crozier et al. 2008; Schulte et al. 2011). Limiting our study to thermal constraints alone may result in overlooking the capacity of species to acclimate or adapt to changing thermal environments in the long run. For instance, if Chinook salmon in the Nechako River can adapt, acclimate, or modify their behaviour to avoid warming, future Te values may be lower than our current predictions. However, it is still uncertain whether this population can effectively respond to increasing temperatures using these strategies. While some species are known to adjust their distribution or timing to track favourable conditions (Crozier et al. 2011; Legrand et al. 2021), it remains unclear whether the Nechako River Chinook salmon possess this ability or if the specific environmental changes will allow for such adaptation.

5 Conclusion

Evidence from this study reinforces the need to revisit and enhance the STMP to ensure the long-term viability of the Nechako River species (Earhart et al. 2023; Oyinlola et al. 2023). Our research suggests that the management strategy for sockeye salmon exposes Chinook salmon parr and adults to thermal-induced stress and unsuitable conditions. Our study highlights the need to manage water releases to ensure that cooler water reaches the key sections that are critical for Chinook salmon survival in the Nechako River. In addition, creating cool-water refugia could offer respite from higher temperatures. Finally, assessing whether the salmon can move upstream to cooler areas, and enhancing their ability to move into such areas could offer a natural way of avoiding the stress. However, our findings are subject to limitations, including underestimating temperature variability and excluding local cooling effects. Moreover, the data used in this study may not fully capture Nechako River Chinook salmon's local adaptations or ecological interactions.

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Data availability The data that support the findings of this study are openly available at https://doi.org/10.5683/SP3/Y6Q8UD

Declarations

Competing interest The authors have declared that no competing interests exist.

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