



Hydrothermal impacts of water release on early life stages of white sturgeon in the Nechako river, B.C. Canada

Muhammed A. Oyinlola^{a,b,c,*}, Mostafa Khorsandi^{a,b}, Rachael Penman^c, Madison L. Earhart^c, Richard Arsenault^d, Colin J. Brauner^c, Andre St-Hilaire^{a,b}

^a Centre Eau Terre Environnement, Institut National de la Recherche Scientifique, 490, rue de la Couronne, Québec G1K 9A9, Canada

^b Canadian Rivers Institute, UNB Fredericton, 28 Dineen Dr Fredericton, New Brunswick, E3B 5A3, Canada

^c Department of Zoology, University of British Columbia, 4200–6270 University Blvd., Vancouver, BC V6T 1Z4, Canada

^d Hydrology, Climate and Climate Change Laboratory, École de technologie supérieure, 1100 Notre-Dame West St., Montreal, QC H3C 1K3, Canada

ARTICLE INFO

Keywords:

Nechako river
Thermal exposure
White sturgeon
Temperature
Physiological limits

ABSTRACT

Water temperature plays a crucial role in the physiology of aquatic species, particularly in their survival and development. Thus, resource programs are commonly used to manage water quality conditions for endemic species. In a river system like the Nechako River system, central British Columbia, a water management program was established in the 1980s to alter water release in the summer months to prevent water temperatures from exceeding a 20 °C threshold downstream during the spawning season of Sockeye salmon (*Oncorhynchus nerka*). Such a management regime could have consequences for other resident species like the white sturgeon (*Acipenser transmontanus*). Here, we use a hydrothermal model and white sturgeon life stage-specific experimental thermal tolerance data to evaluate water releases and potential hydrothermal impacts based on the Nechako water management plan (1980–2019). Our analysis focused mainly on the warmest five-month period of the year (May to September), which includes the water release management period (July–August). Our results show that the thermal exposure risk, an index that measures temperature impact on species physiology of Nechako white sturgeon across all early life stages (embryo, yolk-sac larvae, larvae, and juvenile) has increased substantially, especially in the 2010s relative to the management program implementations' first decade (the 1980s). The embryonic life stage was the most impacted, with a continuous increase in potential adverse thermal exposure in all months examined in the study. We also recorded major impacts of increased thermal exposure on the critical habitats necessary for Nechako white sturgeon recovery. Our study highlights the importance of a holistic management program with consideration for all species of the Nechako River system and the merit of possibly reviewing the current management plan, particularly with the current concerns about climate change impacts on the Nechako River.

1. Introduction

Temperature plays an important role for all aquatic organisms and has been shown to affect species' phenotype, distribution, survival, and development (Pörtner et al., 2001; Perry et al., 2005; Kearney and Porter, 2009). As most aquatic species are poikilothermic ectotherms, their body temperature varies with the environment (Speight et al., 2008), and thus environmental temperature directly influences their physiology, behaviour, and development. For instance, metabolic rate increases with temperature by accelerating biochemical kinetic energy

reaction rates, influencing individual organisms' functioning and performance to be successful in an ecosystem (Angilletta and Angilletta, 2009; Abram et al., 2017), which then may affect species' population and ecology (Lessard and Hayes, 2003; Biro et al., 2007). Indeed, physiological processes increase 2–3 fold for every 10 °C increase in temperature (White et al., 2006; Seebacher et al., 2015; Peck, 2016). This increases up to a temperature optimum, and then performance decreases beyond that (Fig. 1A).

Thermal exposure risk is a vital aspect to consider in aquatic ecosystems due to its potential impacts on the health and functioning of

* Corresponding author. Canadian Rivers Institute and centre Eau Terre Environnement, Institut National de la Recherche Scientifique, 490, rue de la Couronne, Québec G1K 9A9, Canada.

E-mail address: Muhammed.Oyinlola@inrs.ca (M.A. Oyinlola).

<https://doi.org/10.1016/j.jtherbio.2023.103682>

Received 16 December 2022; Received in revised form 6 August 2023; Accepted 7 August 2023

Available online 19 August 2023

0306-4565/© 2023 Elsevier Ltd. All rights reserved.

these ecosystems (Morash et al., 2021). Studies have shown that increased temperatures can enhance metabolic rates and overall organismal functioning, however, beyond an optimum point, further temperature increases can lead to a decline in performance and ultimately mortality (Pörtner et al., 2005; Pörtner and Peck, 2010). These thermal exposures can have significant ecological implications in aquatic systems, leading to altered species distributions, changes in seasonal events, and even the potential for oxygen depletion and the growth of harmful algal blooms (Griffith and Gobler, 2020; Jones and Cheung, 2015; Walters et al., 2018). It is important, therefore, to consider thermal exposure-associated potential risks to aquatic ecosystems and develop frameworks towards better understanding and managing these risks to promote the health and functioning of such aquatic ecosystems.

Anthropogenic activities such as urbanisation, vegetation removal, reservoirs, river regulations, and dams are major contributors to changes in the lotic ecosystem's physio-chemical properties, including temperature (Lessard and Hayes, 2003; Prats et al., 2012; Maheu et al., 2016a). Such activities are beneficial to society; however, they may greatly alter the thermal conditions in rivers, thereby increasing organisms' elevated thermal exposure that may lead to negative impacts (Ahmad et al., 2021; Maheu et al., 2016a,b; Michie et al., 2020; Shi et al., 2021; Zaidel et al., 2021; Zhao et al., 2020).

Many studies have reported the impact of dams on the associated river thermal regime (Larabi et al., 2022; Weber et al., 2017; Zaidel et al., 2021), and have been shown to alter downstream temperature depending on their size and type (Chandesris et al., 2019; Seyedhashemi et al., 2021). Nevertheless, the flow rate can be altered to influence downstream temperature through guided water discharge management to restore, or sustain, the ecological integrity of the river system (Olden and Naiman, 2010). Such management approaches can lead to different thermal pollution magnitudes. For instance, hypolimnetic releases from dams in the summer discharge cold water that reduces downstream temperature, while surface water released from dams may result in considerable downstream warming (Saila et al., 2005; Maheu et al., 2016b). The cooling or warming effect depends on the type of dam. For example, in Eastern Canada, small and medium storage dams are known to have a warming effect during the open water period persisting over river reaches ranging between 4.3 and 16 km (Maheu et al., 2016b).

The Nechako River is an important system in central British Columbia, Canada that is impacted by the presence of a dam through changes in the river system functions (i.e., flow, temperature, sediment etc). To partially mitigate this impact, a water management program has been implemented since the 1980s. The program focused on maintaining a water temperature below or equal to 20 °C during critical times, during the migration and spawning season of Sockeye salmon

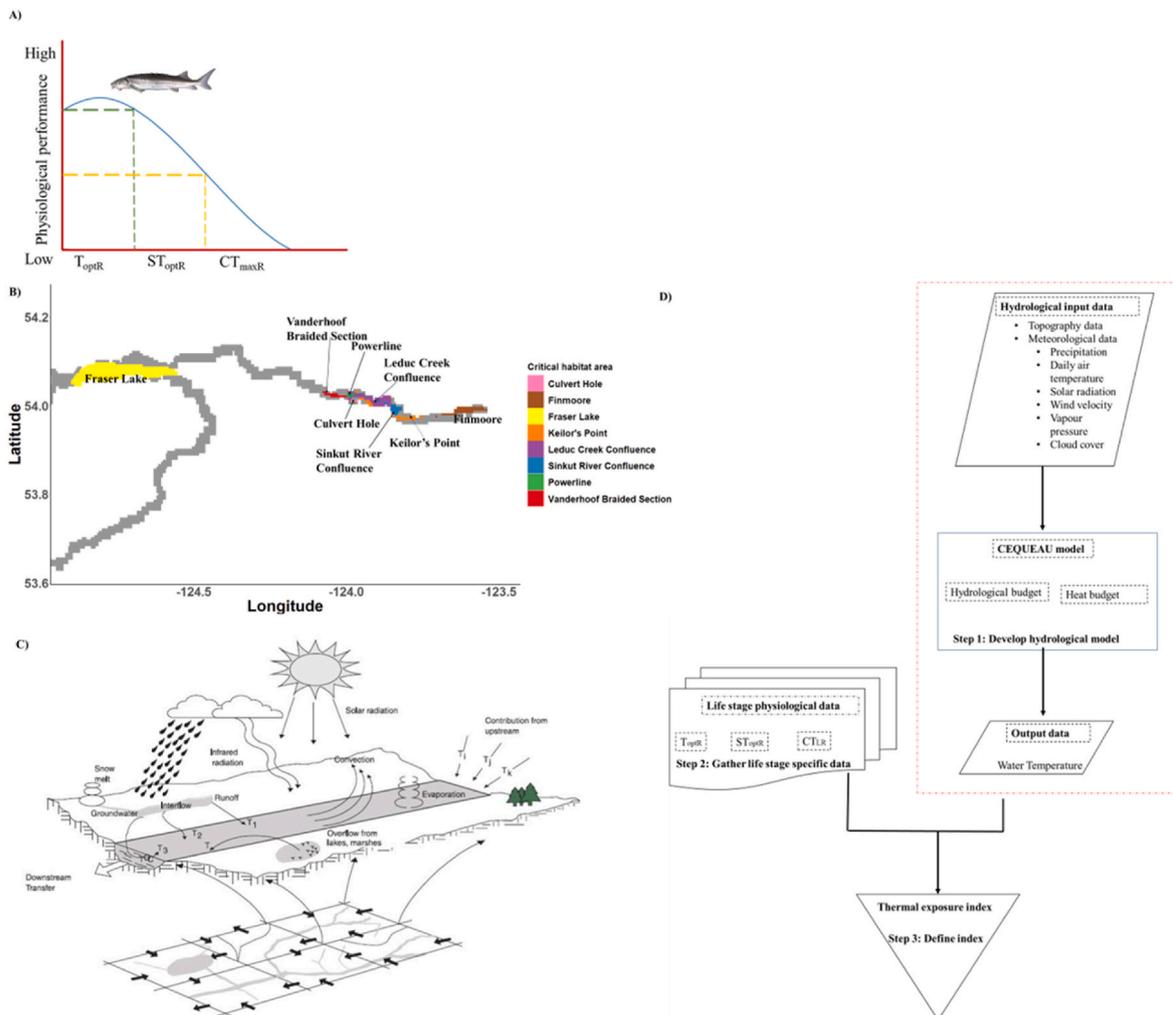


Fig. 1. Graphical representation of the major components of this study. (A) Graphical representation of physiological performance related to temperature. T_{optR} is the optimal temperature range over which fish exhibit their greatest physiological performance, CT_{LR} is a critical thermal temperature range, which coincides with a loss of critical function or death, and the Sub-optimal Temperature Range (ST_{optR}) is the temperature range between T_{optR} upper limits and CT_{LR} lower limits. (B) Critical habitat areas identified in the Species Risk Act (SARA) for the recovery of white sturgeon. (C) Schematic diagram of the framework to derive a thermal exposure index used in this study. (D) CEQUEAU model heat budget representation (see materials and methods for more information).

(*Oncorhynchus nerka*) (Macdonald et al., 2012), when adults migrate through this region to reach their spawning grounds. However, the river system supports many other important and critically endangered species, including white sturgeon (*Acipenser transmontanus*), that are not considered in the present management program. It is therefore essential to develop a better understanding of thermal conditions to which white sturgeon are exposed in the Nechako River and to provide advice on implementing a more comprehensive water management program concerning residents and other migratory fish species requirements.

To mitigate dam impacts and to find a compromise between water impoundment and ecological values, water management programs such as the Summer Temperature Management Program (STMP) of the Nechako River system have been implemented with a focus on water quality, temperature and flow. The STMPs' main objective is to maintain water temperature below 20 °C during the sockeye migration season (July 20 – August 20), in the Nechako River at Finmore (Fig. 1B) (upstream of the Stuart River confluence) (Macdonald et al., 2012). The STMP target is achieved by releasing water discharges of up to 453 m³/s through the Skins Lake Spillway into the Nechako River (Ouellet-Proulx et al., 2017). The management program has been effective in this aim since it started in 1981, which may benefit sockeye salmon spawning success (Macdonald et al., 2012). However, the benefits of this 20 °C target for resident species such as white sturgeon have been questioned (Macdonald et al., 2012). Moreover, reaching the stated thermal objective at Finmore does not guarantee that conditions are optimal elsewhere in the system, such as at locations that constitute habitat for white sturgeon.

The white sturgeon is primarily a freshwater species found only in three major river systems in western North America: the Fraser, Columbia, and Sacramento-San Joaquin rivers (Hildebrand et al., 2016). In British Columbia, the species occurs in the Lower and Upper Fraser, including their tributaries like the Nechako and Stuart Rivers, and the Upper Columbia and Kootenay Rivers (Schreier et al., 2012). The Nechako sturgeon population has declined since 1970 owing to adult natural mortality and negligible recruitment (COSEWIC, 2003). Although several factors, such as fishing, changes to species assemblages, and climate change impacts (Bradford and Irvine, 2000; Hutchings and Reynolds, 2004; Pauly and Palomares, 2005; Johnston and Maceina, 2009; Genner et al., 2010; Cheung et al., 2021) could contribute to the fish population decline, the anthropogenic impacts of dams, such as thermal and sediment alteration, cannot be overlooked (Boucher et al., 2014, 2018; Macdonald et al., 2012). Such alterations might be detrimental to white sturgeon phenotypic characteristics and ultimately survival, especially in the early life stages (i.e., embryo, yolk-sac larvae), which may persist into the juvenile stages (Boucher et al., 2014; Cheung, 2019).

In this study, we developed a framework to evaluate water release-related hydrothermal impacts on the white sturgeon of the Nechako River (B.C. Canada) (Fig. 1C). First, we applied the CEQUEAU model (Charbonneau et al., 1977), a semi-distributed hydrological and water temperature model, to simulate the Nechako River's daily water temperature from 1980 to 2019. Second, we gathered early life stages (i.e., embryo, yolk-sac larvae, larvae and juvenile) specific information on the thermal tolerance and the critical habitats of the white sturgeon in the Nechako River. To assess the effects of water temperature release on Nechako white sturgeon populations, we developed a thermal exposure risk (T_e) index, which ranges from 0 to 3. An index of 0 indicates low thermal exposure risk, while a score of 3 indicates high exposure risk. We employed this index to evaluate the historical impact of the STMP program on the health and survival of Nechako white sturgeon. Finally, we discussed the implication of our results for future water management and Nechako River white sturgeon recovery, especially under global environmental changes. Numerous thermal indicators have been developed and calculated in different lotic systems for salmonids (e.g., Abidi et al., 2022; Edmundson and Mazumder, 2001). However, to our knowledge, this is the first study that designed a thermal exposure index

for white sturgeon in a major system such as the Nechako River basin.

2. Materials and methods

2.1. CEQUEAU model: modelling Nechako river water temperature

CEQUEAU is a semi-distributed hydrological and water temperature model (Fig. 1D) (see (Khorsandi et al., 2022) for model details). The model considers watershed physical characteristics by decomposing them into Elementary Representative Areas (ERA) of equal surface (called “whole squares”) and then defines altitude, percentage of forest cover, and the percentage of ERA covered by lakes and wetlands. The model further defines water routing by subdividing ERAs into a maximum of four so-called “partial squares” according to altitudes, slopes, and the consequent water divides. In each partial square, a hydrological budget is calculated at each time step (daily). CEQUEAU achieves routing by apportioning the water available for runoff proportionally to the partial square areas and identifying the receiving partial square downstream. In addition to physiographic data, the model requires meteorological inputs: daily solid and liquid (or total) precipitation, as well as maximum and minimum daily air temperature. Alongside the hydrological budget, a heat budget is calculated on each partial square. This is done using additional meteorological input variables (solar radiation, wind velocity, vapour pressure, and cloud cover) that are used to compute surface heat fluxes (incoming shortwave radiation, net longwave radiation, latent heat, and sensible heat). In addition to the surface heat budget, heat advected from upstream, local runoff and interflow, as well as groundwater, is accounted for at each time step (Fig. 1D).

2.1.1. CEQUEAU model: modelling temperature and model calibration

The first step in implementing CEQUEAU is calibrating its parameters. This is a two-step process in which the hydrological module is first calibrated using observed streamflow from hydrometric stations on the Nechako River, followed by a similar calibration of the thermal module using water temperature gauges located between the dam and Vanderhoof. In both cases, an automatic calibration algorithm [Covariance Matrix Adaptation Evolution Strategy or CMA-ES (Hansen, 2006)] was implemented after a first manual calibration was used to define the parameters domain. The multi-site temperature calibration method of Khorsandi et al. (2022) was used to adjust the parameters of the water temperature module.

2.2. Thermal tolerance limits and critical habitat for Nechako white sturgeon

First, white sturgeon thermal tolerance thresholds were obtained from laboratory studies conducted at the University of British Columbia, Canada. For each early life stage (i.e., embryo, yolk-sac larvae, larvae, and juvenile), we recorded the Optimal Temperature Range (T_{optR}), Sub-optimal Temperature Range (ST_{optR}), and Critical Thermal Limit Range (CT_{LR}) based on the laboratory results. In this paper, we defined T_{optR} as the temperature range in which fish are at the highest physiological performance, ST_{optR} as the temperature range which coincides with a loss of some critical function and less than 25% mortality is recorded, and CT_{LR} as the temperature range in which more than 50% mortality occurred (Fig. 1A). In cases of missing information, we also gathered T_{optR} from the peer-reviewed literature and government documents. We then defined the thermal exposure risk (T_e) based on T_{optR} , ST_{optR} , and CT_{LR} (Table 1).

$$T_{ei} = 0, \text{ if } [T_a \dots T_b] < T_{optR} \dots \dots \dots (1)$$

$$T_{ei} = 1, \text{ if } [T_a \dots T_b] = T_{optR} \dots \dots \dots (2)$$

$$T_{ei} = 2, \text{ if } [T_a \dots T_b] = ST_{optR} \dots \dots \dots (3)$$

Table 1

White sturgeon thermal exposure (T_e) risk applied for this study, where a value above 1 indicates an elevated thermal exposure risk.

Life stage	Description	Temperature range (°C)	Thermal exposure risk (T_e)	Reference
Embryo	Temperature below optimal temperature (growth/general health condition)	<14	0	
Embryo	The optimal temperature (growth/general health condition)	14–18	1	Earhart et al. (2023)
Embryo	Sub-optimal temperature (loss of some critical function and less than 25% mortality)	>18	2	Earhart et al. (2023)
Embryo	Critical temperature (total loss of critical function and more than 50% mortality)	NA	NA	
Yolk-sac larvae	Temperature below optimal temperature (growth/general health condition)	<14	0	
Yolk-sac larvae	The optimal temperature (growth/general health condition)	14–20	1	Earhart et al. (2023)
Yolk-sac larvae	Sub-optimal temperature (loss of some critical function and less than 25% mortality)	>20	2	Earhart et al. (2023)
Yolk-sac larvae	Critical temperature (total loss of critical function and more than 50% mortality)	NA	NA	
Larvae	Temperature below optimal temperature (growth/general health condition)	<10	0	
Larvae	The optimal temperature (growth/general health condition)	10–16	1	Wang et al. (1985), Wang et al. (1987), DFO (2014), Cheung (2019)
Larvae	Sub-optimal temperature (loss of some critical function and less than 25% mortality)	>16	2	Wang et al. (1985, 1987), Hildebrand et al. (2016)
Larvae	Critical temperature (total loss of critical function and more than 50% mortality)	NA	NA	
Juvenile	Temperature below optimal temperature (growth/general health condition)	<18	0	
Juvenile	The optimal temperature	15–18	1	DFO (2014), Penman (2021),

Table 1 (continued)

Life stage	Description	Temperature range (°C)	Thermal exposure risk (T_e)	Reference
Juvenile	(growth/general health condition) Sub-optimal temperature (loss of some critical function and less than 25% mortality)	>18	2	Penman et al. (2023) DFO (2014), Penman (2021), Penman et al. (2023)
Juvenile	Critical temperature (total loss of critical function and more than 50% mortality)	NA	NA	

$$T_{ei} = 3, \text{ if } [T_a \dots T_b] = CT_{LR} \dots \dots \dots \quad (4a)$$

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

Second, we identified geo-referenced Critical Habitats (CHs) for white sturgeon in the Nechako River based on recovery strategies for species listed under Canada’s Species at Risk Act (SARA) (SARA, 2002) (Fig. 1B, Table 2). The CHs are habitats that are necessary for the survival or recovery of species and that are recognized under the species’ critical habitats for recovery and action plans with the specific significance of the species to each life stage (SARA, 2002).

2.3. Analysis

2.3.1. Spatial predicted temperature evaluation

We tested the CEQUEAU model outputs robustness by comparing the predicted temperature with the observed temperature of two stations, i. e., Nautely and Vanderhoof stations. For each station, we examined the correlation between historical temperature records publicly available at https://climate.weather.gc.ca/historical_data/search_historic_data_e.html and spatially predicted temperature. We then computed the Root Mean Square Error (RMSE), R-squared (R^2) values and percent bias.

2.3.2. Thermal exposure risk

We analysed the life stage thermal exposure risk’s (T_e) Spatio-temporal pattern for the Nechako River from 1980 to 2019. We focused on five months when temperatures are at their highest, i.e., May to September. These months cover the most important time of the year for all white sturgeon early life stages (Cadden, 2000; Triton, 2006) and

Table 2

White sturgeon critical habitats and their significance related to the life stage within the Nechako River system based on the Species at Risk Act (SARA).

Critical Habitat Name	Waterbody	Significant	Life stage
Culvert Hole	Nechako River	Feeding, rearing	Juvenile
Finamore	Nechako River	Feeding, rearing	Juvenile
Fraser Lake	Nautley River	Feeding	Juvenile
Keilor’s Point	Nechako River	Feeding, rearing	Juvenile
Leduc Creek Confluence	Nechako River	Feeding	Juvenile
Powerline	Nechako River	Feeding, rearing	Juvenile
Sinkut River Confluence	Nechako River	Rearing, feeding	Juvenile
Vanderhoof Braided Section	Nechako River	Spawning, rearing, feeding	Yolk-sac larvae, Larvae

include the months when the STMP program is active. We estimated the daily T_e in each $0.005^\circ \times 0.005^\circ$ cell that was calculated from simulated daily temperature data tmmmmm and calculated the average T_e for each decade, i.e., the 1980s (average 1980–1989), the 1990s (average 1990–1999), the 2000s (2000–2009) and the 2010s (average 2010–2019) since the beginning of the STMP program. We then estimated the T_e percentage changes for each life stage in the 1990s, 2000s, and 2010s relative to the 1980s. Also, to evaluate the effect of prolonged lethal temperature and combine temperature and its duration in our analysis, we calculated the cumulative heat degree-days (CHDD °C days) (Neuheimer and Taggart, 2007; Wuenschel et al., 2012) for the days when STMP was active (i.e., between July 20 and August 20). CHDD measures the degree of heating based on the mean daily temperature above the upper optimal temperature range threshold which is calculated as follows.

$$CHDD > T_b = \sum_{d=1}^{d=n} (T_b - T_{di}) \dots\dots\dots (4b)$$

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 further discuss the potential threat and opportunity for white sturgeon recovery and the importance of a holistic management program with much consideration for all species of the Nechako River system. We ran all models and analyses using Matlab (MATLAB, and Statistics Toolbox, 2018a) and the statistical programming software R (R Core Team, 2020).

3. Results

3.1. CEQUEAU model evaluation

We found a significant and positive linear relationship between the historical temperature records in the two stations and the predicted temperature from the CEQUEAU model. For the Nautley station $r = .93$, $p < .001$ and for the Vanderhoof station $r = 0.97$, $p < .001$. For the Nautley station $r = 0.93$, $p < .001$ and for the Vanderhoof station $r = 0.97$, $p < .001$. The RMSE values for each station were 1.86 °C and 1.23 °C, respectively (Fig. 2).

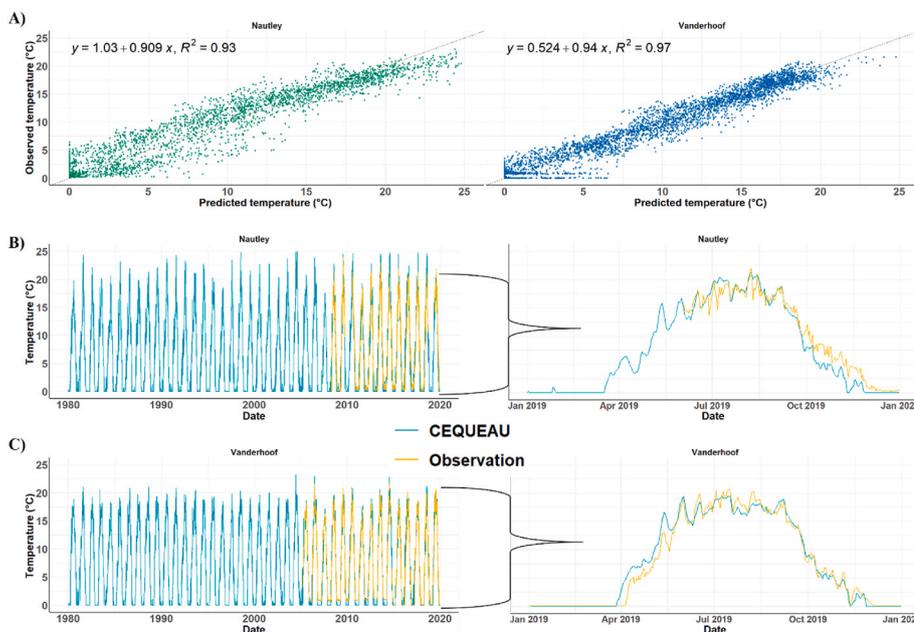


Fig. 2. The relationship between predicted temperature from the CEQUEAU model and the historical temperature data from https://climate.weather.gc.ca/historical_data/search_historic_data_e.html for Nautley and Vanderhoof stations. A) Scatter plots of predicted and observed temperature, with the 1:1 line indicated for comparison. B) and C) Time series of CEQUEAU predicted temperature (blue) and historical observed temperature data (yellow) for these stations, with a 2019 focused plot. In the right panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. Thermal exposure risk of Nechako white sturgeon in the 1980s

3.2.1. Thermal exposure risk across the Nechako river

We analysed the thermal exposure risk (T_e) of Nechako white sturgeon in the 1980s when the STMP program started, where a value above 1 indicates an elevated thermal exposure risk. The results show that across the Nechako River for all life stages (Table 3), average T_e was below 1 (0.02–0.99) for May and June. In July, results indicated that the T_e range was between 0.71 and 0.94 for embryos, yolk-sac larvae and juveniles while T_e was 1.37 ± 0.23 (Mean \pm SD) for Larvae. However, in August, the average T_e was above 1 across all life stages. For September, we estimated T_e lower than 0.5 for embryos, yolk-sac larvae and juveniles while T_e was 1.12 ± 0.05 for Larvae.

3.2.2. Thermal exposure risk in critical habitat area

We evaluated the current white sturgeon habitats on Nechako River, identified as being critical under the Canadian Species at Risk Act (S.C. 2002, c. 29). In total, eight geospatial habitat areas were named critical

Table 3

Average thermal exposure risk for different early life stages of white sturgeon in the 1980s for May to September across the Nechako River.

Life stage	Month	Thermal exposure risk (T_e)
Embryo	May	0.06 \pm 0.04
Yolk-sac larvae	May	0.06 \pm 0.04
Larvae	May	0.45 \pm 0.21
Juvenile	May	0.04 \pm 0.03
Embryo	June	0.30 \pm 0.20
Yolk-sac larvae	June	0.29 \pm 0.18
Larvae	June	0.99 \pm 0.20
Juvenile	June	0.20 \pm 0.17
Embryo	July	0.94 \pm 0.17
Yolk-sac larvae	July	0.85 \pm 0.13
Larvae	July	1.37 \pm 0.23
Juvenile	July	0.71 \pm 0.32
Embryo	August	1.17 \pm 0.18
Yolk-sac larvae	August	1.03 \pm 0.08
Larvae	August	1.68 \pm 0.14
Juvenile	August	1.14 \pm 0.19
Embryo	September	0.44 \pm 0.03
Yolk-sac larvae	September	0.41 \pm 0.04
Larvae	September	1.12 \pm 0.05
Juvenile	September	0.34 \pm 0.04

(Table 2). Overall, for all critical habitats, T_e was above 0.5 for July and August when the STMP program was active compared to other months (May, June, September and October) where T_e was lower than 0.5.

Specifically, our analysis shows the average T_e in the 1980s for the Vanderhoof Braided section area (Fig. 3). The area is recognized as the only known habitat area for spawning and rearing of white sturgeon's early life stages (i.e., embryo, yolk-sac larvae, and larvae) where T_e values of 1.10 ± 0.01 and 1.66 ± 0.01 were calculated for embryo and larvae, respectively while T_e was below 1 for yolk-sac larvae in July. In August, all life stages T_e are above 1 with the highest T_e recorded for larvae (1.80 ± 0.02).

The juvenile life stages of white sturgeon in the Nechako River system use seven critical habitats for feeding and rearing (Table 2). Our

results show that the average T_e in Fraser Lake for May, June and September are the lowest with T_e values below 0.5 in comparison to other juvenile critical habitats in the Nechako River (Fig. 3). However, for the STMP months, we recorded the highest T_e in Keilor's point habitat area (1.14 ± 0.02) in July while in August T_e was the highest at 1.34 ± 0.12 .

3.3. Percentage changes in thermal exposure risk relative to the 1980s

3.3.1. Percentage changes in thermal exposure risk in recent decades across the Nechako river

Generally, our approach shows an increase in percentage change in thermal exposure risk (T_e) across the Nechako River in the 2010s

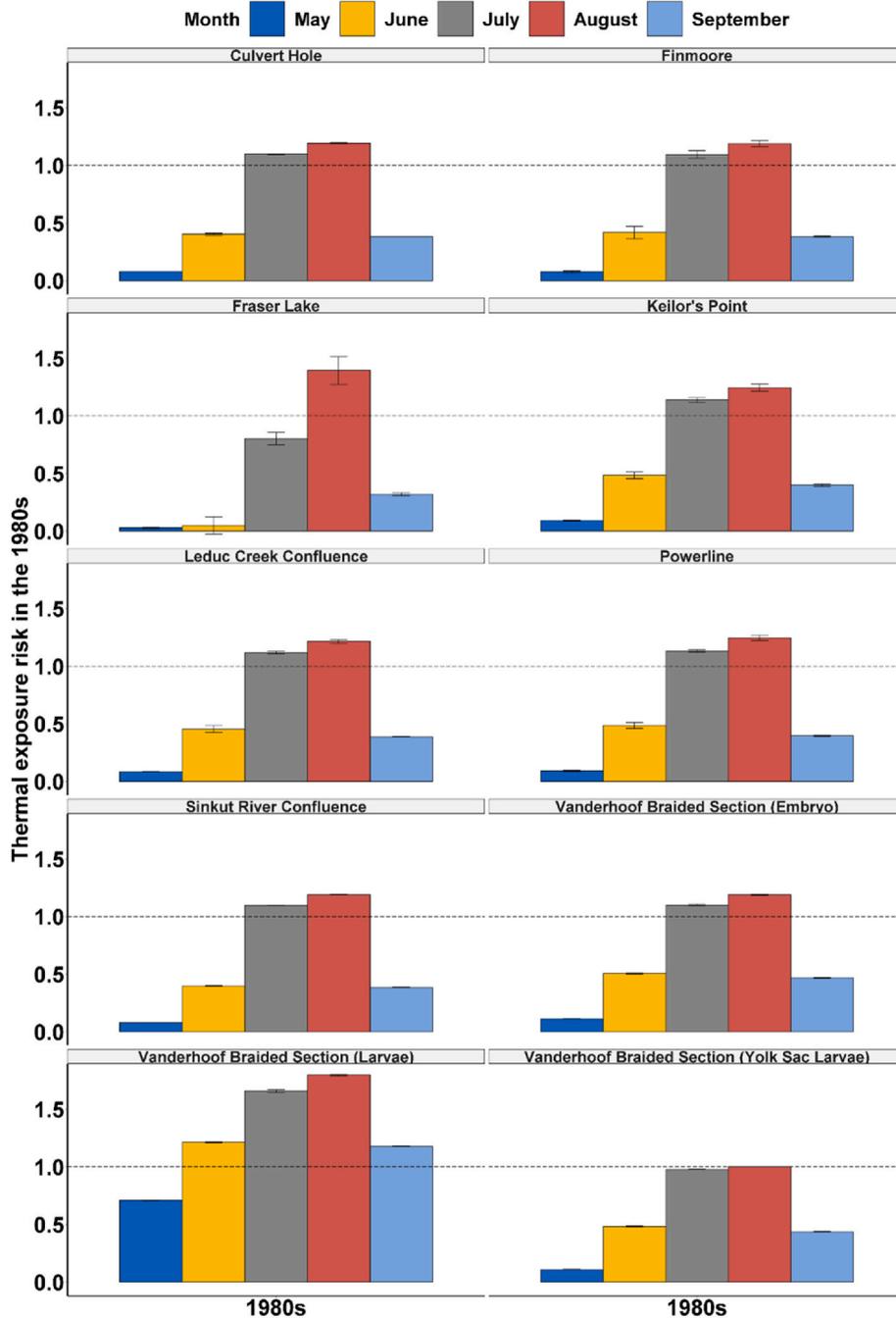


Fig. 3. Nechako River white sturgeon early life stages (embryo, yolk-sac larvae, larvae and juvenile) critical habitats thermal exposure risk for the 1980s (average 1980–1989) for May to September. Vanderhoof Braided Section is used by embryos, yolk-sac larvae and larvae while other habitats are used by the juvenile. The Longdash line indicated a thermal exposure risk of 1.

relative to the 1980s. This increase was apparent in July and August when the STMP program was active (Fig. 4). However, we found a decrease in the T_e for all life stages in the same timeframe for May and June.

Specifically, for the embryo life stage, results show a steady increase in T_e over the months analysed in the 1990s relative to the 1980s (Fig. 4A). We estimated a decrease in T_e for the May ($33.6\% \pm 29$; Mean \pm SD), June ($29.6\% \pm 21$) and July ($9.8\% \pm 3$) respectively (Fig. 4A). While for the same timeframe in August and September, T_e was observed to increase by $2.6\% \pm 2$ and $51\% \pm 4$, respectively. In the 2000s, we found that T_e increased in June ($18.6\% \pm 55$) and decreased ranges from 0.4% to 57% in May, July, August and September. In contrast, we noticed an increase in T_e for all months of the 2010s relative to the 1980s ranging from 4.6% in May to 33.6% in September.

White sturgeon's yolk-sac larvae life stage in the Nechako River experienced a similar thermal exposure as the embryo stage (Fig. 4B). Our analysis indicates that relative to the 1980s, T_e in the 1990s decreased with a range of 7.6%–30% in May, June and July. Nevertheless, increases of $2.2\% \pm 4$ and $47.8\% \pm 3$ were recorded for August and September, respectively. In the 2000s, the T_e decreased substantially in May and September by $54\% \pm 34$ and $13.4\% \pm 3$ respectively. However, an increase of $17.8\% \pm 54$ was recorded for June. For the STMP months, a minimal decrease ($0.7\% \pm 8$ - July) and increase ($0.1\% \pm 2$ - August) were recorded. Whereas in the 2010s relative to the 1980s, T_e increased for all months with the lowest increase estimated for June ($1.2\% \pm 62$) and the highest increase in September ($23.2\% \pm 4$).

Our results estimated a considerable decrease in percentage change of T_e in the 1990s for the larvae life stage in May ($22.0\% \pm 17$) and June ($14.8\% \pm 6$) while an increase of $8.4\% \pm 1$ was recorded for September (Fig. 4C). Also, in the 2000s relative to the 1980s, results show that T_e decreased considerably in May ($34.7\% \pm 20$) and September ($5.7\% \pm 2$). In contrast, for the 2010s, a decrease in T_e was estimated for May ($11.5\% \pm 21$) and June ($1.9\% \pm 29$) while an increase was estimated in August ($2.8\% \pm 1$) and September ($4.1\% \pm 1$).

For the juvenile stage, we found that T_e decreased noticeably in the 1990s relative to the 1980s by $45.2\% \pm 25$, $21.4\% \pm 47$ and $24.3\% \pm 22$ for May, June, and July, respectively (Fig. 4D). However, a considerable increase of $46.3\% \pm 8$ was estimated in September. In the 2000s, results show that T_e decreased in May ($87.7\% \pm 20$), July ($12.5\% \pm 24$), August ($3.4\% \pm 2$), and September ($22.6\% \pm 6$) while an increase of $17.1\% \pm 66$ for June was estimated. In contrast, during the 2010s, a decrease was only estimated in May ($12.2\% \pm 33$), while an increase in thermal exposure was estimated for June ($6.3\% \pm 72$), July ($25.8\% \pm 31$), August ($5.8\% \pm 4$) and September ($26.1\% \pm 3$).

3.3.2. Percentage changes in thermal exposure risk in white sturgeon critical habitat

Our results show that the T_e of the Vanderhoof Braided section area

(habitat used for spawning and rearing of the embryo, yolk-sac larvae, and larvae life stages) has increased substantially across all time frames relative to the 1980s, particularly in the 2010s (Figs. 5 and 6, Figs. S1–5). In the 1990s, T_e increased by $6.6\% \pm 1$ and $53.8\% \pm 1$ for August and September, respectively, while a decrease was estimated for June ($25.0\% \pm 1$) and July ($8.7\% \pm 0.2$). However, in the 2000s, August recorded a noticeable increase in T_e with $23.0\% \pm 2$, compared to a decrease of $13.5\% \pm 1$ and $14.0\% \pm 1$ for May and September. In contrast, T_e in the 2010s increased significantly in June ($7.8\% \pm 0.2$), July ($9.3\% \pm 0.4$), August ($7.6\% \pm 1$), September ($40.6\% \pm 1$) and decreased in May ($0.2\% \pm 2$).

Percentage change in T_e of white sturgeon yolk-sac larvae in Vanderhoof Braided section area in the 1990s relative to the 1980s decreased by $26.5\% \pm 1$ and $8.7\% \pm 0.1$ for June and July while an increase of $47.5\% \pm 0.4$ was recorded for September. In the 2000s, our results show that T_e decreased noticeably in May and September by $11.0\% \pm 2$ and $16.6\% \pm 1$, respectively, while an increase was estimated at $17.8\% \pm 1$ for June. In comparison to the 2010s, T_e decreased in May ($6.0\% \pm 2$) and June ($4.5\% \pm 0.5$) while an increase of $28.2\% \pm 1$ was estimated in September.

For the larvae stages, the Vanderhoof Braided section area T_e decreased in May, June, and July by $18.1\% \pm 0.4$, $10.0\% \pm 0.3$ and $6.7\% \pm 0.2$ respectively in the 1990s and increased by $7.5\% \pm 0.3$ in September within the same time frame relative to the 1980s. However, in the 2000s, our results show a decrease in T_e for all months with the lowest in July ($2.1\% \pm 0.5$) and the highest in May ($28.8\% \pm 01$). In the 2010s relative to the 1980s, the percentage change in T_e decreased considerably by $21.6\% \pm 0.1$ for May while a minimal increase of 4% in T_e was estimated for August and September.

In the 1990s and 2000s, in all juvenile critical habitats except Fraser Lake, our results indicated a similar pattern in percentage changes in T_e . In the 1990s relative to the 1980s, we estimated a substantial decline in T_e for May (lowest 23%- Keilor's Point and highest 37%-Finmoore), June (30%-Sinkut River Confluence and 34%-Leduc Creek Confluence), and July (9%-Powerline and 15%-Sinkut River Confluence) while a considerable increase was estimated in September (34%-Keilor's Point and 39%-Sinkut River Confluence). For Fraser Lake, we estimated a decline in T_e in May (33%) and July (7%) while an increase in T_e was estimated for June (46%) and September (45%). For the 2000s, a substantial decline in T_e was estimated for May (46%-Keilor's Point and 60%-Sinkut River Confluence) and July (7%-Powerline and 9%-Finmoore).

For the 2000s, a decline in T_e was estimated for May (46%-Keilor's Point and 60%-Sinkut River Confluence), July (7%-Powerline and 9%-Finmoore) and August (2%-Finmoore and 3% Keilor's Point) while an increase in exposure was estimated for June (16%- Powerline and 29% Sinkut River Confluence). In Fraser Lake, we estimated a considerable decline in May (100%) and September (30%) and an increase in June

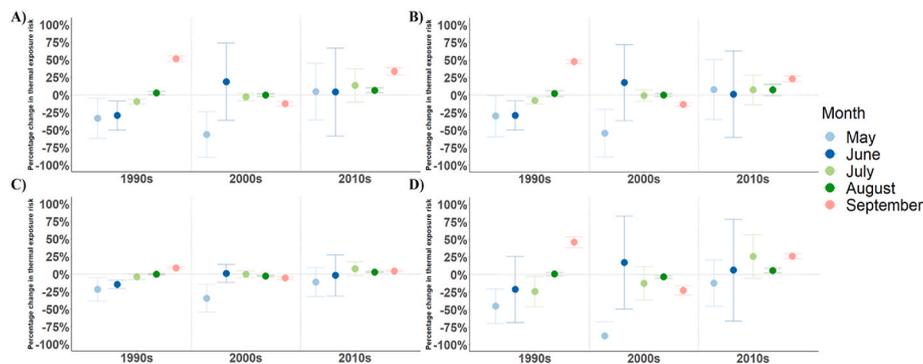


Fig. 4. The percentage change in thermal exposure risk for Nechako River white sturgeon early life stages in the 1990s (average 1990–1999), 2000s (average 2000–2009), and 2010s (average 2010–2010) relative to 1980s (average 1980–1989). A) Embryo B) Yolk-sac larvae C) Larvae D) Juvenile). The Dash line indicated a percentage change in thermal exposure risk of 0%.

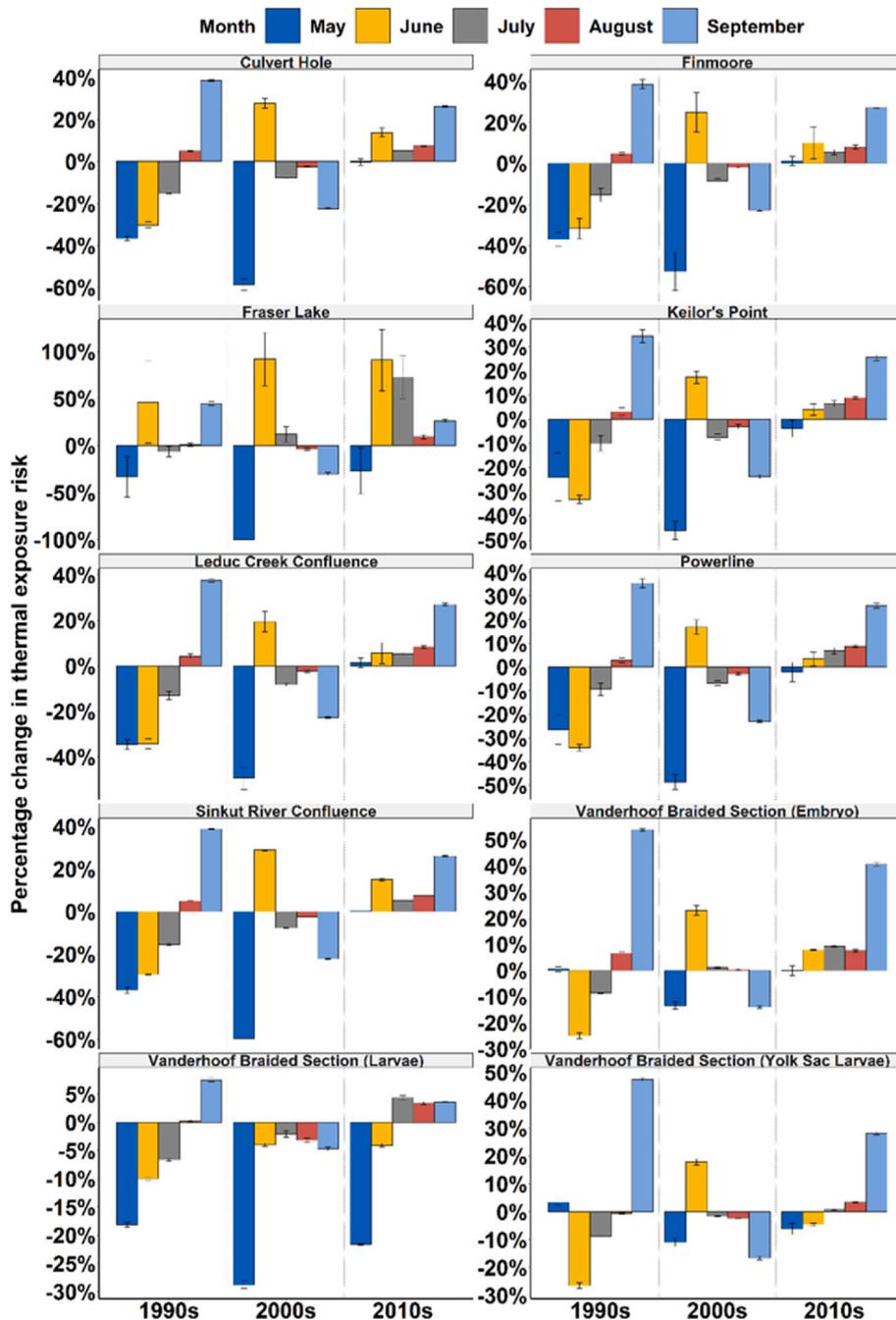


Fig. 5. The percentage change in thermal exposure risk of critical habitat areas of Nechako River white sturgeon early life stages in the 1990s (average 1990–1999), 2000s (average 2000–2009) and 2010s (average 2010–2019) relative to 1980s (average 1980–1989). Vanderhoof Braided Section is used by embryos, yolk-sac larvae and larvae while other habitats are used by the juvenile.

(91%) and July (12%). However, in the 2010s relative to the 1980s, we estimated an increase in percentage change in T_e for June (4%-Keilor's Point and 90% Fraser Lake), July (5%-Culvert Hole and 72%-Fraser Lake), August (7%-Culvert Hole and 9%-Fraser Lake) and September (26%-Keilor's Point and 27%-Finmoore) while a decline in May (0.3%-Culvert Hole and 27%-Fraser Lake).

3.4. Cumulative heat degree days above optimal temperatures for Nechako white sturgeon in critical habitat areas

We calculated the cumulative heat degree days (CHDD) for each life stage above the upper optimal endpoint of the temperature threshold. Specifically, we used 18 °C for embryos and juveniles (CHDD>18), 20 °C

for yolk-sac larvae (CHDD > 20), and 16 °C for larvae (CHDD > 16) since these are the upper limits of the optimal temperature (see Table 1).

Our results show that the CHDD > 18 for the Vanderhoof Braided Section habitat area where the embryo stage is hatched and reared has remained steady between 52 °C-days and 68 °C-days for all timeframe (i. e., the 1980s, 1990s, 2000s and 2010s) (Fig. 7). For the yolk-sac larvae in the same habitat, we estimated the lowest CHDD value ranging from 0.1 °C-days to 3.5 °C-days (CHDD>20) over all the periods in this study. The juvenile life stage uses a wider range of habitats than other early life stages. Our results indicated that Fraser Lake has been the hottest habitat for white sturgeon, especially in the 2010s. CHDD increased from 366 °C-days in the 1980s to 474 °C-days in the 1990s. However, a decrease of 741 °C-days was achieved in the 2000s, which increased

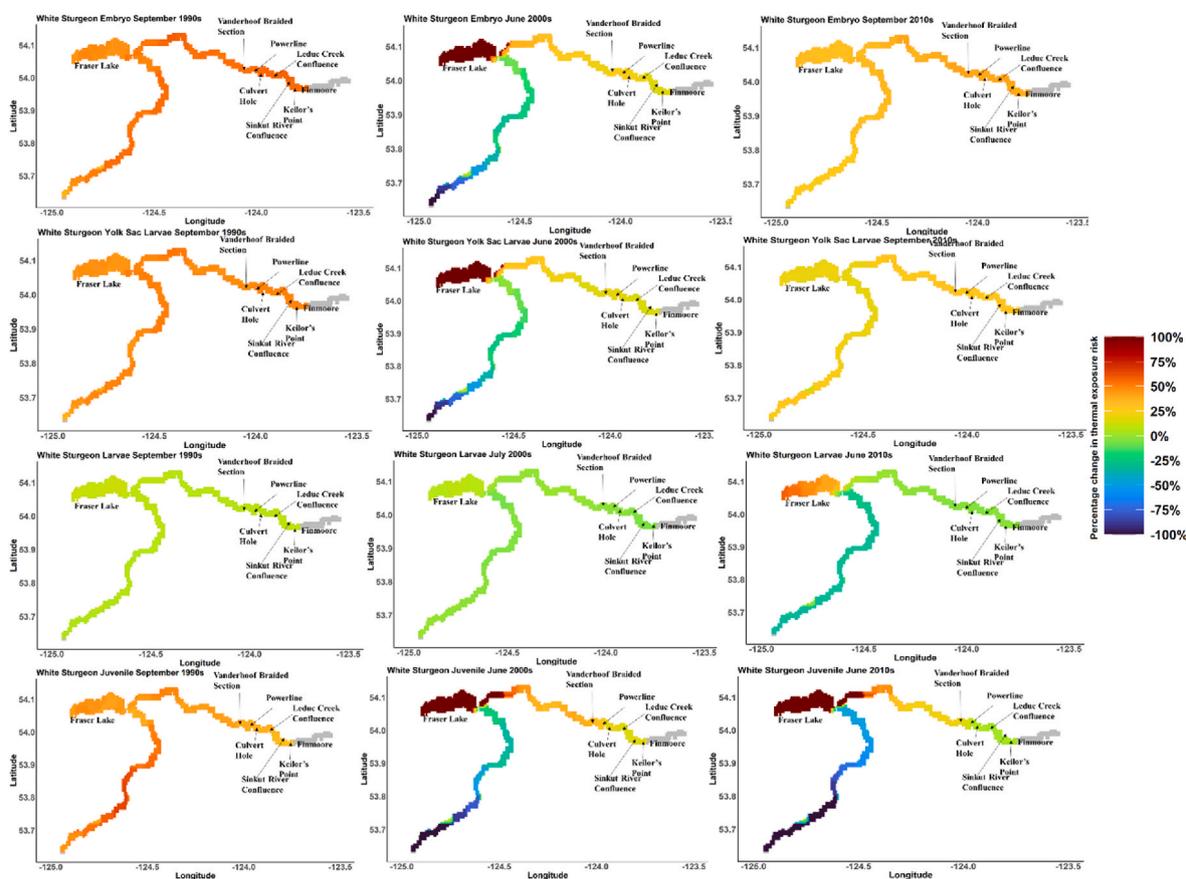


Fig. 6. Spatial map of thermal exposure risk percentage change for Nechako River white sturgeon early life stages (embryo, yolk-sac larvae, larvae and juvenile) in the 1990s (average 1990–1999), 2000s (average 2000–2009) and 2010s (average 2010–2010) relative to 1980s (average 1980–1989) for selected months of high thermal exposure risk represent the largest changes for each decade. Cool and warm colours represent low and high thermal exposure risk, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

substantially to 34 °C-days in the 2010s.

4. Discussion

In recent years, management decisions for dams across the globe have been an important topic of discussion, especially among shareholders, including governmental and non-governmental organisations, Indigenous Nations, communities, fisheries/ecological scientists, and others (Stanley and Doyle, 2003; Lehner et al., 2011; Mims and Olden, 2013; Nguyen et al., 2018). Such discussions centre around human freshwater needs and other related activities, the ecological functional traits, species diversity, and community composition (Nilsson and Berggren, 2000; Poff and Hart, 2002; Asthana and Khare, 2022). With the integrative approach in this study, we were able to spatially explore the thermal exposure risk of the Nechako white sturgeon's early life stages downstream of the Kenney dam in the months before and during the Summer Temperature Management Program (STMP) over 40 years by combining a hydrological model and white sturgeon thermal physiological limits.

The CEQUEAU hydrological model spatially predicts water temperature across the Nechako River system. Our results show comparable projected temperature values with the observed temperature at Nautley and Vanderhoof stations. However, at the Nautley station, very high temperatures are underestimated by the model, which could also be a challenge for projected temperature values in other areas within the Nechako River. Nevertheless, this model represents a novel approach, which allows us to assess the thermal exposure risk for each life stage during white sturgeon early development across the Nechako River and specific habitats over four decades (i.e., the 1980s, 1990s, 2000s and

2010s).

Overall, our study suggests that white sturgeon's early life stages were subjected to minimal thermal exposure risk in the 1980s compared to recent decades (i.e., 1990s, 2000s, and 2010s). Here, a T_e value of 1 indicates an optimal temperature and a value above this indicates thermal exposure risk. This is evident in the low T_e that is estimated for all early life stages across the months investigated in this study. In addition, our study shows a bell-curved T_e pattern in all critical habitat areas, with the peak in July and August falling below the sub-optimal risk. This is an indication of the effectiveness of the STMP program in the 1980s when the program began. Nechako white sturgeon reach the spawning ground (i.e., the Vanderhoof area) by early May (Sykes, 2009), making that month one of the most critical in the early life stages. However, Nechako white sturgeon spawning has been reported between May and June, thus all summer months are critical for early life stages (Sykes, 2009; McAdam et al., 2018). Although a combination of factors such as sediments, water flow rate, adult population size and age structure, among other variables (Jager et al., 2002) all influence the successful recruitment of white sturgeon, the importance of limited exposure to elevated temperature cannot be overemphasised (Challenger et al., 2021).

Contrary to the 1980s, our study indicated that the STMP program, though not targeted at the Nechako white sturgeon conservation, may not be sufficient in reducing the temperature to prevent a thermal exposure risk for early life stages, which appeared especially so in the 1990s and 2010s. Across all life stages in all months, including the STMP months (i.e., July and August), our analysis shows an upward trend in thermal exposure risk compared to the 1980s. However, there was a substantial decline in T_e for white sturgeon in the 2000s with thermal

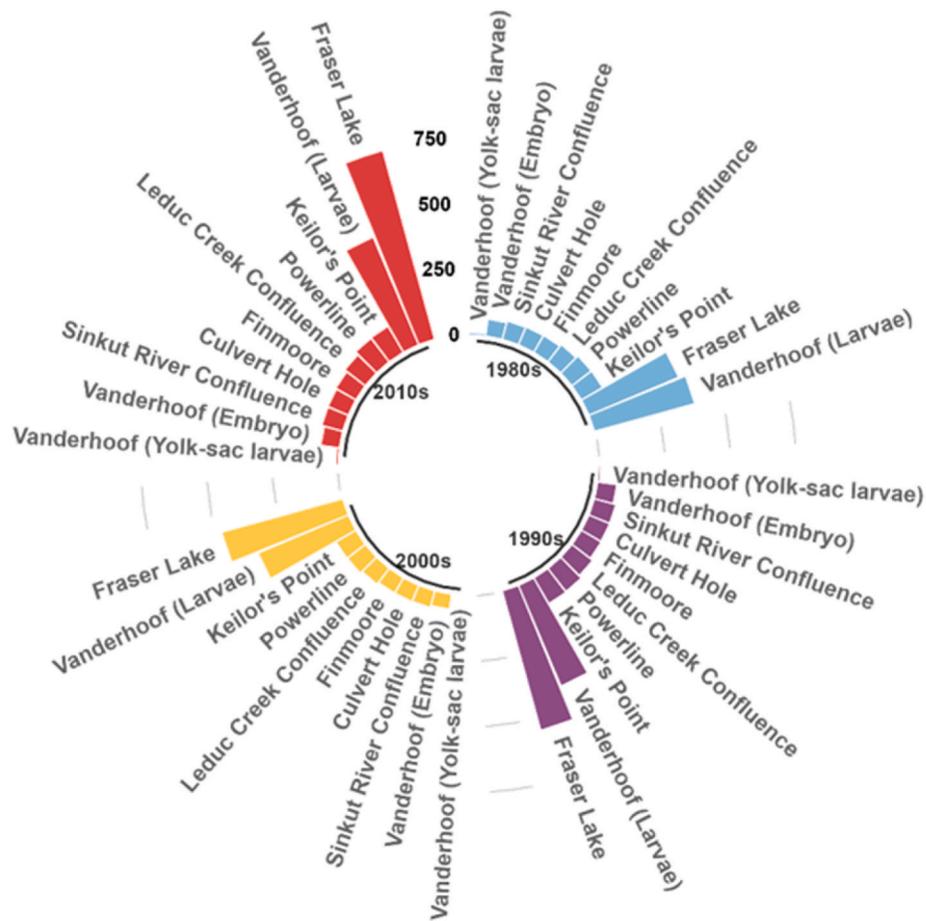


Fig. 7. Cumulative heat degree days above optimal temperature for Nechako white sturgeon early life stages in critical habitat area identified under Species at Risk Act (SARA). The Group of the colour bar represents a decade average (the 1980s, 1990s, 2000s, and 2010s). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

exposure peaking in June (embryo and yolk-sac larvae – 18%, Larvae – 1% and Juvenile-17%) and continuous decline in the remaining months. This might be due to the global climate slowdown ‘hiatus’ recorded in the 2000s (Meehl et al., 2014; Fyfe et al., 2016; Dai and Wang, 2018) rather than the unintended STMP program benefit on Nechako white sturgeon.

The continuous increase in T_e in the 2010s in all Nechako white sturgeon critical habitat areas underscores the threat to white sturgeon recruitment in the Nechako River. High temperatures above optimal limits could affect the spawning habitat quality (Counihan and Chapman, 2018), embryo and larvae survival (Jay et al., 2020) and general growth leading to recruitment failures (Jager et al., 2002; Coutant, 2004; Bates et al., 2014). Our study shows that the Vanderhoof Braided section area, the only known white sturgeon spawning habitat in the Nechako River, has faced high thermal exposure over the years. In addition, we observed a substantial increase in T_e , even though the STMP program was active in July and August. Studies have shown that water temperature within the optimal range plays a dominant effect on sturgeons including white sturgeon’s successful spawning and incubation (Deng et al., 2002; Wang et al., 1985, 1987) and subsequent embryo survival with the optimal temperature between 14 °C and 18 °C (Table 1). Above this optimal temperature range, mortality increases, and physical abnormalities are observed in the hatched embryo (Van Eenennaam et al., 2005; Wang et al., 1985).

In addition to the embryo stage, the Vanderhoof Braided section area serves as an important habitat for yolk-sac larvae and larval stages during initial growth and development. Our study highlights that the water temperature has increased significantly above the optimal value

for the life stages over the decades relative to the 1980s. For instance, we estimated a percentage change in T_e to decline by 26% in the June 1990s, however, a considerable increase of 17% was estimated for the June 2000s. Such high thermal exposure has more significant consequences for the growth and development of the white sturgeon Nechako population. Studies have shown that with optimal temperature, survival rates of yolk-sac larvae, and larvae increase significantly in the presence of gravel substrate (Boucher, 2012; Boucher et al., 2018; Crossman and Hildebrand, 2014; McAdam, 2012).

Of all juvenile white sturgeon critical habitat areas, our study shows that Fraser Lake is an important feeding area due to the lake productivity (Hume et al., 1996; Booth et al., 2001; Davidson and Decker, 2020) and was most impacted. The average T_e value has increased 2-fold in the 2010s relative to the 1980s, with the greatest increases in June (90%), July (72%), August (9%), and September (26%) when the juvenile white sturgeon moves to this habitat for feeding and overwintering (DFO, 2014) (Table 2). However, studies have shown that the juvenile movement into feeding habitats has been further altered with the changes in the flow rate due to the Kenney Dam (McAdam et al., 2005).

Until recently, the degree-day index was used extensively in agriculture and entomology (Herms, 2004; García de Cortázar-Atauri et al., 2009; Unigarro et al., 2017; Murray, 2020). Nevertheless, the degree-day index has been used to describe the relationship between temperature and growth and/or development patterns in fish (Neuheimer and Taggart, 2007; Chezik et al., 2014; Steele and Neuheimer, 2022). Our cumulative heat degree days analysis shows a progressive increase in temperature above optimal for white sturgeon’s early life stages in Nechako River despite the presence of the STMP program. This

indicates that there is an urgent need for a water management program review to include ecological benefits, particularly to Nechako resident species such as white sturgeon.

Our study is in line with previous research that explores the impact of dam systems and water management programs on aquatic ecosystems. These human-induced changes can lead to various negative consequences for the aquatic environment. For instance, they can result in increased severity of algal blooms, habitat fragmentation, altered sediment dynamics, changes in hydrology, shifts in thermal regimes, and disruptions to spawning activities (Buxton and Bradley, 2022; Chen et al., 2022; Li et al., 2022; Qiu et al., 2023; Song, 2023; Tang et al., 2022; Wang et al., 2022). These consequences pose significant threats to freshwater biodiversity and affect the capacity of ecosystems to respond positively to climate change (Cheng et al., 2022).

4.1. Study limitations

Our approach of integrating a spatially distributed hydrological model with the physiological limits of different early life stages of white sturgeon permits insight into how changes in water temperatures may impact this species across the Nechako River and in critical habitat areas. Indeed, this novel approach has provided a relatively coarse spatial resolution better than most analyses focusing on a single river point. This offers an important step in evaluating white sturgeon thermal vulnerability within the reach of the Nechako River. Nevertheless, there are limitations to our approach. Although our simulations did not produce a significant systematic bias, there is a propensity for the CEQUEAU model to underestimate the most extreme temperatures. This might be attributed to the reliability of the observed data used for the model calibration and the changes in the mechanism of production and suspension in some months (Couillard et al., 1988). Also, there may be inaccuracies in the magnitude of the sturgeons' thermal exposure because of the daily timestep temperature outputs of the model. Sturgeons are known to have a high degree of thermal plasticity (Bugg et al., 2020; Penman, 2021; Penman et al., 2023), where thermal tolerance increases with acclimation temperature. This could only be nested in our integrative approach with an hourly time-step hydrological model. The role of thermal acclimation needs to be investigated in more detail and may alter the T_e values in this study.

5. Conclusion

In this study, using a hydrological model and Nechako white sturgeon life stage-specific thermal limits, we explored the influence of water release on hydrothermal impacts associated with a water management program. Our study highlights that water release management to maintain water temperature below 20 °C from July 20 – August 20 might not be sufficient to ensure optimal temperatures for white sturgeon's early life stages, particularly if those earliest life stages occur during this time. It also underscores the necessity to re-evaluate the STMP management program. Hence, it is essential to develop a more comprehensive water management program that meets the resident's and other migratory fish species' requirements, particularly with the current concerns about climate change impacts on the Nechako River. Regional climate projections have shown that mean temperature might increase by ca. 2 °C by the 2050s (Picketts et al., 2017). This would have a major consequence on the Nechako River biotic community. Thus, understanding the possible impacts of the STMP management program on the thermal physiological limit of white sturgeon under climate change is imperative to the future recovery of the species.

CRedit author statement

Conceptualization: Muhammed A. Oyinola, Andre St-Hilaire. Methodology: Muhammed A. Oyinola, Mostafa Khorsandi, Rachael Penman, Madison L. Earhart. Validation: Muhammed A. Oyinola, Andre

St-Hilaire, Colin J Brauner. Formal analysis: Muhammed A. Oyinola. Data Curation: Muhammed A. Oyinola, Mostafa Khorsandi. Writing Original Draft: Muhammed A. Oyinola. Writing - Review & Editing: Muhammed A. Oyinola, Mostafa Khorsandi, Rachael Penman, Madison L. Earhart, Richard Arsenault, Colin J Brauner, Andre St-Hilaire. Visualization: Muhammed A. Oyinola. Funding acquisition: Andre St-Hilaire.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The data that support the findings of this study are openly available at <https://doi.org/10.5683/SP3/EJAVVQ>.

Acknowledgements

We would like to thank the two anonymous reviewers for their suggestions and comments. This work was funded by the Canadian Natural Sciences and Engineering Research Council (NSERC) and Rio Tinto as part of a Collaborative Research and Development grant (Grant 18 Number: CRDPJ 523640-18).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2023.103682>.

References

- Abram, P.K., Boivin, G., Moiroux, J., Brodeur, J., 2017. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. *Biol. Rev.* 92, 1859–1876.
- Abidi, O., St-Hilaire, A., Ouarda, T.B., Charron, C., Boyer, C., Daigle, A., 2022. Regional thermal analysis approach: a management tool for predicting water temperature metrics relevant for thermal fish habitat. *Ecol. Inf.* 70, 101692.
- Ahmad, S.K., Hossain, F., Holtgrieve, G.W., Pavelsky, T., Galelli, S., 2021. Predicting the likely thermal impact of current and future dams around the world. *Earth's Future* 9 (10), e2020EF001916.
- Angilletta Jr., M.J., Angilletta, M.J., 2009. *Thermal Adaptation: a Theoretical and Empirical Synthesis*.
- Asthana, B., Khare, D., 2022. Dams and the Environmental Issues. *Recent Advances in Dam Engineering*. Springer, pp. 339–354.
- Bates, L., Boucher, M., Shrimpton, J., 2014. Effect of temperature and substrate on whole body cortisol and size of larval white sturgeon (*Acipenser transmontanus* Richardson, 1836). *J. Appl. Ichthyol.* 30, 1259–1263.
- Biro, P.A., Post, J.R., Booth, D.J., 2007. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proc. Natl. Acad. Sci. USA* 104, 9715–9719.
- Booth, B.P., Bio, R., Federation, C.N., 2001. *Fraser Lake Important Bird Area Conservation Plan*. Ca. Nature Fed., Bird Studies Can., Fed of BC Naturalists. Wild Bird Trust BC.
- Boucher, M.A., Baker, D., Brauner, C., Shrimpton, J., 2018. The effect of substrate rearing on growth, aerobic scope and physiology of larval white sturgeon *Acipenser transmontanus*. *J. Fish. Biol.* 92 (6), 1731, 174.
- Boucher, M.A., 2012. *The Effect of Substrate Rearing on the Growth, Development, and Survival of Larval White Sturgeon (Acipenser transmontanus) during Early Ontogeny*. University of Northern British Columbia (Canada).
- Boucher, M.A., McAdam, S.O., Shrimpton, J.M., 2014. The effect of temperature and substrate on the growth, development and survival of larval white sturgeon. *Aquaculture* 430, 139–148.
- Bradford, M.J., Irvine, J.R., 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. *Can. J. Fish. Aquat. Sci.* 57, 13–16.
- Bugg, W.S., Yoon, G.R., Schoen, A.N., Laluk, A., Brandt, C., Anderson, W.G., Jeffries, K. M., 2020. Effects of acclimation temperature on the thermal physiology in two geographically distinct populations of lake sturgeon (*Acipenser fulvescens*). *Conserv. Physiol.* 8, coaa087.
- Buxton, T.H., Bradley, D.N., 2022. Evolution of tributary junctions and their capacity for rearing juvenile Chinook salmon (*Oncorhynchus tshawytscha*) on a regulated river. *Ecology* 15 (8), e2463.
- Cadden, V., 2000. *Review of Historical White Sturgeon Distribution within the Nechako River Watershed*. Norcan Consulting Limited, for Ministry of Environment, Lands and Parks.
- Challenger, W., Nelson, T.C., Robichaud, D., English, K.K., Mochizuki, T., Thibault, T., 2021. *Status of White Sturgeon in the Lower Fraser River in 2020*.

- Chandesris, A., Van Looy, K., Diamond, J.S., Souchon, Y., 2019. Small dams alter thermal regimes of downstream water. *Hydrol. Earth Syst. Sci.* 23, 4509–4525.
- Charbonneau, R., Fortin, J., Morin, G., 1977. The CEQUEAU model: description and examples of its use in problems related to water resource management/Le modèle CEQUEAU: description et exemples d'utilisation dans le cadre de problèmes reliés à l'aménagement. *Hydrol. Sci. J.* 22, 193–202.
- Chen, M., You, L.-H., Zhang, L.-L., Liao, N., Song, Y., Wang, H.-W., Li, J., 2022. Mixing processes in a reservoir corresponding to different water level operations caused spatial differences during two phytoplankton bloom events. *J. Hydrol.* 612, 128139.
- Cheng, Y., Nijssen, B., Holtgrieve, G.W., Olden, J.D., 2022. Modeling the freshwater ecological response to changes in flow and thermal regimes influenced by reservoir dynamics. *J. Hydrol.* 608, 127591.
- Cheung, K., 2019. The Effects of Embryonic Incubation Temperature on Subsequent Development, Growth, and Thermal Tolerance through Early Ontogeny of White Sturgeon. University of British Columbia.
- Cheung, W.W., Frölicher, T.L., Lam, V.W., Oyinola, M.A., Reygondeau, G., Sumaila, U. R., Tai, T.C., Teh, L.C., Wabnitz, C.C., 2021. Marine high temperature extremes amplify the impacts of climate change on fish and fisheries. *Sci. Adv.* 7, eabh0895.
- Chezik, K.A., Lester, N.P., Venturelli, P.A., 2014. Fish growth and degree-days I: selecting a base temperature for a within-population study. *Can. J. Fish. Aquat. Sci.* 71, 47–55.
- COSEWIC, 2003. COSEWIC Assessment and Update Status Report on the White Sturgeon (*Acipenser transmontanus*) in Canada.
- Couillard, D., Cluis, D., Morin, G., 1988. An extension of the grid-based hydrological model CEQUEAU to suspended sediment movement through drainage basins. *Water Res.* 22, 991–999.
- Counihan, T.D., Chapman, C.G., 2018. Relating river discharge and water temperature to the recruitment of age-0 White Sturgeon (*Acipenser transmontanus* Richardson, 1836) in the Columbia River using over-dispersed catch data. *J. Appl. Ichthyol.* 34, 279–289.
- Coutant, C.C., 2004. A riparian habitat hypothesis for successful reproduction of white sturgeon. *Rev. Fish. Sci.* 12, 23–73.
- Crossman, J., Hildebrand, L., 2014. Evaluation of spawning substrate enhancement for white sturgeon in a regulated river: effects on larval retention and dispersal. *River Res. Appl.* 30 (1), 1–10.
- Dai, X.-G., Wang, P., 2018. Identifying the early 2000s hiatus associated with internal climate variability. *Sci. Rep.* 8, 1–13.
- Davidson, K.H., Decker, S., 2020. Upstream Fraser River Sockeye (*Oncorhynchus nerka*) Smolt Monitoring Feasibility Project 2019: Nautley River (Nadleh Koh) and Nearby Systems.
- Deng, X., Van Eenennaam, J.P., Doroshov, S.I., 2002. Comparison of Early Life Stages and Growth of Green and White Sturgeon, 28237, 248.
- DFO, 2014. Recovery Strategy for White Sturgeon (*Acipenser transmontanus*) in Canada. Fisheries and Oceans Canada. Species at Risk Act Recovery Strategy Series Ottawa.
- Earhart, M.L., Blanchard, T.S., Morrison, P.R., Strowbridge, N., Penman, R.J., Brauner, C. J., Schulte, P.M., Baker, D.W., 2023. Identification of upper thermal thresholds during development in the endangered Nechako white sturgeon with management implications for a regulated river. *Conserv. Physiol.* 11 (1), coad032. <https://doi.org/10.1093/conphys/coad032>.
- Edmundson, J., Mazumder, A., 2001. Linking growth of juvenile sockeye salmon to habitat temperature in Alaskan lakes. *Trans. Am. Fish. Soc.* 130 (4), 644–662.
- Fyfe, J.C., Meehl, G.A., England, M.H., Mann, M.E., Santer, B.D., Flato, G.M., Hawkins, E., Gillett, N.P., Xie, S.-P., Kosaka, Y., 2016. Making sense of the early-2000s warming slowdown. *Nat. Clim. Change* 6, 224–228.
- García de Cortázar-Atauri, I., Brisson, N., Gaudillere, J.P., 2009. Performance of several models for predicting budburst date of grapevine (*Vitis vinifera* L.). *Int. J. Biometeorol.* 53, 317–326.
- Genner, M.J., Sims, D.W., Southward, A.J., Budd, G.C., Masterson, P., Mchugh, M., Rendle, P., Southall, E.J., Wearmouth, V.J., Hawkins, S.J., 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biol.* 16, 517–527.
- Griffith, A.W., Gobler, C.J., 2020. Harmful algal blooms: a climate change co-stressor in marine and freshwater ecosystems. *Harmful Algae* 91, 101590.
- Hansen, N., 2006. The CMA evolution strategy: a comparing review. *Towards a new evolutionary computation* 75–102.
- Herns, D.A., 2004. Using Degree-Days and Plant Phenology to Predict Pest Activity. IPM (integrated pest management) of midwest landscapes. Minnesota Agricultural Experiment Station Publication St. Paul, MN, pp. 49–59.
- Hildebrand, L., Drauch Schreier, A., Lepla, K., McAdam, S., McLellan, J., Parsley, M.J., Paragamian, V., Young, S., 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. *J. Appl. Ichthyol.* 32, 261–312.
- Hume, J.M., Shortreed, K.S., Morton, K.F., 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. *Can. J. Fish. Aquat. Sci.* 53, 719–733.
- Hutchings, J.A., Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* 54, 297–309.
- Jager, H.I., Van Winkle, W., Chandler, J.A., Lepla, K.B., Bates, P., Counihan, T.D., 2002. A Simulation Study of Factors Controlling White Sturgeon Recruitment in the Snake River. American Fisheries Society Symposium, pp. 127–150.
- Jay, K.J., Crossman, J.A., Scribner, K.T., 2020. Temperature affects transition timing and phenotype between key developmental stages in white sturgeon *Acipenser transmontanus* yolk-sac larvae. *Environ. Biol. Fish.* 103, 1149–1162.
- Johnston, C., Maceina, M., 2009. Fish assemblage shifts and species declines in Alabama, USA streams. *Ecol. Freshw. Fish* 18, 33–40.
- Jones, M.C., Cheung, W.W., 2015. Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES J. Mar. Sci.* 72 (3), 741–752.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Khorsandi, M., St-Hilaire, A., Arsenault, R., 2022. Multisite calibration of a semi-distributed hydrologic and thermal model in a large Canadian watershed. *Hydrol. Sci. J.* 1–28.
- Larabi, S., Schnorbus, M.A., Zwiers, F., 2022. A coupled streamflow and water temperature (VIC-RBM-CE-QUAL-W2) model for the Nechako Reservoir. *J. Hydrol. Reg. Stud.* 44, 101237.
- Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Front. Ecol. Environ.* 9, 494–502.
- Lessard, J.L., Hayes, D.B., 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Res. Appl.* 19, 721–732.
- Li, Y., Fu, X., Chu, X., Liu, S., 2022. A conflict resolution model for reservoir operation in dry seasons under channel alteration. *J. Hydrol.* 610, 127899.
- Macdonald, J., Morrison, J., Patterson, D., 2012. The efficacy of reservoir flow regulation for cooling migration temperature for sockeye salmon in the Nechako River watershed of British Columbia. *North Am. J. Fish. Manag.* 32, 415–427.
- Maheu, A., St-Hilaire, A., Caissie, D., El-Jabi, N., Bourque, G., Boisclair, D., 2016a. A regional analysis of the impact of dams on water temperature in medium-size rivers in eastern Canada. *Can. J. Fish. Aquat. Sci.* 73, 1885–1897.
- Maheu, A., St-Hilaire, A., Caissie, D., El-Jabi, N., 2016b. Understanding the thermal regime of rivers influenced by small and medium size dams in Eastern Canada. *River Res. Appl.* 32, 2032–2044.
- MATLAB, and Statistics Toolbox 2018a. The MathWorks, Inc., Natick, Massachusetts, United States.
- McAdam, D.S.O., 2012. Diagnosing Causes of White Sturgeon (*Acipenser transmontanus*) Recruitment Failure and the Importance of Substrate Condition to Yolk Sac Larvae Survival. University of British Columbia, Vancouver, BC.
- McAdam, S.O., Crossman, J.A., Williamson, C., St-Onge, I., Dion, R., Manny, B.A., Gessner, J., 2018. If you build it, will they come? Spawning habitat remediation for sturgeon. *J. Appl. Ichthyol.* 34, 258–278.
- McAdam, S.O., Walters, C.J., Nistor, C., 2005. Linkages between white sturgeon recruitment and altered bed substrates in the Nechako River, Canada. *Trans. Am. Fish. Soc.* 134, 1448–1456.
- Meehl, G.A., Teng, H., Arblaster, J.M., 2014. Climate model simulations of the observed early-2000s hiatus of global warming. *Nat. Clim. Change* 4, 898–902.
- Michie, L.E., Hitchcock, J.N., Thiem, J.D., Boys, C.A., Mitrovic, S.M., 2020. The effect of varied dam release mechanisms and storage volume on downstream river thermal regimes. *Limnologia* 81, 125760.
- Mims, M.C., Olden, J.D., 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshw. Biol.* 58, 50–62.
- Morash, A.J., Speers-Roesch, B., Andrew, S., Currie, S., 2021. The physiological ups and downs of thermal variability in temperate freshwater ecosystems. *J. Fish. Biol.* 98 (6), 1524–1535.
- Murray, M., 2020. Using Degree Days to Time Treatments for Insect Pests.
- Neuheimer, A.B., Taggart, C.T., 2007. The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci.* 64, 375–385.
- Nguyen, T.H.T., Everaert, G., Boets, P., Forio, M.A.E., Bennetsen, E., Volk, M., Hoang, T. H.T., Goethals, P.L., 2018. Modelling tools to analyze and assess the ecological impact of hydropower dams. *Water* 10, 259.
- Nilsson, C., Berggren, K., 2000. Alterations of riparian ecosystems caused by river regulation: dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. *Bioscience* 50, 783–792.
- Olden, J.D., Naiman, R.J., 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshw. Biol.* 55, 86–107.
- Ouellet-Proulx, S., St-Hilaire, A., Boucher, M.-A., 2017. Water temperature ensemble forecasts: implementation using the CEQUEAU model on two contrasted river systems. *Water* 9, 457.
- Pauly, D., Palomares, M.-L., 2005. Fishing down marine food web: it is far more pervasive than we thought. *Bull. Mar. Sci.* 76, 197–212.
- Peck, L.S., 2016. A cold limit to adaptation in the sea. *Trends Ecol. Evol.* 31, 13–26.
- Penman, R., 2021. The Effects of Temperature Acclimation and Heating Rate on the Thermal Tolerance of Juvenile White Sturgeon (*Acipenser transmontanus*). University of British Columbia.
- Penman, R.J., Bugg, W., Rost-Komiya, B., Earhart, M.L., Brauner, C.J., 2023. Slow heating rates increase thermal tolerance and alter mRNA HSP expression in juvenile white sturgeon (*Acipenser transmontanus*). *J. Therm. Biol.* 103599.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308 (5730), 1912–1915.
- Picketts, I.M., Parkes, M.W., Déry, S.J., 2017. Climate change and resource development impacts in watersheds: insights from the Nechako River Basin, Canada. *Can. Geogr./Le Géogr. Can.* 61, 196–211.
- Poff, N.L., Hart, D.D., 2002. How dams vary and why it matters for the emerging science of dam removal: an ecological classification of dams is needed to characterize how the tremendous variation in the size, operational mode, age, and number of dams in a river basin influences the potential for restoring regulated rivers via dam removal. *Bioscience* 52, 659–668.
- Pörtner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Contin. Shelf Res.* 21, 1975–1997.

- Pörtner, H.O., Langenbuch, M., Michaelidis, B., 2005. Synergistic effects of temperature extremes, hypoxia, and increases in CO₂ on marine animals: from Earth history to global change. *J. Geophys. Res.: Oceans* 110 (C9).
- Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish. Biol.* 77 (8), 1745–1779.
- Prats, J., Val, R., Dolz, J., Armengol, J., 2012. Water temperature modeling in the Lower Ebro River (Spain): heat fluxes, equilibrium temperature, and magnitude of alteration caused by reservoirs and thermal effluent. *Water Resour. Res.* 48.
- Qiu, R., Wang, D., Singh, V.P., Zhang, H., Tao, Y., Wu, J., Wang, Y., 2023. Ecological responses of spawning habitat suitability to changes in flow and thermal regimes influenced by hydropower operation. *Ecohydrology* 16 (2), e2507.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. Available online at: R Foundation for Statistical Computing, Vienna, Austria <https://www.r-project.org/>.
- Saila, S., Poyer, D., Aube, D., 2005. Small dams and habitat quality in low order streams. Wood-Pawcatuck Watershed Association, Hope Valley, RI. Retrieved from <http://www.wpwa.org>.
- SARA, 2002. Species at Risk Act: an Act Respecting the Protection of Wildlife Species at Risk in Canada.
- Schreier, A.D., Mahardja, B., May, B., 2012. Hierarchical patterns of population structure in the endangered Fraser River white sturgeon (*Acipenser transmontanus*) and implications for conservation. *Can. J. Fish. Aquat. Sci.* 69, 1968–1980.
- Seebacher, F., White, C.R., Franklin, C.E., 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Change* 5, 61–66.
- Seyedhashemi, H., Moatar, F., Vidal, J.-P., Diamond, J.S., Beaufort, A., Chandresris, A., Valette, L., 2021. Thermal signatures identify the influence of dams and ponds on stream temperature at the regional scale. *Sci. Total Environ.* 766, 142667.
- Shi, X., Sun, J., Xiao, Z., 2021. Investigation on river thermal regime under dam influence by integrating remote sensing and water temperature model. *Water* 13 (2), 133.
- Song, Y., 2023. Hydrodynamic impacts on algal blooms in reservoirs and bloom mitigation using reservoir operation strategies: a review. *J. Hydrol.*, 129375.
- Speight, M., Hunter, M., Watt, A., 2008. Insects and climate. In: Speight, M.R., Hunter, M.D., Watt, A.D. (Eds.), *Ecology of Insects Concepts and Applications*, pp. 33–60.
- Stanley, E.H., Doyle, M.W., 2003. Trading off: the ecological effects of dam removal. *Front. Ecol. Environ.* 1, 15–22.
- Steele, R.W., Neuheimer, A.B., 2022. Assessing the ability of the growing degree-day metric to explain variation in size-at-age and duration-to-moult of lobsters and crabs. *Can. J. Fish. Aquat. Sci.* 79, 850–860.
- Sykes, G., 2009. Adult White Sturgeon Monitoring-Nechako River 2008.
- Tang, C., Yan, Q., Li, W., Yang, X., Zhang, S., 2022. Impact of dam construction on the spawning grounds of the four major Chinese carps in the Three Gorges Reservoir. *J. Hydrol.* 609, 127694.
- Triton, 2006. Potential Effects of Mountain Pine Beetle on Nechako River Hydrology and White Sturgeon (2006) Environmental Consultants Ltd. Prepared for Ministry of Environment.
- Unigarro, C.A., Bermúdez, L.N., Medina, R.D., Jaramillo, Á., Flórez, C.P., 2017. Evaluation of four degree-day estimation methods in eight Colombian coffee-growing areas. *Agron. Colomb.* 35, 374–381.
- Van Eenennaam, J.P., Linares-Casenave, J., Deng, X., Doroshov, S.I., 2005. Effect of incubation temperature on green sturgeon embryos, *Acipenser medirostris*. *Environ. Biol. Fish.* 72, 145–154.
- Walters, A.W., Mandeville, C.P., Rahel, F.J., 2018. The interaction of exposure and warming tolerance determines fish species vulnerability to warming stream temperatures. *Biol. Lett.* 14 (9), 20180342.
- Wang, Y., Tao, Y., Qiu, R., Wang, D., Wu, J., 2022. A framework for assessing river thermal regime alteration: a case study of the Hanjiang River. *J. Hydrol.* 610, 127798.
- Wang, Y., Buodington, R., Doroshov, S., 1987. Influence of temperature on yolk utilization by the white sturgeon, *Acipenser transmontanus*. *J. Fish. Biol.* 30, 263–271.
- Wang, Y.L., Binkowski, F.P., Doroshov, S.I., 1985. Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. *Environ. Biol. Fish.* 14, 43–50.
- Weber, N., Bouwes, N., Pollock, M.M., Volk, C., Wheaton, J.M., Wathen, G., Wirtz, J., Jordan, C.E., 2017. Alteration of stream temperature by natural and artificial beaver dams. *PLoS One* 12, e0176313.
- White, C.R., Phillips, N.F., Seymour, R.S., 2006. The scaling and temperature dependence of vertebrate metabolism. *Biol. Lett.* 2, 125–127.
- Wuenschel, M.J., Hare, J.A., Kimball, M.E., Able, K.W., 2012. Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (*Lutjanus griseus*): a combined laboratory, field and modeling approach. *J. Exp. Mar. Biol. Ecol.* 436, 19–27.
- Zaidel, P.A., Roy, A.H., Houle, K.M., Lambert, B., Letcher, B.H., Nislow, K.H., Smith, C., 2021. Impacts of small dams on stream temperature. *Ecol. Indicat.* 120, 106878.
- Zhao, J., Li, H., Cai, X., Chen, F., Wang, L., Yu, D., 2020. Long-term (2002–2017) impacts of Danjiangkou dam on thermal regimes of downstream Han River (China) using Landsat thermal infrared imagery. *J. Hydrol.* 589, 125135.