Comparative Biochemistry and Physiology, Part A 284 (2023) 111469

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Bioenergetic consequences of repeated catch-and-release fisheries interactions on adult steelhead across a range of ecologically relevant water temperatures

Amanda L. Jeanson [a], Jamie C. Madden [a,*], Andreas Ekström [b], Andy J. Danylchuk [c], Nathan Young [d], Andrew Howarth [a], William M. Twardek [a], Ronald G. Twibell [e], Roger P. Root [e], Kyle C. Hanson [f], Steven J. Cooke [a]

[a] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada*
[b] *Department of biological and environmental sciences, University of Gothenburg, Medicinaregatan 18, 41390 Gothenburg, Sweden*
[c] *Department of Environmental Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, MA 01003, USA*
[d] *School of Sociological and Anthropological Studies, University of Ottawa, 75 Laurier Ave. E, Ottawa, Ontario K1N 6N5, Canada*
[e] *U.S. Fish and Wildlife Service, Abernathy Fish Technology Center, 1440 Abernathy Creek Road, Longview, WA 98632, USA*
[f] *U.S. Fish and Wildlife Service, Pacific Region, Fish and Aquatic Conservation, 11th Ave., Portland, OR 97232, USA*

ARTICLE INFO

Edited by Michael Hedrick

Keywords:
Recreational fishing
Fisheries management
Cardiac monitoring
Warming
Oncorhynchus mykiss

ABSTRACT

The biological consequences of catch-and-release angling have been studied for decades, yet little is known about the compounding effects of repeated recreational fisheries recaptures on the physiology and behaviour of angled fish. Using heart rate biologgers and behavioural assays, this study investigated the physiological and behavioural consequences of multiple simulated angling events (i.e., repeated stressors) on female steelhead (*Oncorhynchus mykiss*), under current (6 °C) and future (11 °C) water temperature scenarios. While steelhead in the warmer water temperature scenario demonstrated alterations in cardiac function (e.g., increases in maximum heart rate and scope of heart rate) and evidence of behavioural impairments (e.g., decreases in chase activity and landing time) over the course of two simulated angling events, cold water treated fish had negligible change. Fish subjected to two simulated angling events under warm water temperature conditions tended to demonstrate an increase in recovery time and scope for heart rate, and a decrease in resting heart rate. A second experiment was conducted to test for sex-specific differences in the heart rate response of steelhead subjected to an increase in water temperature. Females demonstrated a higher scope for heart rate when compared to males during the event and during recovery. More work is needed to better understand the interaction between multiple angling events and recovery from these events at various water temperatures, and the biological basis for sex-specific differences in cardiac function and response to challenges. This study contributes to a growing body of evidence on the effects of repeated stressors on wild fish.

1. Introduction

Repeated stressors represent inherent challenges to animals whether in captivity or in the wild (Tyack et al., 2022). When faced with a stressor animals must attempt to regain homeostasis. When a subsequent stressor is applied, especially prior to an animal fully achieving homeostasis, it is possible that allostatic load is exceeded potentially leading to serious fitness impairments or even death (Romero et al., 2009). Stressors come with bioenergetic costs (Parsons, 1994) so repeated stressors are additive and can collectively lead to reductions in energetic resources available to allocate to maintenance (e.g., immune function), growth, and reproduction (Schreck, 2010; Sokolova, 2013). The effects of repeated stressors have been explored in fish often in the context of applied issues such as repeated handling in captivity or during fisheries interactions. For example, Barton et al. (1986) revealed that multiple acute stressors collectively led to significant cumulative stressors for fish in a hatchery. In the context of fisheries interactions, fish may be captured, released, and then recaptured again which equates

* Corresponding author.
E-mail address: jamiemadden@cmail.carleton.ca (J.C. Madden).
@AmandaJeanson (A.L. Jeanson), @jamiecmadden_ (J.C. Madden), @SJC_fishy (S.J. Cooke)

https://doi.org/10.1016/j.cbpa.2023.111469
Received 5 December 2022; Received in revised form 20 June 2023; Accepted 21 June 2023
Available online 17 July 2023

to repeated stressors with associated bioenergetic costs (Watson et al., 2020).

Steelhead, the anadromous life-history type of the rainbow trout (*Oncorhynchus mykiss*), are an iteroparous salmonid often targeted by recreational anglers due to the high-quality angling experiences they provide (Morten and Branch, 2000; Kelch et al., 2006). Anglers typically fish for steelhead during their spawning migrations up rivers and often target steelhead at holding pools, where the fish congregate to rest, forage, and await ideal migratory conditions (Nelson et al., 2005; Nakamoto, 1994; Richard et al., 2014). As a result of population declines throughout their North American native range (Nakamoto, 1994; Kendall et al., 2017; Scheuerell et al., 2021), many recreational steelhead fisheries are now catch-and-release only (as a conservation strategy), meaning fish are immediately released so that they can continue their migration to spawning grounds. The catch-and-release nature of steelhead recreational fisheries, along with high catch success at holding pools, makes recapture of steelhead in short time intervals possible and even likely (Nelson et al., 2005; Twardek et al., 2018). With continued warming predicted for steelhead migration paths in North America (Keefer et al., 2018), the physiological and behavioural consequences of multiple (repeated over days) catch-and-release angling events coupled with warming waters is of interest to anglers and fisheries managers alike.

Few studies have investigated the impacts of repeated stressors on fish in the context of fisheries interactions. Cline et al. (2012) found that multiple angling events resulted in the short-term weight loss of largemouth bass (*Micropterus salmoides*). Fish lost weight for six days following multiple capture-and-release events, but later re-gained the weight (i.e., compensatory growth), and thus did not demonstrate a net weight loss at the end of the angling season. Using blue-finned mahseer (*Tor khudree*) in India, Bower et al. (2022) revealed that as many as three simulated fisheries encounters did not lead to any progressive changes in reflex impairment (accurate predictors of stress extent and mortality; Davis, 2010). This suggests that blue-finned mahseer are relatively robust to multiple capture events even in close succession. Nelson et al. (2005) evaluated the consequences of multiple recaptures on survival rates of caught and released steelhead at moderate temperatures and found that multiple angling events did not greatly impact survival rates. However, that does not preclude sublethal impacts which may be magnified by more extreme thermal conditions (Meka and McCormick, 2005). Increases in water temperature beyond the thermal optimal are a major concern for sport fishes such as steelhead (Gale et al., 2013), as warming may impair their physiological capacity to adequately handle other stressors such as those from angling interactions (Prystay et al., 2017; Wilkie et al., 1996, 1997), potentially leading to death (Holder et al., 2022).

Bioenergetics serves as a useful framework to consider how fisheries interactions, especially those involving multiple recaptures, may influence fish condition and fitness (Watson et al., 2020). Although this can be done in a modeling context (e.g., Stockwell et al., 2002; Meka and Margraf, 2007), there is also need for empirical studies. Electronic tags that measure heart rate and either transmit data (i.e., transmitters) or store data for later downloading (i.e., biologgers) are a useful tool for assessing the consequences of multiple fisheries interactions by generating data relevant to bioenergetics (Cooke et al., 2016). Changes in heart rate can serve as an indicator of stress in fish (Sopinka et al., 2016) and can provide insight on the magnitude of effects resulting from angling events (Anderson et al., 1998; Cooke et al., 2003). Unlike blood-based stress parameters (e.g., cortisol, glucose) and behavioural impairment indices, electronic tags equipped with heart rate sensors can yield assessments of a stress response at consistent time intervals for continuous, long periods (Donaldson et al., 2010). Although cardiac output (determined by stroke volume and heart rate) is a more robust indicator of energetic costs than solely heart rate (Thorarensen et al., 1996), heart rate is still considered a strong proxy of cardiac output and oxygen consumption in rainbow trout (Brodeur et al., 2001).

Using heart rate biologgers and a series of behavioural assays, we investigated the physiological and behavioural consequences of repeated stressors (simulated angling events) on hatchery-reared, free-swimming steelhead in 'cold' (~ 6 °C) and 'warm' (~ 11 °C) water treatments. We hypothesized that fish in the warm water treatment would experience greater physiological (increased heart rate) and behavioural (decreased chase activity and landing time) alterations due to repeated simulated angling events than fish in the cold water treatment. Second, we hypothesized that the recovery time and heart rate during recovery between those undergoing one vs. two simulated angling events would be significantly increased for those in the warm water treatment, but not in the cold water treatment. Finally, based on a growing body of research on sex-specific physiological alterations and mortality in salmonids when fish are exposed to environmental challenges (reviewed in Hinch et al., 2021), we hypothesized that females would be more sensitive to simulated angling events and water temperature than males demonstrated by higher values for maximum heart rate, resting heart rate and scope for heart rate during a water temperature increase event.

2. Methods

This experiment was conducted in accordance with Canadian Council on Animal Care guidelines administered by the Carleton University Animal Care Committee (Protocol #s: 110588 & 110,723).

2.1. Collection and husbandry

2.1.1. For this experiment, 72

female adult and 8 male adult (4-year-old) hatchery-reared steelhead were provided by the Abernathy Fish Technology Center in Longview, Washington, USA (mean length of 37.35 ± 4.36 cm, mean weight 580.89 ± 108.4 g). During the experiments, fish were housed in 3-m diameter flow-through fiberglass cylindrical tanks supplied with water from Abernathy Creek, and a well located on the land of the Abernathy Fish Technology Center. Water temperature in Abernathy Creek during the study period (February 2020) ranged from 5 to 7 °C, and the water temperature from the well that supplied the tanks during the study period ranged from 10.5 to 11.5 °C. Temperatures during the period for both water supplies were within, or close to the optimal temperature range of 7.8 to 11.1 °C for migration in adult steelhead (DWR and USBR 1999).

2.2. Implantation of PIT tags and heart rate biologgers

Each fish underwent surgery to implant both a heart rate biologger (DST milli HRT, 13 mm × 39.5 mm, 11.8 g; Star-Oddi, Iceland; http://www.staroddi.com/), and a passive integrated transponder (PIT) tag (for identification purposes throughout the study; Prystay et al., 2017). Fish were immobilized for surgery using TENS (transcutaneous electrical nerve simulation) unit e-gloves (Reid et al., 2019). Surgery took place on a surgery table with re-circulating water constantly flushed over the gills. Each fish received a PIT tag, and a heart rate biologger (programmed to take a heart rate reading every three minutes at 200 Hz; Prystay et al., 2017) which were placed within the body cavity via an incision of about four centimeters in the abdominal wall. The heart rate biologgers were positioned vertically immediately posterior to the pericardium and anchored to the ventral abdominal wall musculature using a 3–0 monofilament suture, and the incision was thereafter closed with three to five 3–0 monofilament sutures. Immediately after surgery, all treatment groups were housed in tanks receiving creek water, with trickling well water (to increase consistency in water chemistry across tanks). As recommended by previous studies using heart rate biologgers, fish were given ~72 h between surgery and experimental testing to provide ample time for recovery (Raby et al., 2015; Prystay et al., 2017; Brijs et al., 2019).

2.3. Experiment one: the effects of recapture on steelhead behaviour and physiology under current and predicted water temperature conditions

Sixty-four fish were divided across two replicates, and four treatment groups following surgery (Fig. 1). These groups were: 1) fish in cold water (~ 6 °C) subjected to one simulated angling event, 2) fish in cold water subjected to two simulated two angling events, 3) fish in warm water (~ 11 °C) subjected to one simulated angling event, 4) fish in warm water subjected to two simulated angling events. This group of fish consisted of 62 females and 2 males (males in group one and three). Following the ~72-h surgery recovery period, fish in the two warm water treatment groups were subjected to a water temperature increase at a rate of approximately 1 °C per hour. Temperature increases were carried out by lowering the inflow of creek water and increasing the inflow of well water until water temperatures reached between 10.5 and 11.5 °C. Fish in the two cold water temperature treatments received creek water with trickling well water during the entirety of the study.

Fish in the two temperature treatment groups were held at their respective temperatures for ~48 h following the increase in water temperature event for fish in the warm water treatment groups, after which each fish was removed from their holding tank and transferred into a 1.2 m diameter plastic pool, where they were chased for three minutes, and air exposed for 30 s to replicate the exercise and handling associated with an angling event (Kieffer, 2000; Cooke et al., 2001; Suski et al., 2004). During each chase, the number of times each fish moved into a new quadrant of the pool was counted (measuring chase activity), and the time until fish stopped swimming, representing when a fish on the line stops fighting, was also recorded (termed as landing time herein; see Prystay et al., 2017). After being air exposed, each fish was returned to their treatment group tank. Half the fish in each temperature condition were chased and air exposed again ~24 h following the first chase and air exposure, to simulate re-occurring angling events. Fish were left to recover in their treatment group tanks for ~48 h.

2.4. Experiment two: temperature increase event with females and males

A second experiment was conducted to test whether females were more sensitive to thermal change than males. Fish implanted with heart rate biologgers and PIT tags were placed in one of two identical 3-m diameter fiberglass cylindrical tanks (one housed five females and four males, and the other housed three females and four males). Both tanks received flowing creek water for ~48 h, after which, some of the flow into the tank was replaced by well water to increase water temperature to ~11 °C at a rate of approximately 1 °C per hour. Fish were left in their holding tanks for 24 h following the end of the water temperature increase event to capture their physiological response.

Following the end of the experiments, fish were euthanized by cerebral concussion, according to the animal care protocols. Sutures were removed to allow for the retrieval of heart rate biologgers and PIT tags. The total weight (average weight was 570.1 g), as well as standard length (average length was 38.0 cm) was taken for each fish. Gonads were then removed and weighed for each fish and used to measure GSI.

$$GSI = (gonad\ weight \div total\ weight) \times 100$$

2.5. Data and statistical analyses

Only heart rate data recordings from the biologgers with a quality index (QI) value of 0 were retained, and fish were excluded from the study in the case of failed monitors. Heart rate recordings were removed if they appeared unrealistic (heart rate reading of over 120 or under 20), and/or if the ECG obtained from the biologgers indicated that the reading was not an accurate measure of heart rate. Omitted data accounted for <1% of values. Statistical analyses and figure creation were completed in SPSS Version 27 and R Studio version 4.2.2.

2.5.1. Analyses of the effects of water temperature on fish subjected to two simulated angling events

Heart rate data during each simulated angling event were extracted for each fish exposed to two simulated angling events. Fish were excluded from the study if extracted datasets were missing more than 25% of values because of heart rate biologgers losing memory or not having enough storage space during the study, data exclusion due to poor QI scores, and/or data deletion due to unrealistic values, and/or missing data due to mortality. This resulted in $n = 10$ in the cold water treatment group, and $n = 10$ in the warm water treatment group (i.e., 20 out of 32 fish were retained for analysis). Heart rate data were extracted from 10:30–11:30 AM the day of the first chase so that resting heart rate

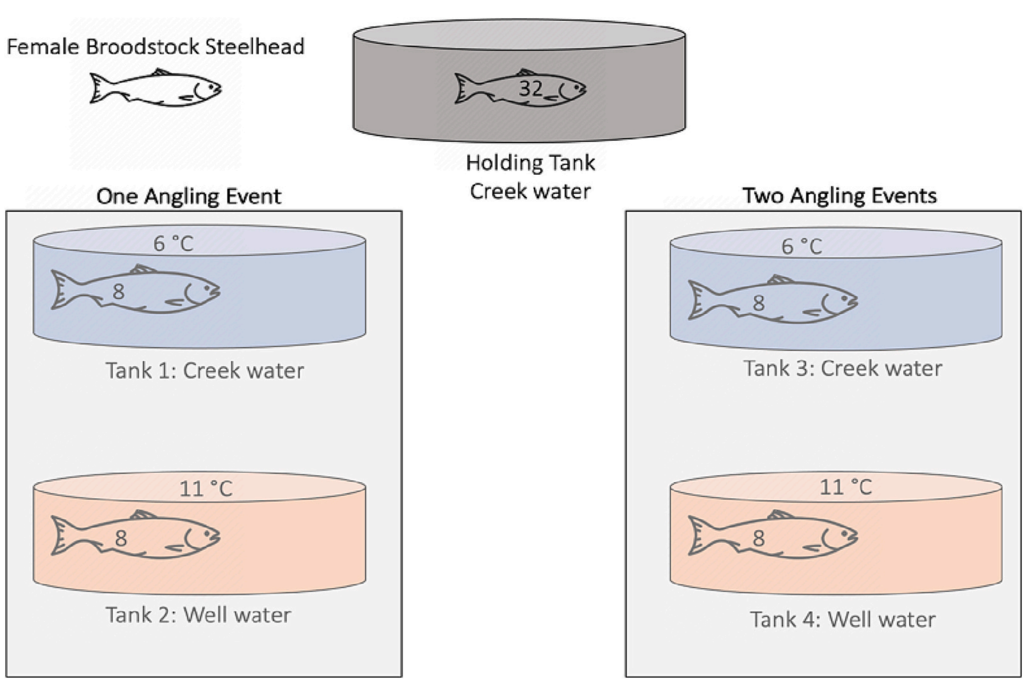

Fig. 1. Experimental set-up depicting the distribution of female hatchery steelhead across capture-event and temperature treatments.

(average heart rate during normal activity) prior to the chase could be determined for each fish. The difference (delta) in values of 1) chase activity (number of quadrant lines crossed during simulated chase), 2) landing time (time it took for fish to slow down during simulated chase), 3) maximum heart rate (95th percentile), 4) resting heart rate (10th percentile), and 5) scope for heart rate (maximum – resting heart rate), between the second and first simulated angler event were determined for all fish that underwent two simulated angling events. Four General Linear Models (GLMs) for each of the variables listed above (dependent variables) were performed and subsequently ranked with an Akaike Information Criterion corrected for small sample size (AICc; Mazerolle, 2020). Data met all assumptions for GLM tests (normality, equal variance). Temperature was included as a categorical factor, and fish weight, standard length, and GSI were included individually as linear predictors with interactions in all GLMs.

2.5.2. Analyses of the effects of recapture on steelhead recovery of simulated angling events under cold and hot water temperature conditions

Resting heart rate for each fish was extracted from heart rate data taken from 10:30–11:30 AM the day of the first chase in each round and calculated as explained above. Heart rate data for each fish for the 24-h period (heart rate measured in three-minute intervals) following their last simulated angling event (for half of the fish, this is after the first and only angling event, for the other half, this after the second simulated angling event) was also extracted. From that 24-h block, heart rate from the start of the last simulated angling event, to when fish had returned to resting heart rate (identified as two subsequent heart rate readings at determined resting heart rate) was further extracted. This data represents the time in which each fish was recovering from their final simulated angling event. Fish were excluded from the study if datasets were missing more than 25% of values (as explained above) during the extracted recovery period, in addition to the fish already excluded. From the extracted block of heart rate data taken during the period in which each fish was recovering from their final simulated angling event, values for maximum heart rate (95th percentile), resting heart rate (10th percentile), scope for heart rate (maximum – resting heart rate) and time to return to resting heart rate were calculated. Two one-way ANOVAs were conducted (one for warm water treatments, and one for cold water treatments) with number of simulated angler events as the fixed factor, and maximum heart rate, resting heart rate, and scope for heart rate and time taken to return to resting heart rate following the last simulated angling event, included as dependent variables. An ANOVA was selected for this test as fish from both temperature conditions did not recover from surgery at the same rate.

Following the completion of this experiment, the mean heart rate data for each water temperature treatment group were plotted, and it became evident that the time given for fish to recover from surgery (~72 h), as recommended in the literature (Raby et al., 2015; Prystay et al., 2017; Brijs et al., 2019), was possibly insufficient. Fish in the cold water temperature treatment groups continued to demonstrate recovery from surgery the day of, and the day following the water temperature increase event for fish in the warm water temperature group (Appendix Fig. A1). This could have influenced findings related to maximum and resting heart rates recorded during recovery. For this reason, heart rate, metrics for our second hypothesis were not compared across warm and cold water treatment groups and were only contrasted against fish from the same water temperature treatment undergoing one or two simulated angling events.

2.5.3. Analyses of sex specific differences in heart rate variables during warming

Heart rate data during the warming event and during the 24-h recovery period following the warming event was extracted for each fish. Fish were excluded from the study if extracted datasets were missing 45% or more values (because of heart rate biologgers losing memory or not having enough storage space during the study, data exclusion due to poor QI scores, and/or data deletion due to unrealistic values, and/or fish mortality). We increased the exclusion threshold in this exploratory experiment due to reduced data quality, and to retain an adequate sample size. After exclusions of fish with poor data quality, there were 6 males and 4 females left in this experiment. Two one-way ANOVAs were conducted (one with data taken during the water temperature increase event, and one with data taken during the 24-h recovery period following the event) with fish sex (male or female) as the fixed factor, and maximum heart rate, resting heart rate and scope for heart rate as dependent variables.

3. Results

3.1. Effects of water temperature on fish subjected to two simulated angling events

3.1.1. Effects of temperature on chase activity during simulated angling events

Temperature was found to be the best predictor of change in chase activity by the AICc and GLM results (Appendix Table A1). Temperature significantly influenced change in chase activity with $p = 0.024$. The difference in chase activity between the second and first angling event was significantly lower in the warm water treatment group (mean change of −27.1 quadrant lines crossed) relative to the cold water treatment group (mean change of 5.6 quadrant lines crossed; Fig. 2B).

3.1.2. Effects of temperature on landing time during simulated angling events

The GLM and AICc results revealed that the best ranking model predicting change in landing time contained only water temperature as a response variable (see Appendix Table A2). The significance of temperature in this best scoring model was found to be $p = 0.014$. The difference in landing time between the second and first simulated angling event was significantly lower in the warm water treatment group (mean change of −13.1 s) than in the cold water treatment group (mean change of 10.8 s.; Fig. 2A).

3.1.3. Effects of temperature on heart rate in fish subjected to simulated angling

No GLM in the AICc results was found to be superior to the null model in predicting change in resting heart rate (Appendix Table A3). The significance of temperature was found to be $p = 0.56$. The difference in resting heart rate between the second and first simulated angling event in the warm water treatment group increased slightly (mean change of 0.64 beats per minute; bpm), as did resting heart rate in the cold water treatment group (mean change of 2.09 bpm).

The GLM with solely temperature as a predictor variable for maximum heart rate was the highest ranking model, though not ranking more than delta two AICc more than the null model (see Appendix Table A4). The effect of temperature on maximum heart rate trended towards significance ($p = 0.076$) as did the effect of GSI on maximum heart rate ($p = 0.067$). The change in maximum heart rate between the second and first simulated angling event in the cold water treatment group decreased (mean change of −0.66 bpm), yet there was an increased change in heart rate in the warm water treatment group (mean change of 2.21 bpm; Appendix Fig. A2.). Plotting the data revealed a significant difference in slope (i.e., change in maximum heart rate in relation to GSI; Fig. 3.)

The AICc results revealed that the highest ranking model predicting change in scope for heart rate contained solely temperature as a predictor variable, though not more than delta two AICc more than the null model (Appendix Table 5). Temperature was found to be significant ($p = 0.047$). The mean for change in heart rate scope across both simulated angling events increased in the warm water temperature condition (mean change of 1.55) and decreased in the cold water temperature condition (mean change of −2.75; Appendix Fig. A3.).

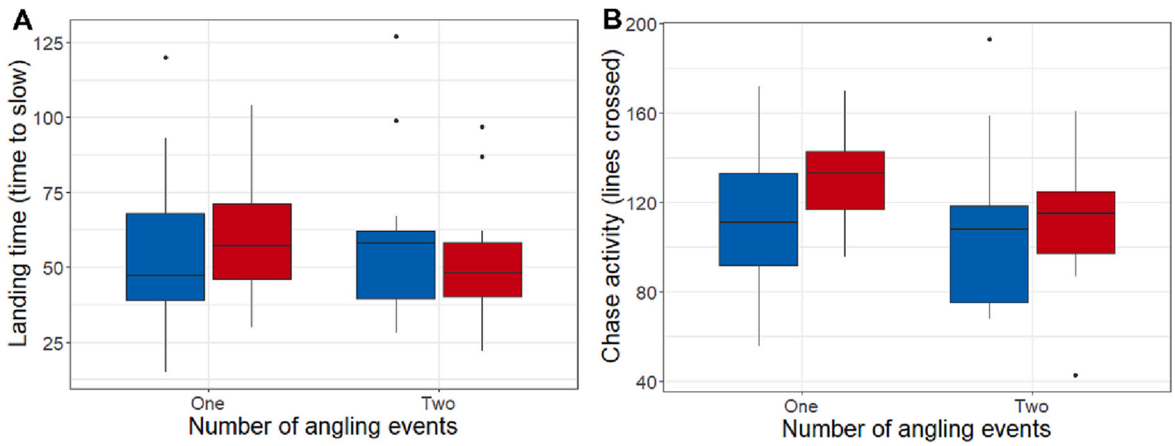

Fig. 2. Behaviour parameters of steelhead undergoing two simulated angling events. A) Landing time (time to slow during chase events) during one and two simulated angling events in the warm water (11 °C, red) and cold water (6 °C, blue) treatment group and B) Chase activity during one and two simulated angling events in the warm water (11 °C, red) and cold water (6 °C, blue) treatment group. Boxes indicate median, first and third quartile, as well as minimum and maximum values with outliers represented as dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

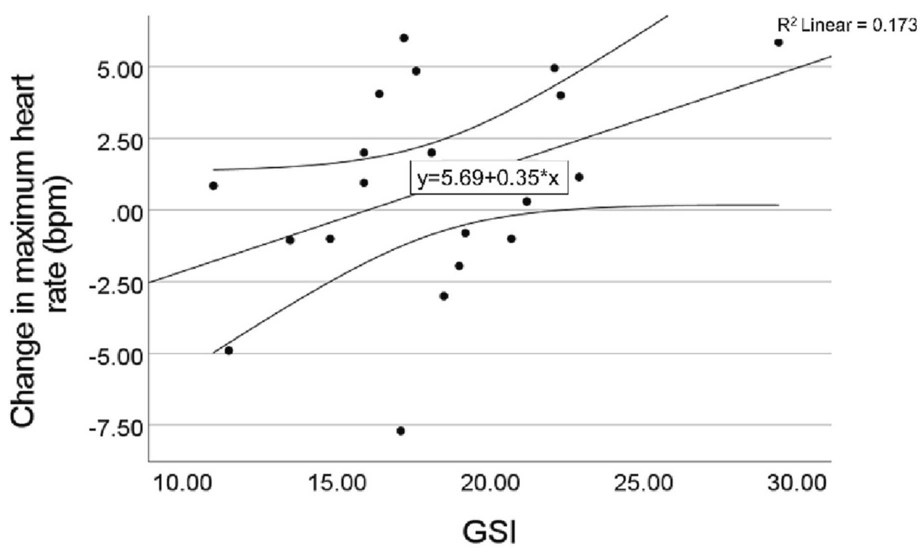

Fig. 3. Relationship between gonadosomatic index (GSI) and change in maximum heart rate with a linear line of best fit and mean standard error (curved lines).

3.2. Effects of recapture on steelhead recovery of simulated angling events under cold and hot water temperature conditions

3.2.1. Warm water temperature treatment group

The ANOVA results for the warm water temperature treatment group found no significant effect of number of simulated angling events on scope for heart rate, maximum heart rate, time to return to resting heart rate, or resting heart rate during recovery (see Table 1).

Maximum heart rate remained constant amongst fish subjected to one and two simulated angling events, with average maximum heart rate for both groups being 84 beats per minute (bpm). There was no significant change in resting heart rate amongst those subjected to two compared to one simulated angling events during recovery, yet fish subjected to only one event demonstrated an average resting heart rate of 67 bpm, which tended to be higher than those subjected to two events, as they demonstrated an average resting heart rate of 61 bpm. Scope for heart rate during recovery trended towards being lower in fish subjected to only one simulated angling event (mean scope for heart rate of 17 bpm) when compared to fish subjected to two simulated angling events (mean scope for heart rate of 23 bpm). Recovery time, or time taken to return to resting heart rate, trended towards being lower in fish subjected to only one simulated angling event (mean recovery time of 507 min), when compared to fish subjected to two simulated angling events (mean recovery time of 606 min).

Table 1
Effect of the number of simulated angling events on steelhead max heart rate, scope for heart rate, resting heart rate and time taken to return to resting heart rate for the warm water treatment group.

	df	Mean Square	F	Significance
Maximum heart rate				
Between Groups	1	0.013	0.001	0.98
Within Groups	16	20.1		
Total	17			
Resting heart rate				
Between Groups	1	167.554	2.23	0.155
Within Groups	16	75.144		
Total	17			
Scope for heart rate				
Between Groups	1	163.755	3.441	0.082
Within Groups	16	42.633		
Total	17			

Table 2
Effect of the number of simulated angling events on steelhead max heart rate, scope for heart rate, resting heart rate, and time taken to return to resting heart rate for the cold water treatment group.

	df	Mean Square	F	Significance
Maximum heart rate				
Between Groups	1	3.636	0.456	0.509
Within Groups	17	7.9733		
Total	18			
Resting heart rate				
Between Groups	1	1.737	0.079	0.783
Within Groups	17	22.102		
Total	18			
Scope for heart rate				
Between Groups	1	0.745	0.024	0.879
Within Groups	17	31.166		
Total	18			

3.2.2. Cold water temperature treatment group

The ANOVA results for the cold water temperature treatment group did not reveal a significant effect of number of simulated angling events on maximum or resting heart rate, scope for heart rate and time to return to resting heart rate during recovery (see Table 2).

Maximum heart rate remained almost constant amongst fish subjected to one and two simulated angling events, with average maximum heart rate for those subjected to one simulated angling event being 67 bpm, and for those subjected to two simulated angling events being 68 bpm. Resting heart rate also remained almost the same amongst fish subjected to one and two simulated angling events, with average resting heart rate for fish subjected to one simulated angling event being 43 bpm, and for fish subjected to two simulated angling events being 44 bpm. Average scope for heart rate remained constant across fish subjected to two and one simulated angling events, with both groups demonstrating a scope for heart rate of 14 bpm. The ANOVA results did not suggest any trend in recovery time (time taken for fish to return to resting heart rate following their last simulated angling event), yet fish subjected to one simulated angling event had an average recovery time of 985 min, and fish subjected to two simulated angling events had an average recovery time of 862 min.

3.3. Differences between female and male heart rates during an increase in water temperature event

3.3.1. Water temperature increase event

Sex significantly influenced resulting scope for heart rate during a temperature increase event (Table 3), where females had a higher scope for heart rate (33 bpm) relative to males (22 bpm). On average, females had slightly lower resting heart rates (38 bpm) and slightly higher maximum heart rates (71 bpm) during a temperature increase event compared to males (44 bpm and 66 bpm, respectively) (Fig. 4A).

Table 3
Difference between male ($n = 6$) and female ($n = 4$) max heart rate, scope for heart rate, and resting heart rate during temperature increase event.

	df	Mean Square	F	Significance
Scope for heart rate				
Between Groups	1	301.504	28.253	0.001**
Within Groups	8	10.672		
Total	9			
Maximum Heart rate				
Between Groups	1	58.411	0.894	0.372
Within Groups	8	65.344		
Total	9			
Resting Heart rate				
Between Groups	1	94.501	2.272	0.17
Within Groups	8	41.588		
Total	9			

3.3.2. Recovery from the warming event

Sex significantly influenced scope for heart rate during the recovery period during the warming event (Table 4), where females had a higher scope for heart rate during recovery (21 bpm) relative to males (13 bpm). Resting heart rate during a temperature increase event was 49 and 55 bpm in females and males, respectively, and the average maximum heart rate was 70 versus 67 bpm in females and males, respectively (Fig. 4B).

4. Discussion

Consistent with our first hypothesis, fish in the warm water temperature treatment that underwent two simulated angling events showed greater physiological alterations and behavioural impairments resulting from a simulated recapture angling event than fish under cold water temperatures. Fish in the warm water temperature treatment displayed a higher maximum heart rate and scope for heart rate during the second simulated angling event, whereas fish in the cold water temperature treatment displayed slightly lower maximum heart rate and scope. Moreover, fish in the warm water temperature treatment did poorly in behavioural measures during the second simulated angling event with significantly lower chase activity and landing time. Conversely, cold water temperature treated fish had unchanged chase activity and improved landing time during the second event when compared to the first. An increase in physiological alterations (in this case, heart rate parameters) and a decrease in behavioural measures suggests fish in the warm water temperature treatment faced additional stress because of the simulated recapture event (Gale et al., 2013). Fish in the cold water temperature treatment did not demonstrate much evidence of compounding effects from multiple simulated angler recaptures.

The current findings are largely consistent with the literature suggesting that water temperature compounds the effects of other stressors (Whitney et al., 2016; McCormick et al., 2021), such as an angling recapture event. Angling events force fish to engage in both aerobic and anaerobic metabolism (Ferguson and Tufts, 1992; Kieffer, 2000), which is known to increase cardiac output (heart rate and/or stroke volume). Anaerobic metabolism is common during the “fight” and air exposure aspects of a catch-and-release event whereas aerobic metabolism is used by fish to recover from the resultant oxygen debt (Blažka, 1958; Scarabello et al., 1991). Temperature also increases cardiac activity (Farrell et al., 2001; Farrell et al., 2009), meaning fish subjected to angling events under warm water temperatures would be expected to demonstrate higher heart rates compared to those in cold water temperatures, both during and after exercise. This is evident in our study as fish in the warm water temperature treatment showed higher resting and maximum heart rate during simulated re-occurring angling events, suggestive of increased cardiac output likely sustaining increased tissue metabolic demand.

The second hypothesis that recovery heart rate and time would be increased over one and two simulated angling events in warm water, but not in cold water, was not supported. Yet, trends in the data suggest a recapture event may lead to longer recovery time and an increase in scope for heart rate in warm water temperature conditions. Resting heart rate, scope for heart rate and recovery time trended towards being higher during the recovery of fish subjected to two simulated angling events under warm water temperatures and no such trends were found across cold water temperature treatment groups, though these findings were not statistically different. It is important to emphasize that we could not compare across water temperatures in this study due to surgery recovery times, and thus are only comparing between one and two angling events in each temperature group. More work is needed to determine effects of multiple angling events on recovery. Laboratory research on juvenile rainbow trout where fish were exercised twice found more rapid recovery for the second swimming challenge which was interpreted as a potential training effect (Scarabello et al., 1991).

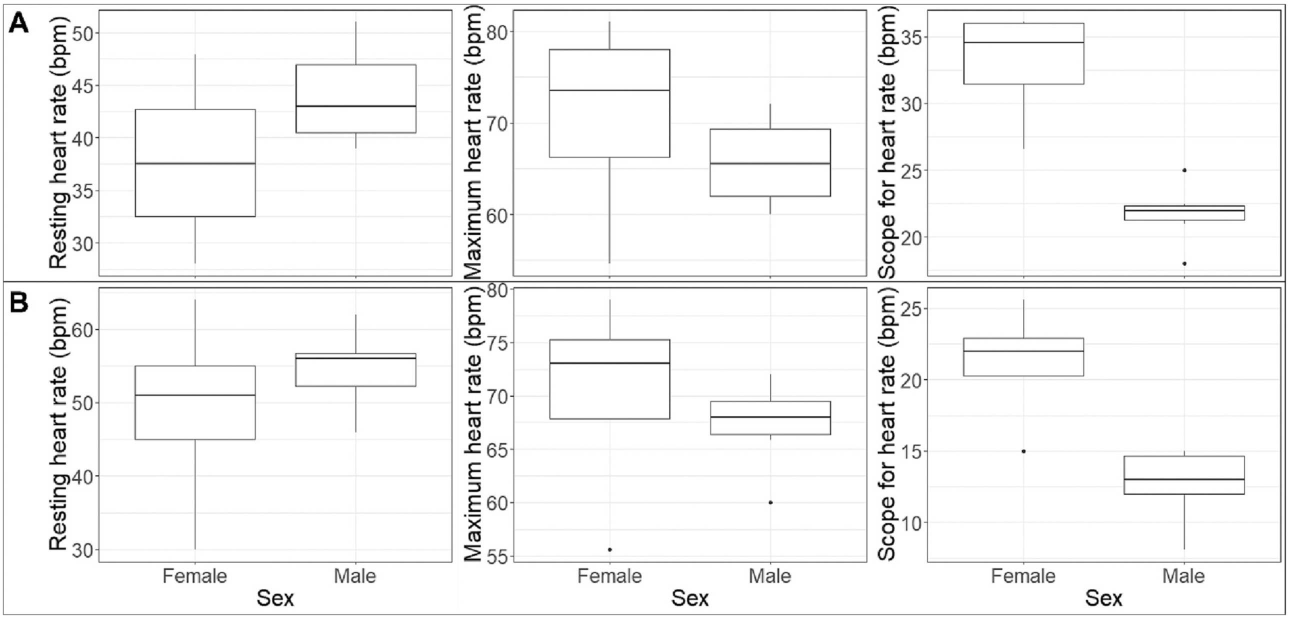

Fig. 4. Average male ($n = 6$) and female ($n = 4$) resting heart rate, maximum heart rate, and scope for heart rate A) during and B) following a temperature increase event. Error bars reflect 95% confidence intervals. Boxes indicate median, first and third quartile, as well as minimum and maximum values with outliers represented as dots.

Table 4
Difference between male and female max heart rate, scope for heart rate, and resting heart rate following a temperature increase event.

	df	Mean Square	F	Significance
Scope for heart rate				
Between Groups	1	173.06	14.919	0.005**
Within Groups	8	11.6		
Total	9			
Maximum Heart rate				
Between Groups	1	19.38	0.393	0.548
Within Groups	8	49.253		
Total	9			
Resting Heart rate				
Between Groups	1	76.614	0.822	0.391
Within Groups	8	93.234		
Total	9			

There is a substantial literature on exercise training in fish (reviewed in Davison, 1997) although most of that work has been done in the laboratory where fish are not free-swimming during recovery and where recovery (e.g., in a sensory deprivation chamber) may be easier to detect. Future work should assess recovery following angling events at varying time intervals, as well as under a larger range of temperatures so that patterns between temperature increase and recovery from multiple angling events can be identified. To date, recovery times have been linked to the extent of aerobic activity (Lee et al., 2003a), but not temperature (Anderson et al., 1998; Schreer et al., 2001; Prystay et al., 2017). It is reasonable to predict that temperature increases can affect recovery from angling events, as fish engage in excess post-exercise oxygen consumption (EPOC) during recovery (Lee et al., 2003a), and temperature is linked to an increased cardiac output (Farrell et al., 2001; Farrell et al., 2009). However, it is possible that those effects are only manifested in a meaningful way at even more extreme water temperatures.

Consistent with our third hypothesis, females demonstrated significant differences in heart rate during an increase in water temperature, as well as during the recovery period from the warming event. However, our sample size for this experiment is low and thus reduces the power of our results here. Regardless, these findings fit with Eliason et al. (2020)'s findings demonstrating sex-specific differences in Pacific salmonids regarding recovery times from stressors, and oxygen delivery to the heart. These differences demonstrate the importance of accounting for sex-specific differences when conducting research assessing cardiac function in salmonids. Females showed a larger scope for heart rate and demonstrated higher maximum heart rate values as well as lower resting heart rate. Females in this study were sexually mature, which may have influenced sex-specific differences in heart rate as sexual maturity is known to increase sex-specific differences in physiological performance of fishes (Franklin and Davie, 1992). Indeed, sexual maturation could lead to an increased metabolic demand associated with egg maturation in females during reproduction reflecting an increased gonadal metabolic demand, which thus requires an elevation in cardiac output and gonadal blood flow. Our findings here also support this, as plotting GSI with change in maximum heart rate showed a positive relationship which trended towards being significant. As in different sexes, behavioural phenotype may also affect the physiological response of fish undergoing a stressor (Pottinger and Carrick, 2001; Øverli et al., 2004), and would be best investigated with plasma cortisol readings in future studies.

Our assessments of heart rate indicate that the ~72 h recovery period as has been suggested by several studies (e.g., Raby et al., 2015; Prystay et al., 2017; Brijs et al., 2019), was insufficient for allowing full recovery from the surgical procedures (see above) and hindered the ability to directly compare warm and cold treatments in this study. Future studies should allow for longer post-surgical recovery times, especially when coupled with temperature treatment protocols. The mechanisms underpinning these protracted post-surgery recovery times are unclear and could vary with tag burden, anesthetic method or other factors.

In conclusion, this study demonstrates that repeated capture impacts the physiological and behavioural state of steelhead with significant bioenergetic consequences. When water temperatures are cool, steelhead can compensate for additional stressors associated with repeated simulated angling events. However, when subjected to stressors such as those associated with warming water temperatures, steelhead will most certainly demonstrate physiological and behavioural indicators of stress. This study did not find any evidence of prolonged impacts of repeated simulated angling events on fish recovery, yet trends in the data suggest fish in warmer waters may not be able to recover from multiple angling events as easily as those in cooler waters. As temperatures are predicted to continue increasing due to global warming, managing effects of angling in increasingly warmer waters will only grow more crucial. Our work contributes to our fundamental understanding of the effects of repeated stressors on fish while also providing valuable knowledge that may be relevant to fisheries managers.

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

Data will be made available on request.

Acknowledgements

The authors would like to thank the Abernathy Fish Technology Centre for providing fish, equipment and expertise that supported this work. SJC was supported by NSERC and the Canada Research Chairs program. AJD was supported by the National Institute of Food & Agriculture, U.S. Department of Agriculture, the Massachusetts Agricultural Experiment Station and Department of Environmental Conservation. ALJ and JCM was supported by the Fonds de Recherche du Québec – Nature et Technologies (FRQNT). Findings and conclusions are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. The use of trade names does not imply endorsement by the Federal government. We thank Trevor Avery for thoughtful comments on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2023.111469.

References

Anderson, W.G., Booth, R., Beddow, T.A., McKinley, R.S., Finstad, B., Økland, F., Scruton, D., 1998. Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon, Salmo salar (L.). Hydrobiologia 371, 233–240.

Barton, B.A., Schreck, C.B., Sigismondi, L.A., 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. Trans. Am. Fish. Soc. 115 (2), 245–251.

Blažka, P., 1958. The anaerobic metabolism of fish. Physiol. Zool. 31 (2), 117–128.

Bower, S.D., Szekeres, P., Raghavan, R., Danylchuk, A.J., Cooke, S.J., 2022. Consequences of simulated multiple catch-and-release events and different handling procedures on reflex impairment, ventilation rate, and body condition in Tor khudree. Fish. Res. 246, 106175.

Brijs, J., Sandblom, E., Rosengren, M., Sundell, K., Berg, C., Axelsson, M., Gräns, A., 2019. Prospects and pitfalls of using heart rate bio-loggers to assess the welfare of rainbow trout (*Oncorhynchus mykiss*) in aquaculture. Aquaculture 509, 188–197.

Brodeur, J.C., Dixon, D.G., McKinly, R.S., 2001. Assessment of cardiac output as a predictor of metabolic rate in rainbow trout. J. Fish Biol. 58 (2), 439–452.

Cline, T.J., Weidel, B.C., Kitchell, J.F., Hodgson, J.R., 2012. Growth response of largemouth bass (*Micropterus salmoides*) to catch-and-release angling: a 27-year mark–recapture study. Can. J. Fish. Aquat. Sci. 69 (2), 224–230.

Cooke, S.J., Philipp, D.P., Dunmall, K.M., Schreer, J.F., 2001. The influence of terminal tackle on injury, handling time, and cardiac disturbance of rock bass. N. Am. J. Fish Manag. 21 (2), 333–342.

Cooke, S.J., Ostrand, K.G., Bunt, C.M., Schreer, J.F., Wahl, D.H., Philipp, D.P., 2003. Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of water temperatures. Trans. Am. Fish. Soc. 132 (6), 1154–1165.

Cooke, S.J., Brownscombe, J.W., Raby, G.D., Broell, F., Hinch, S.G., Clark, T.D., Semmens, J.M., 2016. Remote bioenergetics measurements in wild fish: opportunities and challenges. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 202, 23–37.

Davis, M.W., 2010. Fish stress and mortality can be predicted using reflex impairment. Fish Fish. 11 (1), 1–11.

Davison, W., 1997. The effects of exercise training on teleost fish, a review of recent literature. Comp. Biochem. Physiol. A Physiol. 117 (1), 67–75.

Donaldson, M.R., Clark, T.D., Hinch, S.G., Cooke, S.J., Patterson, D.A., Gale, M.K., Frappell, P.B., Farrell, A.P., 2010. Physiological responses of free-swimming adult coho salmon to simulated predator and fisheries encounters. Physiol. Biochem. Zool. 83 (6), 973–983.

Eliason, E.J., Dick, M., Patterson, D.A., Robinson, K.A., Lotto, J., Hinch, S.G., Cooke, S.J., 2020. Sex-specific differences in physiological recovery and short-term behaviour following fisheries capture in adult sockeye salmon (Oncorhynchus nerka). Can. J. Fish. Aquat. Sci. 77 (11), 1749–1757.

Farrell, A.P., Thorarensen, H., Axelsson, M., Crocker, C.E., Gamperl, A.K., Cech Jr., J.J., 2001. Gut blood flow in fish during exercise and severe hypercapnia. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 128 (3), 549–561.

Farrell, A.P., Eliason, E.J., Sandblom, E., Clark, T.D., 2009. Fish cardiorespiratory physiology in an era of climate change. Can. J. Zool. 87 (10), 835–851.

Ferguson, R.A., Tufts, B.L., 1992. Physioloical effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for catch-and-release fisheries. Can. J. Fish. Aquat. Sci. 49, 1157–1162.

Franklin, C.E., Davie, P.S., 1992. Sexual maturity can double heart mass and cardiac power output in male rainbow trout. J. Exp. Biol. 171 (1), 139–148.

Gale, M.K., Hinch, S.G., Donaldson, M.R., 2013. The role of temperature in the capture and release of fish. Fish Fish. 14 (1), 1–33.

Hinch, S.G., Bett, N.N., Eliason, E.J., Farrell, A.P., Cooke, S.J., Patterson, D.A., 2021. Exceptionally high mortality of adult female salmon: a large-scale pattern and a conservation concern. Can. J. Fish. Aquat. Sci. 78 (6), 639–654.

Holder, P.E., Wood, C.M., Lawrence, M.J., Clark, T.D., Suski, C.D., Weber, J.M., et al., 2022. Are we any closer to understanding why fish can die after severe exercise? Fish Fish. 23 (6), 1400–1417.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Johnson, E.L., Peery, C.A., Caudill, C.C., 2018. Thermal exposure of adult Chinook salmon and steelhead: diverse behavioral strategies in a large and warming river system. PLoS One 13 (9), e0204274.

Kelch, D., Lichtkoppler, F., Sohngen, B., Daigneault, A., 2006. The value of steelhead (*Onchorhynchus mykiss*) angling in Lake Erie tributaries. J. Great Lakes Res. 32 (3), 424–433.

Kendall, N.W., Marston, G.W., Klungle, M.M., 2017. Declining patterns of Pacific northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. Can. J. Fish. Aquat. Sci. 74 (8), 1275–1290.

Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 126 (2), 161–179.

Lee, C.G., Farrell, A.P., Lotto, A., Hinch, S.G., Healey, M.C., 2003a. Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. J. Exp. Biol. 206 (18), 3253–3260.

Mazerolle, M.J., 2020. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.3–1. https://cran.r-project.org/package=AICcmodavg.

McCormick, J.L., Dobos, M.E., Bowersox, B.J., Copeland, T., 2021. Evaluation of management strategies for an incidental catch-and-release steelhead fishery. N. Am. J. Fish Manag. 41 (2), 498–512.

Meka, J.M., Margraf, F.J., 2007. Using a bioenergetic model to assess growth reduction from catch-and-release fishing and hooking injury in rainbow trout, *Oncorhynchus mykiss*. Fish. Manag. Ecol. 14 (2), 131–139.

Meka, J.M., McCormick, S.D., 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. Fish. Res. 72 (2–3), 311–322.

Morten, K.L., Branch, F., 2000. A survey of Zymoetz (Copper) River steelhead anglers in 1999. Report by Cascadia Natural Resource Consulting, Duncan, BC for Fisheries Branch, British Columbia Ministry of Environment, Lands and Parks, Smithers, BC Skeena Fisheries Report Series SK, 127.

Nakamoto, R.J., 1994. Characteristics of pools used by adult summer steelhead Oversummering in the New River, California. Trans. Am. Fish. Soc. 123 (5), 757–765.

Nelson, T.C., Rosenau, M.L., Johnston, N.T., 2005. Behavior and survival of wild and hatchery-origin winter steelhead spawners caught and released in a recreational fishery. N. Am. J. Fish Manag. 25 (3), 931–943.

Øverli, Ø., Korzan, W.J., Höglund, E., Winberg, S., Bollig, H., Watt, M., Summers, C.H., 2004. Stress coping style predicts aggression and social dominance in rainbow trout. Horm. Behav. 45 (4), 235–241.

Parsons, P.A., 1994. The energetic cost of stress. Can biodiversity be preserved? Biodivers. Lett. 11–15.

Pottinger, T.G., Carrick, T.R., 2001. Stress responsiveness affects dominant–subordinate relationships in rainbow trout. Horm. Behav. 40 (3), 419–427.

Prystay, T.S., Eliason, E.J., Lawrence, M.J., Dick, M., Brownscombe, J.W., Patterson, D. A., Crossin, G.T., Hinch, S.G., Cooke, S.J., 2017. The influence of water temperature on sockeye salmon heart rate recovery following simulated fisheries interactions. Conserv. Physiol. 5 (1).

Raby, G.D., Clark, T.D., Farrell, A.P., Patterson, D.A., Bett, N.N., Wilson, S.M., Willmore, W.G., Suski, C.D., Hinch, S.G., Cooke, S.J., 2015. Facing the river gauntlet: understanding the effects of fisheries capture and water temperature on the physiology of coho salmon. PLoS One 10 (4), e0124023.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., et al., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873.

Richard, A., Bernatchez, L., Valiquette, E., Dionne, M., 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 71 (11), 1730–1739.

Romero, L.M., Dickens, M.J., Cyr, N.E., 2009. The reactive scope model—a new model integrating homeostasis, allostasis, and stress. Horm. Behav. 55 (3), 375–389.

Scarabello, M., Heigenhauser, G.J.F., Wood, C.M., 1991. The oxygen debt hypothesis in juvenile rainbow trout after exhaustive exercise. Respir. Physiol. 84 (2), 245–259.
Scheuerell, M.D., Ruff, C.P., Anderson, J.H., Beamer, E.M., 2021. An integrated population model for estimating the relative effects of natural and anthropogenic factors on a threatened population of steelhead trout. J. Appl. Ecol. 58 (1), 114–124.
Schreck, C.B., 2010. Stress and fish reproduction: the roles of allostasis and hormesis. Gen. Comp. Endocrinol. 165 (3), 549–556.
Schreer, J.F., Cooke, S.J., McKinley, R.S., 2001. Cardiac response to variable forced exercise at different temperatures: an angling simulation for smallmouth bass. Trans. Am. Fish. Soc. 130 (5), 783–795.
Sokolova, I.M., 2013. Energy-limited tolerance to stress as a conceptual framework to integrate the effects of multiple stressors. Integr. Comp. Biol. 53 (4), 597–608.
Sopinka, N.M., Donaldson, M.R., O'Connor, C.M., Suski, C.D., Cooke, S.J., 2016. Stress indicators in fish. In: Fish Physiology, vol. 35. Academic Press, pp. 405–462.
Stockwell, J.D., Diodati, P.J., Armstrong, M.P., 2002. A bioenergetic evaluation of the chronic-stress hypothesis: can catch-and-release fishing constrain striped bass growth? Am. Fish. Soc. Symp. 30, 144–147.
Suski, C.D., Killen, S.S., Cooke, S.J., Kieffer, J.D., Philipp, D.P., Tufts, B.L., 2004. Physiological significance of the weigh-in during live-release angling tournaments for largemouth bass. Trans. Am. Fish. Soc. 133 (6), 1291–1303.
Thorarensen, H., Gallaugher, P.E., Farrell, A.P., 1996. The limitations of heart rate as a predictor of metabolic rate in fish. J. Fish Biol. 49 (2), 226–236.
Twardek, W.M., Gagne, T.O., Elmer, L.K., Cooke, S.J., Beere, M.C., Danylchuk, A.J., 2018. Consequences of catch-and-release angling on the physiology, behaviour and survival of wild steelhead Oncorhynchus mykiss in the Bulkley River, British Columbia. Fish. Res. 206, 235–246.
Tyack, P.L., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., et al., 2022. Managing the effects of multiple stressors on wildlife populations in their ecosystems: developing a cumulative risk approach. Proc. R. Soc. B 289 (1987), 20222058.
Watson, J.W., Hyder, K., Boyd, R., Thorpe, R., Weltersbach, M.S., Ferter, K., Sibly, M., 2020. Assessing the sublethal impacts of anthropogenic stressors on fish: an energy-budget approach. Fish Fish. 21 (5), 1034–1045.
Whitney, J.E., Al-Chokhachy, R., Bunnell, D.B., Caldwell, C.A., Cooke, S.J., Eliason, E.J., et al., 2016. Physiological basis of climate change impacts on North American inland fishes. Fisheries 41 (7), 332–345.
Wilkie, M.P., Brobbel, M.A., Davidson, K.G., Forsyth, L., Tufts, B.L., 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 54 (3), 503–511.
Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T., Tufts, B. L., 1996. Physiology and survival of wild Atlantic salmon following angling in warm summer waters. Trans. Am. Fish. Soc. 125 (4), 572–580.