Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures

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ABSTRACT

Sockeye salmon abundance in the Fraser River has declined precipitously over the past two decades, reducing fishing opportunities for this ecologically, culturally and economically valuable species. Release of non-target species that are captured incidentally is a growing conservation measure used in managing mixed species fisheries. Fraser River sockeye salmon are released from commercial, First Nations, and recreational fisheries, however little research exists investigating the fitness and fate of released sockeye salmon, and none examine how the effect of ecologically relevant temperature ranges interact with capture stressors. We exposed adult migrating summer-run sockeye in freshwater to simulated capture and release stressors, including exhaustive exercise and air exposure, at temperatures spanning the range of historic, current and predicted future migration conditions in the Fraser River (13 °C, 19 °C, and 21 °C) to understand the physiological consequences of these stressors acting in synergy. Three minutes of exhaustive exercise significantly raised the plasma lactate, chloride, sodium, and osmolality, and lowered the plasma potassium of these fish, and one minute of air exposure following exercise elevated glucose (females only) and exacerbated high lactate levels. The inability of all air-exposed fish in the warmest temperatures to maintain equilibrium upon return to the water is evidence of the effects of warm temperatures. Fewer than half of the air-exposed fish in the coolest temperature demonstrated this impairment. Further, air exposure resulted in a marked depression of ventilation rates in the warmest temperatures. This is the first experiment investigating the physiological disturbance of capture and release at various temperatures on adult Pacific salmon, and the results suggest a need for better understanding of the potential fitness consequences to improve the management of this important resource.

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1. Introduction

Fisheries management agencies frequently impose harvest regulations (e.g. gear selection, bag limits, closed seasons for some species) that require the release of non-target species (i.e., bycatch) in both commercial and recreational fisheries. In the recreational sector, some fish are also released voluntarily due to a conservation ethic among anglers (Arlinghaus et al., 2007). A major assumption involved with capture and release fishing, irrespective of the sector, is that released fish do not have significantly reduced survival or fitness relative to conspecifics that are not exposed to the same stressors (Cooke and Schramm, 2007; Wydoski et al., 1976). Although there are a number of inherent

differences between commercial and recreational fisheries, fish are exposed to stress and injury in both sectors, with the potential for mortality during the process. Studies have examined the effects of capture and release on immediate, short-term, and delayed mortality of various species and they have found that the survival of released fish can range from zero to almost 100% (Alverson et al., 1994; Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Davis, 2002; Muoneke and Childress, 1994). In these examples, survival was dependant upon species, anatomical hooking location, capture depth, hook, bait, gear types, air exposure, life history stage and/or size, and handling. Mortality arising from capture and release is often not incorporated into management models, which can impede the ability of management agencies to develop sustainable fishing practices (Coggins et al., 2007). In addition, considerable research has examined the specific influence of water temperature on post-release survival of fish (Cooke and Suski, 2005; Davis, 2002; Wilkie et al., 1997, e.g. Wilkie

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et al., 1996). Results of this research have been used to develop some general guidelines adopted by management agencies, such as recommending avoiding catch-and-release fishing or reducing air exposure during high temperatures (e.g. Fisheries and Oceans Canada; DFO, 2010a, Atlantic Salmon Federation; ASF, 2010). However, these guidelines often provide vague or even contradictory advice when it comes to catch-and-release best practices (for example with regard to air exposure and resuscitation; Pelletier et al., 2007). It is known that fish have adapted to and depend upon the thermal environment in which they live (Pörtner, 2002), and that temperatures exceeding an optimal range can cause impairment of physiological processes and decreased survival (Brett et al., 1958; Eliason et al., 2011; Elliot, 1981). The degree to which the optimal thermal range may narrow when fish experience capture and thermal stress simultaneously remains to be understood.

In British Columbia, sockeye salmon (*Oncorhynchus nerka*) are the most commercially valuable Pacific salmon species (BCMOE, 2008) and are highly valued by anglers and First Nations (aboriginal) fishers. Owing to an abundant return in 2010, approximately 13 million Fraser River sockeye salmon were caught in commercial seine, troll, and gill-net fisheries, and an additional 1.4 million were caught in First Nations gill-net and seine fisheries (DFO, 2010b). Both sectors fish primarily where sockeye salmon are approaching, and then transitioning to, fresh water from the Pacific Ocean. The recreational fishery for sockeye salmon in the Fraser River is focused mainly in the lower Fraser River and has grown from being almost non-existent a decade ago (between 1984 and 1990, a total of 370 sockeye were caught by anglers) to a catch of 190,000 (2002), 155,000 (2006) and 300,000 (2010) in dominant cycle years (DFO, 2010c). Temporal closures of the sockeye fisheries and catch limits are implemented to protect threatened stocks and ensure adequate escapement to spawning grounds, forcing the periodic release of captured sockeye salmon. For example, anglers released one third of captured sockeye salmon (100,000 fish) in 2010 in the Fraser River, and on average released 21,000 fish per year in the previous four years (DFO, 2010c). There are no direct estimates of how many sockeye salmon escape from different gear types but fail to complete their migration. However, a recent study in Alaska (Baker and Schindler, 2009) and a report on Fraser River sockeye salmon (Clarke et al., 1994) demonstrate up to 50% of spawning adults had characteristic net mark scars on their bodies. The authors also found that Alaskan sockeye salmon with moderate to severe gillnet injuries were far less likely to successfully enter natal streams than non-injured fish (Baker and Schindler, 2009).

A recent review of 83 studies, involving an examination of capture-release and thermal stress (Gale et al., in press), found that the majority detected deleterious physiological and survival consequences of warm temperatures on released fish. However, more than half failed to put the study temperatures into an ecologically or biologically meaningful context. For most species, there exists little or no data on the consequences of capture and release at ecologically relevant high temperatures. This is true for all Pacific salmon species (*Oncorhynchus* spp.), and perhaps most notably for sockeye salmon, which are well-studied in regards to temperature tolerance (Brett, 1971; Cooke et al., 2004; Crossin et al., 2008; Eliason et al., 2011; Farrell et al., 2008) yet there is little known about how temperature affects survival of released sockeye following capture.

Summer water temperatures in the Fraser River have increased by ~2 °C over the last 60 years (Patterson et al., 2007) with 13 of the past 20 years being the warmest on record. Extremely high levels of migration mortality (>90% in some populations) have been attributed to high temperatures in Fraser River sockeye salmon (Cooke et al., 2004; Farrell et al., 2008; Martins et al., 2011), and are presumed to result from factors including energy exhaustion, collapse of aerobic and cardiac scope, physiological stress, diseases and parasites (Eliason et al., 2011; Farrell et al., 2008; Mathes et al.,
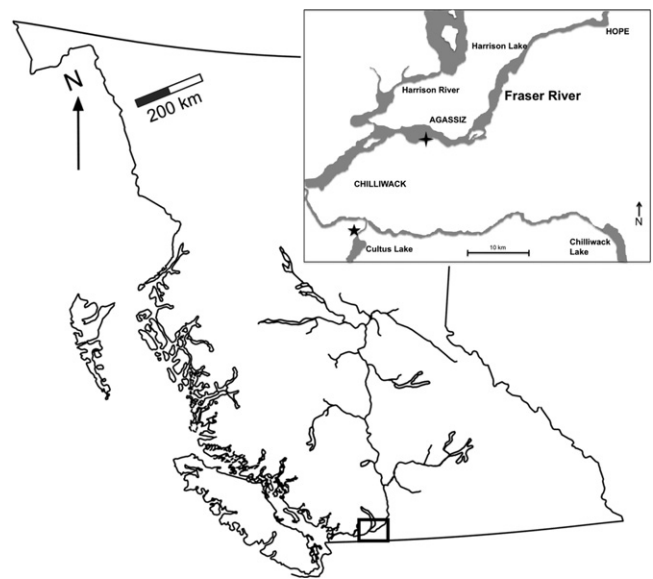

Fig. 1. British Columbia and the Fraser River, which drains almost one-third of the province. Inset is the study area, with the cross marking the fish capture site on the Fraser River in Chilliwack, and the star marking the Cultus Lake Salmon Research Laboratory, where experiments took place.

2010; Rand and Hinch, 1998). Fisheries gear interactions occur as a stressor overlaid on the inherent migration challenges, and consist of burst swimming behaviour in attempt to escape, injury from gear entanglement/hooking, and often air exposure during handling and release. Given that Fraser River sockeye salmon are experiencing temperatures in freshwater that can affect migration survivorship, and that capture and release (or capture and escape) is frequently occurring, there is a pressing need to examine the how temperature and capture-related stressors may interact to influence the survival and physiological responses of fish, particularly Pacific salmon.

The objective of this study was to use sockeye salmon to investigate the interactions between temperature and capture-related stressors and their consequences for post-release blood physiology and survival. To that end, Fraser River sockeye were exposed to three different simulated capture-related stressors – no applied capture stressor, simulated capture, or simulated capture including air exposure – under a range of water temperatures. They were then assessed for the magnitude of physiological impairments using plasma metabolite, ion, and hormone concentrations. Water temperatures reflected a natural range that this run has historically encountered, including temperatures both cooler (13 °C) and warmer (19 °C) than the window for maximum aerobic scope (Farrell et al., 2008; Fry, 1971), as well as a high temperature (21 °C) that is approaching the critical thermal limit for this group of fish (Eliason et al., 2011; Farrell et al., 2008). Capture stressors were intended to simulate the flight response and exhaustive exercise, with or without air exposure, that might be experienced by a sockeye salmon caught in a net or on a hook. We hypothesized that the capture stressor coupling exhaustive exercise with air exposure would cause the highest physiological impairments, and that these effects would be most severe at the highest temperature.

2. Methods

2.1. Study site and animals

Capture of study animals took place on August 11–12, 2009 in the main-stem of the Fraser River in Chilliwack, British Columbia (Fig. 1). Fraser River sockeye salmon are managed as four consecutive "run-timing" groups based on the timing of entry to the Fraser River: early Stuart, early summer, summer-run, and late-run.

Adult summer-run sockeye salmon were intercepted soon after they departed the ocean and commenced their freshwater spawning migration towards natal streams. River temperature at this time was measured at approximately $18 \pm 1\,^{\circ}C$. Sockeye salmon were captured using a beach seine deployed from a small boat and pulled close to shore, to allow dip-netting of individual fish into truck-mounted transport tanks. In total, 101 fish were transported approximately 26 kilometers in cool ($\sim$11 $^{\circ}C$) water to the Fisheries and Oceans Canada (DFO) Cultus Lake Salmon Research Laboratory (CLL), where all experiments took place. Dissolved oxygen was monitored continuously throughout transport, and was maintained above 80% by transporting fish in cool water and the diffusion of oxygen from truck-mounted cylinders.

After arrival at the CLL facility, Passive Integrated Transponder (PIT) tags (approximately 8.5 mm $\times$ 2 mm size, 134.2 kHz, Biomark Inc., Boise, Idaho) were injected into the coelomic cavity for individual identification and fish were randomly placed into one of nine circular 1400 l aquaria (2 m diameter, maximum 13 fish tank^{-1}, or $\sim$0.028 kg l^{-1}). Aquaria (holding tanks) were supplied with filtered and UV sterilized fresh water ($\sim$40 l min^{-1}; LS-Permabead Filtration System, Integrated Aqua Systems Inc., Escondido, California) from Cultus Lake. All aquaria were $13 \pm 0.2\,^{\circ}C$ at fish arrival, and were maintained at this temperature for 24 h to allow fish to recover from the stress of transport. Tank temperatures were monitored carefully in real time (checked at least every 30 min during temperature ramp-up periods and every hour between 0700 and 0100 h at all other times during the experimental period), and later confirmed using data collected using iButton temperature data loggers (Maxim Integrated Products, Inc., Sunnyvale, California).

2.2. Thermal and simulated capture treatments

Summer-run fish can encounter migration temperatures through the lower Fraser River which can range from <13 $^{\circ}C$ to >21 $^{\circ}C$ (Patterson et al., 2007). We selected temperatures for our experiments that spanned this range. The temperatures of three tanks were maintained at $13 \pm 0.2\,^{\circ}C$ while the temperatures of the other six tanks were slowly (<1 $^{\circ}C$ h^{-1}) ramped up to treatment temperatures of $19 \pm 0.2\,^{\circ}C$ (3 tanks) and $21 \pm 0.2\,^{\circ}C$ (3 tanks), where they remained until the end of the experiment. Due to logistical constraints, we elected to expose fish to an equal rate of temperature increase at the cost of equal lengths of temperature exposure before capture treatments in order to reduce mortality due to excessively rapid warming. Therefore, after 12 h (in the case of 21 $^{\circ}C$ treatments) to 24 h (in the case of 13 $^{\circ}C$ treatments), fish were individually netted into a doughnut shaped aquaria (2 m diameter, 2 fish per tank) at temperatures equal to that of their holding tanks, scanned for PIT tag numbers, and their ventilation rates were counted by observing opercular beats for 30 s. Fish were randomly assigned one of three simulated capture treatments: (1) "handling only", which included handling, transfer, and monitoring in an identical fashion to fish exposed to the other treatments, only the chase, exercise and air exposure protocols were omitted, (2) "capture", which included three minutes of manual chasing, eliciting a flight response and exhaustive exercise, or (3) "capture plus air exposure," which included "capture" immediately followed by one minute air exposure. Fish were stimulated to exercise by four experimenters, who leaned over the perimeter of the tank and touched the tails of the fish or splashed vigorously behind them. Fish were stimulated each time they stopped burst swimming in order to elicit the maximum anaerobic exercise possible using this method, a common approach in studies of fish responses to exercise (Kieffer, 2000; Milligan, 1996). Air exposure was achieved by rapidly dip netting the individual fish immediately after the three minute exercise had elapsed, and elevating it in the net just above the surface of the water for 60 s. Immediately after the assigned treatment, ventilation rates were counted for 30 s and observable impairments such as the inability to maintain dorso-ventral equilibrium were recorded for presence/absence and duration. Fish were continuously visually monitored for 25 min after the cessation of treatments. Midway through this monitoring period, fish were moved to smaller (100 l, 1 m $\times$ 0.5 m $\times$ 0.3 m) individual holding tanks with fresh flowing water until 30 min had elapsed fish since were transferred to the initial treatment tanks. For logistic purposes, fish were subjected to treatments in pairs; treatments for a pair of fish occurred in the same tank at the same time, however each fish was netted, moved, handled, exercised, air-exposed, and sampled individually and simultaneously. All procedures and fish care were approved by the Canadian Council on Animal Care (#A08-0388).

2.3. Blood sampling, processing and analysis

Thirty minutes after the fish entered the initial treatment tank (onset of stressor), they were moved to a flow-through, foam-lined v-shaped trough, where they were sampled for blood by holding them in a supine position. This sampling time allowed both the detection of elevation of stress indices in the blood, and logistically allowed for the inclusion of 101 individuals over 2 days. The anterior end of their body was kept completely underwater to allow for normal respiratory gas exchange. Three milliliters of blood was collected via caudal venipuncture using a heparinized Vacutainer (Becton, Dickinson and Company – Canada, Mississauga, Ontario), and stored in an ice-slurry until subsequent processing (<45 min). This technique took less than one minute to complete, and is a component of a suite of biopsies and sampling techniques used in several past studies involving adult sockeye salmon and have been shown to have negligible effects on fish health and behaviour (reviewed in Cooke et al., 2005, 2008).

After blood samples were collected, fish were moved to large ($\sim$7000 l, 3 m diameter) circular aquaria supplied with fresh water in the same manner as the smaller aquaria described above. Fish were monitored carefully for morbidity by observing their behaviour and physical condition every 5 min for at least 2 h after blood samples were collected. Thereafter they were observed at least once per hour between 0700 and 0100 h until the end of the experiment at approximately 72 h. Fish were judged to be moribund if they exhibited permanent loss of equilibrium or if they became unable to swim, but were still ventilating. Fish that ceased ventilating completely were deemed dead. Moribund and dead fish, as well as fish surviving to the end of the experiment, were removed immediately from the tank by dip net with minimum disruption to the remaining fish, and both moribund fish and those surviving to the end (i.e., 72 h post treatment) were euthanized by cerebral concussion. This 72 h period enabled us to evaluate short-term mortality (frequently regarded as 2–3 days post release; Arlinghaus et al., 2007), and also provided the opportunity to assess physiological recovery at a standardized time-point. Fish were then immediately sampled for blood in the same manner as the initial sample collection; if more than 10–15 min had elapsed since death, fish were not sampled. A small (5 mm) piece of adipose fin tissue was removed to identify individuals to stock (Beacham et al., 2004, 1995). For each fish we recorded time of death, sex, post-orbital-hypural (POH) length, girth (at the fattest point of the fish), somatic fat content (using a handheld microwave fat meter, Distell Fish Fatmeter FM 692, Distell.com Inc., West Lotham, UK; following the protocol and conversion equation described in Crossin and Hinch, 2005), and whole body mass. Morphometric and energetic measures were recorded so that physiological results could not be attributable to differential size or energy status between treatment groups.
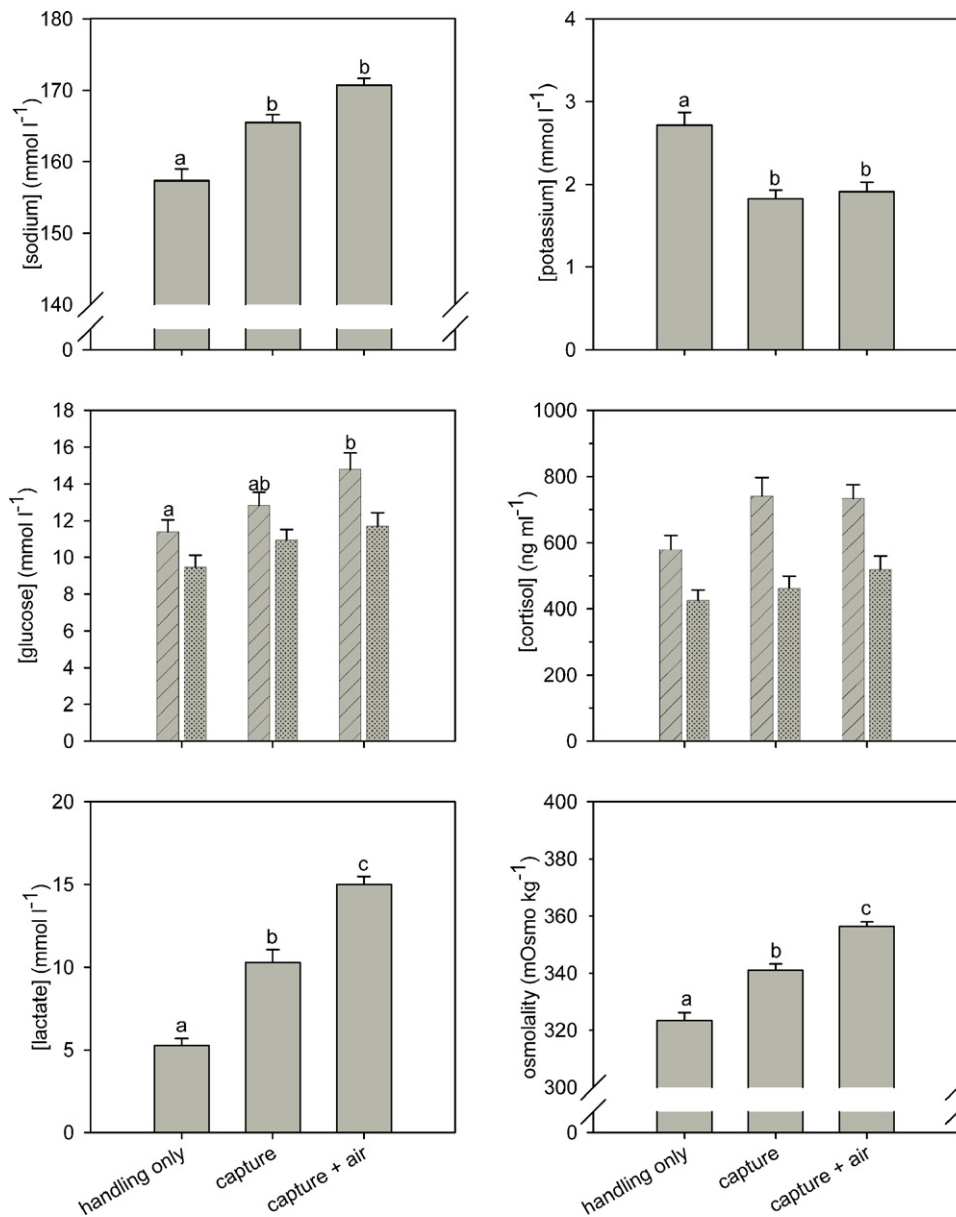
Fig. 2. Mean plasma sodium, potassium, glucose, cortisol, and lactate concentrations and osmolality by capture treatment group, collected 30 min after capture treatment, with standard error bars ($n = 34 \pm 2$). Where sexes responded differently to capture, bars are patterned (lines indicate females and stipples indicate males, $n = 17 \pm 5$). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

2.4. Assays

Whole blood was centrifuged at $7000 \times g$ for 6 min and plasma was stored at $-80\,°C$ until further analysis. Plasma was subsequently analyzed for cortisol, testosterone and 17β-estradiol (Neogen ELISA with Molecular Devices Spectramax 240pc plate reader), lactate, glucose (YSI 2300 Stat Plus analyzer), osmolality (Advanced Instruments 3320 freezing-point osmometer), chloride (Haake Buchler digital chloridometer), sodium, and potassium (Cole-Parmer, model 410 single-channel flame photometer) in the manner described in Farrell et al. (2001).

2.5. Statistical analysis

In order to test for an effect of fish sex on physiological responses to treatments, each were analyzed using three-way Analysis of Variance (ANOVA) with interactions to assess the joint effects of sex, capture treatment, and temperature. In cases where sex

had no effect we removed it from the analysis and used two-way ANOVA on each variable, and where sex was determined to be a significant effect we separated the genders and used 2-way ANOVA on each separately to determine the effect of capture treatment and temperature. Where statistical differences were detected between capture treatment or temperature groups, Welch's t-tests were performed post-hoc to determine the nature of those differences. Pearson's Chi-square tests were used to detect effects of capture treatment or temperature on the frequency of equilibrium loss after treatment and mortality prior to the termination of the experiment. Significance levels were set at 0.05. We present the p-values for individual tests and indicate significance using False Detection Rate (Curran-Everett, 2000) to correct for multiple comparisons. All tests were performed using R statistical software (R Foundation for Statistical Computing, Vienna, Austria). Data were $\log_{10}$-transformed if they failed to meet statistical assumptions of normality and equal variance. Prior to other analyses, treatment and temperature groups were checked for
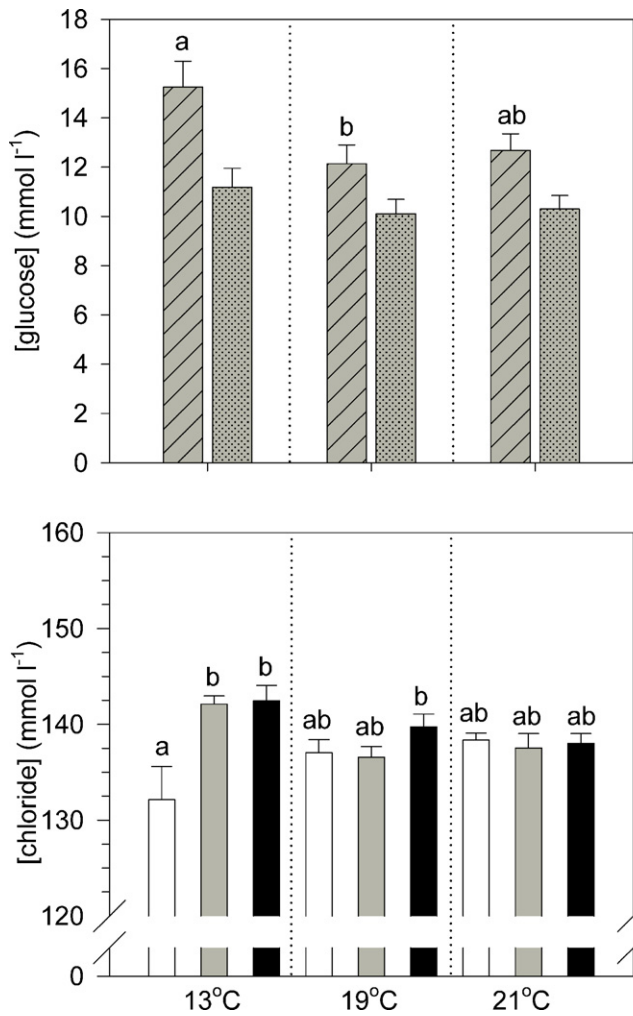
Fig. 3. Mean plasma glucose by temperature ($n = 17 \pm 4$) for females (lines) and males (stipples), and plasma chloride by capture × temperature group (sexes pooled, $n = 11$–12), collected 30 min after capture treatment, with standard error bars. Bar shading indicates capture treatment—handing only (white bars), capture (grey bars), capture + air exposure (black bars). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

differences in size (length, mass) or energy status using two-way ANOVA.

3. Results

All 101 sockeye were confirmed to be from the summer run-timing group of stocks, primarily from the Late Stuart/Stellako, Chilko, and Quesnel stocks. There were no morphological or energetic differences between fish in different temperature or capture treatment groups (ANOVA: $p > 0.05$).

3.1. Immediate responses to treatment

All fish appeared exhausted before the end of the three-minute exercise component of simulated capture, and were barely responsive to tactile or visual stimuli (no longer bursting away from experimenters hands). Most fish rested on the bottom of the tank or drifted in the current following cessation of treatment, while non-exercised fish generally held position in the current or moved around the tank. Capture treatment had a significant effect on the frequency of equilibrium loss (Pearson's Chi-square: $\chi^2 = 61$, d.f. = 2, $p < 0.0001$), while the effect of temperature was significant only before correction for multiple comparisons (Pearson's Chi-square:
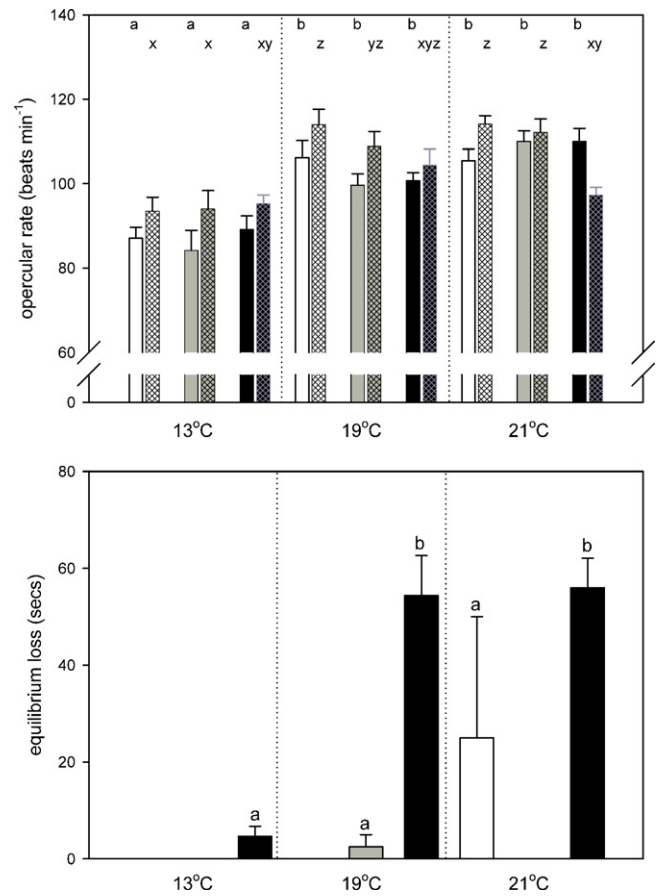

Fig. 4. (Top) Mean ventilation rate for each capture treatment × temperature group, measured immediately before (no pattern) and after (cross-hatched) capture treatments were applied, with standard error bars. Bar shading indicates capture treatment—handing only (white bars), capture (grey bars), capture + air exposure (black bars). Lower-case letters a,b indicate significant differences between temperatures in ventilation rates pre-treatment ($n = 11$–12), and lower-case letters x, y, z indicate the significant differences after False Detection Rate correction for multiple comparisons between capture treatment × temperature groups on post-treatment ventilation rates. (Bottom) Mean duration of equilibrium loss immediately after capture treatment, for each capture treatment × temperature group ($n = 11$–12), with standard error bars. Bar shading indicates capture treatment—handing only (white bars), capture (grey bars), capture + air exposure (black bars). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons. Bars with the small letter (a) are not significantly different from zero.

$\chi^2 = 6.3$, d.f. = 2, $p = 0.042$). All 23 fish in the 19 °C and 21 °C air-exposed groups, as compared to five (42%) of the cool-temperature air-exposed fish lost equilibrium after application of the capture-stressor. The duration of equilibrium loss was longer (19–98 s) for the 19 °C and 21 °C fish, than for the 13 °C fish (5–23 s; Fig. 4). Only two (3%) fish that were not air-exposed demonstrated a loss of equilibrium after treatment (duration of equilibrium loss showed a significant temperature × capture treatment interaction, ANOVA: $F_{4,92} = 21.46$, $p < 0.0001$). Ventilation rates measured before exercise treatments were lower in 13 °C fish compared to fish in 19 °C or 21 °C (ANOVA: $F_{2,92} = 11.6$, $p < 0.0001$), whereas immediately after exercise treatment, ventilation rates were depressed in 21 °C air-exposed fish (Fig. 4; significant temperature × treatment interaction (ANOVA: $F_{4,92} = 2.9$, $p = 0.027$).

3.2. Post-capture samples—30 min after treatment

Capture treatment had a significant effect on sodium (ANOVA: $F_{2,92} = 19.0$, $p < 0.0001$), potassium (ANOVA: $F_{2,92} = 7.0$, $p = 0.0015$), lactate (ANOVA: $F_{2,92} = 38.5$, $p < 0.0001$), osmolality (ANOVA:
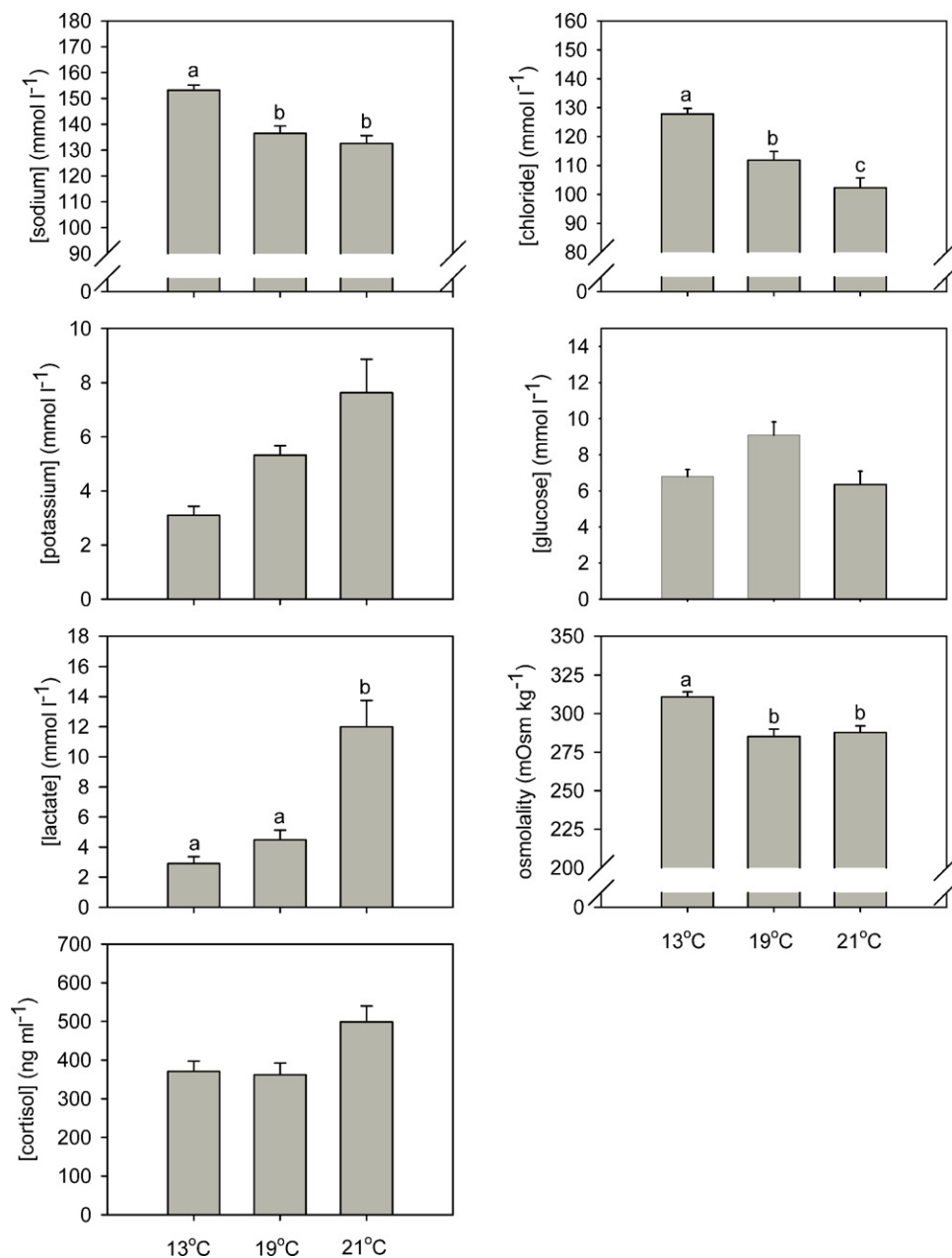
Fig. 5. Mean plasma sodium, chloride, potassium, glucose, lactate, osmolality and cortisol by temperature group ($n = 32 \pm 2$), collected 72 h after capture treatment, with standard error bars. Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

$F_{2,91} = 36.3$, $p < 0.0001$; Fig. 2), and glucose (females only; ANOVA: $F_{2,44} = 4.2$, $p = 0.022$) measured at 30 min (Fig. 3). In contrast, temperature treatment did not have a significant effect on any of the plasma parameters at this sampling (ANOVA: $p > 0.2$) with the exception of glucose (females only; ANOVA: $F_{2,44} = 5.3$, $p = 0.0089$). In some cases, capture alone significantly elevated parameters above values for "handling only" fish. Plasma chloride concentrations were higher in captured than in "handling only" fish, however with chloride a significant temperature $\times$ treatment interaction (ANOVA: $F_{4,92} = 4.4$, $p = 0.0026$) prevented statistical confirmation of this difference. We detected no effect of capture treatment or temperature on cortisol for either sex (ANOVA: $p > 0.2$).

3.3. Terminal samples—72 h after treatment

The effects of the capture treatments were no longer evident in any plasma variable at the terminal sampling, 72 h post treatment.

In contrast, temperature treatment did have a detectable effect on chloride (ANOVA: $F_{2,89} = 9.2$, $p = 0.00023$), sodium (ANOVA: $F_{2,89} = 7.7$, $p = 0.00084$), lactate (ANOVA: $F_{2,89} = 5.0$, $p = 0.0086$), and osmolality (ANOVA: $F_{2,87} = 4.5$, $p = 0.014$) at terminal sampling (Fig. 5). Plasma lactate concentrations had approximately halved for the 13 °C and 19 °C groups since the first sampling (decreased from ~9 to ~4 mmol l^{-1}), however lactate for the 21 °C fish had not recovered at all (~12.0 mmol l^{-1}). During terminal sampling, on the last day of the experiment, we began to observe mortality in the 21 °C fish and therefore sampled moribund or dead fish between terminal sampling of the survivors. Fourteen female (14%) and six male (6%) fish from the 21 °C treatment died before the termination of the experiment (sex not statistically significant, Pearson's Chi-square: $\chi^2 = 2.50$, d.f. = 1, $p = 0.11$; deaths occurred 46–76 h after chase treatments), while no fish from the 13 °C or 19 °C treatments died during this time. Capture treatment did not have a significant effect on survival (Pearson's Chi-square, 21 °C fish only: $\chi^2 = 1.22$,

d.f. = 2, $p = 0.54$), however captured fish trended towards higher mortality (45% handling only, 64% captured, and 67% captured and air-exposed fish died).

We evaluated analyses of 72 hour plasma constituents including all 21 °C fish, and then repeated the analysis excluding samples taken from moribund or dead fish to account for the fact that these fish were inherently different from the 21 °C survivors. Overall, fish that were found dead or moribund had much higher lactate levels ($\sim$16.9 mmol l^{-1}) than 21 °C fish that were live-sampled at the end of the experiment (Welch's t-test: $t = 4.77$, $p < 0.0001$), despite the similar time of sampling, although six individuals that died had lactate levels well within the range of the 72 h samples from 21 °C survivors ($\sim$4.9 mmol l^{-1}). When we excluded the 20 moribund or dead fish, there was no significant effect of temperature on terminal lactate levels. All fish were checked for signs of being moribund every 5–10 min on the last experimental day (when mortalities were occurring), therefore we are confident that samples were taken from dead fish were collected only minutes after death. Plasma chloride and sodium concentrations at this sampling were lower for the 21 °C and 19 °C groups than for the 13 °C group, a result that was significant whether or not we excluded mortalities (Welch's t-test: $p \leq 0.011$; and 21 °C survivors were not different than 21 °C mortalities in terms of plasma sodium, potassium, osmolality, or cortisol after correction for multiple comparisons; Welch's t-test: $p > 0.01$). No other effects of temperature in the plasma were detected at this sample time.

4. Discussion

This is the first experiment examining the synergistic effects of ecologically relevant high temperatures and capture stressors on any species of adult river-migrating Pacific salmon. Contrary to our expectations, there was no substantial relationship between direct short-term mortality and capture treatment at any temperature. However, in the only published research quantifying the relative survival of wild migrating sockeye salmon in the Fraser River caught by angling compared to beach seine (at 17–19 °C, Donaldson et al., 2011), lower survival of angled fish became most apparent when evaluated at arrival at sub-natal watersheds (after > 96 h post-release). Since we observed no mortality of fish held at comparable temperatures for the duration of our study, there remains the possibility that mortality associated with capture treatments would become apparent over a longer time-course. The observed mortality at 21 °C was not unexpected, as this temperature is believed to be at or approaching the critical thermal limits for adult sockeye salmon (Eliason et al., 2011).

4.1. Capture treatment effects

We used manual chasing (Kieffer, 2000, e.g. Milligan, 1996) to elicit the burst swimming behaviour that is typical of a fish fighting on a hook and line, or struggling to escape from trawl, seine, or gill nets. Three minutes of exhaustive exercise is a capture stressor consistent with angler handling of sockeye salmon during catch and release (Donaldson et al., 2011), but it is likely a conservative time estimate in comparison to the experience of sockeye salmon being released from other gear types. Up to one minute of air exposure may occur during release by a commercial or recreational fisher, depending on the difficulty of hook removal or net disentanglement (Donaldson et al., 2011). When fish burst swim, they utilize anaerobic respiration fuelled by energy stores found in white muscle tissue, producing lactic acid as a by-product (Wood, 1991). The dissociation of a proton results in the production of lactate anions, and a portion of both compounds move from the muscle to the blood. Consequently, elevation of lactate in the blood indicates

elevations of these metabolites in the white muscle. We were interested in measuring plasma lactate concentrations after applying simulated capture stressors to assess the relative impacts of our capture treatments. Compared to the handling only treatment ($\sim$5 mmol l^{-1}; similar to sockeye salmon sampled immediately after beach-seining; Donaldson et al., 2011), plasma lactate was doubled in captured fish and tripled in air-exposed fish 30 minutes after treatment. Overall, we detected up to a 13-fold increase in plasma lactate above baseline levels of sockeye being held in the same conditions ($\sim$1.5 mmol l^{-1}; Jeffries et al., 2011), thus it was surprising that we did not see reduced survival of the captured and air-exposed fish. Donaldson et al. (2010a) detected equally high lactate levels in hatchery coho salmon (O. kisutch) using identical capture simulation procedures at 8 °C without significant mortality. These results suggest that Pacific salmon have the ability to recover from substantial (acute) instances of lactic acidosis in fresh water, confirming prior marine work on coho salmon (Farrell et al., 2001) and in-river work on sockeye salmon (Donaldson et al., 2010b). However, Jain and Farrell (2003) found that repeat swim performance was reduced in rainbow trout (O. mykiss) with lactate levels above a threshold of $\sim$12 mmol l^{-1}, suggesting that salmonids may be more susceptible to subsequent capture by fisheries or predators if their ability to escape is impaired.

Elevations in cortisol are a characteristic response of fish to stress (Barton, 2002). Consequently, cortisol is the principle corticosteroid measured in response to catch and release stressors (Arlinghaus et al., 2007). Previous research has shown that female Pacific salmon may demonstrate a greater increase of plasma cortisol than males in response to stress (Fagerlund, 1967; McQuillan et al., 2003), and cortisol is involved in the regulation of energy metabolism and the hydromineral balance (Barton, 2002). Stress hormones trigger mobilization of stored aerobic energy (Gamperl et al., 1994; Wendelaar Bonga, 1997) resulting in increased glucose levels in the plasma. Therefore, we analyzed the sexes separately when they differed in their response to the treatments. The lack of significant effect of capture stressors on cortisol levels in our study was surprising, however both glucose and cortisol levels did trend higher with the application of capture stressors, and we detected higher plasma glucose in air-exposed compared to "handling only" females. Both cortisol and glucose in the sockeye in our study were high compared to other studies on adult sockeye salmon. Glucose levels from our experimental fish (4.4–22.2 mmol l^{-1}) were double to triple those of bio-sampled migrating sockeye captured by dip-net (Young et al., 2006), depending on capture treatment. The rapidity of sampling after capture with a dip-net ensured that glucose levels have not yet had a chance to respond to the stress of capture and handling, and our experimental fish were likely demonstrating elevated glucose and cortisol concentrations in part due to the chronic stress from their days in captivity (Portz et al., 2006; Roscoe et al., 2011). Sockeye salmon in our experiment demonstrated a more than 10-fold elevation in cortisol levels above the river-migrating sockeye salmon in Young et al. (2006), and an approximately five-fold elevation above quiescent sockeye salmon held in captivity and sampled via catheter in Sandblom et al. (2009), presumably in part due to handling and capture stressors.

Exercise and stress can disrupt ionic and osmotic balances within the blood and tissues, by affecting water or ion uptake or elimination mechanisms (Wendelaar Bonga, 1997). Plasma sodium and chloride ion levels respond to the accumulation of metabolites in the muscle tissues due to exercise and stress; this osmoregulatory disturbance can cause water to move out of the plasma and into the muscle, increasing plasma ion concentrations (Wood, 1991). Consistent with this, captured sockeye salmon in this study had higher plasma concentrations of sodium and chloride ions 30 min after treatment than did "handling only" fish. Values from our study were similar to data ranges from other studies

on river-migrating sockeye salmon (Clark et al., 2010; Donaldson et al., 2010b; Young et al., 2006) and for capture-simulation treated coho salmon (Donaldson et al., 2010a), suggesting that capture treatments had caused some osmoregulatory disturbance, but most fish were still within normal limits for this stage of their life history. Differences in total osmolality were predictable as they are likely driven primarily by differences in the main plasma solutes, lactate, sodium and chloride, among the capture treatment groups. A surprising result of this study was the lower plasma potassium levels in captured fish compared to "handling only" fish, since exercise is known to increase plasma potassium as it is lost from the muscle cells (Sejersted and Sjøgaard, 2000; Thomas et al., 1987). We can only speculate that the lower levels 30 min after exercise are a function of sampling time and the rapid re-uptake of potassium ions from the extracellular space (Nielsen and Lykkeboe, 1992). Whereas blood sampling 1–2 h post-stressor may have yielded different results in the suite of variables measured here, 30 min post-stressor blood sampling was chosen in order to capture responses to treatments and to maximize the number of individuals we were able to treat and sample in a short time. Results from an experiment on coho salmon using identical simulated capture protocols yielded the same patterns in blood chemistry when sampled one hour post-stressor (Donaldson et al., 2010a).

4.2. Temperature effects

Temperature had an observable effect on whole animal physiology both before and immediately after capture treatment, therefore we were surprised at the lack of detectable effect in the plasma constituents measured 30 min after simulated capture. We offer two possible explanations: (1) the relatively short exposure to high temperatures prior to capture treatments resulted in minimal disturbance to blood physiology; or (2) while the warmest temperatures were already having physiological consequences, the effects of the different thermal stress levels may have been masked by the more recently imposed simulated capture stressors. It is possible that the effects of capture stressor and temperature on the plasma stress indicators would have been additive had we applied the capture treatment after a longer high temperature exposure ($21\,^\circ$C is known to be stressful for sockeye salmon; Brett, 1971; Eliason et al., 2011; Farrell et al., 2008; Gilhousen, 1990; Keefer et al., 2008; Martins et al., 2011). The exposure time to elevated temperatures of 12–24 h is meaningful, however, as it represents our approximation of fish encountering warm water and concentrated fisheries as they enter and migrate through the lower river.

Warm temperatures had an effect on ventilation rates and the ability of fish to maintain equilibrium immediately after treatment. Compared to fish in $13\,^\circ$C, ventilation rates were 18% higher in $19\,^\circ$C fish and 25% higher in $21\,^\circ$C fish before treatment, likely reflecting an increase in resting metabolism due to warmer body temperature. After exercise, sockeye salmon exhibit an increased rate of oxygen consumption (termed excess post-exercise oxygen consumption, EPOC) as they re-establish homeostasis (Lee et al., 2003). EPOC has been shown to increase with temperature in juvenile and adult sockeye salmon (Brett, 1964; Lee et al., 2003). Oxygen is required to fuel the processes that correct metabolic and ionic biochemical imbalances and restore oxygen and phosphate stores to the tissues (Gaesser and Brooks, 1984; Lee et al., 2003). Interestingly, fish that were captured (burst swimming fuelled by anaerobic metabolism) then air-exposed (preventing respiratory gas exchange) in the warmest water demonstrated an 11% decrease in ventilation rate once returned to the water. While we did not quantify ventilatory volume, if we assume that slower ventilation frequency translated to reduced gas exchange and lower oxygen uptake, then fish that presumably had the greatest need to recover oxygen were the least able to do so quickly. This combined with

the inability of air-exposed fish in $19\,^\circ$C and $21\,^\circ$C to maintain equilibrium when first returned to the water is evidence that the warm water temperatures were having deleterious physiological effects on the fish at this time. This supports our second explanation that temperature effects were undetectable in the plasma simply because they were masked by the other stressors.

At the end of the experiment fish had been allowed ~72 h to recover from simulated capture treatments, and at final sampling we detected no legacy effects of those treatments. We elected to terminate the experiment at 72 h because it allowed us to sample moribund and surviving fish at the same time-point. Also, our previous work on sockeye salmon demonstrated there were no detectable legacy effects of capture treatment on survival or physiology after approximately 48 h. In the current experiment, the physiological effects of warm temperatures were evident in the high plasma lactate and depressed chloride and sodium concentrations in the $21\,^\circ$C fish at 72 h. Being a by-product of glycolysis, plasma lactate is an indicator of anaerobic metabolism, which results when systemic oxygen demand exceeds supply, such as during burst swimming or high-temperature induced hypoxia (Pörtner, 2001). As a group, the 72 h mean plasma lactate in $21\,^\circ$C fish ($\sim$12 mmol l^{-1}) was similar to those measured after capture treatment, including some fish with concentrations up to 20-fold higher than baseline. Our data comparing surviving fish with mortalities also suggest that lactate levels either elevate drastically immediately before death (Bradford et al., 2010; Hruska et al., 2010; Tierney et al., 2009), and/or that lactate levels this high contributed to mortality. For example, these individuals may have been experiencing oxygen deficiency caused by temperatures beyond critical thermal limits, resulting in passive survival using anaerobic mitochondrial metabolism (Pörtner, 2001, 2002). Unfortunately, our design does not permit us to determine whether some mortality may have been attributable to acidosis, but certainly other mechanisms were also important. The lower concentrations of plasma sodium and chloride ions detected in the $19\,^\circ$C and $21\,^\circ$C temperature treatments after 72 h were still significant when we analyzed only the live-sampled fish. Thus, we are confident that these patterns truly did relate to thermal stress, although potentially indirectly, as it may have been a consequence of impending death (Jeffries et al., 2011) or advanced stages of gill and kidney pathogen infection (Bradford et al., 2010), both of which may be modulated by warm temperatures. Consistent with these results, chronic stress can be a cause of osmoregulatory dysfunction, which in freshwater would cause a net loss of ions to the environment (Barton and Iwama, 1991; Wendelaar Bonga, 1997). Studies examining the physiology of sockeye salmon on spawning grounds suggest that metabolite accumulation, elevations of corticosteroids, immunosuppression, and osmo/ionoregulatory dysfunction may all contribute to natural senescence (Hruska et al., 2010; Morbey et al., 2005).

4.3. Conclusions and management considerations

Through river warming and changes in migration behaviour an increasing proportion of adult Fraser River sockeye salmon are undertaking migrations at temperatures that are well above their optimum and occasionally approaching their critical thermal limits, and hence have relatively low aerobic and cardiac scope available to migrate (Eliason et al., 2011; Farrell et al., 2008). Large proportions of the returning runs have perished during migrations as a result of high temperatures (Macdonald et al., 2010; Martins et al., 2011). Our results confirm that even without physical injury, which is a frequent consequence of gear encounters (Davis, 2002), the exhaustive exercise associated with fisheries capture results in substantial physiological stress in sockeye salmon. Air exposure during release results in additional disturbances as was evident from the plasma

analyses and the inability of air-exposed fish to maintain equilibrium after release. Even a temporary loss of equilibrium is likely dangerous to fish since it makes them far more vulnerable to repeat fisheries capture, predation, and drifting downstream. Due to the nature of the lower Fraser River fishery, sockeye salmon are very likely to encounter fishing gear (either recreational or commercial) more than once. If release of captured fish is intended as a conservation measure employed by managers, the increased probability of mortality may be a consideration when planning for openings and desired escapement numbers, or when accounting for the impact of non-retention fisheries.

While laboratory experiments such as this one on adult salmon have limitations in their applicability to wild migrants, this study was an important first step to understanding thermal impacts on capture-and-release stressors in sockeye salmon. We must acknowledge the caveats that fish in our study benefited from the absence of injuries typically incurred when encountering fishing gears, but were artificially challenged with the stress of captivity. However, the findings still have important implications for capture-and-release of river-migrating fish. Sockeye salmon exposed to our simulated capture treatments were characterized by elevated lactate, sodium, and chloride levels and lower potassium levels compared to their "handling only" counterparts, cortisol and glucose concentrations above expected levels for river-migrants, depressed ventilation, and the inability to maintain equilibrium. In order to survive, released fish will have to cope with ionoregulatory imbalances, oxygen deficits, and altered acid-base status, and clear lactate and other metabolites from the blood and tissues. The elimination of air exposure in sockeye salmon that will be released, particularly in temperatures $\geq 19\,^{\circ}\mathrm{C}$, will increase the probability of their survival through a reduction in equilibrium loss, as well as reducing the magnitude of physiological impairments. We also suggest that future research should investigate easily observable metrics such as equilibrium loss, ventilation rates, and reflex impairment (Davis, 2010; Davis and Ottmar, 2006) that could be developed into real-time tools to understand the physiological status of fish as they are being released. Given that temperatures in the Fraser River are expected to continue to warm in future years (Ferrari et al., 2007; Morrison et al., 2002) and Fraser sockeye salmon have shown declines in productivity over the past 20 years (a federal judicial inquiry is currently examining the potential causes of this decline), field research on survival and fitness consequences on sockeye salmon escaping from fishing gear (e.g. using telemetry to track released fish), particularly on stocks that are less tolerant of high temperatures, is warranted.

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