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Consequences of winter air exposure on walleye (*Sander vitreus*) physiology and impairment following a simulated ice-angling event

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ABSTRACT

Length-based harvest restriction is common in fisheries management and can result in a substantial number of fish being released after capture. Science on live release confirms that the practice allows individuals to return to the population and reproduce; however, little is known about how handling practices influence mortality or the sub-lethal physiological alterations in fish that are released during the winter. In this study, walleye (*Sander vitreus*; Mitchill 1818) were angled through the ice in Lake Nipissing, Ontario to evaluate the contribution of air exposure to the reflex impairment, post-release mortality, and the stress response of fish in the winter. Following 24 h holding, fish were exposed to a simulated angling event and exposed to air or snow across a range of exposure durations. Fish were non-lethally blood sampled and were assessed for reflex impairment and mortality 24 h after capture. No mortalities were recorded during the study and reflex impairment was not linked to exposure type or duration. Blood [lactate] at 1 h post-capture was comparable across treatment groups but was significantly higher than respective baselines. Plasma [cortisol], blood [glucose], and aspartate aminotransferase activities were comparable to baseline levels. Walleye appeared to be resilient to catch-and-release angling in the winter given that no mortalities occurred and fish suffered minimal reflex impairment and physiological disturbance following capture. Findings from this study suggest that mandatory catch-and-release regulations for sub-adult walleye are a useful tool for the management of winter walleye ice fisheries.

1. Introduction

Recreational fishing in inland waters is a popular pass-time and is growing in popularity (Cooke et al., 2015). As a result, recreational fisheries can be highly exploitative and ultimately share similar conservation concerns as commercial fisheries (Cooke and Cowx, 2006a,b). The over exploitation of fish stocks by recreational fisheries can have significant implications for biodiversity, trophic interactions, and ecosystem functioning (Cooke and Cowx, 2006a,b) such that fisheries managers use a variety of management strategies to reduce harvest in order to achieve fisheries and ecosystem management objectives (FAO, 2012). Various forms of harvest regulations include size limits (e.g. minimum or maximum size limits, slot limits), creel reductions, and/or spatiotemporal closures that mandate some fish be released (Johnson and Martinez, 1995; Coggins et al., 2007; Post, 2012). In addition, some anglers release fish voluntarily (Arlinghaus et al., 2007). Catch-and-release (C&R) is a valuable conservation and management tool for fisheries managers to prevent the overexploitation of fish populations (Wydoski, 1977; Post et al., 2002). The efficacy of C&R as a management tool relies on the tenant that released fish survive and suffer negligible fitness consequences (Wydoski, 1977; Cooke and Schramm, 2007). Although C&R has been widely adopted by anglers and managers (Arlinghaus et al., 2007), not all fish survive following release and all fish will experience some sub-lethal injury and stress (Muoneke and Childress, 1994; Arlinghaus et al., 2007). As such, there is a growing literature base focused on characterizing the consequences of C&R and optimizing C&R methods to inform management and ensure that C&R best practices are employed to maximize fish welfare.

Hooking injury, strenuous exercise, and prolonged air exposure because of C&R can result in a physiological stress response (Cooke et al., 2002; Gingerich et al., 2007) and mortality of released fish (Ferguson and Tufts, 1992; Danylchuk et al., 2007). Increased concentrations of the corticosteroid hormone cortisol is a primary indicator of the stress response in teleosts (Mommsen et al., 1999; Barton, 2002;

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Schreck and Tort, 2016). Following a stressor, cortisol acts to re-establish the internal homeostasis of the animal, which generally occurs by enhancing energy mobilization/availability (e.g. gluconeogenesis, glycogenolysis, etc.) and correcting hydromineral imbalances (reviewed in Wendelaar Bonga, 1997; Mommsen et al., 1999; Schreck and Tort, 2016). As such, cortisol is often associated with circulating concentrations of glucose, reduced hepatic glycogen content, and increased metabolic rates (reviewed in Wendelaar Bonga, 1997; Mommsen et al., 1999; Schreck and Tort, 2016). Moreover, lactate is typically elevated given that anaerobic metabolism is induced by exercise (i.e. fighting; Kieffer, 2000) and air exposure (Cook et al., 2015). In some instances, tissue damage (inferred from release of intracellular enzymes into the plasma; see Morrissey et al., 2005) can occur if environmental conditions are too extreme, exercise too vigorous, or air exposures too long. Consequently, these metrics are widely used to assess the stress status of an organism in field conditions (Iwama et al., 2005; Sopinka et al., 2016).

In C&R events, air exposure is one of the most commonly encountered stressors. Air exposure temporarily eliminates gas exchange at the gills leading to the development of hypoxemia and anaerobic metabolism (Ferguson and Tufts, 1992). Anaerobic metabolism during air exposure may result in metabolic acidosis through an accumulation of metabolic acid (i.e. lactate) wherein cardiovascular function and swimming performance may be adversely affected (Wood, 1983; Ferguson and Tufts, 1992; Cooke et al., 2001; Schreer et al., 2005; Cook et al., 2015). The degree to which air exposure impacts physiological operation is highly context and species specific (Cook et al., 2015). As with most aspects of ectotherm physiology, temperature is a driving factor in determining the magnitude of response during a stressor as well as in determining recovery dynamics during an air exposure event (Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007; Gingerich et al., 2007; Cook et al., 2015; Raby et al., 2015; Prystay et al., 2017). In some instances, the interaction of a number of stressors, including temperature and air exposure, during an angling event may result in post-release mortality (Bartholomew and Bohnsack, 2005; Gingerich et al., 2007). Although the influence of warm temperatures on caught and released fish has been investigated extensively (reviewed in Gale et al., 2013), little research has evaluated the influence of extreme cold temperatures and its interactive effects with air exposure on the fate of fish released in an ice-angling context.

Ice angling is a common recreational activity at northern latitudes (Margenau et al., 2003; Deroba et al., 2007) that subjects fish to capture stress during cold winter extremes. Despite the popularity of ice-angling, there is a paucity of information related to the effects of C&R during the winter months (Lavery, 2016; Louison et al., 2017a, b; Lennox et al., 2018). The stress response of ice-angled fish has been found to be slower and less pronounced than fish angled during the summer months (Louison et al., 2017a, b). However, rapid changes to ambient temperatures such as those experienced by fish captured during the winter can also elicit a stress response (Donaldson et al., 2008). Studies performed during the summer found that decreased water temperatures resulted in a corresponding decrease in walleye mortality following an angling event (Graeb et al., 2005; Schramm et al., 2010). The effect of air exposure during ice-angling is complex given the exposure of tissues to possibly harsh and freezing environmental conditions and, conversely, cooler water temperatures resulting in a delayed stress response. Therefore, it is unclear how fish may respond to air exposure stress during a period of lowered metabolism and correspondingly slower blood flow (Egginton, 1997). Thus, the objective of the following study was to address how handling stressors (especially related to air exposure) associated with a typical ice fishing event influenced the physiology and mortality of wild walleye (*Sander vitreus*; Mitchill 1818). It was predicted walleye exposed to air or snow following ice fishing would elicit a greater physiological stress response than those not exposed to these conditions.

2. Methods

2.1. Sampling site

Field work was conducted from January 10th to February 26th, 2017 on Lake Nipissing; an 87,325-ha lake situated in Ontario, Canada. Lake Nipissing is a relatively shallow lake with a mean depth of only 4.5 m and hosts a diverse fish community consisting of 42 species. Walleye in Lake Nipissing receive considerable fishing pressure from recreational anglers, a commercial fishery, and local Indigenous communities. Any walleye angled with a total length less than 46 cm must be released (OMNRF, 2017). For this study, all fish were collected from South Bay (46.18 °N, 79.59 °W) in four different sampling locations at depths ranging from 6.0 to 12.5 m. Water temperature remained 4 °C throughout the study period in the depth of water that walleye were angled from. Air temperatures ranged from −19.4 °C outside to 15 °C inside heated shacks. Air temperature data was retrieved from the weather station in Callander, Ontario (46.22 °N, 79.37 °W). All procedures were done in accordance with the ethical standards set by the Canadian Council for Animal care and approved by the Carleton University Animal Care Committee (AUP # 106247).

2.2. Ice angling

This work followed a similar methodological approach to that of Twardek et al. (2018). Fish were caught using either active or passive methods through drilled ice fishing holes (diameter of 20.3 cm). Active fishing involved an angler jigging a lure 15–30 cm from the bottom with a medium-light action ice fishing rod. Rods used for active fishing were spooled with 2.7 kg monofilament line rigged with 7.1–10.6 g treble-hooked jigging spoons or jigheads. Hooks were baited with an emerald shiner (*Notropis atherinoides*; Rafinesque, 1818). Once the angler detected a fish strike, the rod was jerked swiftly upward to set the hook and the fish was reeled quickly to the surface in < 15 s. Passive fishing typically involved the use of a tip-up, which is used to suspend a lure at a desired depth (15–30 cm from bottom) in the water and alerts the angler when a fish has begun to spool out the line by an indicator flag. Tip-ups were prepared with 9.1 kg braided line, a 7 g lead sinker, and either Gamakatsu Octopus #4 J-hooks or Gamakatsu Octopus #4 circle hooks baited with a live emerald shiner. Tip-ups were attended to immediately after an indication of a fish strike (i.e. raised flag) or every 15–45 minutes regardless of an indicator. Fish caught on tip-ups were retrieved hand-over-hand. Another passive fishing method that was employed involved using an unattended rod to simulate a tip-up. The rod was placed firmly in the snow and suspended a lure 15–30 cm from bottom. Passive rods were equipped with 2.7 kg monofilament line with Gamakatsu Octopus #4 J-hooks, Gamakatsu Octopus #4 circle hooks, or 7.1–10.6 g treble-hooked jigging spoons baited with a live emerald shiner. Using passive methods, the fight times were also short (< 15 s); although, the total time spent on the hook was unknown. The variation in angling techniques used here represents a suite of strategies to ensure that we could capture sufficient numbers of fish for use in this study. As outlined below, fish used in the mortality assessment were recovered for a 24 h period following the angling event to ensure that no adverse physiological effects of the angling event would appear in our experimental design. Gear type was not included in our statistical models as the recovery period meant that issues arising from hooking injury (e.g., deep hooking) would have likely manifested in death. As such, by focusing on survivors from that initial holding period we were able to control for hooking-related injury and mortality and focus our efforts on understanding the consequences of handling-related stressors such as air exposure.

2.3. Mortality and reflex impairment assessment

Once a walleye was caught, the hook was promptly removed, total fish length was measured, and anatomical hooking location was noted. During this period, air exposure was limited to < 10 s. Fish were then held in a submerged net pen for a 24 h holding period (0.5 175 m^3, radius = 0.5 m × height = 1.9 m, 1” diameter nylon mesh, conical net pen, H. Christiansen Company, Minnesota; see Twardek et al., 2018). Individual fish were fin clipped for identification purposes and the density of the submerged pen was limited to a maximum of 15 walleye per pen. The 24 h holding period prior to the experimental series was conducted to generate hooking mortality estimates published elsewhere (Twardek et al., 2018), focused on generating management-relevant gear-specific mortality rates. Here, we used survivors and asked different questions about the consequences of different handling procedures on fish condition and survival.

After the holding period, fish were returned to the surface and tested for reflex impairment using the reflex action mortality predictors (RAMP) assessment method (Davis, 2010; Raby et al., 2012). Fish were assessed based on body flex (the ability to flex and move when removed from the water while being held by the midsection), tail grab (attempted escape while in water when gently pinched on the caudal fin), orientation (ability to re-orient themselves in the water and maintain equilibrium when turned upside down), head complex (whether the fish continued to ventilate when removed from the water), and vestibular-ocular response (the ability of the fish to track the handler with eye movements when placed on its side out of water; Raby et al., 2012). Following the initial reflex impairment test, fish that showed no signs of impairment were chased for 2 min in a 189 L plastic tote to simulate an angling event. Reflex impairment was tested again using the RAMP method following the chase. Fish were then exposed to either snow or air for a random period that ranged from 0 s to 300 s based on the output of a random number generator in R using the sample function (R Core Team, 2017). Snow exposure consisted of simply laying the fish on the ice/snow, a common practice amongst walleye anglers in the winter (personal observations and communication with outfitters). Air exposure consisted of holding the fish out of water in the air for the designated period. Reflex impairment was tested again following the exposure treatments. Fish were then transferred to the submerged net pen and held for an additional 24 h monitoring period. After the final holding period, fish were brought to the surface, mortality was ascertained, reflex impairment was assessed, and live fish were released.

2.4. Physiological biomarkers

A subset of walleye caught with passive angling methods were exposed to one of four treatment groups following angling and processing (hook removal and measurement). These treatment groups consisted of a baseline group, a handling control, a 2 min snow exposure (laid on the ice), and a 2 min air exposure (held out of water). Baseline fish consisted of animals that were bled immediately following capture from the angling event (i.e. within 3 min) and were not subject to any of the experimental treatment. Ideally, these fish represented an undisturbed animal (Cooke et al., 2013; Lawrence et al., 2018). The handling controls were subject to the same transport and levels of handling as the snow and air exposed fish but were maintained within a water filled cooler such as not to be exposed to either the air or the snow. Snow exposure fish were simply laid on the ice for two minutes. This exposure is reflective of the common practices used by ice anglers when dehooking a captured animal (Personal observations). Air exposure fish were held in the air and represented conditions where an angler would be either de-hooking the animal or posing for a photograph with it (Cooke and Schramm, 2007). Fish were assigned to treatment groups systematically to avoid temporal bias and ensure even sample size distribution between treatment groups. Following treatments, a RAMP evaluation was performed on each fish prior to blood sampling (Raby et al., 2012). The handling control, air exposure group, and snow exposure group were held in submerged net pens for one hour to allow blood parameters to obtain elevated values for these physiological indices (Barton and Iwama, 1991). Only one fish was held per submerged net pen for the physiological stress assessments. After the holding period, fish were removed from the submerged net and bled within 3 min of being brought to the surface (Lawrence et al., 2018). Fish were bled through a caudal venipuncture using a 21 G needle and a heparinized (Na^+ heparin, 10, 000 USP units/ml; Sandoz Canada Inc., Boucherville, QC, Canada) 1 ml syringe. Blood lactate (mmol•L-1, Lactate Plus, Nova Biomedical Corporation Canada Ltd, Mississauga, ON, Canada) and glucose (mmol•L-1, Accu-Chek Compact Plus, Hoffman-La Roche Limited, Mississauga, ON, Canada) concentrations were assessed with handheld point-of-care-devices immediately following bleeding. Both the Lactate Pro lactate meter (Beecham et al., 2006; Brown et al., 2008) and Accuchek glucose meter (Beecham et al., 2006; Cooke et al., 2008) have been validated previously for use in teleosts. Furthermore, these types of devices are widely used in the assessment of teleost blood biomarkers in a variety of settings, species and contexts (reviewed in Stoot et al., 2014). Blood was then centrifuged for 2 min (2000 *g*; Mandel Scientific, Guelph, ON, Canada). The separated plasma was then decanted and stored at −80 °C. Plasma cortisol titres were made using a commercially available radioimmunoassay (RIA; ImmuChem Cortisol Coated Tube RIA Kit, MP Biomedicals, Solon, OH, USA) kit that has been previously validated for use in teleosts (Gamperl et al., 1994). Plasma cortisol was run on a single plate and had an intraplate assay variation of 6.18%. The activity of aspartate aminotransferase (E.C. 2.6.1.1.) in the plasma was assayed using a kinetic enzyme assay observing the oxidation of NADH in solution. This assay was assessed using the methods provided in Mommsen et al. (1980).

2.5. Statistical analysis

Statistical analysis was performed using R Statistical Software (R Core Team, 2017) with the level of statistical significance set at $\alpha = 0.05$. A mixed effects linear regression was implemented with the lme function in the R package nlme (Pinheiro et al. 2017). Because reflexes were assessed for the same individual at four timepoints (i.e. initial, after chase, after exposure, final), individual ID was incorporated as a random intercept in the model with the fixed effect being the assessment timepoint. To compare among assessment timepoints, a Tukey HSD test was implemented with the glht function in multcomp (Hothorn et al., 2008). To assess whether exposure duration or treatment in air/snow affected the extent of reflex impairment, a linear model was implemented investigating the change in reflexes between chase and exposure with exposure time and treatment as fixed effects. For the physiology component, separate one-way analysis of variance (ANOVA) models using the Welch’s test were completed to compare the concentrations of glucose, lactate, and cortisol; aspartate aminotransferase activities; and RAMP scores across treatment groups. Figures were plotted with the ggplot2 package (Wickham, 2016).

3. Results

The total sample size of walleye used for the mortality and reflex impairment component was n = 26. The mean total length of the 26 fish was 342 mm (± 55 mm SD) with only one fish being legal harvest size (460 mm) as per the Ontario Ministry of Natural Resources and Forestry fishing regulations (OMNRF, 2017).

3.1. Reflex impairment and mortality

Walleye were exposed for 176 ± 68 s in air or 140 ± 104 s in snow ($t = 1.04$, $df = 20.64$, $P = 0.31$). After exposure, 73.0% of the fish showed some symptoms of reflex impairment with 46.0% failing to body flex, 26.9% failing to maintain equilibrium, and 23.1% failing to respond to tail grab. All fish maintained ventilation and had a discernible vestibular-ocular response after exposure. Upon release, only one of the 26 fish showed minor reflex impairment (failed to body flex)

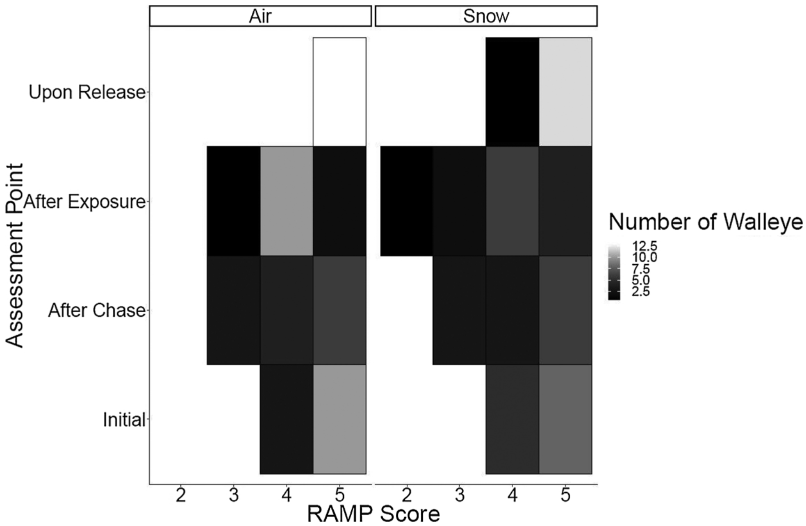

Fig. 1. Walleye (*Sander vitreus*) reflex impairment (RAMP) scores (sum of five tested reflex variables) at four time points. Body flex, tail grab, equilibrium, vestibular-ocular response, and head complex were tested prior to experimentation, after being chased, after being air exposed in air (left) or on snow (right), and prior to release. A RAMP score of 5 indicates no reflex impairment. Tiles are shaded by the number of fish in each RAMP score category at each time point.

with all other fish showing no signs of impairment whatsoever. No mortalities were recorded in either treatment group. Relative to initial values, reflexes were significantly lowered following chase ($z = -2.94$, $P = 0.02$) and exposure ($z = -4.27$, $P < 0.01$; Fig. 1). However, reflexes were not significantly different between the post-chase and post-exposure assessment periods ($z = -1.28$, $P = 0.29$; Fig. 1). There was then a significant improvement in reflexes when fish were released ($z = 6.03$, $P < 0.01$), which was similar to the initial reflex impairment observed and suggestive of recovery ($z = 1.76$, $P = 0.29$). Exposure time had no effect on reflex impairment ($t = -1.36$, $P = 0.19$) nor did treatment ($t = -0.63$, $P = 0.53$), suggesting that reflex impairment was not exacerbated by air exposure of walleye (Fig. 1).

3.2. Physiological biomarkers

Glucose, lactate, and cortisol concentrations in circulation were elevated in all treatment groups relative to the baseline group. However, no significant difference existed between treatment and baseline groups in both mean plasma cortisol concentrations ($p = 0.274$; Fig. 2) and blood glucose concentrations ($p = 0.092$; Fig. 3). Mean baseline blood lactate concentrations were significantly lower than the lactate levels of the control group, and both air and snow exposure groups (all $|t| > 3.74$, all $P < 0.01$; Fig. 4). Plasma aspartate aminotransferase activity was highest in the baseline and 2 min snow exposure treatment groups with activities of 16.4 µmol/min/L of plasma (± 9.1 µmol/min/L of plasma SD) and 16.5 µmol/min/L of plasma (± 7.8 µmol/min/L of plasma SD), respectively compared to the activity of the air exposure group (air: 12.7 ± 4.5, snow: 16.5 ± 7.8 µmol/min/L; Fig. 5). There was no significant difference in plasma aspartate aminotransferase activity between treatment groups ($p = 0.227$). Additionally, no significant difference in post-exposure RAMP scores was observed between treatment groups ($p = 0.344$).

4. Discussion

All 23 walleye undergoing simulated angling for the mortality and reflex impairment component of the study survived a 24 h post-release holding period. This result is consistent with a previous study on walleye captured via ice angling that found a post-release mortality rate of 0% (Cano et al., 2001). However, studies performed on Lake Nipissing found the post-release mortality of ice-angled walleye had a lower estimate of 7% (Twardek et al., 2018) and an upper estimate of 23% (Rowe and Esseltine, 2001). The large discrepancy between studies in walleye survival rates also appears in the literature in studies performed during the summer months. In some instances, the post-release mortality of walleyes has been as low as 0.8%–1.1% (Fletcher, 1987; Schaefer, 1989). However, more recent studies have found post-release mortality rates of angled walleyes ranging from 25%–31% (Reeves and Staples, 2011; Talmage and Staples, 2011) and even extending to 79% during angling tournament scenarios (Graeb et al., 2005). Walleye

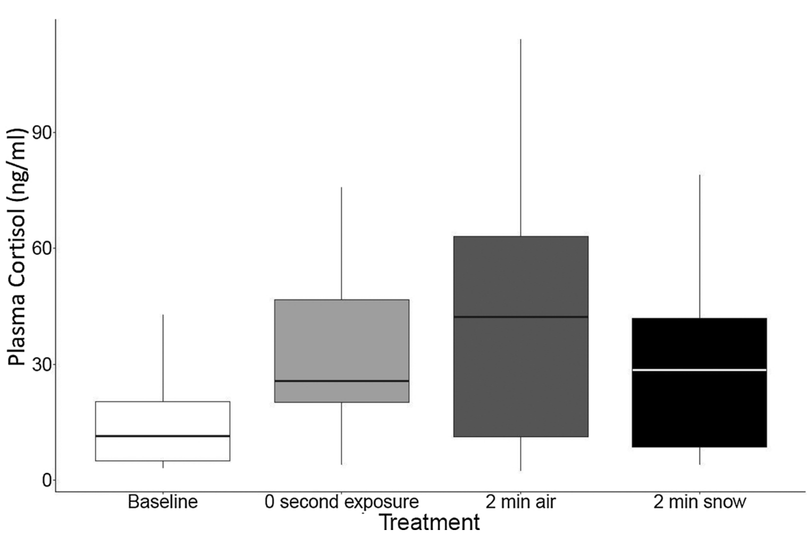

Fig. 2. Boxplots depicting plasma cortisol concentrations of ice-angled walleye at baseline levels (i.e. immediately following capture, t = 0; white bar; N = 7) or at 1 h post-stressor for fish treated as handling controls (0 s exposure; light grey bar; N = 8), after a 2 min air exposure (dark grey bar; N = 10), or following a 2 min snow exposure (black bar; N = 10). No statistical effects of treatment were found. Statistical analysis was conducted using a one-way analysis of variance (ANOVA) coupled with a post-hoc Welch's test. Statistical significance being accepted at $\alpha = 0.05$. Box plots depict the median difference score value, delineated by the interquartile range (1 st to 3rd quantile) and an accompanying whisker that represents 1.5x beyond this range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

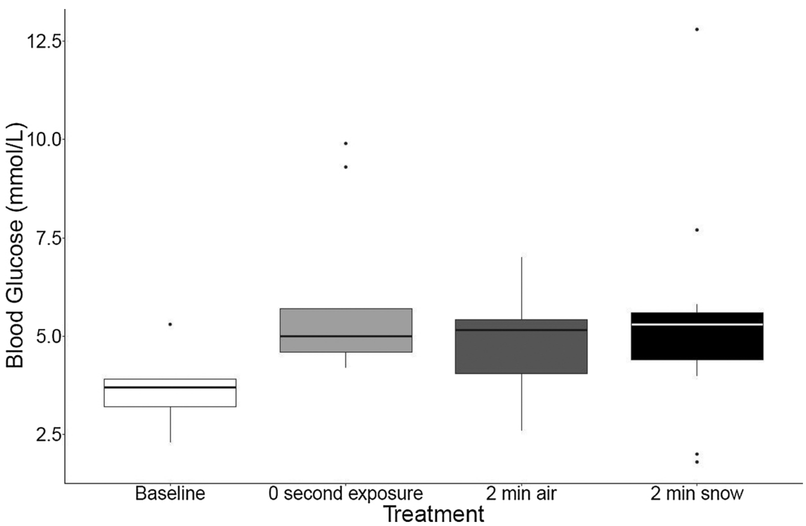

Fig. 3. Boxplots depicting blood glucose concentrations of ice-angled walleye at baseline levels (i.e. immediately following capture, t = 0; white bar; N = 9) or at 1 h post-stressor for fish treated as handling controls (0 s exposure; light grey bar; N = 10), after a 2 min air exposure (dark grey bar; N = 12), or following a 2 min snow exposure (black bar; N = 11). No statistical effects of treatment were found. Statistical analysis was conducted using a one-way analysis of variance (ANOVA) coupled with a post-hoc Welch's test. Statistical significance being accepted at α = 0.05. Box plots depict the median difference score value, delineated by the interquartile range (1 st to 3rd quantile) and an accompanying whisker that represents 1.5x beyond this range. Suspected statistical outliers are presented as black circles outside of the interquartile range (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

mortality rates have also been shown to vary drastically within a study depending on the water body (Payer et al., 1989) or the month that the fish were angled in (Reeves and Brusewitz, 2007). Evidently, several factors such as water temperature, handling, equipment used, anatomical hooking location, and depth of water being fished (ie. barotrauma) are important factors in determining the post-release survival of angled walleye (Graeb et al., 2005; Reeves and Brusewitz, 2007; Reeves and Staples, 2011; Talmage and Staples, 2011). Colder water temperatures correlate strongly with higher survival rates following angling during the ice-free period (Graeb et al., 2005; Reeves and Brusewitz, 2007). Therefore, the high survival rate of walleye captured via ice angling is logical due to the cold winter water temperatures and longevity of these fish in cold northern latitudes (Quist et al., 2003).

In addition to water temperature, air exposure is an important variable in determining the post-release survival of angled fish (Cook et al., 2015). Although no relationship was found between post-release mortality and air exposure duration, it is possible that damage to tissues such as gill filaments caused by exposure to freezing temperatures may have long-term consequences not initially apparent within the 24 h holding period. Indeed, Ferguson and Tufts (1992) identified damage to gill lamellae following air exposure that we did not quantify here. Most studies on walleye mortality have used a 120 h holding period (Reeves and Brusewitz, 2007; Reeves and Staples, 2011; Talmage and Staples, 2011) with one study holding fish up to 12 d (Fletcher, 1987). Extrapolating relationships between exposure and mortality based on our results is further complicated because fish used for the mortality and reflex impairment component of the study were held for an initial 24 h holding period prior to a simulated angling event and exposure. Following the initial holding period, only fish showing no signs of impairment were included in the study. As a result of this sampling methodology, this component of the study was inherently biased by selecting for hardier fish that may have had a higher likelihood of survival. Nonetheless, the high post-release survival rate of walleye after simulated capture via ice angling bodes well for the use of C&R as a conservation tool. Although there were no mortalities resulting from simulated capture, there were sublethal consequences that should also be accounted for.

The majority of fish subject to simulated capture experienced reflex impairment immediately after exposure. Reflex impairment was significantly lower following 24 h of holding/recovery with all but one fish being fully recovered prior to release. Despite a high prevalence of immediate reflex impairment, there was no significant relationship between exposure times and this response, nor was there a difference in reflex impairment for fish exposed to air or snow. The relationship between air exposure and stress is well understood and has been thoroughly researched with respect to summer C&R angling (Cook et al., 2015; Lawrence et al., 2018). However, there is a dearth of information regarding the consequences of ice-angling; particularly air exposure in harsh winter conditions (Lavery, 2016). The RAMP method was a highly effective proxy for migratory success in coho salmon

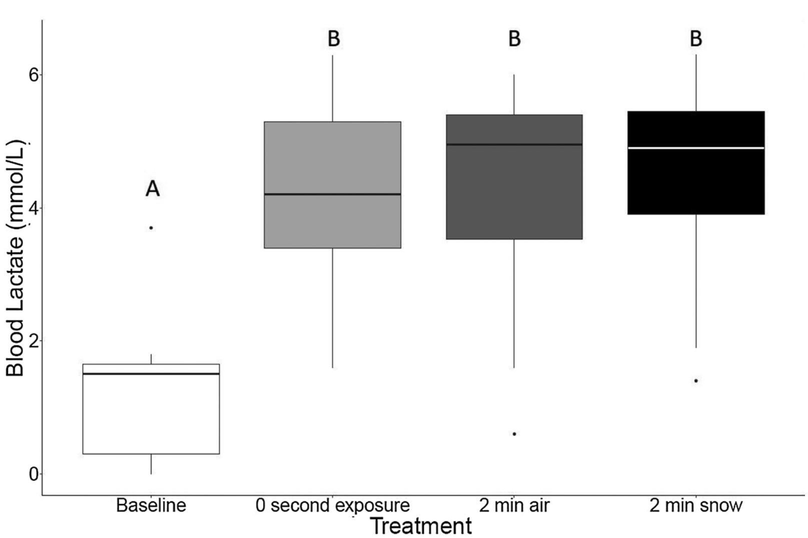

Fig. 4. Boxplots depicting blood lactate concentrations of ice-angled walleye at baseline levels (i.e. immediately following capture, t = 0; white bar; N = 8) or at 1 h post-stressor for fish treated as handling controls (0 s exposure; light grey bar; N = 10), after a 2 min air exposure (dark grey bar; N = 12), or following a 2 min snow exposure (black bar; N = 11). A significant treatment effect was found. Unique letters denote statistically significant differences among treatment groups. Statistical analysis was conducted using a one-way analysis of variance (ANOVA) coupled with a post-hoc Welch's test. Statistical significance being accepted at α = 0.05. Box plots depict the median difference score value, delineated by the interquartile range (1 st to 3rd quantile) and an accompanying whisker that represents 1.5x beyond this range. Suspected statistical outliers are presented as black circles outside of the interquartile range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

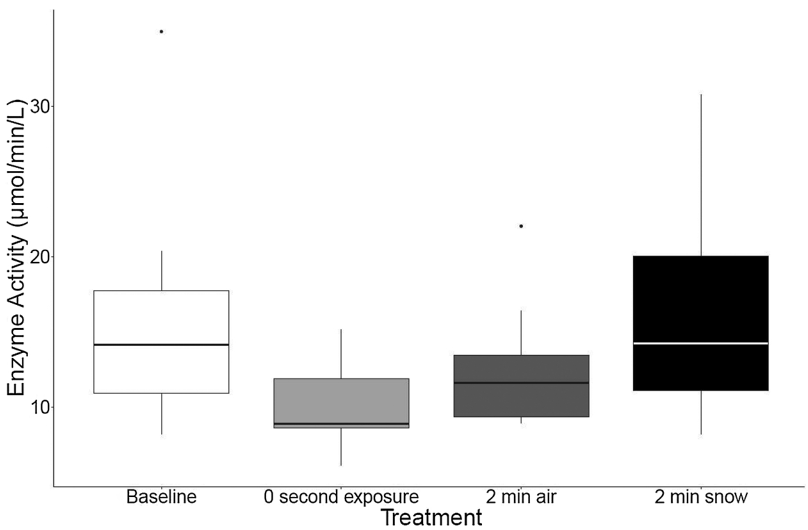

Fig. 5. Boxplots depicting activity of aspartate aminotransferase (E.C. 2.6.1.1.) in the plasma of ice-angled walleye at baseline levels (i.e. immediately following capture, t = 0; white bar; N = 7) or at 1 h post-stressor for fish treated as handling controls (0 s exposure; light grey bar; N = 7), after a 2 min air exposure (dark grey bar; N = 8), or following a 2 min snow exposure (black bar; N = 7). A no significant effects of treatment were found. Statistical analysis was conducted using a one-way analysis of variance (ANOVA) coupled with a post-hoc Welch's test. Statistical significance being accepted at α = 0.05. Box plots depict the median difference score value, delineated by the interquartile range (1 st to 3rd quantile) and an accompanying whisker that represents 1.5x beyond this range. Suspected statistical outliers are presented as black circles outside of the interquartile range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(*Onchorhynchus kisutch*; Walbaum, 1792) during September in southern British Columbia, which is drastically different from the conditions in our study site (Raby et al., 2012). Interestingly, it was observed that many of the fish handled in this study were lethargic, regardless of treatment group or exposure duration which may have had a slight effect on the interpretation of RAMP scoring used here. Although, Louison et al. (2017b) did show that RAMP scores are an effective means of assessing fish impairment in winter angled fish. We suggest that further lab-based studies be performed to assess the consistency of RAMP scores across environmental temperature regimes. Similar to the mortality results, the reflex impairment results must be interpreted cautiously because the sampling methodology selected for hardier fish. Furthermore, the use of multiple stressors in this study (Cooke et al., 1999) makes it difficult to ascertain which particular stressor or combination of stressors was responsible for the reflex impairment noted immediately after exposure. In addition to observed reflex impairment, there was some evidence that walleye underwent physiological alterations in response to simulated capture and handling.

It was expected that treatment groups would experience an elevation in plasma cortisol titres, relative to our controls. Elevations in plasma cortisol concentrations following an acute stressor have been well established in the literature (reviewed in Wendelaar Bonga, 1997 and Schreck and Tort, 2016). The lack of a discernible difference in plasma cortisol concentrations amongst our groups likely represents a contextual response. Factors such as prior stress history, life history stage, and personality/behavioural syndromes can all influence the degree of baseline and responsiveness of the stress axis in teleost fishes (reviewed in Barton, 2002 and Spagnoli et al., 2016). Thus, it is possible that individual/contextual effects may be attributed to the variation in cortisol responses observed here, producing a null effect.

Blood glucose concentrations were also unaffected by treatment group. Because of cortisol's role in energy mobilization and the fact that stressed teleosts exhibit elevated blood glucose concentrations (reviewed in Wendelaar Bonga, 1997; Mommsen et al., 1999 & Schreck and Tort, 2016), we expected walleye to demonstrate a similar increase in blood glucose concentrations to non-baseline treatments. However, blood glucose concentrations were consistent across all groups (Fig. 3). A proportion of our variation in blood [glucose] may be explained by catecholamine release following the angling event which results in glycogen breakdown and hyperglycemia typically (reviewed in Randall and Ferry, 1992; & Wendelaar Bonga, 1997). Although, this remains speculative as catecholamines were not measured in the current study. Blood lactate concentrations were significantly lower in the baseline group compared to the exposure treatment groups. Elevations in blood lactate titres in the non-baseline groups were expected given that air exposure produces a hypoxemia wherein the animal employs anaerobic metabolism consequently producing lactate as a metabolic by-product (reviewed in Wood, 1991). Moreover, lactate formation has been well characterized in angled fish as a direct consequence of exhaustive exercise during the angling event that elicits the use of anaerobic, white muscle fibres (Wood, 1991; Suski et al., 2003, 2004; Meka and McCormick, 2005; Lawrence et al., 2018). Together, stress associated with handling (i.e. all non-baseline fish) coupled with a lack of oxygen exchange in the air/snow exposure groups likely resulted in accruing oxygen debt that manifests as an accumulation of lactate in circulation and is likely the best explanation for our results. Interestingly, baseline fish did not have near zero concentrations of lactate in the blood (~2 mM; Fig. 4). This is likely the product of the animals burst swimming on the line (i.e. fighting the hook) before capture thereby resulting in some lactate accumulation.

Presence of aspartate aminotransferase in the blood plasma is indicative of potential damage to tissues (Oluah, 1999), especially damage to renal tissues where the activity of this enzyme is relatively high (Lawrence et al., 2015). Stress-induced fish have been shown to have increased plasma activity of aspartate amintotransferase (Wells et al., 1986; Butcher et al., 2010; Pullen et al., 2017). However, there was also no significant difference between aspartate aminotransferase activities between treatment groups suggesting that the degree of renal/hepatic damage was comparable between our treatment groups.

The magnitude of the stress response of fish has been shown to be greatly affected by temperature with colder water temperatures resulting in a delayed and attenuated stress response (Van Ham et al., 2003; Meka and McCormick, 2005; Brownscombe et al., 2015). Previous work on the physiological stress response in fish following capture by ice-angling have also revealed an attenuated and delayed stress response (Louison et al., 2017a, b). Northern pike (*Esox lusius*; Linnaeus, 1758) exposed to capture via ice-angling attained peak lactate concentrations between 45 min to 2 h following an acute stressor whereas glucose and cortisol concentrations failed to reach peak values even 4 h post-stressor (Louison et al., 2017a). Although blood lactate levels peaked after 2 h, they did not recover from peak levels within 4 h post-capture (Louison et al., 2017a). In the present study, it is possible that the 1 h period between air exposure and drawing blood was not sufficient to capture peak values for our physiological indices. Perhaps a longer period would allow metabolite concentrations to reach a level that is truly reflective of a "peak" response but this was not explored in our current study. Future work should look to investigate the specific time course by which walleye blood physiological metrics are altered over the initial hours following angling stressors as in Louison et al. (2017a,b). This would allow for a selection of a more appropriate time point for taking peak blood physiological values in this species.

5. Conclusions

The 100% survival rate and complete recovery of reflex impairment by all but one of the fish is a positive indication that C&R is a useful tool in the management of the winter harvest of fish stocks. There was no significant difference in the concentrations of blood glucose, blood lactate, or plasma cortisol between the exposure treatment groups nor was there a significant difference between the aspartate aminotransferase activities. It is possible that the lack of significance was a result of the combination of a muted and delayed stress response at colder temperatures, reduced enzymatic activity at colder temperatures, and relatively short exhaustion times. Future studies should assess the timing of stress-related metabolites following capture via ice-angling to ensure that peak values are being accurately represented. Although exposure duration did not contribute significantly to mortality or reflex impairment in this study, it is suggested nonetheless that ice-anglers minimize air exposure (especially in periods of extreme cold) whenever possible given the preponderance of evidence in the literature (reviewed in Cook et al., 2015) suggesting that exposure is harmful to the welfare of the fish. This is particularly salient given that we did not conduct any histological analysis of gills that could have been damaged by sub-zero temperatures. Presumably, there is a temperature-mediated threshold of handling and air exposure beyond which there would be significant physiological disturbance or death. On particularly cold days when humidity is low and wind chill is high, even short durations of air exposure could freeze the sensitive gill tissue. Nonetheless, the results of this study are encouraging as they suggest that walleye may be resilient to ice angling and are able to recover following capture and handling in cold air temperatures. It should be noted however, that our mortality estimates do not account for hooking mortality, which are often the primary source of mortality in caught-and-released fish (Bartholomew and Bohnsack, 2005; Huhn and Arlinghaus, 2011). However, in previous works on this species, hooking related mortalities were quite rare (Twardek et al., 2018). Furthermore, C&R could potentially be more effective during the winter months due to the attenuated stress response exhibited by fish following release and the relatively low mortality rates.

Author contributions

All authors contributed to the design of the experiment. The experimental trials were conducted by J.M.L., M.J.L., W.M.T., and R.J.L. Data analyses were performed by J.M.L. with help from R.J.L. The manuscript was written by J.M.L., with all authors contributing to revisions.

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