Canadian Journal of
Fisheries and
Aquatic Sciences

OPEN ACCESS | Article

# Lake trout reflex impairment and physiological status following ice-angling

**Bradley E. Howell**[a], **Giulio Navarroli**[a], **Eric J. Mullen**[b], **Steven J. Cooke**[c], **and Caleb T. Hasler**[a]

[a]Fish Biology and Conservation Laboratory, Department of Biology, The University of Winnipeg, Winnipeg, MB R3B 2E9, Canada; [b]Department of Natural Resources and Northern Development, Province of Manitoba, Lac du Bonnet, MB R0E 1A0, Canada; [c]Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, ON K1S 5B6, Canada

Corresponding author: **Bradley E. Howell** (email: bradleyhowell@trentu.ca)



## Abstract

We examined behaviour and physiology of lake trout (*Salvelinus namaycush*) following ice-angling. Fish were ice-angled and placed in a water-filled tub for 0.5, 4, and 6 h to recover ($n = 19$). Reflex impairment and physiological status were assessed repeatedly for every individual. Longer fight times lead to higher lactate and glucose, and lower extracellular pH 0.5 h post-angling. Loss of orientation was the most common reflex impairment (84% of fish) 4 h post-angling. Mortality (36.8%) was observed during the study; however, variation in handling, barotrauma, and issues with sampling may have confounded angling effects. To determine if barotrauma impacted impairment and mortality, lake trout at a later sampling date ($n = 29$) were exposed to air for either 60, 120, 180, 240, 300, or 420 s before assessment (3.4% mortality). For fish air-exposed for 300 s or more, 14% lost orientation during immediate assessment. Bloating occurred in 20% of fish air-exposed for 60 s. An air exposure duration of 420 s significantly impaired reflexes. Recreationally caught lake trout show behavioural and physiological impairment with such impairments magnified by extended air exposure.

**Key words:** catch-and-release, winter, stress, mortality, barotrauma

## Introduction

Catch-and-release angling (C&R) relies on the assumption that fish survive and exhibit negligible long-term impairment (Wydoski 1977). If those assumptions are satisfied, C&R can be a valuable conservation tool and enable use of various harvest management regulations (Arlinghaus et al. 2007; Danylchuk et al. 2018). However, negative consequences for fish are observed following angling (e.g., Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Sass and Shaw 2020) and these consequences compound with water temperature and air exposure to induce mortality (Gingerich et al. 2007) or sublethal effects on reproduction and growth (Watson et al. 2020; Papatheodoulou et al. 2022). Additionally, fish released immediately upon capture may not necessarily exhibit external signs of harm and thus, cryptic impairment may lead to unobserved delayed mortality (Coggins Jr. et al. 2007; Gilman et al. 2013). It is, therefore, imperative to incorporate behaviour, physiology, and mortality assessments into C&R science to fully assess angling impacts on fishes (e.g., Cooke and Schramm 2007; Brownscombe et al. 2022).

For fish, the process of angling involves fighting the line, air exposure, and being handled. These individual stressors can combine to induce a generalized stress response (Cooke and Suski 2005), which allows fish to regain homeostasis through coordinated physiological changes (Schreck and Tort 2016). Responses to stress in fish are tiered. The immediate response includes endocrine changes such as higher levels of catecholamines and corticosteroids (Wendelaar Bonga 1997). Endocrine changes then induce effects on cardiac output, oxygen uptake, and the mobilization of energy substrates (Wendelaar Bonga 1997). Should homeostasis not be regained, reduction in growth, poor disease resistance, or altered behaviour may affect long-term reproduction and survival (Barton 2002). The generalized stress response varies with environmental factors, for example, fish exhibit a more pronounced hormonal or metabolic response in warmer temperatures (Barton and Schreck 1987; Wilkie et al. 1996), compared to colder temperatures (Guderley 2004).

An understudied fish in the context of C&R science is the lake trout (*Salvelinus namaycush*), despite many jurisdictions across North America promoting all-season angling opportunities. These fish exhibit slow growth, longevity, late maturation, low reproductive potential, and slow replacement of adults, making them vulnerable to fishing pressure (Shuter et al. 1998). Other closely related salmonid species, like brook trout (*Salvelinus fontinalis*), experience blood chemistry disturbances such as elevated blood glucose (Wedemeyer and Wydoski 2008) and reflex impairment (Brownscombe et al. 2022) following angling. Lake trout are one of only a handful of species that have pre-existing research on the consequences of winter angling, leaving a gap in our understanding of related impairment or mortality (e.g., Dextrase and Ball 1991; Persons and Hirsch 1994). The scarcity of information regarding physiology, behaviour, and survival inhibits our ability to assess effects of unique environmental conditions and specialized fishing techniques associated with ice-angling (Lawrence et al. 2022). Despite our understanding of seasonal differences in growth, movement, and habitat use (Binder et al. 2017; Gallagher et al. 2018; Hébert and Dunlop 2020), we have yet to fully describe how winter angling directly impacts post-release behaviours and physiology of lake trout.

Lake trout share similar trophic ecologies and habitat use with other salmonids that inhabit deep and cold oligotrophic lakes (Ivanova et al. 2021; Nawrocki et al. 2022; Ridgway et al. 2022). These salmonids are adapted for rapid vertical movement, displaying diel vertical migration and air gulping from the surface to fill their swim bladders (Saunders 1953; Keyler et al. 2019; Macaulay et al. 2020; Pelster 2021; Larocque et al. 2022). Despite this, fish angled from depths $>$ 30 m are sensitive to pressure and temperature changes (McLennan et al. 2014; Sitar et al. 2017) and may experience barotrauma regardless of season. Barotrauma occurs in fish that are rapidly brought towards the surface from depth due to the decompression of gases in the blood and organs (Carlson 2012). The change in gas pressure can result in a range of injuries such as displaced organs, internal bleeding, and lung tissue damage (Rummer and Bennett 2005; Hannah et al. 2008; Pribyl et al. 2011). Physostomous species, like lake trout, are vulnerable to barotrauma despite the ability to belch excess gas from the swim bladder through the esophagus via a pneumatic duct (Saunders 1953; St John 2003). This is becoming widely recognized as a conservation concern by anglers (Schreer et al. 2009; Elliot et al. 2021). Barotrauma symptoms have been more heavily explored during open water angling, but recent research has shown high post-release mortality from barotrauma in cold lakes where fish are angled from deep depths (Althoff et al. 2021).

Another important issue associated with lake trout and C&R science is that lake trout are often considered “trophy” fish. Lake trout reach large sizes ($>$1 m), and size is an important factor with regard to effects of angling on fish because larger fish often have longer fight times (Reeves and Staples 2011), experience higher levels of angling-induced stress (Wydoski et al. 1976; Meka and McCormick 2005), and mortality (Loftus et al. 1988; Nuhfer and Alexander 1992; Lee and Bergersen 1996). Therefore, trophy-sized lake trout fisheries may be at risk from angler-induced effects. Beyond size, mortality in angled lake trout can also be explained by hook placement and bleeding (Falk et al. 1974; Persons and Hirsch 1994) and hook type (Dextrase and Ball 1991).

In our study, we examined the physiological and behavioural responses of lake trout to C&R ice-angling in Clearwater Lake, Manitoba. The objectives of this study were to (1) quantify reflex impairment and recovery post-capture, (2) explore how plasma stress metrics (i.e., cortisol, lactate, glucose, and pH) differ with time post-capture (samples taken at 0.5, 4, and 6 h), (3) examine interactions of blood metrics and reflex impairment responses to angling to predict mortality, (4) characterize factors that influence reflex impairment and physiology, including size, fight time, and length of air exposure, and (5) determine if barotrauma might be occurring in lake trout angled during the winter. For the extended recovery sampling (objectives 1–4), we hypothesized that fish capture would induce stress and impair behaviour that would affect survivorship. Specifically, we expected that fish would have delayed recovery but low reflex impairment, stress metrics would increase with time, high behavioural and physiological responses would be predictive of mortality, and fish length would affect stress and impairment. For the immediate recovery sampling (objective 5), we hypothesized that fish capture would impair behaviour and lead to barotrauma. We expected that fish would display reflex impairment within the first several minutes following capture.

# Methods

## Study location

We angled lake trout from Clearwater Lake, Manitoba, Canada (54.0570°N, 101.0564°W) between 10–16 January 2022 and 28 March–8 April 2022. The surface area of the lake is 593 km$^2$ and its average depth is 13.1 m. In January, air temperatures fluctuated between −30 °C and −1.3 °C (mean = −16.50 °C) (Environment and Climate Change Canada 2022) and water temperatures 10 m below the lake surface were between −0.2 °C and 0 °C (mean = −0.05 °C) (Pro20 model, YSI Inc., Yellow Springs, OH, USA; range = −5 °C to −55 °C, accuracy = ±0.3 °C). We angled for fish between 16 and 18.6 m (mean = 16.40 m) where dissolved oxygen levels were between 122.43% and 150.92% air saturation (mean = 126.09% air saturation) (17.36–21.4 mg·L$^{-1}$, mean = 18.84 mg·L$^{-1}$). In March, air temperatures were between −13 °C and 6.2 °C (mean = −1.60 °C) and water temperatures 10 m below the lake surface were between 0.2 °C and 1 °C (mean = 0.53 °C). We angled for fish between 6.1 and 21.3 m (mean = 15.23 m) where dissolved oxygen levels were between 84.15% and 123.91% air saturation (mean = 100.28% air saturation) (11.73–17.42 mg·L$^{-1}$, mean = 14.02 mg·L$^{-1}$).

## Fish capture and holding

Our research was conducted in accordance with animal care protocols approved by the Animal Care Committee of The University of Winnipeg (Animal Use Protocol #AE10491), following guidance by the Canadian Council on Animal Care. We also had a Provincial Scientific Collection (General) Permit (#22758865). We divided our study into two sampling periods. In January, after fish capture, we held fish in tubs for up to 6 h to monitor physiological recovery in blood parameters and reflex impairment (extended recovery). In March, after fish capture, we held fish for 420 s to quantify barotrauma and reflex impairment (immediate recovery).

During both sampling periods, we captured fish using 1.17 m extra heavy-action fiberglass ice fishing rods (46XH Slugger, Fish Frostbite, CA, USA) that were spooled with 13.61 kg braided line and a 1.22 m, 5.44 kg fluorocarbon leader on a size 35 reel (Pflueger President XT, Pure Fishing, Columbia, SC, USA). We either held the rods or fitted them to a tip-up (I Fish Pro 2.0, Tactical Ice Gear, CA, USA). For rods we held, we rigged them with spoons, plastic swimbaits, jigging tubes, or quick-strike rigs with size 1/0 treble hooks. For the tip-ups, we baited size 1/0 treble hooks with dead whole cisco (*Coregonus artedi*) (152–330 mm) and placed these within 50 m of each angler (12 experienced anglers). We angled fish from various locations on the lake and we caught fish within and outside uninsulated heated ice fishing tents. Once an angler felt a strike or observed a tip-up flag, they quickly raised the rod to set the hook and lift the fish from the water. An observer recorded the time between hooking the fish and the fish clearing the ice hole (i.e., fight time). We then immediately unhooked the fish, noted the hooking location, and scored the level of bleeding using a three-point scale (adapted from Falk et al. 1974): 0 score, none, no external bleeding near the hook entry point; 1 score, slight, a small amount of bleeding localized near the hook entry point; 2 score, flowing, blood surrounding and obscuring the hook entry point. Because anglers were spread out in a general area around our sampling tent, we transported fish within a tub filled with fresh lake water on a sleigh. The maximum distance we transported a fish was 400 m. For each fish we captured, we recorded the duration of air exposure time during handling.

## Extended recovery sampling

During the first sampling period, in January, upon entry into the sampling tent, we measured each fish ($n = 19$) for length and weight, and then transferred it to a tub of fresh surface water for reflex assessment (see below). Once we completed the reflex assessment, we moved fish to a covered 378 L stock tank filled with fresh surface water. We frequently changed the water in the tank and water temperature fluctuated between 0 °C and 0.1 °C (mean = 0.05 °C) with dissolved oxygen levels between 61.67% and 131.83% air saturation (mean = 99.83% air saturation) (12.8–18.64 $mg{\cdot}L^{-1}$, mean = 14.12 $mg{\cdot}L^{-1}$). We left fish to recover in the tank for 0.5, 4, and 6 h. We never held more than four fish at a time in the stock tank and were cognisant of total fish size in the tank.

At each time point, we assessed fish for impairment using a reflex assessment and a blood sample (size dependent, see below). For the reflex assessment, we followed previously established methods (Davis 2007; Raby et al. 2012; McLean et al. 2016; Brownscombe et al. 2022) and conducted it in a tub (78.74 × 45.72 × 30.48 cm) that we filled with fresh lake water. The assessment included the following metrics: (1) tail grab, burst swimming response to caudal peduncle grab; (2) body flex, attempted escape when held out of the water by midsection; (3) head complex, opening of jaws in normal ventilation pattern when held out of water; (4) vestibular–ocular response, tracking of eye to remain level when rotated horizontally and held out of water; (5) orientation, vertical alignment after being placed upside-down in the holding bin. We scored failure to demonstrate a metric “1”, and we calculated total reflex impairment score as the sum of each of the five impairments that were not present for all individuals at each time point. A single observer (BEH) conducted all reflex assessments to limit variation between samplers. The assessment took less than 60 s.

Following each of our reflex assessments, we sampled fish for blood using best practices described in Lawrence et al. (2020). Briefly, we held fish ventral-side up with their gills submerged in the water of the tub. We drew 1.5 mL of blood via caudle puncture with a 10 mL lithium heparin vacutainer and 21-G needle. We then immediately centrifuged the blood at 6000 g for 3 min to separate plasma from other blood components (red blood cells) and allocated the plasma into three 0.6 mL vials. We stored the plasma and other blood component samples in a vapour shipper that was charged with liquid nitrogen (Cryopro 3.6 L, VWR International, Radnor, PA, USA) until we could move them to a laboratory freezer (−80 °C). Total blood sampling time varied between fish due to difficulties associated with outside temperatures, and we sampled fish (>1500 g) during each of the three time points. We could only sample fish (<1500 g) twice (i.e., a random two out of the three time points) to ensure less than 10% of total blood volume was removed (Lawrence et al. 2020). Following the end of sampling at the 6 h time point, we inserted a T-bar anchor tag on the left side of the dorsal fin of each released fish to ensure fish were not resampled. No fish were recaptured.

For each fish and time point, we quantified concentrations of plasma cortisol, lactate, and glucose and measured intracellular and extracellular pH. For plasma cortisol, we used a commercially available enzyme-linked immunosorbent assay (ELISA) kit (#402710, Neogen, Lexington, KY, USA) and a microplate spectrophotometer (SpectraMax i3, Molecular Devices, San Jose, CA, USA). The ELISA kit that we used was previously validated for analysis of salmonid plasma samples (Raby et al. 2015). We ran the assay in triplicate at a dilution factor of 200 after completing a dilution series of 25, 50, 100, 200, and 400 to choose the appropriate dilution factor based on a standard curve. The intra-assay variation (% CV) for our plates was 7.48% and the interassay variation was 12.2%, which are acceptable ranges for plasma cortisol in salmonids (Barry et al. 1993). We determined concentrations of plasma lactate and glucose following the enzymatic methods of Lowry and Passonneau (1972). We tested each sample in triplicate and used a dilution factor of 3.75 for plasma lactate. The intra-assay variation for plasma lactate was 5.08% and interassay variation was 15%. The intra-assay variation for plasma glucose was 4.22% and interassay variation was 12.9%. We measured extracellular pH from thawed plasma and intracellular pH from lysed red blood cells that went through five freeze–thaw cycles (e.g., Mullen et al. 2020) (HI98165 pH Meter, HANNA Instruments, Woonsocket, RI, USA).

## Barotrauma and immediate recovery sampling

In April, we sampled a second group of lake trout ($n = 29$). We angled these fish using the same methods described above. We monitored angler interaction with fish according to four time intervals defined by times $T_0$–$T_4$ (adapted from Lyon et al. 2022). The first time interval ($T_0$–$T_1$) began when an angler set the hook ($T_0$) and ended when fish were out of the ice hole and exposed to the air ($T_1$). The second time interval ($T_1$–$T_2$) began when fish were exposed to the air ($T_1$) and ended after fish had been placed onto the ice surface and exposed to air for a randomly specified amount of time (60, 120, 180, 240, 300, and 420 s) before we placed it into a tub filled with fresh water ($T_2$). Between $T_1$ and $T_2$, we recorded hooking location, level of bleeding, length, and weight in the same fashion as described above. We also attached to each fish a coloured T-bar anchor tag on the left side of the dorsal fin to ensure fish were not resampled. The third time interval ($T_2$–$T_3$) began once fish were placed into water inside the assessment tub ($T_2$) and ended once the reflex and barotrauma assessments (described below) had been completed and we returned the fish to the ice hole ($T_3$). The fourth time interval ($T_3$–$T_4$) began once we placed the fish into the ice hole and ended when the fish kicked-off ($T_4$). During this time, we retained a loose grip on the caudal peduncle in case we had to retrieve the fish because it was unable to swim away. We scored the vigour of release using a three-point scale: 0 or poor, lethargic movement, and lack of consistent tail beats; 1 or good, regular movement and consistent tail beats; and 2 or excellent, energetic movement and fast-paced tail beats.

During the $T_2$ and $T_3$ time period, after fish were air-exposed for one of the randomly selected time intervals, we completed two assessments of the captured fish. First, we performed a reflex assessment, which was carried out in the same manner as the first sampling period. The second assessment was a barotrauma assessment (adapted from Althoff et al. 2021; indicators are noted in several studies, e.g., Morrissey et al. 2005; Gravel and Cooke 2008; Schreer et al. 2009; Eberts et al. 2018), which we performed in the same tub as the reflex assessment (Fig. 1). For the barotrauma assessment, we scored the presence of the following metrics ("1" present, "0" not present): (1) oral organ eversion, gastric herniation into the buccal cavity; (2) exophthalmia, bulging eyes; (3) bloating, overinflation of the midsection; (4) anal organ eversion, prolapsed anus; (5) hemorrhaging, redness in the mouth/gills/fins/anus. Similar to the reflex assessment, a single observer (BEH) performed the barotrauma assessment. We calculated total barotrauma score as the sum of each of the five impairments that were not present for all individuals at each time point. It took us less than 60 s to complete the assessment.

## Data analysis and statistics

We used R version 4.1.2 (R Core Team 2021) and assessed significance at $\leq 0.05$, unless noted otherwise. For the first sampling period (i.e., extended recovery experiment), we tested whether blood plasma and pH parameters differed across recovery times using paired *t* tests ("stats" package, R Core Team 2021). We could not use repeated-measures analysis of variance because not all fish were sampled at each time point. Prior to analysis, we tested for outliers using Grubbs' tests for outliers ("outliers" package, Komsta 2022) and removed them from the analysis. Then, to ensure model assumptions were met, we tested homogeneity of variance using a Levene's test ("cars" package, Fox and Weisberg 2019) and normality using a Shapiro–Wilk test ("stats" package, R Core Team 2021). When the model assumption tests failed for the blood parameters, we used a square root transformation prior to the paired *t* test. For significant comparisons, we calculated effect size using Cohen's D test ("effsize" package, Torchiano 2020). When individuals were missing a blood parameter value at a particular recovery time, we removed it from the data set for comparisons using that recovery time and blood parameter. Because we undertook multiple statistical analyses using the blood, we used a Bonferroni correction to offset the likelihood of a type-I error, thus for the tests involving the blood metrics, we used a significance level of $\alpha = 0.01$. To relate mortality with the blood parameters we used binary logistic regression models ("stats" package, R Core Team 2021). We regressed mortality against each blood parameter at all the recovery time (0.5, 4.0, and 6.0 h) to address whether the blood parameters predicted death. Again, we used a Bonferroni correction to account for multiple statistical tests being performed and thus, we used $\alpha = 0.01$ to determine significance of the blood parameter versus mortality models. The next analysis we performed was to determine, at each recovery time point, the effects of total length, fight time, air exposure, and reflex impairment on all the blood parameters. To accomplish this, we created 17 candidate linear models based on various combinations of the independent variables and used an information theoretic approach (second-order Akaike's Information Criterion; "AICcmodavg" package, Mazerolle 2020; "lme4" package, Bates et al. 2015). Likewise to above, outliers were removed, model assumptions were validated, and data were transformed as needed. The last statistical analysis we carried out for the first sampling period was to analyze whether reflex impairment could be predicted by any of the independent variables, including recovery time, total length, fight time, and air exposure. To accomplish this, we used binary multiple logistic regression mixed models ("lme4" package, Bates et al. 2015). Notably, we originally included interactions of the independent variables; however, they were not significant and removed from the final analysis. There were no interactions between variables. Additionally, we included individual ID as a random effect because, unlike blood parameters, we had reflex scores for every individual.

For the second sampling period (i.e., immediate recovery experiment), we used binary multiple logistic regression models ("stats" package, R Core Team 2021) to determine the effects of total length, fight time, and air exposure on either reflex or barotrauma impairment. We originally included depth and interactions of the independent variables in the model but removed them due to insignificance. Lastly, we compared reflex and barotrauma scores using a Pearson correlation ("devtools" package, Wickham et al. 2022) to determine if the two response variables were associated.

# Results

## Extended recovery

Overall, we caught 19 lake trout during the first sampling period. These fish had a mean (±S.D.) total length of 633 ± 149 mm with a range of 450–952 mm. The mean weight of the lake trout caught during the first sampling period was

**Fig. 1.** Images showing barotrauma assessment metrics including (A) oral organ eversion, (B) exophthalmia, (C) bloating and anal organ eversion, (D) hemorrhaging in the eye, and (E) hemorrhaging in the fins observed in lake trout (*Salvelinus namaycush*) following angling.




3130 ± 2484 g with a range of 454–9667 g. There was a 36.8% mortality rate. Of the seven mortalities observed, only one occurred prior to the 0.5 h sampling point, three after the 4 h sampling point, and three shortly after the 6 h sampling point. In all fish, bleeding and injury were minimal, hooks were not swallowed, and fish were active upon hook removal.

Recovery time, total length, fight time, and air exposure did not have any effect on reflex scores (Table 1). Total reflex impairment immediately following capture was 4 and peaked to 18 at 4 h. Reflex impairment then began to decline at 6 h. Loss of orientation was the most observed reflex impairment with 84% of fish displaying it 4 h post-angling (Fig. 2). At 4 h post-capture, cortisol was 70% higher than it was at 0.5 h (paired $t$ test: $t_{12} = -5.7$, $P < 0.001$) and it doubled at 6 h (paired $t$ test: $t_8 = -4.4$, $P \leq 0.01$) with large effect sizes for both comparisons (Fig. 3). At 4 h, lactate was 28% higher than it was at 0.5 h (paired $t$ test: $t_{12} = -5.3$, $P \leq 0.001$) and at 6 h it was 31% higher (paired $t$ test: $t_8 = -6.5$, $P \leq 0.001$) with large effect sizes for both comparisons. Glucose was not significantly higher at 4 or 6 h post-capture when compared to the 0.5 h sample point. Extracellular pH decreased from 7.59 at 0.5 h to 7.43 (1%) at 4 h (paired $t$ test: $t_{11} = 5.9$, $P < 0.001$) with a large effect size but not at 6 h post-capture. Intracellular pH did not significantly change at 4 or 6 h post-capture when compared to the 0.5 h sample point. No relationships were found between blood metrics at any recovery time and mortality (Table 2). The most parsimonious models to predict cortisol, lactate, glucose, extracellular pH, and intracellular pH were found via Akaike information criterion (AICc) (Table 3). Thirty minutes after the angling event,

**Table 1.** Summary of binary multiple logistic regression models assessing the effects of recovery time (h), fish total length (mm), fight time (s), and air exposure (s) on whether lake trout (*Salvelinus namaycush*) showed impairment for any of the five reflex impairment indicators assessed after ice-angling during an extended recovery experiment (L.L., effect estimate lower limit; U.L., effect estimate upper limit).

| Variable | Estimate | L.L. | U.L. |
|---|---|---|---|
| (Intercept) | −68.77 | −158.66 | 21.11 |
| Recovery time 0.5 | 7.07 | −2.75 | 16.90 |
| Recovery time 4 | 7.07 | −2.75 | 16.90 |
| Recovery time 6 | 8.06 | −2.46 | 18.59 |
| Total length | 0.09 | −0.03 | 0.22 |
| Fight | −0.03 | −0.07 | 0.02 |
| Air exposure | 0.05 | −0.04 | 0.13 |

fight time was a significant predictor of lactate ($R^2 = 0.42$), the interaction of fight time + reflex score was a significant predictor of glucose ($R^2 = 0.51$), and fight time was a significant predictor of plasma pH ($R^2 = 0.24$) (Table 3). Four hours after the angling event the interaction of fight time + reflex score was a significant predictor of lactate ($R^2 = 0.81$) and again at 6 h ($R^2 = 0.80$).

### Immediate recovery

During the second sampling period, 29 lake trout were angled. These fish had a mean total length of 599 ± 184 mm with a range of 310–1040 mm. The mean weight of the lake trout caught during the second sampling period was 2619 ± 3113 g with a range of 190–11 310 g. There was a 3.4% mortality rate (one fish was hooked in the gill arches and died). Air exposure, total length, and fight time did not influence barotrauma scores. Totaled barotrauma scores peaked at 60 s of air exposure and then fluctuated throughout the rest of the time points up to 420 s. Bloating of the abdomen was the most observed barotrauma impairment with 20% of fish displaying it 60 s post-angling. Oral organ eversion was the only reflex indicator not observed in any fish captured. Only an air exposure time of 420 s influenced reflex score (Table 4). Total reflex scores continued to increase across the 420 s and loss of orientation was the most observed reflex impairment with 14% of fish displaying it 300 s post-angling (Fig. 2). Reflex impairment and extent of barotrauma were not correlated (Pearson correlation: $t_{27} = 0.23$, $r = 0.05$, $P > 0.05$).

## Discussion

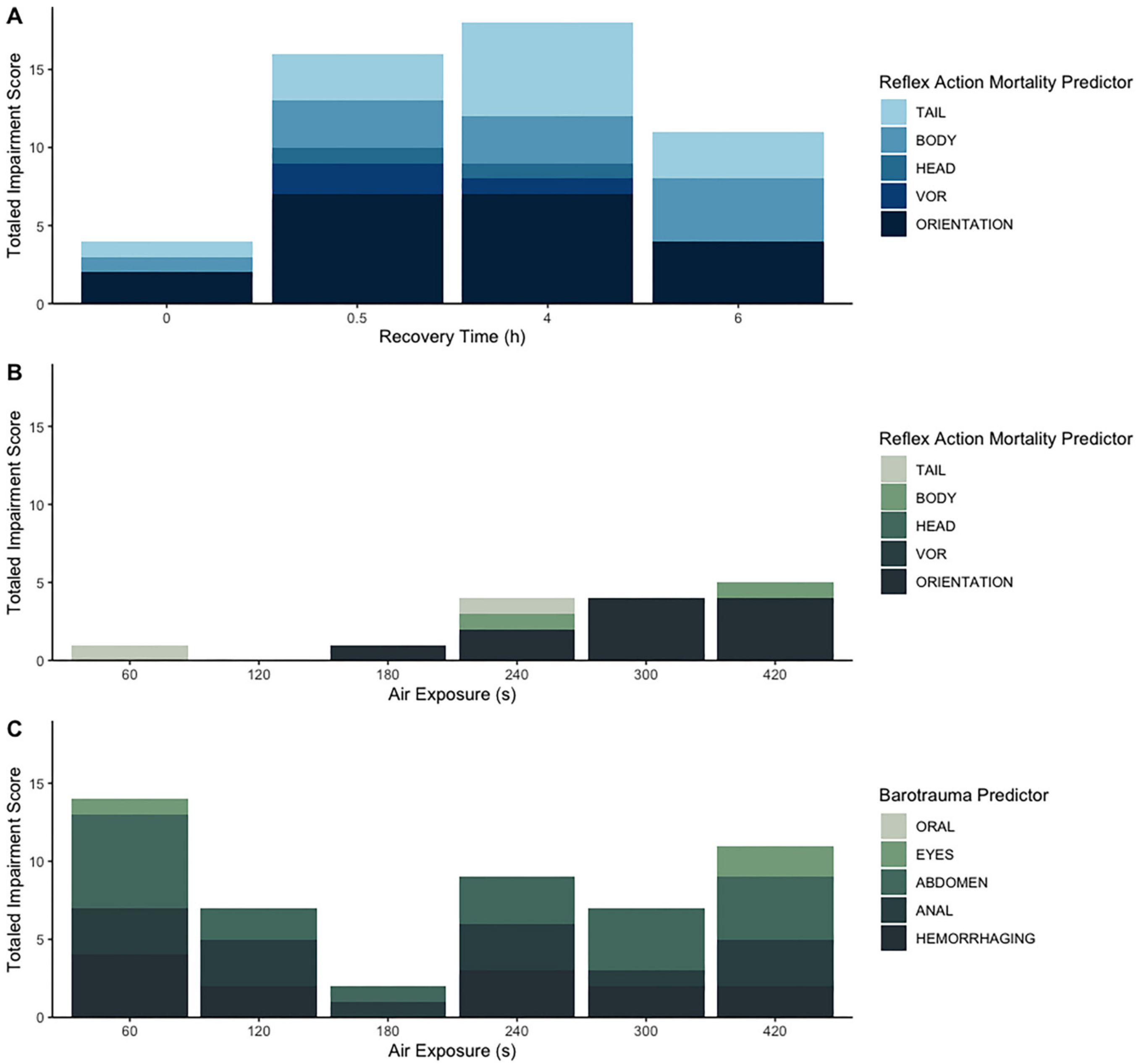
### Mortality

The 36.8% mortality rate observed in the extended recovery experiment was higher than expected for a physostomous species, which are typically robust to stressors like barotrauma (Brown et al. 2014). However, these mortalities could not be confidently attributed to the hooking and retrieval, as immediately following capture, fish were responsive and had minimal injury or bleeding. Sampling and handling of fish, as well as holding the fish in tubs at surface rather than at capture depth, were additional stressors that could have contributed to the observed mortality (Ferter et al. 2015). Additionally, the low sample size during the extended sampling and the lack of variation in capture depth limit our interpretation of the mortality rate. Nonetheless, the mortality rate observed in this experiment is higher than what has been seen in other studies examining the effects of ice-angling on lake trout. For example, mortality rates in other studies that ice-angled lake trout were 10% (Dextrase and Ball 1991) and 24% (Persons and Hirsch 1994); however, fish in these studies were not held for extended periods of time like in our experiment and so delayed mortality was not assessed. Delayed mortality has been documented following exhaustive exercise or post-angling in other salmonids (Wood et al. 1983; Ferguson and Tufts 1992), with most angling-induced mortality occurring within the first 48 h (Mongillo 1984; Dedual 1996). In our experiment, lake trout died within 6 h following capture at ∼16 m. Holding conditions and handling can potentially exacerbate stress responses and behaviour (Portz et al. 2006; Mullen et al. 2020). Based on our higher than expected mortality rate, either angling caused a much more serious impact than found in other lake trout and ice-angling studies or some aspect of the fish holding induced unintended consequences. Due to fish capture depth, and our observation that lake trout were not releasing gas at the surface, we speculate that the fish may have suffered from barotrauma. Anecdotally, we observed swim bladder inflation in certain fish dissected after mortality had occurred. The addition of a barotrauma assessment during the second sampling period allowed us to deduce that pressure-related impairment was occurring in the lake trout, though based on observations between the two sampling periods, we do not think barotrauma was as severe as it was in the first sampling event. Holding fish to obtain physiological and reflex endpoints are one of the main challenges with C&R studies in the winter and refinement of methodology is needed to remove sampling and handling stressors (Lawrence et al. 2022).

### Behaviour

Coupling behaviour with physiological parameters can provide insight into a fish's state following angling (Arlinghaus et al. 2009; Cooke et al. 2013). Reflex indicator scores showed signs of behavioural recovery within 6 h. Loss of orientation was the most observed reflex impairment with 84% of fish displaying it 4 h post-angling during extended recovery and 14% of fish displaying it 300 s post-angling during immediate recovery. Impaired orientation has been shown to be a crucial predictor of mortality in other species (Gingerich et al. 2007; Raby et al. 2012) and is necessary for fish to return to desired depths upon release (Louison et al. 2023). Fish experiencing an orientation impairment are likely forced to float just under the ice surface after release and, therefore, experience low temperatures and potential tissue freezing (Card et al. 2022). Behavioural impairments, such as floating, force fish to continue exhaustive activity through the act of trying to return to depth, further perpetuating changes in

**Fig. 2.** Totaled impairment scores for (A) extended recovery reflex impairment ($n$ = 19), (B) immediate recovery reflex impairment ($n$ = 29), and (C) immediate recovery barotrauma ($n$ = 29) predictors in lake trout (*Salvelinus namaycush*) sampled following ice-angling. Reflex metrics include (1) tail grab, (2) body flex, (3) head complex, (4) vestibular–ocular response, and (5) orientation. Barotrauma metrics include (1) oral organ eversion, (2) exophthalmia, (3) bloating, (4) anal organ eversion, and (5) hemorrhaging.



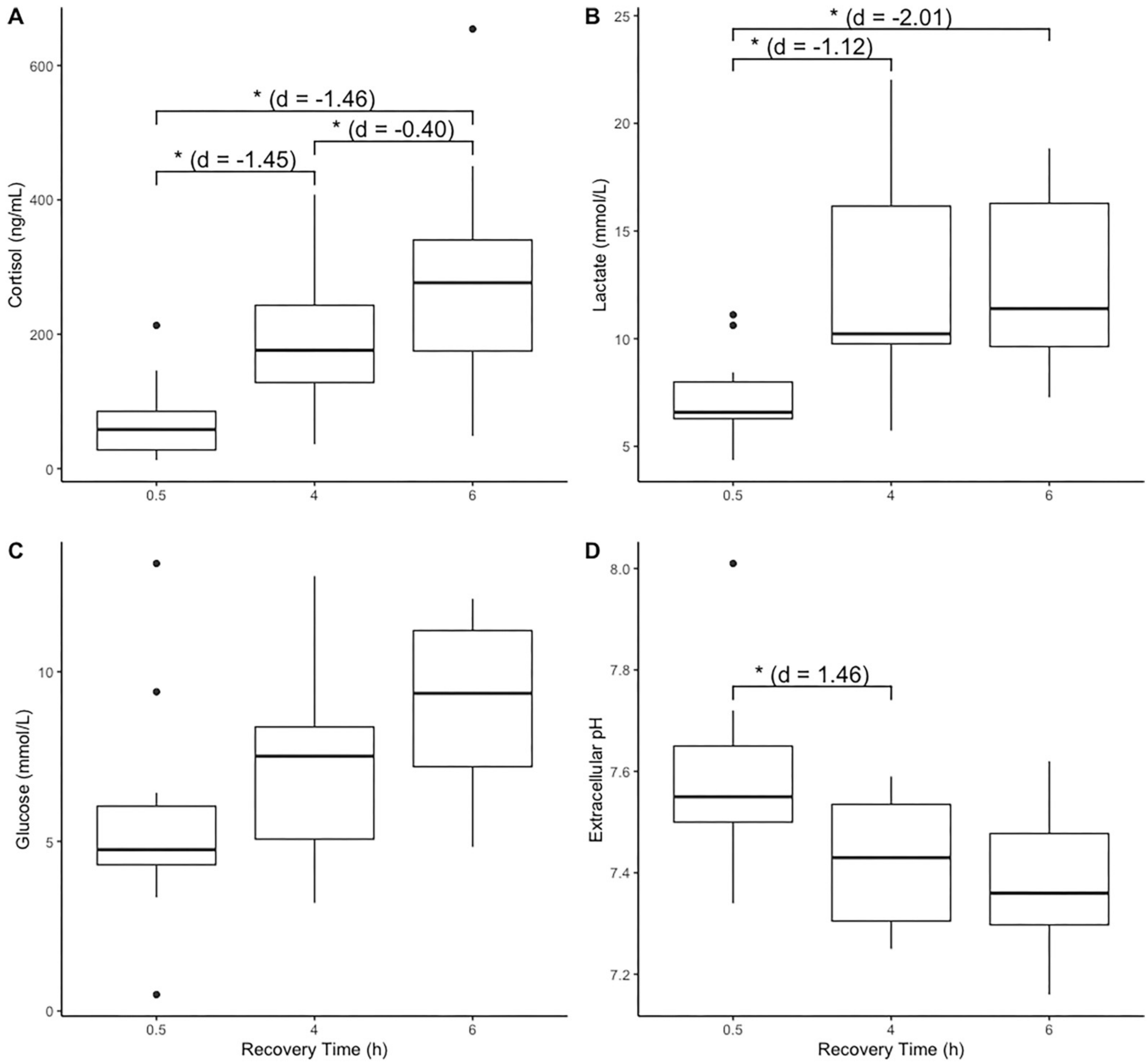



physiological variables and possibly accelerating mortality (Wood 1991; Ross and Hokenson 1997).

Oral organ eversion is one of the most recognizable and commonly observed injuries resulting from barotrauma (Schreer et al. 2009). This occurs when the stomach is inverted and expelled through the esophagus due to the overexpansion of the swim bladder (Fig. 1A). Physoclistous fish are typically more susceptible to barotrauma then physostomous fish like lake trout because their swim bladder is not connected to the stomach via a pneumatic duct (Saunders 1953; St. John 2003). These fish must instead diffuse gases through a capillary mesh that supplies blood to the swim bladder and is the interface for gas exchange (Ferguson 1989). Despite being physostomous, lake trout in this study exhibited barotrauma impairment which would not have been captured by using only the reflex assessment. We, therefore, recommend using both assessments in succession to provide a better estimate of the range of impairments.

Barotrauma may be exacerbated by varying factors. Other studies have found effects of depth and duration that fish were held at the surface on barotrauma (Schreer et al. 2009; Wegner et al. 2021). In our study, air exposure, total length,

**Fig. 3.** Concentrations of (A) plasma cortisol, (B) plasma lactate, (C) plasma glucose, and (D) extracellular pH in lake trout (*Salvelinus namaycush*) sampled at 0.5 h ($n = 13$), 4 h ($n = 13$), or 6 h ($n = 11$) following ice-angling. Thick black horizontal lines denote median values, boxes contain all data within the 25th and 75th quartiles, whiskers show the range of data, and outliers are depicted as black dots. Asterisks above horizontal brackets denote statistical significance at corrected $\alpha = 0.01$. Cohen's $d$ values (i.e., standardized difference of the means) are within parentheses.






and fight time did not affect barotrauma scores. Angling for lake trout often occurs at depths > 40 m with bait either resting-on or jigging just above the bottom of the lake (Lamont 2017). Water pressure increases with depth and thus, fish angled from the bottom experience the full gradient of pressure changes on the way to the surface. Lake trout typically display their belching mechanism to expel excess gas through their mouths during an angling event. However, the high barotrauma scores observed in this study suggest that this mechanism was not entirely reliable during rapid decompression. Lake trout have previously been documented to display signs of barotrauma but not in relation to ice-angling (Ng et al. 2015; Sitar et al. 2017). Interestingly, reflex impairment and barotrauma were not meaningfully correlated despite similarities in certain impairment metrics such as orientation in the reflex assessment and abdominal bloating in the barotrauma assessment.

## Blood physiology

Ice-angling induced changes to plasma cortisol, plasma lactate, plasma glucose, extracellular pH, and intracellular pH in lake trout. Cortisol, lactate, and glucose were highest at

**Table 2.** Summary of binary logistic regression models assessing the effects of cortisol (ng·mL$^{-1}$), lactate (mmol·L$^{-1}$), glucose (mmol·L$^{-1}$), extracellular pH, or intracellular pH of lake trout (*Salvelinus namaycush*) sampled at 0.5, 4, and 6 h post-angling on whether a fish survived the angling event or not.

| Time (in hours) | Blood metric | Estimate | S.E. | *z* value | df | *P* |
|---|---|---|---|---|---|---|
| 0.5 | Cortisol | 0.28 | 0.22 | 1.30 | 12 | 0.19 |
| | Lactate | 0.96 | 1.69 | 0.57 | 12 | 0.57 |
| | Glucose | −2.10 | 1.70 | −1.24 | 12 | 0.22 |
| | Extracellular pH | 13.76 | 21.17 | 0.65 | 12 | 0.52 |
| | Intracellular pH | 91.41 | 64.73 | 1.41 | 12 | 0.16 |
| 4 | Cortisol | 0.14 | 0.15 | 0.92 | 14 | 0.36 |
| | Lactate | 4.12 | 1.87 | 2.21 | 14 | 0.03 |
| | Glucose | 1.04 | 1.21 | 0.86 | 14 | 0.39 |
| | Extracellular pH | 10.23 | 24.52 | 0.42 | 14 | 0.68 |
| | Intracellular pH | 24.69 | 44.15 | 0.56 | 12 | 0.58 |
| 6 | Cortisol | 0.01 | 0.12 | 0.05 | 10 | 0.96 |
| | Lactate | 3.33 | 1.85 | 1.80 | 10 | 0.07 |
| | Glucose | −0.19 | 1.31 | −0.14 | 10 | 0.89 |
| | Extracellular pH | −4.75 | 25.30 | −0.19 | 10 | 0.85 |
| | Intracellular pH | 18.76 | 43.36 | 0.43 | 10 | 0.67 |

**Note:** Statistical significance was determined at a corrected $\alpha = 0.01$.

6 h post-angling when sampling ended. Despite below-ice water temperatures and the expectation that physiological processes, such as metabolism and the stress response, should be slowed (Davis et al. 1984; Barton and Schreck 1987; Guderley 2004; Louison et al. 2017*b*), the observed values for each variable were higher than what has been found in previous lake trout studies during summer months (Wedemeyer and Wydoski 2008; Pottinger 2010). These values may have been influenced by holding conditions, as described earlier. Typically, cortisol and lactate values peak between 0.5 and 2 h before recovery after exhaustive exercise or handling (Milligan and Wood 1986; Barton and Iwama 1991). In female pink salmon, cortisol, lactate, and glucose peaked between 0.5 and 2 h after being exposed to 3 min of exhaustive exercise and 1 min of air exposure (Donaldson et al. 2014). Maximum intracellular and extracellular pH values were within similar ranges of other C&R studies (Brobbel et al. 1996; Mullen et al. 2020). The continued decrease in pH up to 6 h post-angling was expected because anerobic use of glycogen to meet energy demands leads to an excess of lactate and reduced pH (Milligan and Wood 1986). Quantifying maximum peak values for all other blood metrics was not possible since they increased continuously up to 6 h. The delayed onset of the stress response and heightened blood metrics after 4 h seen in this study has also been noted in other ice-angling research (Louison et al. 2017*a*,*b*). Recovery profiles differ by species and context (Ruane et al. 1999; Barton 2000; Logan et al. 2019; Lawrence et al. 2022), so generalized physiological responses of ice-angled lake trout remain poorly characterized. Understanding fish recovery is important for conservation, so further research is needed to understand the full amount of time required for fish to return to baseline physiological levels. Fish that continue to experience stress after being released can be more susceptible to other factors such as predation (Campbell et al. 2010; Holder et al. 2020). Therefore, quantifying physiological recovery time can improve understanding of delayed mortality.

Plasma cortisol, lactate, glucose, and pH were not predictors of mortality. All metrics examined in this study are physiological variables that are well explored in other fishes as physiological disturbance markers (Wood 1991; Suski et al. 2003; Cooke et al. 2013; Twardek et al. 2018). Cortisol is a primary stress hormone, lactate and glucose are metabolites, and pH indicates acid–base status (Wendelaar Bonga 1997). Collectively, they are a result of internal coordination to increase the availability of oxygen and energy (Rodnick and Planas 2016; Schreck and Tort 2016). Lactate is valuable in predicting mortality because it is a by-product of exhaustive exercise (Wood 1991). Lactate anion is produced via glycolysis while metabolic protons are produced during adenosine triphosphate breakdown (Robergs et al. 2004). It has been implicated with post-exercise mortality and may play a role in mitigating pathological effects of exhaustion (Wang et al. 1994; Holder et al. 2022). Minimizing factors that influence changes in metabolites during collection and handling in field settings is difficult since the process of collecting blood itself inherently changes blood metabolite profiles through the stress of confinement (Kiilerch et al. 2018), handling (Sopinka et al. 2016), and technical ability (Lawrence et al. 2020). In this study, holding time was limited to mitigate effects from fasting and altered environment (Morata et al. 1982; Scarabello et al. 1991; Brobbel et al. 1996) but fish may have experienced increased handling due to logistical challenges with winter sampling.

Fight time and the interaction of fight time + reflex impairment were the only variables that predicted lactate at 0.5, 4,

**Table 3.** Summary of model selection results based on second-order Akaike information criterion (AICc) for linear models predicting the cortisol (ng·mL$^{-1}$), lactate (mmol·L$^{-1}$), glucose (mmol·L$^{-1}$), extracellular pH, and intracellular pH concentrations of lake trout (*Salvelinus namaycush*) sampled at 0.5, 4, and 6 h post-angling.

| Time (in hours) | Metric | Model name | K | AICc | ΔAICc | AICc Wt | Cum. Wt | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| 0.5 | Cortisol | Null | 2 | 61.90 | 0.00 | 0.41 | 0.41 | – |
| | Lactate | **Fight** | **3** | **10.10** | **0.00** | **0.46** | **0.46** | **0.42** |
| | | Length + Fight + Reflex | 5 | 11.94 | 1.84 | 0.18 | 0.65 | 0.72 |
| | Glucose | **Fight + Reflex** | **4** | **19.83** | **0.00** | **0.32** | **0.32** | **0.51** |
| | | Reflex | 3 | 20.64 | 0.80 | 0.21 | 0.53 | 0.24 |
| | | Null | 2 | 20.92 | 1.09 | 0.19 | 0.72 | – |
| | Plasma pH | **Fight** | **3** | **−53.07** | **0.00** | **0.22** | **0.22** | **0.24** |
| | | Null | 2 | −52.86 | 0.21 | 0.20 | 0.41 | – |
| | | Air | 3 | −52.40 | 0.66 | 0.16 | 0.57 | 0.19 |
| | | Length | 3 | −52.28 | 0.78 | 0.15 | 0.72 | 0.18 |
| | | Fight + Air | 4 | −51.23 | 1.84 | 0.09 | 0.80 | 0.37 |
| | Blood pH | Null | 2 | −65.80 | 0.00 | 0.56 | 0.56 | – |
| 4 | Cortisol | Null | 2 | 67.10 | 0.00 | 0.38 | 0.38 | – |
| | | Reflex | 3 | 68.50 | 1.40 | 0.19 | 0.57 | 0.09 |
| | Lactate | **Fight + Reflex** | **4** | **15.09** | **0.00** | **0.57** | **0.57** | **0.81** |
| | | Length + Fight + Reflex | 5 | 16.38 | 1.29 | 0.30 | 0.87 | 0.86 |
| | Glucose | Null | 2 | 19.61 | 0.00 | 0.23 | 0.23 | – |
| | | Air | 3 | 19.63 | 0.02 | 0.23 | 0.46 | 0.19 |
| | | Reflex | 3 | 20.14 | 0.53 | 0.18 | 0.63 | 0.15 |
| | | Air + Reflex | 4 | 20.74 | 1.13 | 0.13 | 0.76 | 0.33 |
| | Plasma pH | Null | 2 | −51.16 | 0.00 | 0.46 | 0.46 | – |
| | Blood pH | Null | 2 | −64.13 | 0.00 | 0.30 | 0.30 | – |
| | | Fight | 3 | −63.81 | 0.32 | 0.26 | 0.55 | 0.10 |
| | | Length | 3 | −63.04 | 1.09 | 0.17 | 0.73 | 0.11 |
| 6 | Cortisol | Null | 2 | 65.09 | 0.00 | 0.53 | 0.53 | – |
| | Lactate | **Fight + Reflex** | **4** | **13.75** | **0.00** | **0.85** | **0.85** | **0.80** |
| | Glucose | Null | 2 | 16.91 | 0.00 | 0.35 | 0.35 | – |
| | | Fight | 3 | 18.08 | 1.17 | 0.20 | 0.55 | 0.18 |
| | | Reflex | 3 | 18.43 | 1.52 | 0.16 | 0.71 | 0.15 |
| | Plasma pH | Null | 2 | −39.06 | 0.00 | 0.48 | 0.48 | – |
| | | Fight | 3 | −37.72 | 1.33 | 0.24 | 0.72 | 0.16 |
| | Blood pH | Null | 2 | −49.86 | 0.00 | 0.48 | 0.48 | – |
| | | Fight | 3 | −48.61 | 1.25 | 0.26 | 0.74 | 0.17 |

**Note:** The most parsimonious models are in bold.

or 6 h post-angling. Longer fight times increase exhaustive activity and thus, lactate production (Holder et al. 2022). Exhaustion following line-fighting may also impair reflexes that require the depleted energy stores such as body flex, orientation, and tail grab. In this study, only an air exposure of 420 s influenced reflex impairment score. A large body of research has previously demonstrated the effects of holding (Cooke et al. 2002; Donaldson et al. 2013; Chhor et al. 2022*b*), fish size (Loftus et al. 1988; McLean et al. 2020), fight time (Cooke et al. 2016; Blyth and Bower 2022), and air exposure (Gingerich et al. 2007; Donaldson et al. 2014; Logan et al. 2019; Chhor et al. 2022*a*) on reflex impairment. For example, brook trout > 328 mm with air exposure times >10 s exhibit higher reflex impairment measures (Brownscombe et al. 2022).

## Effect of size

While fish body length was not found to influence mortality or impairment in this study, larger rainbow trout (*Oncorhynchus mykiss*) have been shown to experience a higher degree of angling-induced stress (Wydoski et al. 1976) and hooking mortality (Schisler and Bergersen 1996). The lack of effect observed in this study may be attributed to a low number of large individuals (i.e., 5 fish > 890 mm) captured during sampling periods. Larger fish may be more likely to fight to exhaustion and thus often experience negative survival outcomes after angling due to increased length of time fighting the line (Reeves and Staples 2011; Twardek et al. 2018). Angler-induced C&R mortality is in direct conflict with fishery conservation aims and thus, management decisions

**Table 4.** Summary of binary multiple logistic regression models assessing the effects of air exposure time (s), fish total length (mm), and fight time (s) on whether lake trout (*Salvelinus namaycush*) showed impairment for any of the five reflex impairment indicators or barotrauma metrics assessed after ice-angling during an immediate recovery experiment.

| | Variable | Estimate | S.E. | *z* value | df | *P* |
|---|---|---|---|---|---|---|
| Reflex | (Intercept) | −11.74 | 6190 | −1.90 | 28 | 0.06 |
| | Exposure time 120 s | −19.21 | 4265 | −0.01 | 28 | 1.00 |
| | Exposure time 180 s | 1.68 | 3.12 | 0.54 | 28 | 0.59 |
| | Exposure time 240 s | 1.88 | 2.18 | 0.86 | 28 | 0.39 |
| | Exposure time 300 s | 2.97 | 2.13 | 1.39 | 28 | 0.16 |
| | **Exposure time 420 s** | **4.57** | **2.31** | **1.97** | **28** | **0.05** |
| | Total length | 0.02 | 1.10 | 1.48 | 28 | 0.14 |
| | Fight | −0.00 | 0.02 | −0.32 | 28 | 0.75 |
| Barotrauma | (Intercept) | 18.30 | 6389 | 0.00 | 28 | 1.00 |
| | Exposure time 120 | −19.02 | 6389 | −0.00 | 28 | 1.00 |
| | Exposure time 180 | −22.70 | 6389 | −0.00 | 28 | 1.00 |
| | Exposure time 240 | −0.75 | 9544 | 0.00 | 28 | 1.00 |
| | Exposure time 300 | −20.64 | 6389 | −0.00 | 28 | 1.00 |
| | Exposure time 420 | 0.59 | 9804 | 0.00 | 28 | 1.00 |
| | Total length | 0.00 | 0 | 0.02 | 28 | 0.98 |
| | Fight | 0.05 | 0.07 | 0.67 | 28 | 0.50 |

**Note:** Statistical significance was determined at $\alpha = 0.05$ and is in bold.

should focus on methods to improve survivorship in released fish.

### Management

The results of this study provide new information on the susceptibility of physostomes to angling-induced impairment during the winter. Specifically, lake trout exhibited delayed behavioural and physiological recovery in the extended recovery experiment and a high degree of impaired barotrauma metrics in the immediate recovery experiment. Understanding how to effectively manage this population during winter months is vital to prevent a decline in fish abundance. Generally, fisheries managers lack scientific information to inform decision-making around winter C&R fisheries. Basic estimates of fish hooking mortality are necessary and can range from 1% to >90% depending on species, angler skill, and environmental factors (Muoneke and Childress 1994; Arlinghaus et al. 2007). This study provides estimates of immediate and extended mortality following angling which may be used to inform strategies aimed at protecting and enhancing fishing opportunities. Additionally, we describe other factors such as physiological changes and reflex impairment that may predict mortality. Further research on ice-angling needs to explore extended impacts on spatial ecology (Lawrence et al. 2022). Monitoring after release is especially difficult due to a lack of pre-established telemetry infrastructure in many northern lakes in addition logistical difficulties associated with ice cover. General best practices must continue to be promoted for this fishery such as preventing air exposure, limiting fight times, and careful handling upon capture (Brownscombe et al. 2017, 2022; Danylchuk et al. 2018; Chhor et al. 2022*a*). Wider implementation of commercially available descending devices may combat fish mortality by returning fish to a depth that allows them to relieve barotrauma pressure (Curtis et al. 2015; Bellquist et al. 2019; Davies et al. 2022; Louison et al. 2023). These devices are an alternative to more invasive methods such as fizzing which has the potential to harm vital organs if done improperly (Kerr 2001; Nguyen et al. 2009; Drumhiller et al. 2014). Further research should explore the efficacy of descending devices to relieve barotrauma in lake trout during winter months.

## Acknowledgements

We respectfully acknowledge that the work and learning was conducted on the traditional territory of the Saulteaux and Swampy Cree Peoples (Treaty 5 Territory). We offer gratitude to the First Nations for their ongoing stewardship of this land. The project was supported by Manitoba Natural Resources and Northern Development (MNRND). We thank Ian Kitch (MNRND) and Derek Kroeker (MNRND) for assisting in the design of this study. We appreciate Cole Phillips (MNRND), Ethan Dobbs (MNRND), Darren Smith (OMNDMNRF), Mike Parna (OMNDMNRF), Ayden Ricker-Held, and all other volunteers for assistance during the field programs. Contributions from Evergreen Lodge and Resort (Ken Kobelka) and Clearwater Outfitters (Josh Kobelka) were also vital to our success.

## Article information

### History dates

Received: 7 February 2023
Accepted: 26 May 2023
Accepted manuscript online: 9 June 2023
Version of record online: 26 July 2023

## Data availability

Data will be made openly available upon request.

# Author information

## Author ORCIDs

Bradley E. Howell https://orcid.org/0000-0001-8552-6957
Giulio Navarroli https://orcid.org/0000-0003-3486-474X
Steven J. Cooke https://orcid.org/0000-0002-5407-0659
Caleb T. Hasler https://orcid.org/0000-0003-3242-7415

## Author contributions

Conceptualization: BEH, EJM, SJC, CTH
Formal analysis: BEH
Funding acquisition: BEH, SJC, CTH
Investigation: BEH, GN, EJM
Methodology: BEH, EJM, CTH
Project administration: BEH, EJM
Resources: SJC, CTH
Supervision: CTH
Visualization: BEH
Writing – original draft: BEH
Writing – review & editing: BEH, GN, EJM, SJC, CTH

## Competing interests

There is no conflict of interest declared in this article.

## Funding information

This project received funding from the Manitoba Fish and Wildlife Enhancement Fund (#FES20-006) and a Natural Sciences and Engineering Research Council (NSERC) Alliance Grant (ALLRP 562034-21). BEH was supported by The Northern Scientific Training Program (NSTP) and the University of Winnipeg Graduate Studies Scholarship.

# References

Althoff, A.L., Suski, C.D., and Louison, M.J. 2021. Depth-based barotrauma severity, reflex impairment and stress response in two species of ice-angled fish. Fish. Manag. Ecol. **28**: 383–392. doi:10.1111/fme.12493.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., et al. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev. Fish. Sci. **15**: 75–167. doi:10.1080/10641260601149432.

Arlinghaus, R., Klefoth, T., Cooke, S.J., Gingerich, A., and Suski, C.D. 2009. A combined laboratory and field study to understand physiological and behavioral disturbance and recovery from catch-and-release recreational angling in northern pike (*Esox lucius*). Fish. Res. **97**: 223–233. doi:10.1016/j.fishres.2009.02.005.

Barry, T.P., Lapp, A.F., Kayes, T.B., and Malison, J.A. 1993. Validation of a microtitre plate ELISA for measuring cortisol in fish and comparison of stress responses of rainbow trout (*Oncorhynchus mykiss*) and lake trout (*Salvelinus namaycush*). Aquaculture, **117**: 351–363. doi:10.1016/0044-8486(93)90331-R.

Bartholomew, A., and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. **15**: 129–154. doi:10.1007/s11160-005-2175-1.

Barton, B.A. 2000. Salmonid fishes differ in their cortisol and glucose responses to handling and transport stress. N. Am. J. Aquac. **62**: 12–18. doi:10.1577/1548-8454(2000)062⟨0012:SFDITC⟩2.0.CO;2.

Barton, B.A. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integr. Comp. Biol. **42**: 517–525. doi:10.1093/icb/42.3.517.

Barton, B.A., and Iwama, G.K. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Annu. Rev. Fish Dis. **1**: 3–26. doi:10.1016/0959-8030(91)90019-G.

Barton, B.A., and Schreck, C.B. 1987. Influence of acclimation temperature on interrenal and carbohydrate stress responses in juvenile chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture, **62**: 299–310. doi:10.1016/0044-8486(87)90172-4.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**: 1–48. doi:10.18637/jss.v067.i01.

Bellquist, L., Beyer, S., Arrington, M., Maeding, J., Siddall, A., Fischer, P., et al. 2019. Effectiveness of descending devices to mitigate the effects of barotrauma among rockfishes (*Sebastes spp.*) in California recreational fisheries. Fish. Res. **215**: 44–52. doi:10.1016/j.fishres.2019.03.003.

Binder, T.R., Marsden, J.E., Riley, S.C., Johnson, J.E., Johnson, N.S., He, J., et al. 2017. Movement patterns and spatial segregation of two populations of lake trout *Salvelinus namaycush* in Lake Huron. J. Great Lakes Res. **43**: 108–118. doi:10.1016/j.jglr.2017.03.023.

Blyth, S.A., and Bower, S.D. 2022. After the spawn and on the hook: sea trout *Salmo trutta* biophysical responses to different components of catch and release in a coastal fishery. J. Fish Biol. **101**: 464–477. doi:10.1111/jfb.15108.

Brobbel, M.A., Wilkie, M.P., Davidson, K., Kieffer, J.D., Bielak, A.T., and Tufts, B.L. 1996. Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. Can. J. Fish. Aquat. Sci. **53**: 2036–2043. doi:10.1139/f96-143.

Brown, R.S., Colotelo, A.H., Pflugrath, B.D., Boys, C.A., Baumgartner, L.J., Deng, Z.D., et al. 2014. Understanding barotrauma in fish passing hydro structures: a global strategy for sustainable development of water resources. Fisheries, **39**: 108–122. doi:10.1080/03632415.2014.883570.

Brownscombe, J.W., Danylchuk, A.J., Chapman, J.M., Gutowsky, L.F., and Cooke, S.J. 2017. Best practices for catch-and-release recreational fisheries–angling tools and tactics. Fish. Res. **186**: 693–705. doi:10.1016/j.fishres.2016.04.018.

Brownscombe, J.W., Ward, T.D., Nowell, L., Lennox, R.J., Chapman, J.M., Danylchuk, A.J., and Cooke, S.J. 2022. Identifying thresholds in air exposure, water temperature and fish size that determine reflex impairment in brook trout exposed to catch-and-release angling. Conserv. Physiol. **10**: coac070. doi:10.1093/conphys/coac070.

Campbell, M.D., Patino, R., Tolan, J., Strauss, R., and Diamond, S.L. 2010. Sublethal effects of catch-and-release fishing: measuring capture stress, fish impairment, and predation risk using a condition index. ICES J. Mar. Sci. **67**: 513–521. doi:10.1093/icesjms/fsp255.

Card, J.T., Louison, M.J., Bieber, J.F., Suski, C.D., and Hasler, C.T. 2022. An examination of freezing in yellow perch (*Perca flavescens*) following ice fishing using a histological approach. J. Appl. Ichthyol. **38**: 285–292. doi:10.1111/jai.14304.

Carlson, T.J. 2012. Barotrauma in fish and barotrauma metrics. *In* The Effects of Noise on Aquatic Life. Vol. **730**, pp. 229–233. doi:10.1007/978-1-4419-7311-5_51.

Chhor, A.D., Glassman, D.M., Brownscombe, J.W., Trahan, A.T., Danylchuk, A.J., and Cooke, S.J. 2022a. Short-term behavioural impacts of air-exposure in three species of recreationally angled freshwater fish. Fish. Res. **253**: 106342. doi:10.1016/j.fishres.2022.106342.

Chhor, A.D., Reid, J.L., Holder, P.E., Nowell, L.B., Brownscombe, J.W., Danylchuk, A.J., and Cooke, S.J. 2022b. Temporary retention in cold water reduces postrelease behavioral impairment in angled rainbow trout. N. Am. J. Fish. Manag. **42**: 140–150. doi:10.1002/nafm.10731.

Coggins, L.G., Jr., Catalano, M.J., Allen, M.S., Pine, W.E., III, and Walters, C.J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. **8**: 196–210. doi:10.1111/j.1467-2679.2007.00247.x.

Cooke, S.J., and Schramm, H.L. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. Fish. Manag. Ecol. **14**: 73–79. doi:10.1111/j.1365-2400.2007.00527.x.

Cooke, S.J., and Suski, C.D. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources?. Biodivers. Conserv. **14**: 1195–1209. doi:10.1007/s10531-004-7845-0.

Cooke, S.J., Cooke, C.J.A., and Brownscombe, J.W. 2016. Ultralight or heavyweight? The interactive effects of gear strength and air exposure on reflex impairment in largemouth bass. Trans. Am. Fish. Soc. **145**: 1202–1207. doi:10.1080/00028487.2016.1208116.

Cooke, S.J., Donaldson, M.R., O'Connor, C.M., Raby, G.D., Arlinghaus, R., Danylchuk, A.J., et al. 2013. The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. Fish. Manag. Ecol. **20**: 268–287. doi:10.1111/j.1365-2400.2012.00867.x.

Cooke, S.J., Schreer, J.F., Wahl, D.H., and Philipp, D.P. 2002. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Am. Fish. Soc. Symp. 489–512. Retrieved June 2023 from https://www3.carleton.ca/fecpl/pdfs/C%20and%20R%20LMB%20SMB%20MS.pdf.

Curtis, J.M., Johnson, M.W., Diamond, S.L., and Stunz, G.W. 2015. Quantifying delayed mortality from barotrauma impairment in discarded red snapper using acoustic telemetry. Mar. Coast. Fish. **7**: 434–449. doi:10.1080/19425120.2015.1074968.

Danylchuk, A.J., Danylchuk, S.C., Kosiarski, A., Cooke, S. J., and Huskey, B. 2018. Keepemwet fishing—an emerging social brand for disseminating best practices for catch-and-release in recreational fisheries. Fish. Res. **205**: 52–56. doi:10.1016/j.fishres.2018.04.005.

Davies, H.L., Gross, S., Haggarty, D.R., and Juanes, F. 2022. Conserving rockfishes: barotrauma and descending devices in the Northeast Pacific. Fisheries, **47**: 406–411. doi:10.1002/fsh.10810.

Davis, K.B., Suttle, M.A., and Parker, N.C. 1984. Biotic and abiotic influences on corticosteroid hormone rhythms in channel catfish. Trans. Am. Fish. Soc. **113**: 414–421. doi:10.1577/1548-8659(1984)113⟨414:BAAIOC⟩2.0.CO;2.

Davis, M.W. 2007. Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. ICES J. Mar. Sci. **64**: 1535–1542. doi:10.1093/icesjms/fsm087.

Dedual, M. 1996. Observed mortality of rainbow trout caught by different angling techniques in Lake Taupo, New Zealand. N. Am. J. Fish. Manag. **16**: 357–363. doi:10.1577/1548-8675(1996)016%3C0357:OMORTC%3E2.3.CO;2.

Dextrase, A.J., and Ball, H.E. 1991. Hooking mortality of lake trout angled through the ice. N. Am. J. Fish. Manag. **11**: 477–479. doi:10.1577/1548-8675(1991)011%3C0477:HMOLTA%3E2.3.CO;2.

Donaldson, M.R., Hinch, S.G., Jeffries, K.M., Patterson, D.A., Cooke, S.J., Farrell, A.P., and Miller, K.M. 2014. Species-and sex-specific responses and recovery of wild, mature pacific salmon to an exhaustive exercise and air exposure stressor. Comp. Biochem. Physiol. A Mol. Integr. Physiol. **173**: 7–16. doi:10.1016/j.cbpa.2014.02.019.

Donaldson, M.R., Raby, G.D., Nguyen, V.N., Hinch, S.G., Patterson, D.A., Farrell, A.P., et al. 2013. Evaluation of a simple technique for recovering fish from capture stress: integrating physiology, biotelemetry, and social science to solve a conservation problem. Can. J. Fish. Aquat. Sci. **70**: 90–100. doi:10.1139/cjfas-2012-0218.

Drumhiller, K.L., Johnson, M.W., Diamond, S.L., Reese Robillard, M.M., and Stunz, G.W. 2014. Venting or rapid recompression increase survival and improve recovery of Red Snapper with barotrauma. Mar. Coast. Fish. **6**: 190–199. doi:10.1080/19425120.2014.920746.

Eberts, R.L., Zak, M.A., Manzon, R.G., and Somers, C.M. 2018. Walleye responses to barotrauma relief treatments for catch-and-release angling: short-term changes to condition and behavior. J. Fish Wildl. Manag. **9**: 415–430. doi:10.3996/112017-JFWM-096.

Elliott, C.W., Row, A.J., and Tufts, B.L. 2021. Comparison of angler interventions for smallmouth bass experiencing barotrauma in catch-and-release angling tournaments. N. Am. J. Fish. Manag. **41**: 834–843. doi:10.1002/nafm.10590.

Environment and Climate Change Canada. 2022. Hourly Data Report 2022 [data set]. Government of Canada. Retrieved June 2023 from https://climate.weather.gc.ca/climate_data/hourly_data_e.html?hlyRange=2005-08-22%7C2022-05-26&dlyRange=2005-08-22%7C2022-05-25&mlyRange=2007-08-01%7C2007-11-01&StationID=43983&Prov=MB&urlExtension=_e.html&searchType=stnName&optLimit=specDate&StartYear=2021&EndYear=2022&selRowPerPage=25&Line=1&searchMethod=contains&txtStationName=The+Pas&timeframe=1&time=LST&time=LST&Year=2022&Month=1&Day=10#.

Falk, M.R., Gillman, D.V., and Dahlke, L.W. 1974. Comparison of mortality between barbed and barbless hooked lake trout, Winnipeg, Manitoba. Can. Fish. Mar. Serv. Tech. Rep. CEN/T-74-1.

Ferguson, H.W. 1989. Systemic pathology of fish. A text and atlas of comparative tissue responses in diseases of teleosts. Iowa State University Press.

Ferguson, R.A., and Tufts, B.L. 1992. Physiological 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. doi:10.1139/f92-129.

Ferter, K., Weltersbach, M.S., Humborstad, O. B., Fjelldal, P. G., Sambraus, F., Strehlow, H. V., and Vølstad, J. H. 2015. Dive to survive: effects of capture depth on barotrauma and post-release survival of Atlantic cod (*Gadus morhua*) in recreational fisheries. ICES J. Mar. Sci. **72**: 2467–2481. doi:10.1093/icesjms/fsv102.

Fox, J., and Weisberg, S. 2019. An R companion to applied regression. 3rd ed. Sage Publications, Thousand Oaks, CA. Retrieved June 2023 from https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Gallagher, C.P., Guzzo, M.M., and Dick, T.A. 2018. Seasonal depth and temperature use, and diel movements of lake trout (*Salvelinus namaycush*) in a subarctic lake. Arct. Sci. **5**: 71–89. doi:10.1139/as-2017-0003.

Gilman, E., Suuronen, P., Hall, M., and Kennelly, S. 2013. Causes and methods to estimate cryptic sources of fishing mortality. J. Fish Biol. **83**: 766–803. doi:10.1111/jfb.12148.

Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., and Arlinghaus, R. 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. Fish. Res. **86**: 169–178. doi:10.1016/j.fishres.2007.06.002.

Gravel, M.A., and Cooke, S.J. 2008. Severity of barotrauma influences the physiological status, postrelease behavior, and fate of tournament-caught smallmouth bass. N. Am. J. Fish. Manag. **28**: 607–617. doi:10.1577/M07-013.1.

Guderley, H. 2004. Metabolic responses to low temperature in fish muscle. Biol. Rev. **79**: 409–427. doi:10.1017/S1464793103006328.

Hannah, R.W., Rankin, P.S., Penny, A.N., and Parker, S.J. 2008. Physical model of the development of external signs of barotrauma in Pacific rockfish. Aquat. Biol. **3**: 29–296. doi:10.3354/ab00088.

Hébert, I., and Dunlop, E.S. 2020. Temperature response in the physiology and growth of lake trout strains stocked in the Laurentian Great Lakes. J. Great Lakes Res. **46**: 366–375. doi:10.1016/j.jglr.2020.01.012.

Holder, P.E., Griffin, L.P., Adams, A.J., Danylchuk, A.J., Cooke, S.J., and Brownscombe, J.W. 2020. Stress, predators, and survival: exploring permit (*Trachinotus falcatus*) catch-and-release fishing mortality in the Florida Keys. J. Exp. Mar. Biol. Ecol. **524**: 151289. doi:10.1016/j.jembe.2019.151289.

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**: 1400–1417. doi:10.1111/faf.12696.

Ivanova, S.V., Johnson, T.B., Metcalfe, B., and Fisk, A.T. 2021. Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. Freshw. Biol. **66**: 615–627. doi:10.1111/fwb.13665.

Kerr, S.J. 2001. A review of fizzing, a technique for swim bladder deflation. Ministry of Natural Resources, Fish & Wildlife Branch, Fisheries Section.

Keyler, T.D., Hrabik, T.R., Mensinger, A.F., Rogers, L.S., and Gorman, O.T. 2019. Effect of light intensity and substrate type on siscowet lake trout (*Salvelinus namaycush siscowet*) predation on deepwater sculpin (*Myoxocephalus thompsonii*). Hydrobiologia, **840**: 77–88. doi:10.1007/s10750-019-3944-5.

Kiilerich, P., Servili, A., Peron, S., Valotaire, C., Goardon, L., Leguen, I., and Prunet, P. 2018. Regulation of the corticosteroid signalling system in rainbow trout HPI axis during confinement stress. Gen. Comp. Endocrinol. **258**: 184–193. doi:10.1016/j.ygcen.2017.08.013.

Komsta, L. 2022. Outliers: tests for outliers. R package version 0.15. Retrieved June 2023 from https://CRAN.R-project.org/package=outliers.

Lamont, D. 2017. Hardwater lake trout. Hooked Magazine. Available from https://www.hookedmagazine.ca/hardwater-lake-trout/ [accessed 8 January 2022].

Larocque, S.M., Lake, C., Johnson, T.B., and Fisk, A.T. 2022. Patterns in spatial use of land-locked Atlantic salmon (*Salmo salar*) in a large lake. J. Great Lakes Res. **48**: 381–391. doi:10.1016/j.jglr.2021.12.002.

Lawrence, M.J., Jeffries, K.M., Cooke, S.J., Enders, E.C., Hasler, C.T., Somers, C. M., et al. 2022. Catch-and-release ice fishing: status, issues, and research needs. Trans. Am. Fish. Soc. **151**: 322–332. doi:10.1002/tafs.10349.

Lawrence, M.J., Raby, G.D., Teffer, A.K., Jeffries, K.M., Danylchuk, A.J., Eliason, E.J., et al. 2020. Best practices for non-lethal blood sampling of fish via the caudal vasculature. J. Fish Biol. **97**: 4–15. doi:10.1111/jfb.14339.

Lee, W.C., and Bergersen, E.P. 1996. Influence of thermal and oxygen stratification on lake trout hooking mortality. N. Am. J. Fish. Manag. **16**: 175–181. doi:10.1577/1548-8675(1996)016%3C0175:IOTAOS%3E2.3.CO;2.

Loftus, A.J., Taylor, W.W., and Keller, M. 1988. An evaluation of lake trout (*Salvelinus namaycush*) hooking mortality in the upper Great Lakes. Can. J. Fish. Aquat. Sci. **45**: 1473–1479. doi:10.1139/f88-172.

Logan, J.M., Lawrence, M.J., Morgan, G.E., Twardek, W.M., Lennox, R.J., and Cooke, S.J. 2019. Consequences of winter air exposure on walleye (*Sander vitreus*) physiology and impairment following a simulated ice-angling event. Fish. Res. **215**: 106–113. doi:10.1016/j.fishres.2019.03.014.

Louison, M.J., Hasler, C.T., Fenske, M.M., Suski, C.D., and Stein, J.A. 2017a. Physiological effects of ice-angling capture and handling on Northern Pike, Esox lucius. Fish. Manag. Ecol. **24**: 10–18. doi:10.1111/fme.12196.

Louison, M.J., Hasler, C.T., Raby, G.D., Suski, C.D., and Stein, J.A. 2017b. Chill out: physiological responses to winter ice-angling in two temperate freshwater fishes. Conserv. Physiol. **5**: cox027. doi:10.1093/conphys/cox027.

Louison, M.J., LaRochelle, L., and Cooke, S.J. 2023. Effectiveness of barotrauma mitigation methods in ice-angled bluegill and black crappie. Fish. Manag. Ecol.doi:10.1111/fme.12615.

Lowry, O.H., and Passonneau, J.V. 1972. A flexible system of enzymatic analysis. Academic Press, New York. Retrieved June 2023 from https://books.google.ca/books?hl=en&lr=&id=R23cNZbBByMC&oi=fnd&pg=PP1&dq=a+flexible+system+of+enzymatic&ots=X8PKxh4CDJ&sig=Z8qDTaMuf2BdjxXevBv19zXG1VM&redir_esc=y#v=onepage&q=a%20flexible%20system%20of%20enzymatic&f=false.

Lyon, C.A., Davis, J.L., Fincel, M.J., and Chipps, S.R. 2022. Effects of capture depth on walleye hooking mortality during ice fishing. Lake Reserv. Manag. **38**: 334–340. doi:10.1080/10402381.2022.2130118.

Macaulay, G., Wright, D., Oppedal, F., and Dempster, T. 2020. Buoyancy matters: establishing the maximum neutral buoyancy depth of Atlantic salmon. Aquaculture, **519**: 734925. doi:10.1016/j.aquaculture.2020.734925.

Mazerolle, M.J. 2020. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. Retrieved June 2023 from https://cran.r-project.org/package=AICcmodavg.

McLean, M.F., Hanson, K.C., Cooke, S.J., Hinch, S.G., Patterson, D.A., Nettles, T.L., et al. 2016. Physiological stress response, reflex impairment and delayed mortality of white sturgeon Acipenser transmontanus exposed to simulated fisheries stressors. Conserv. Physiol. **4**: cow031. doi:10.1093/conphys/cow031.

McLean, M.F., Litvak, M.K., Stoddard, E.M., Cooke, S.J., Patterson, D.A., Hinch, S.G., et al. 2020. Linking environmental factors with reflex action mortality predictors, physiological stress, and post-release movement behaviour to evaluate the response of white sturgeon (*Acipenser transmontanus* Richardson, 1836) to catch-and-release angling. Comp. Biochem. Physiol. A Mol. Integr. Physiol. **240**: 110618. doi:10.1016/j.cbpa.2019.110618.

McLennan, M.F., Campbell, M.J., and Sumpton, W.D. 2014. Surviving the effects of barotrauma: assessing treatment options and a ‘natural’ remedy to enhance the release survival of line caught pink snapper (*Pagrus auratus*). Fish. Manag. Ecol. **21**: 330–337. doi:10.1111/fme.12083.

Meka, J.M., and 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**: 311–322. doi:10.1016/j.fishres.2004.10.006.

Milligan, C.L., and Wood, C.M. 1986. Tissue intracellular acid-base status and the fate of lactate after exhaustive exercise in the rainbow trout. J. Exp. Biol. **123**: 123–144. doi:10.1242/jeb.123.1.123.

Mongillo, P.E. 1984. A summary of salmonid hooking mortality. Washington Department of Game, Fisheries Management Division,Olympia.

Morata, P., Vargas, A.M., Sanchez-Medina, F., Garcia, M., Cardenete, G., and Zamora, S. 1982. Evolution of gluconeogenic enzyme activities during starvation in liver and kidney of the rainbow trout (*Salmo gairdneri*). Comp. Biochem. Physiol. B Comp. Biochem. **71**: 65–70. doi:10.1016/0305-0491(82)90176-6.

Morrissey, M.B., Suski, C.D., Esseltine, K.R., and Tufts, B.L. 2005. Incidence and physiological consequences of decompression in smallmouth bass after live-release angling tournaments. Trans. Am. Fish. Soc. **134**: 1038–1047. doi:10.1577/T05-010.1.

Mullen, E.J., Schoen, A.N., Hauger, M.D., Murray, L., and Anderson, W.G. 2020. Angler experience and seasonal effects on the response of the lake sturgeon to catch-and-release angling. Trans. Am. Fish. Soc. **149**: 709–720. doi:10.1002/tafs.10266.

Muoneke, M.I., and Childress, W.M. 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. **2**: 123–156. doi:10.1080/10641269409388555.

Nawrocki, B.M., Zhu, C., and Johnson, T.B. 2022. Comparative trophic ecology of nearshore juvenile salmonids in Lake Ontario. J. Great Lakes Res. **48**: 1669–1680. doi:10.1016/j.jglr.2022.09.004.

Ng, E.L., Fredericks, J.P., and Quist, M.C. 2015. Effects of gill-net trauma, barotrauma, and deep release on postrelease mortality of lake trout. J. Fish Wildl. Manag. **6**: 265–277. doi:10.3996/122014-JFWM-096.

Nguyen, V., Gravel, M.A., Mapleston, A., Hanson, K.C., and Cooke, S.J. 2009. The post-release behaviour and fate of tournament-caught smallmouth bass after ‘fizzing’ to alleviate distended swim bladders. Fish. Res. **96**: 313–318. doi:10.1016/j.fishres.2008.12.003.

Nuhfer, A.J., and Alexander, G. R. 1992. Hooking mortality of trophy-sized wild brook trout caught on artificial lures. N. Am. J. Fish. Manag. **12**: 634–644. doi:10.1577/1548-8675(1992)012⟨0634:HMOTSW⟩2.3.CO;2.

Papatheodoulou, M., Závorka, L., Koeck, B., Metcalfe, N.B., and Killen, S.S. 2022. Simulated pre-spawning catch and release of wild Atlantic salmon (*Salmo salar*) results in faster fungal spread and opposing effects on female and male proxies of fecundity. Can. J. Fish. Aquat. Sci. **79**: 267–276. doi:10.1139/cjfas-2021-0089.

Pelster, B. 2021. Using the swimbladder as a respiratory organ and/or a buoyancy structure—Benefits and consequences. J. Exp. Zool. A Ecol. Integr. Physiol. **335**: 831–842. doi:10.1002/jez.2460.

Persons, S.E., and Hirsch, S.A. 1994. Hooking mortality of lake trout angled through the ice by jigging and set-lining. N. Am. J. Fish. Manag. **14**: 664–668. doi:10.1577/1548-8675(1994)014⟨0664:HMOLTA⟩2.3.CO;2.

Portz, D.E., Woodley, C.M., and Cech, J.J. 2006. Stress-associated impacts of short-term holding on fishes. Rev. Fish Biol. Fish. **16**: 125–170. doi:10.1007/s11160-006-9012-z.

Pottinger, T.G. 2010. A multivariate comparison of the stress response in three salmonid and three cyprinid species: evidence for inter-family differences. J. Fish Biol. **76**: 601–621. doi:10.1111/j.1095-8649.2009.02516.x.

Pribyl, A.L., Kent, M.L., Parker, S.J., and Schreck, C.B. 2011. The response to forced decompression in six species of Pacific rockfish. Trans. Am. Fish. Soc. **140**: 374–383. doi:10.1080/00028487.2011.567858.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved June 2023 from https://www.R-project.org/.

Raby, G.D., Donaldson, M.R., Hinch, S.G., Patterson, D.A., Lotto, A.G., Robichaud, D., et al. 2012. Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild coho salmon bycatch released from fishing gears. J. Appl. Ecol. **49**: 90–98. doi:10.1111/j.1365-2664.2011.02073.x.

Raby, G.D., Hinch, S.G., Patterson, D.A., Hills, J.A., Thompson, L.A., and Cooke, S.J. 2015. Mechanisms to explain purse seine bycatch mortality of coho salmon. Ecol. Appl. **25**: 1757–1775. doi:10.1890/14-0798.1.

Reeves, K.A., and Staples, D.F. 2011. Relative hooking mortality among Walleyes caught on barbed and barbless octopus hooks and barbed jigs. N. Am. J. Fish. Manag. **31**: 32–40. doi:10.1080/02755947.2011.557944.

Ridgway, M.S., Bell, A.H., Lacombe, N.A., Mitchell, K.J., Smith, D.A., Taylor, C.E., and Middel, T.A. 2022. Thermal niche and habitat use by co-occurring lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) in stratified lakes. Environ. Biol. Fishes, 1–15. doi:10.1007/s10641-022-01368-9.

Robergs, R.A., Ghiasvand, F., and Parker, D. 2004. Biochemistry of exercise-induced metabolic acidosis. Am. J. Physiol. Regul. Integr. Comp. Physiol. **287**: R502–R516. doi:10.1152/ajpregu.00114.2004.

Rodnick, K.J., and Planas, J.V. 2016. The stress and stress mitigation effects of exercise: cardiovascular, metabolic, and skeletal muscle adjustments. Fish Physiol. **35**: 251–294. doi:10.1016/B978-0-12-802728-8.00007-2.

Ross, M.R., and Hokenson, S. R. 1997. Short-term mortality of discarded finfish bycatch in the Gulf of Maine fishery for northern shrimp Pandalus borealis. N. Am. J. Fish. Manag. **17**: 902–909. doi:10.1577/1548-8675(1997)017%3C0902:STMODF%3E2.3.CO;2.

Ruane, N.M., Bonga, S.W., and Balm, P.H.M. 1999. Differences between rainbow trout and brown trout in the regulation of the pituitary–interrenal axis and physiological performance during confinement. Gen. Comp. Endocrinol. **115**: 210–219. doi:10.1006/gcen.1999.7292.

Rummer, J.L., and Bennett, W.A. 2005. Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. Trans. Am. Fish. Soc. **134**: 1457–1470. doi:10.1577/T04-235.1.

Sass, G.G., and Shaw, S.L. 2020. Catch-and-release influences on inland recreational fisheries. Rev. Fish. Sci. Aquac. **28**: 211–227. doi:10.1080/23308249.2019.1701407.

Saunders, R.L. 1953. The swimbladder gas content of some freshwater fish with particular reference to the physostomes. Can. J. Zool. **31**: 547–560. doi:10.1139/z53-039.

Scarabello, M., Wood, C.M., and Heigenhauser, G.J.F. 1991. Glycogen depletion in juvenile rainbow trout as an experimental test of the oxygen debt hypothesis. Can. J. Zool. **69**: 2562–2568. doi:10.1139/z91-361.

Schisler, G.J., and Bergersen, E.P. 1996. Postrelease hooking mortality of rainbow trout caught on scented artificial baits. N. Am. J. Fish. Manag. **16**: 570–578. doi:10.1577/1548-8675(1996)016%3C0570:PHMORT%3E2.3.CO;2.

Schreck, C.B., and Tort, L. 2016. The concept of stress in fish. Fish Physiol. **35**: 1–34. doi:10.1016/B978-0-12-802728-8.00001-1.

Schreer, J.F., Gokey, J., and DeGhett, V. J. 2009. The incidence and consequences of barotrauma in fish in the St. Lawrence River. N. Am. J. Fish. Manag. **29**: 1707–1713. doi:10.1577/M09-013.1.

Shuter, B.J., Jones, M.L., Korver, R.M., and Lester, N.P. 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Can. J. Fish. Aquat. **55**: 2161–2177. doi:10.1139/f98-055.

Sitar, S.P., Brenden, T.O., He, J.X., and Johnson, J.E. 2017. Recreational postrelease mortality of lake trout in lakes Superior and Huron. N. Am. J. Fish. Manag. **37**: 789–808. doi:10.1080/02755947.2017.1327903.

Sopinka, N.M., Donaldson, M.R., O'Connor, C.M., Suski, C.D., and Cooke, S.J. 2016. Stress indicators in fish. Fish Physiol. **35**: 405–462. doi:10.1016/B978-0-12-802728-8.00011-4.

St John, J. 2003. Is your fish "bent" and will it survive? SPC Live Reef Fish Information Bulletin #11. pp. 31–35. Retrieved June 2023 from https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=6a427477bfb34fba20fc5775ac979565f0bc15ac.

Suski, C.D., Killen, S.S., Morrissey, M.B., Lund, S.G., and Tufts, B.L. 2003. Physiological changes in largemouth bass caused by live-release angling tournaments in southeastern Ontario. N. Am. J. Fish. Manag. **23**: 760–769. doi:10.1577/M02-042.

Torchiano, M. 2020. Effsize: efficient effect size computation, https://CRAN.R-project.org/package=effsize⟩.

Twardek, W.M., Gagne, T.O., Elmer, L.K., Cooke, S.J., Beere, M.C., and 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. doi:10.1016/j.fishres.2018.05.019.

Wang, Y., Heigenhauser, G.J., and Wood, C. M. 1994. Integrated responses to exhaustive exercise and recovery in rainbow trout white muscle: acid-base, phosphogen, carbohydrate, lipid, ammonia, fluid volume and electrolyte metabolism. J. Exp. Biol. **195**: 227–258. doi:10.1242/jeb.195.1.227.

Watson, J.W., Hyder, K., Boyd, R., Thorpe, R., Weltersbach, M.S., Ferter, K., et al. 2020. Assessing the sublethal impacts of anthropogenic stressors on fish: An energy-budget approach. Fish Fish. **21**: 1034–1045. doi:10.1111/faf.12487.

Wedemeyer, G.A., and Wydoski, R.S. 2008. Physiological response of some economically important freshwater salmonids to catch-and-release fishing. N. Am. J. Fish. Manag. **28**: 1587–1596. doi:10.1577/M07-186.1.

Wegner, N.C., Portner, E.J., Nguyen, D.T., Bellquist, L., Nosal, A.P., Pribyl, A.L., et al. 2021. Post-release survival and prolonged sublethal effects of capture and barotrauma on deep-dwelling rockfishes (genus *Sebastes*): implications for fish management and conservation. ICES J. Mar. Sci **78**: 3230–3244. doi:10.1093/icesjms/fsab188.

Wendelaar Bonga, S.E. 1997. The stress response in fish. Physiol. Rev. **77**: 591–625. doi:10.1152/physrev.1997.77.3.591.

Wickham, H., Hester, J., Chang, W., and Bryan, J. 2022. devtools: tools to make developing R packages easier. Retrieved June 2023 from https://CRAN.R-project.org/package=devtools.

Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T., and Tufts, B. L. 1996. Physiology and survival of wild Atlantic salmon following angling in warm summer waters. Trans. Am. Fish. Soc. **125**: 572–580. doi:10.1577/1548-8659(1996)125⟨0572:PASOWA⟩2.3.CO;2.

Wood, C.M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. J. Exp. Biol. **160**: 285–308. doi:10.1242/jeb.160.1.285.

Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? J. Fish Biol. **22**: 189–201. doi:10.1111/j.1095-8649.1983.tb04739.x.

Wydoski, R.S. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. Catch and release fishing as a management tool: a national sport fishing symposium. Humboldt State University, Arcata, California. pp. 43–87.

Wydoski, R.S., Wedemeyer, G.A., and Nelson, N.C. 1976. Physiological response to hooking stress in hatchery and wild rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. **105**: 601–606. doi:10.1577/1548-8659(1976)105⟨601:PRTHSI⟩2.0.CO;2.