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Ice-fishing handling practices and their effects on the short-term post-release behaviour of Largemouth bass

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ABSTRACT

Numerous studies have investigated the impacts of catch-and-release on the post-release behaviour of fish during periods characterized by warm air and water temperatures. Comparatively little is known about the post-release behaviour of fish caught while ice fishing. Largemouth bass (LMB), a popular sportfish in North America, is sometimes encountered during ice fishing and is often released due to angler conservation ethic or to comply with regulations. To examine the impacts of ice angling on the post-release behaviour of LMB, we exposed them to a range of handling practices and assessed their skin temperatures prior to release, as well as short-term post-release swimming activity using biologgers equipped with a tri-axial accelerometer, temperature and pressure sensors. Skin temperature of LMB had a significant positive relationship with windchill temperature. Generally, the longer that LMB were exposed to air or placed on the ice, the colder their skin became. Overall, water depth and water temperature selected by LMB increased with time during the post-release period. Overall dynamic body acceleration (ODBA), a proxy for locomotory activity, decreased as time progressed in the release period, while ODBA decreased with increasing depth and water temperatures. LMB with warmer skin temperatures had lower locomotory activity compared to those with colder skin temperatures. Further, the effect of skin temperature on locomotory activity became more amplified with increasing depth and warming water temperatures selected by LMB post-release. Anglers practicing catch-and-release angling during the winter should adopt best handling practices by reducing the time fish are removed from the water when windchill temperatures are sub-freezing to avoid alteration in post-release behaviour.

1. Introduction

Recreational angling is a leisure activity enjoyed worldwide, year-round, in different climates, and spans across various habitats from saltwater to freshwater. Fish that are angled recreationally are sometimes harvested for food (Cooke et al. 2018), or may be caught and released (Arlinghaus et al. 2007). Although some catch-and-release (C&R) is voluntary (Pitcher and Hollingworth, 2002), often times anglers are required to release fish to comply with fishing regulations (e.g., closed seasons, slot size limits; (Cooke and Schramm, 2007)). There has been a great amount of research on the effects of C&R on the survival and sublethal outcomes for a wide range of freshwater and marine fish after an interaction with an angler (reviewed in Bartholomew and Bohnsack, 2005, Arlinghaus et al. 2007). Such knowledge has informed fisheries management regulations and has also equipped anglers with best practices to improve the welfare of angled fish (reviewed in Brownscombe et al. 2017). Until recently, the majority of this research has focused on fish angled during the open water seasons. In contrast, comparatively little is known about outcomes for angled fish that are caught during the winter through the ice.

In cold climate regions where winter is often accompanied with ice cover on freshwater systems (McMeans et al. 2020, Studd et al. 2021), ice fishing is a common recreational activity but it comes with added problems of fish care when practicing C&R due to the presence of extreme cold temperatures (Deroba et al. 2007). Fish that are angled during the colder periods of the year show a reduced response to stress

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and a reduced mortality rate compared to when angled and released in warmer water temperatures (Louison et al. 2017a, Louison et al. 2017b, Twardek et al. 2018). Nonetheless, fish that are removed from the water are exposed to a combination of air and wind (windchill) and thus undergo a rapid change in the ambient temperature during periods with sub-freezing temperatures. It is known that damage to essential tissues can occur when aquatic ectotherms are exposed to air temperatures near or below freezing, and this exposure can prolong the recovery period (Warrenchuck and Shirley, 2002). For example, extensive damage to epithelial tissues (eyes, skin and gills) of fish occurs as a result of air exposure during cold periods, which can impair physiological functions (Tilney and Hocutt, 1987). Similarly, Haukenes et al. (2009) observed that exposure to freezing temperatures promoted cellular damage to the gill structure of tanner crabs (*Chionoecetes bairdi*) which had a negative impact on oxygen uptake.

Many studies have identified the risks and damage caused to fish when exposed to air in warm temperatures (Cook et al. 2015), but limited research has been focused on the extent of damage that is associated with C&R angling during the winter period when air temperatures are sub-freezing (Gale et al. 2013). There are many challenges with trying to investigate the effects of C&R angling during the winter, including ice cover that makes it difficult to observe fish once released. Common approaches to studying C&R in the winter involves holding fish in a net below the ice for a 24-48 -h period to characterize mortality (Twardek et al. 2018, Logan et al. 2019). Although these studies assessed post-release survival, little information is available about the immediate post-release behaviour of fish after encountering an ice-fishing C&R event.

In recent years, the use of biologgers has enabled researchers to assess the short-term behaviour of fish in the wild (Cooke et al. 2016) including in the context of C&R (Donaldson et al. 2008). For example, tri-axial accelerometer, pressure and temperature sensors on electronic tags can be used to quantify short-term swimming activity, depth and water temperature used by fish during the post-release period (Bettoli and Osborne, 1998, Freire et al. 2012, Brownscombe et al. 2013, Ferter et al. 2015, Lennox et al. 2018, Holder et al. 2020). Angling often leads to physiological alterations characterized by heightened cardiovascular and respiratory activity (Cooke et al. 2001), depleted tissue energy stores and alterations in blood chemistry (Ferguson and Tufts 1992, Kieffer 2000), which collectively contribute to swimming impairments, disorientation, increased risk of predation and loss of equilibrium (Kieffer 2000, Cooke et al. 2002, Cooke and Philipp, 2004, Danylchuk et al. 2007). Deviations in routine swimming behaviour and patterns during the short-term post-release period are good proxies for determining the long-term fate of fish, which is often correlated with the survival of fish (Beitinger 1990, Brownscombe et al. 2014). It is also known that cold water temperatures delay the response to stress created from being air exposed (Louison et al. 2017a, Louison et al. 2017b), which further warrants the need for assessing the post-release behaviour of fish captured in the winter. As previously mentioned, exposure to harsh environmental conditions with sub-freezing temperatures promotes the risk of freezing and damaging essential tissues and fins (Tilney and Hocutt, 1987), which may impact the locomotory capabilities of a fish.

Largemouth bass (*Micropterus salmoides*) (LMB) are a popular sportfish species in recreational angling that is primarily C&R and a common target species for competitive tournaments (Cooke et al. 2002). There are various ways that LMB are regulated across jurisdictions, with fisheries regulations in some northern jurisdictions (e.g., parts of Ontario and Michigan) that do not permit targeting LMB during the winter (closed season), while other areas allow a winter C&R angling season for LMB. Some jurisdictions even permit the harvest of LMB during the winter. With little knowledge about how this valued species responds to angling stressors in the winter, it is difficult to determine which best practices should be encouraged when handling LMB in both jurisdictions that allow anglers to target LMB in the winter or where they are encountered incidentally. Although the biological basis for regulations that limit fishing for LMB in the winter is unclear, it is presumably to reduce stress prior to reproduction (i.e., spring spawning), to reduce potential for overharvesting while LMB are aggregated in the winter, and/or to protect LMB when they are primarily in deep water and at risk of barotrauma (Gustaveson et al. 1991, Morrissey et al. 2005, Granfors 2013). While there is limited information available associated with the impacts of air exposure of LMB during sub-freezing temperatures, Bieber et al. (2019) found that swimming performance of Bluegill (*Lepomis macrohirus*) was significantly reduced when exposed to sub-freezing temperatures for 5 minutes. As suggested by Bieber et al. (2019), reducing air exposure duration during sub-freezing temperatures would ensure the survival of released *Centrarchidae* species.

The objective of this study was to examine how LMB respond to a C&R event in the winter. Specifically, we quantified how different air and ice exposures during a typical C&R event under a range of winter conditions (i.e., windchill, wind speed) influenced skin temperature and post-release behaviour of LMB. Data were recorded on biologgers attached to wild LMB caught in the winter using Velcro harnesses for roughly ten minutes. This study provides insight on how environmental conditions and angler behaviour influence the behaviour and condition of LMB angled in the winter.

2. Materials and Methods

2.1. Fish capture and tagging

LMB were captured between January 24th, 2020 and February 12th, 2020 in Elbow Lake in South Frontenac, Ontario, Canada (44°28'27.2"N, 76°25'43.0"W). LMB were captured by two different angling techniques: still lines (tip-ups) and actively jigging with ice fishing rods. Tip-ups were spooled with 9.1 kg breaking strength braided Dacron line and tipped with a 4.5 kg breaking strength fluorocarbon leader line to a single barbless size 4 Gamakatsu octopus hook, baited with a dead minnow. Ice fishing rods used were medium light to medium action rods, spooled with 2.7 kg to 3.6 kg breaking strength monofilament or braided line. Small invertebrate-like plastics and jigging spoons (tipped with a piece of minnow) were used to actively jig LMB. All fish were captured and released between 5.5 meters and 6.5 meters of water. Once fish were landed, they were transferred to a water filled trough and total length (mm) was measured. All locomotory, water temperature and water depth data were collected on Axy-Depth biologgers (12×31 x 11 mm, 7.5 g in air; TechnoSmArt, Guidonia Montecelio, Italy) epoxied to an acrylic plate (1 mm thick) and secured to the mid-section of the LMB using a Velcro strap (Fig. 1; see Chhor et al. In Press). These tri-axial biologgers had the same configuration parameters across all fish in the study. The acceleration (g) of LMB was measured across three axes (A_x = surge, A_y = sway, A_z = heave, with respect to attachment orientation) with a sample rate of 25 Hz at an 8-bit resolution. This model of biologger has a temperature resolution of $\pm$ 0.1 °C and a depth resolution of $\pm$5 cm. As described in Shepard et al. (2008), Brownscombe et al. (2018), static acceleration (gravity) was removed from the dynamic acceleration (fish movement) using a 2 second box smoother. Overall dynamic body acceleration (ODBA), an index of locomotor activity (Halsey et al., 2009; Gleiss et al., 2011; Brownscombe et al., 2013; Wright et al., 2014), was calculated using the absolute sum of the dynamic acceleration from all three axes (A_X, A_Y and A_Z) (Halsey et al. 2011). Biologgers were placed on the ventral side of the fish, between the two pectoral fins. Fixing the biologgers to the fish took place in the trough, keeping the fish submerged in water, immediately after taking length measurements. Attachment process of the biologger with the Velcro harness never exceeded 60 seconds. Once the biologger was attached, LMB were immediately released (control fish), or subjected to an additional handling treatment (see below). After the treatment process and prior to being resubmerged and released, skin temperature of the fish was recorded with an infrared temperature meter ($\pm$ 1 °C,

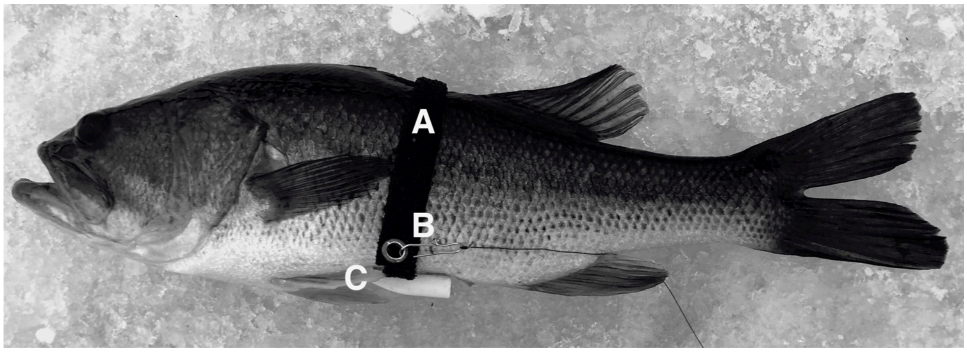

Fig. 1. Largemouth bass (*Micropterus salmoides*) with the Velcro strap (A) configuration used. The fast-attach clip (B) is used for retrieval of the biologger at the end of the trials. The biologger is placed on the ventral side of the Largemouth bass between the pectoral fins (C).

AstroAl, Placentia, California, United-States of America). Windspeed (km/h) and windchill (°C) was also measured using a handheld weather station (wind speed ± 5%, ± 2 °C, Hold Peak, Zhuhai, China). Prior to release, a Velcro harness to which the biologgers were affixed, was attached to a rod and reel that was spooled with 13.6 kg breaking strength braided line to allow for retrieval of the accelerometer, including the harness, at the end of the monitoring period. The bail of the spinning reel was kept open, allowing the fish to freely swim with the biologger for 10 -minute post-release monitoring period after which the bail of the reel was closed, creating tension on the braided line allowing the Velcro harness, including the biologger, to unstrap and dislodge from the fish. The logger package was then retrieved (i.e., reeled in). The location of the attachment strap was standardized for all fish (Fig. 1).

2.2. Treatments

Fish were exposed to different air and ice exposure treatments, including (0, 10, 30, and 90 seconds) of exposure, upon capture of the LMB. Each exposure treatment besides the control treatment (0 seconds), was comprised of two separate treatments, where fish were removed from the water and were either held in air or laid on the ice for the duration of the exposure period (zero, 10-air, 10-ice, 30-air, 30-ice, 90-air, 90-ice). These chosen durations represent a range of common exposure periods seen in ice angling events (Gingerich et al. 2007, Louison et al. 2017b).

2.3. Data Analysis

Model assumptions were checked following the outlined protocols in Zuur et al. (2010). For the purpose of this study, minutes post-release was treated as ordinal numbers accounting for individual minute blocks from the 10-minute post-release monitoring period. All models had fish length as a covariate to account for the size differences among the various treatment (Table 1). The model with skin temperature as the response variable was fit with a linear model using *lm* with windspeed (km/h), windchill (°C) and treatment as predictor variables. All other models were fit using a linear mixed effects model (*lmer*) function from the *nlme* package (Pinheiro et al. 2020). Analysis of variance (ANOVA), with a threshold alpha value of 0.05 (95% confidence), was then used to determine the significant predictors in the *lm* and *lmer* model, which were then followed up with a Dunnet or Tukey post-hoc test with the *glht* function from the *multcomp* package (Hothorn et al. 2008). A one-way ANOVA was used to determine if there were any differences in windchill temperatures across treatments, which was then followed up with a post-hoc test to identify pairwise differences. All analyses ware preformed in R (3.6.2) via R Studio (version 1.2.5033).

For the linear mixed effects model with ODBA as the response variable, treatment, windchill, water temperature, minutes post-release and the interaction of treatment and minutes post-release were fit as the predictor variables. Due to restrictions on correlated predictor variables (depth and water temperature), another model with ODBA as the response variable was also fit with treatment, windchill, depth, minutes post-release and the interaction of treatment and minutes post-release were fit as the predictor variables. Model with water temperature as the response variable was fit with treatment, windchill, minutes post-release and the interaction between treatment and minutes post-release as the predictor variables. Similarly, a model with the relationship of water depth and temperature as the response variable was fit with treatment, windchill, minutes post-release and the interaction between treatment and minutes post-release as the predictor variables. Finally, to understand how the interaction of external environment factors (out of water) interacting with the internal environmental factors (in the water) influence the locomotory activity, a second model with ODBA as a response variable was fit with skin temperature, the residuals from the relationship of water temperature and water depth, and the interaction of skin temperature with the residuals of the water temperature and depth relationship. All linear mixed effect models were fit with fish ID as the random effect variable to account for repeated measures across individuals.

Table 1
Total amount of Largemouth bass (*Micropterus salmoides*) per treatment, including the size of range within each treatment and the average size with the standard deviation.

Treatment	*n*	Mean (mm) ± S.D.	Smallest (mm)	Longest (mm)
Control	10	383 ± 34	315	430
10 sec air	10	370 ± 23	330	401
10 sec ice	10	340 ± 33	290	380
30 sec air	7	356 ± 58	272	425
30 sec ice	11	357 ± 35	284	385
90 sec air	8	338 ± 39	263	374
90 sec ice	9	364 ± 22	325	405

3. Results

3.1. Fish Metrics

A total of sixty-three LMB (mean ± (S.D.) total length (L_T) = 356 ± 36 mm, 263– 430 mm range) were captured for this study and each fish was only used once (Table 1). There was a significant difference between the mean lengths of LMB among the various treatments (ANOVA, $F_6 = 11.244$, $p < 0.001$) and therefore body sizes was incorporated into analysis models to account for this body size effect.

3.2. Skin Temperature

There was a positive relationship between LMB skin temperature and windchill temperature ($r^2 = 0.53$, $F_{620,1} = 264.095$, $p < 0.001$) (Fig. 2),

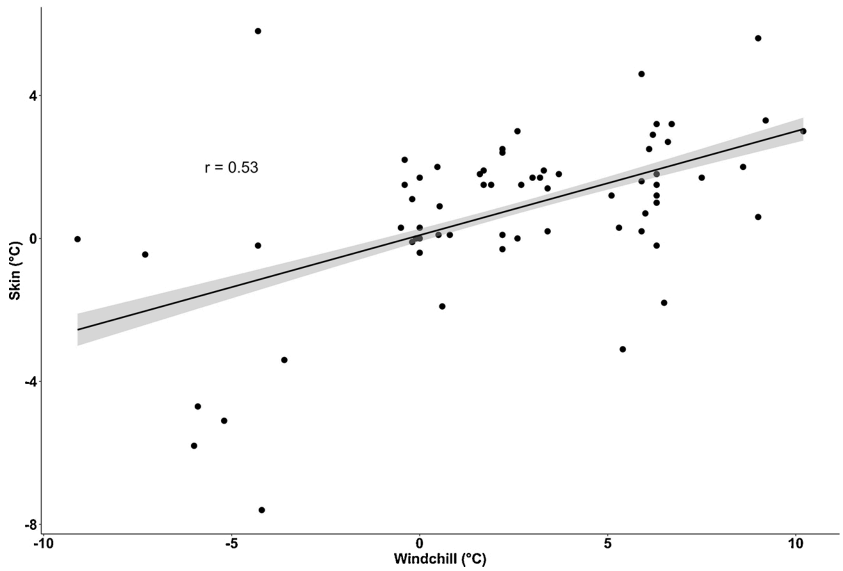

Fig. 2. Linear relationship between windchill and skin temperature of Largemouth bass (*Micropterus salmoides*) taken after being exposed to various air or ice exposures. Shaded area around the line of best fit represents the 95% confidence interval (y = 0.091 + 0.291x).

an index accounting for body heat loss of an individual at a given ambient temperature with the combination of wind speed. Wind speed alone did not have a significant effect on skin temperature ($F_{620,1}$ = *2.772, p = 0.096*). Skin temperature had a significant negative relationship with the total length of LMB ($F_{620,1}$ = *29.978, p < 0.001*). There was a significant difference in the windchill temperature between treatments ($F_{620,6}$ = *15.357, p < 0.001*) and the 90-air exposure handling treatment had significantly elevated windchill temperature compared to the control treatment, which was not air exposed (*t = 3.631, p = 0.002;* Fig. 3). Skin temperature of LMB was significantly different among handling treatments ($F_{621,6}$ = *14.670, p < 0.001*; Fig. 4). Skin temperatures were lower in all air and ice exposure treatments, compared to the control treatment with no exposure period. Within the air exposure treatments, the greatest difference in skin temperature was in the 30 second exposure (*t = -5.228, p < 0.001*), followed by the 10 second air exposure (*t = -3.168, p = 0.009*) and lastly the 90 second air exposure (*t = -2.853, p < 0.026*). As for LMB skin temperatures in the ice exposure treatments, compared to the control treatment, the biggest difference was seen in the 30 second ice exposure (*t = -7.665, p < 0.001*), followed by the 90 second ice exposure (*t = -5.233, p < 0.001*), and finally the 10 second ice exposure (*t = -5.015, p < 0.001*). There was also a greater reduction in skin temperature in LMB that are put on the ice, compared to those just air exposed (Fig. 4).

3.3. Post-Release Behaviour

As the monitoring period progressed, LMB used significantly warmer ($F_{630,8}$ = *46.004, p = < 0.001*) and deeper water ($F_{630,8}$ = *23.419, p = < 0.001*) following release, specifically when compared to the first minute of monitoring (Fig. 5). There was also a significant positive relationship between windchill temperature and water temperature selected during the release period ($F_{630,1}$ = *5.028, p = 0.028*). There was no significant relationship between windchill temperatures experienced and the depth selected by LMB upon release ($F_{630,1}$ = *2.787, p = 0.099*). LMB that experienced colder windchill were found in cooler water temperatures when released. There was no significant effect of treatment ($F_{630,48}$ = *0.649, p = 0.691*), nor the interaction between treatment and minutes post-release on the water temperature selected during the post-release

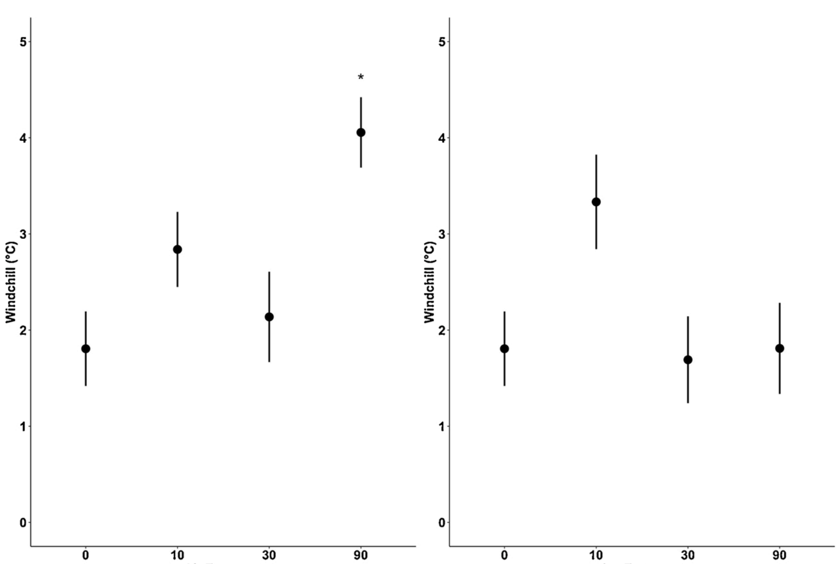

Fig. 3. Mean windchill experienced (n = 63, 2.47 °C ± 0.17 °C SE) by Largemouth bass (*Micropterus salmoides*) during an air exposure period for 10 seconds (n = 10, 1.19 °C ± 0.24 °C SE), 30 seconds (n = 7, 2.14 °C ± 0.47 °C SE) and 90 seconds (n = 8, 4.06 °C ± 0.37 °C SE). Mean skin temperature of Largemouth bass after experiencing an ice exposure for 10 seconds (n = 8, 3.33 °C ± 0.49 °C SE), 30 seconds (n = 11, 1.69 °C ± 0.45 °C SE) and 90 seconds (n = 9, 1.81 °C ± 0.47 °C SE) is also shown in the figure. Asterisks indicate the level of significance between 0 second exposure, control treatment (n = 10, 1.81 °C ± 0.39 °C SE) and the respective air or ice exposure.

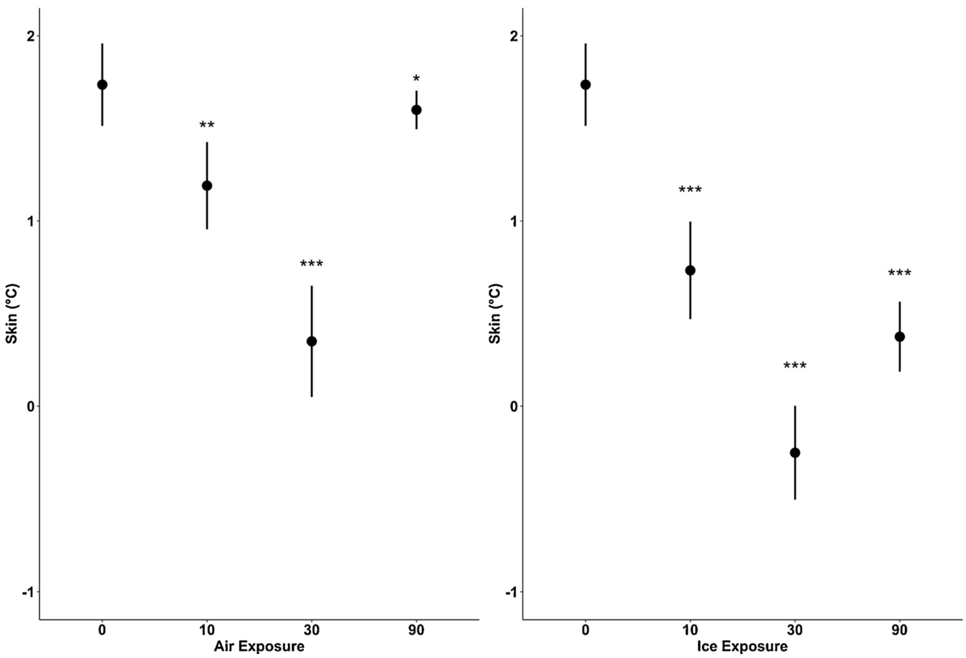

Fig. 4. Mean skin temperature (n = 63, 0.81 °C ± 0.09 °C SE) of Largemouth bass (*Micropterus salmoides*) after experiencing an air exposure for 10 seconds (n = 10, 1.19 °C ± 0.24 °C SE), 30 seconds (n = 7, 0.35 °C ± 0.30 °C SE) and 90 seconds (n = 8, 1.60 °C ± 0.10 °C SE). Mean skin temperature of Largemouth bass after experiencing an ice exposure for 10 seconds (n = 8, 0.73 °C ± 0.26 °C SE), 30 seconds (n = 11, -0.25 °C ± 0.25 °C SE) and 90 seconds (n = 9, 0.38 °C ± 0.19 °C SE) is also shown in the figure. Asterisks indicate the level of significance between 0 second exposure, control treatment (n = 10, 1.74 °C ± 0.22 °C SE) and the respective air or ice exposure.

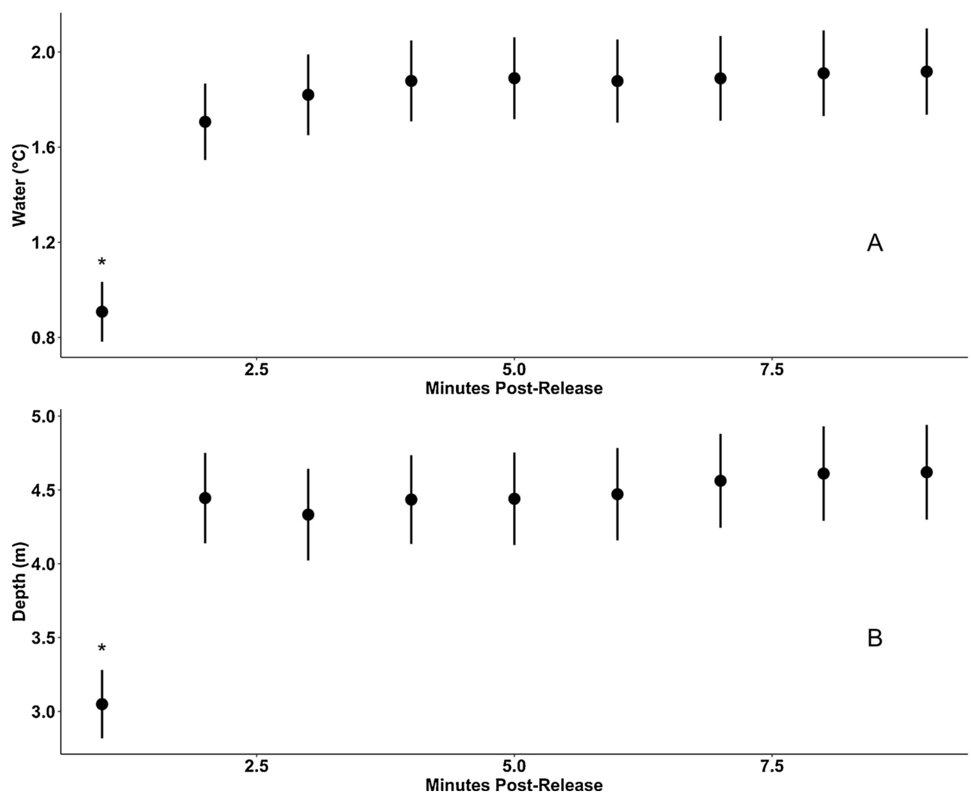

Fig. 5. Two-part figure representing the progressive increase of mean water temperature (4.33 °C ± 0.10 °C SE) (A) and mean depth (1.76 m ± 0.06 m SE) selected (B) by Largemouth bass (*Micropterus salmoides*) during the nine-minute post-release period. Asterisks are used to indicate water temperature and depth selected during the first minute post-release was significantly different than the following minutes post-release.

period ($F_{630,48} = 0.847, p = 0.759$). There was also no significant effect of treatment ($F_{630,1} = 0.723, p = 0.631$), or the interaction of treatment and minutes post-release on the selected water depth during the post-release period ($F_{630,48} = 0.786, p = 0.850$). Fish size did not influence water depth ($F_{630,1} = 0.003, p = 0.960$) or water temperature selected when released ($F_{630,1} = 0.297, p = 0.588$).

Locomotory activity (ODBA) of LMB significantly decreased as depth ($F_{630,1} = 56.373, p < 0.001$) and water temperature increased ($F_{630,1} = 5.432, p = 0.021$; Fig. 6). ODBA did not differ between treatments in the model with depth ($F_{630,6} = 0.901, p = 0.497$) and water temperature ($F_{630,6} = 1.041, p = 0.407$). However, there was a significant negative relationship between ODBA and time post-release in the depth model

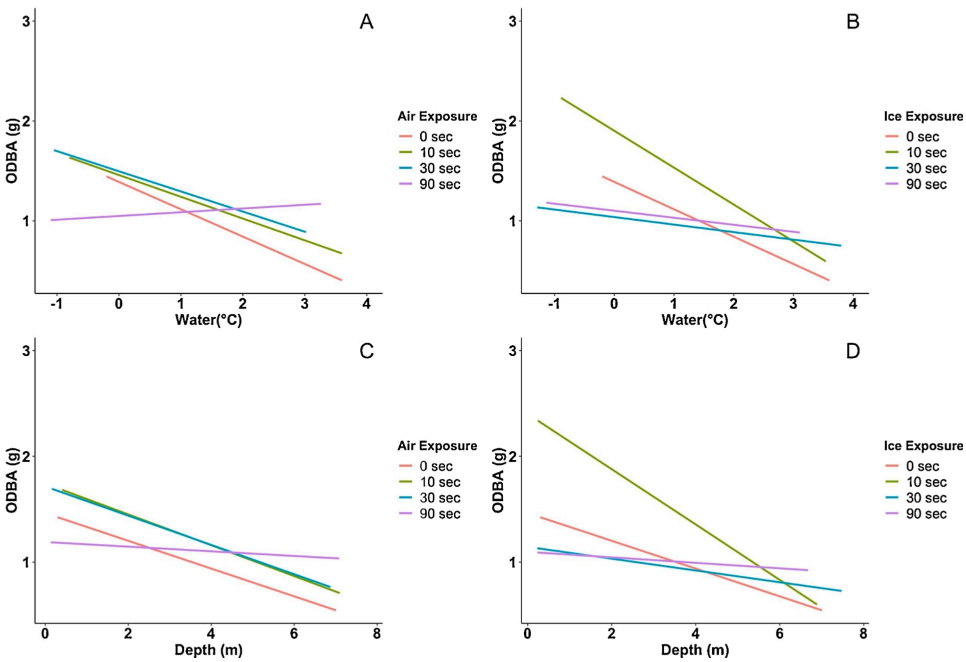

Fig. 6. Change in the mean overall dynamic body acceleration (ODBA) of Largemouth bass (*Micropterus salmoides*) when selecting different water temperatures and depth during the post-release period. The various colours represent different air or ice exposures experienced by the Largemouth bass prior to release. Figure A shows the change in locomotory activity when selecting water temperatures upon release after an air exposure, or ice exposure (B). Figure C shows the change in locomotory activity when selecting water temperatures upon release after an air exposure, or ice exposure (D). Colours within the figures represent the various durations of exposure.

($F_{630,8} = 177.606, p < 0.001$) and water temperature model ($F_{630,8} = 157.482, p < 0.001$). There was a significant difference in ODBA over the course of the post-release monitoring period (Fig. 7). Windchill and ODBA had a significant positive relationship in the model with ODBA as the response variable and depth as a predictor variable, ($F_{630,1} = 4.122, p = 0.048$). LMB experienced a reduction in locomotion after being exposed to colder windchill temperatures. Fish size did not significantly influence locomotory activity upon release in the water depth model ($F_{630,1} = 0.237, p = 0.628$), nor did fish size significantly influence activity in the water temperature model ($F_{630,1} = 0.406, p = 0.526$).

Skin temperature alone did not have a significant effect on ODBA of LMB ($F_{630,1} = 1.414, p = 0.238$). When considering the interaction effect of skin temperature with the residuals obtained from the relationship between water temperature and water depth, there is a significant positive relationship on the locomotory activity of LMB ($F_{630,1} = 15.788, p < 0.001$). Therefore, as water depth and water temperature selected increased during the post-release period, the greater the effect skin temperature had on the locomotory activity of LMB.

4. Discussion

Fish become prone to an extreme and abrupt gradient in ambient temperature when anglers remove fish from the water post-capture during the winter, given the variation in air temperatures and wind intensities. Environmental conditions have an important influence on ectothermic organisms and their behaviour (Magnuson et al. 1979, Deroba et al. 2007). Skin temperature of LMB was lowest during exposure periods where windchill temperatures were the coldest (Fig. 2). There was a significant positive relationship between windchill temperatures and skin temperature of LMB in the winter. Skin temperature

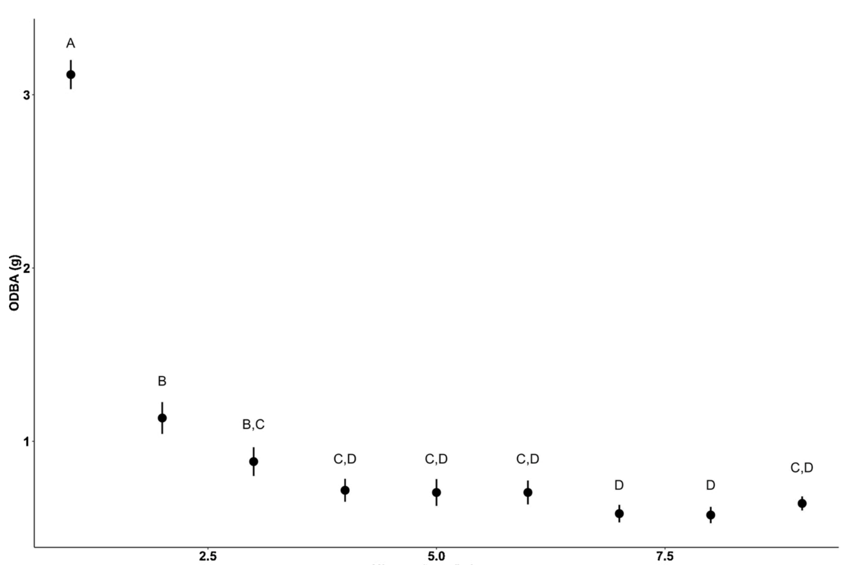

Fig. 7. Mean overall dynamic body acceleration (ODBA) (1.00 g ± 0.04 g SE) of Largemouth bass (*Micropterus salmoides*) at each individual minute post-release. Letters represent the results of a Tukey post-hoc test. Similar letters indicate that there are no differences in ODBA between the respective minutes, while differing letters indicate significant dissimilarities in ODBA at the respective minutes.

of LMB was also negatively influenced by the body size of fish. Colder skin temperatures were observed in larger fish as they have more skin exposure, allowing for greater amounts of heat loss when removed from the water. As noted by Ortega et al. (2017), wind speed and windchill temperatures increases the rate of heat exchange between animals, specifically ectotherms, and their surrounding environment (Porter and Gates, 1969, Stevenson 1985). Wind also increases the rate of water loss in ectotherms with wet skin, further increasing desiccation (Winne et al. 2001). Air temperature is often one of the most important driving factors that determines the response and recovery rate of fish after an air exposure event (Arlinghaus et al. 2007, Gingerich et al. 2007, Cook et al. 2015). Colder skin temperatures in LMB were present in all treatments that removed fish from the water, compared to the control treatment (0 seconds) that did not remove LMB from the water (Fig. 4). Post-capture, there are several reasons fish may be removed from the water, including hook(s) extraction, weighing and measuring the fish, and/or an admiration period (including taking photographs; Cooke and Suski (2005)). LMB that were removed from the water and air or ice exposed for a longer period of time, generally experienced a greater amount of heat loss with a reduction in skin temperature (Fig. 4). Although skin temperature rarely drops below 0 °C, it is critical to keep in mind that the skin temperature of LMB, an ectotherm, prior to being removed from the water, is that of their previous environment (~ 4 °C). It is clear that increasing time that fish are removed from the water and exposed to sub-freezing windchill temperatures, greater the potential for windchill temperatures to negatively affect the skin temperature of the fish via rapid cooling and/or contact freezing.

Generally, skin temperature decreased as time removed from the water increased. This trend was also present in LMB placed on the ice during the exposure period. LMB placed on the ice typically showed greater heat loss with colder skin temperatures compared to those only exposed to air. This suggests that anglers should consider not placing fish on the ice or snow while removed from the water. Although it seems that the average skin temperature is elevated (warmer) in the 90 second exposure treatments, further investigation indicates that individuals in these treatments experienced warmer mean windchill temperatures when removed from the water, supporting that windchill temperatures has a significant impact on the skin temperature (Fig. 3). Consideration must also be place on the difference in amount of skin that is exposed to windchill between air and ice treatments. LMB that are held strictly in the air, have their entire body exposed to the windchill, whereas LMB that were placed on the ice only had one side of the body exposed to the windchill. However, there is limited knowledge available surrounding the extent of physiological damage and behaviour changes associated with fish that are caught, exposed to environmental elements during cold temperatures and released back into cold water (Deroba et al. 2007). In fact, the extent of the damage caused by air exposure with the added stress of temperature in fish, is very context specific to the ambient air temperature that fish are air exposed to (Cook et al. 2015, Raby et al. 2015, Bieber et al. 2019). In fact, majority of the catch-and-release studies have focused on the challenges associated with air exposures during warm periods of the year, focused on the physiological damages, resulting in immediate, or delayed mortality (Cooke and Suski, 2005). Consequently, there is a paucity of research and understanding regarding how these same air-exposure events affect fish during the winter with the presence of harsh environmental conditions.

During the winter, it is common that cooler water temperatures remain near the surface of lakes with warming at depth (typically to 4 °C). Upon release, it was clear that LMB progressively selected deeper and warmer water as time increased during the post-release period (Fig. 5). Although the amount time spent removed from the water exposed to air or on ice did not have a direct significant effect on the depth and water temperature selected during the post-release period, windchill temperatures did have a significant effect on the water temperature selected upon release by LMB. Specifically, LMB that experienced warmer windchill temperatures were found to select warmer water temperatures. As previously mentioned, environmental conditions play an important role in fish behaviour (Magnuson et al. 1979, Deroba et al. 2007). Fish that experience warmer windchill temperatures are more likely to select warmer water temperatures during the post-release period in attempts to avoid a large fluctuation in body temperature compared to the surrounding environmental temperature, in this case the water temperature. Fish that experienced colder windchill temperatures when removed from the water and exposed to air or ice, remained in slightly shallower and cooler water temperatures for a greater duration in the post-release period. Similar to water depth and temperature selected during the post-release period, locomotory activity of LMB decreased as time progressed during the monitoring period (Fig. 7), regardless of the exposure length and type. There was a negative relationship between swimming activity levels of LMB and the depth and water temperature selected during the post-release period. LMB that were found in deeper and warmer water had reduced amounts of locomotory activity, as compared to those that were found in cooler shallower water (Fig. 6).

Stress response from air exposure is often delayed in colder water temperatures, compared to in warm water temperatures where there is often an immediate response (Louison et al. 2017a, Louison et al. 2017b). Our findings further support previous knowledge that water temperature is an important influence on fish behaviour. However, there was an increase in locomotory activity seen in LMB that selected shallower and cooler water upon release. Although previous studies indicate that fish have greater levels of locomotory activity in warmer water (Hasler et al. 2009), results from this study suggest that fish caught-and-released during the winter, after experiencing an ice angling event, have reduced locomotory activity in warmer water at the bottom of the lake, compared to fish shallower in the water column in cooler water (Fig. 6). These findings suggest that air and ice exposure may show some immediate behaviour alterations upon release, compared to what was previously presumed about cold water responses in fish, but further investigation is required. As seen in Cooke et al. (2003), disturbances created by an angling event, with the added stresses created from an air exposure period, may have caused an elevation in heart rate when returned to the water, which could have also increased the cardiac output of LMB upon release due to oxygen debt (Priede 1974, Wardle and Kanwisher, 1974). Nonetheless, the reason for increased locomotory activity in cooler water warrants further investigation.

There was a significant interaction of skin temperature and relationship between water depth and temperature on the locomotory activity of LMB during the post-release period. As previously mentioned, locomotory activity had a negative relationship with water depth and temperature selected during the post-release period. LMB that selected deeper and warmer water temperature had reduced (colder) skin temperature compared to the individuals in shallower and cooler water. In other words, when LMB selected deeper and warmer water temperatures, the effect of skin temperature was amplified on locomotory activity. We can conclude from this that removing LMB from the water, when windchill temperatures are predominantly cold, reducing the skin temperature, the greater the increase in locomotory activity of LMB. When LMB were not removed from the water (control treatment), warmer skin temperatures were present with lower levels of locomotory activity. This increase in locomotory activity, a clear alteration of behaviour, may indicate that there is impairment associated with these reduced skin temperatures. Previous studies have shown that when fish are removed from the water during periods with sub-freezing temperatures, are prone to damage to their essential tissues including fins, gills, and eyes (Tilney and Hocutt, 1987). Damage to these soft tissues may result in impaired locomotory ability, inhibited oxygen uptake capacity, and reduced visual sensory ability (Boutilier 1990, Ferguson and Tufts 1992, Suski et al. 2004). During this study, only short-term behaviour was investigated and does not provide information on how skin temperature might alter and impact the long-term fate of fish captured and released during the winter. Although there is limitation associated with monitoring behaviour for a short period of time (first 10-minutes post-release), there is sufficient evidence supporting the link between immediate impairments from stress (reflex action mortality predictors - RAMP) with the long-term fate of released fish (Raby et al. 2012). Further, Brownscombe et al. (2013) revealed that there is a link between immediate reflex impairment and short-term behaviour of fish released from fisheries related stressors. Further work is needed to understand the extent of physical damage associated with winter exposure in fish. Nonetheless, based on our findings we recommend anglers consider reducing the amount of time fish are kept out of the water in sub-freezing temperatures, while also avoiding placing fish on the ice or snow if they are fish they intend to released. Although there was no significant difference between the air and ice treatments with respect to the duration they were removed from the water, skin temperature of fish placed on the ice or snow was slightly lower than the LMB that were only held in the air (Fig. 4).

CRediT authorship contribution statement

L. LaRochelle: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Resources, Writing - original draft, Visualization. **A.D. Chhor:** Software, Investigation, Resources, Writing - review & editing. **J.W. Brownscombe:** Software, Formal analysis, Investigation, Writing - review & editing. **A.J. Zolderdo:** Resources, Writing - review & editing. **A.J. Danylchuk:** Writing - review & editing, Supervision. **S.J. Cooke:** Conceptualization, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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