



MANAGEMENT BRIEF

Impact of Ice-Angling and Handling on Swimming Performance in Bluegill and Largemouth Bass

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Abstract

Many recreational anglers practice catch-and-release; however, research indicates that capture and handling has the potential to adversely affect fish. Numerous catch-and-release studies have been conducted during warmer months, but little work has been done during the winter when ice-anglers in temperate regions target fish. We conducted an ice angling simulation that quantified the impacts of air temperature and air exposure duration on swimming performance and gill physiology of Bluegill *Lepomis macrochirus* and Largemouth Bass *Micropterus salmoides*. In all experiments, fish were first subjected to a simulated angling bout in water at 5°C, followed by 30 s or 5 min of air exposure at above freezing (3–8°C) or subfreezing (–7°C) temperatures. The fish were then assessed for critical swimming speed (Bluegill), oxygen consumption (Bluegill), burst swimming (Largemouth Bass), or gill damage (Largemouth Bass). Results showed that Bluegill subjected to 5 min of air exposure at –7°C suffered impaired swimming, with a 47% loss in critical swimming speed (U_{crit}) compared with the controls. Treatment had no impact on burst swimming or gill damage in Largemouth Bass. The results demonstrate the possible impacts of air exposure on fish, and we recommend that ice-anglers make an effort to minimize air exposure duration, especially when air temperatures are low.

Winter conditions can cause major physiological changes to temperate freshwater fish. Drops in both temperature and dissolved oxygen (DO; Magnuson et al. 1985), as well as alterations to available habitat (Garvey et al. 2004) observed in the winter, can result in reductions in metabolism (Fullerton et al. 2000; Hasler et al. 2009) and decreased physiological performance (Kolok 1992; Larsen et al. 2001). More importantly, these factors can increase mortality risk for fish in winter, creating a period when populations may undergo a bottleneck effect (Hurst 2007). Cold conditions can also impact how fish respond to acute stressors; studies conducted outside the winter season have found that colder temperatures can lead to delays in physiological recovery (Wilkie et al. 1997; Davis 2004). Therefore, understanding how winter conditions can impact the ability of fish to recover following a stressful event is important, especially in environments where human activity can be a source of stress (Meka and McCormick 2005; King et al. 2016).

Catch-and-release angling can also be a source of physiological disturbance for fish. The capture process during angling typically involves a bout of anaerobic exercise

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followed by a period of air exposure when hooks are removed, photographs are taken, and the decision of whether to release the fish is made. When combined, these stressors can result in changes in blood ion concentrations, rises in lactate levels, and the depletion of energy reserves, which can impair postrelease swimming performance should the fish be returned to the water rather than harvested (Cooke and Suski 2005; Schreer et al. 2005; Arlinghaus et al. 2009). In addition, it is well known that temperature can impact the ability of fish to capture food and recover from stressors (Gale et al. 2013). The magnitude of physiological disturbances following capture have been shown to correlate with water temperature during summer conditions (15°C and above) (Gustaveson et al. 1991; Klefoth et al. 2008; Cooke et al. 2013). However, examinations of how fish respond to angling at cooler water temperatures (10°C and below as with ice-angling) have only recently been conducted, with the few studies on this topic generally finding a muted stress response and low postrelease mortality relative to angling in warmer water (Louison et al. 2017a; Twardek et al. 2018). No studies have quantified how winter capture impacts the swimming performance of fish during recovery following angling. Swimming ability is a critical characteristic given the fact that reductions in swimming performance can lead to increased risk of mortality via predation (Raby et al. 2014). In addition, work to date has not quantified how variation in air exposure temperature (i.e., as a result of de-hooking and examining the size of the fish) can influence stress response and recovery. This is a particularly critical issue during winter angling as air exposure at near-freezing temperatures can result in tissue damage that can exacerbate the stress response or prolong recovery times (Warrenchuck and Shirley 2002). For example, Haukenes et al. (2009) found that tanner crabs *Chionoecetes bairdi* that experienced emersion stressors at freezing temperatures experienced cellular damage at the gills, which impaired oxygen uptake.

The current study was designed to further our knowledge of how fish respond to ice-angling capture by conducting complementary experiments to quantify the impacts of air exposure time (via handling) and air temperature on critical swimming performance (U_{crit}), burst swimming performance (U_{burst}), and gill damage following a simulated catch-and-release event. We chose to examine these two metrics of swimming performance separately as they are controlled by separate mechanisms, with aerobically-powered swimming driven by vascularized red muscle tissue while anaerobic burst swimming is powered by anaerobic glycolysis in fast-twitch white muscle fiber (Rome et al. 1984; Sidell and Moerland 1989). In addition, it is possible that exercise and air exposure could impact one system in a more pronounced way than the other. In addition to metrics of swimming performance, the aerobic

scope, burst swimming ability, and physical damage to gill tissue after simulated angling were quantified, thereby providing an extensive assessment of potential consequences from winter angling. In addition, we chose to conduct this work using two popular sport fish species (Bluegill *Lepomis macrochirus* and Largemouth Bass *Micropterus salmoides*; Gaeta et al. 2013) to formulate best practice recommendations to minimize ice angler impacts on target fish during winter. Based on the previous literature, we hypothesized that long exposure to subfreezing air temperatures will have a greater impact on gill damage than will shorter air exposure durations or warmer air temperatures, and that this damage to gill tissue will consequently negatively impact aerobic swimming. Together, results from this work will provide management recommendations related to air exposure durations that can benefit fish that are angled through the ice.

MATERIALS AND METHODS

Study site and fish care.—Bluegill used in this study were acquired in the spring of 2016 from Jake Wolf Fish Hatchery in Topeka, Illinois, and transported to the Illinois Natural History Survey's Aquatic Research Facility in Champaign. The ponds at the facility featured naturally occurring macroinvertebrate food items and were stocked with Fathead Minnows *Pimphales promelas* for additional forage. At the research facility, Bluegill were held in a single 0.04-ha earthen-bottom pond that they shared with approximately 50 Yellow Perch *Perca flavescens*. On January 11, 2018, the pond was drained and 40 Bluegill were retrieved (length: mean \pm SE = 18.1 \pm 3 cm, range = 13.0–19.9 cm; weight: mean \pm SE = 130.2 \pm 6 g, range = 42.8–180.2 g). Following collection from the pond, Bluegill were held for 7 d in a single, common 1,175-L circular holding tank outside with ambient air temperature of -8°C to 3°C , while water temperature ranged from 4°C to 6°C . The outdoor holding tank contained an air stone connected to a PentAir Sweetwater compressor for aeration. Initially, Bluegill were offered a portion of bloodworms (family Chironomidae; approximately 3% of their body weight per fish) from a local pet store for food. The feeding rates were low (this is common for fish in winter; Keast 1968) to be reflective of conditions experienced by free-swimming fish in the wild.

Largemouth Bass used in this study were acquired from Keystone Hatchery in Richmond, Illinois, in 2017. Before the experiment, they were held in a single 0.04-ha pond identical to the Bluegill pond. On February 3, 2018, the holding pond containing Largemouth Bass was drained and 54 Largemouth Bass (length: mean \pm SE = 19.6 \pm 0.3 cm, range = 17.0–23.0 cm; weight: mean \pm SE = 103.6 \pm 6.0 g, range = 56.6–185.3 g) were collected and distributed evenly across four different circular holding tanks,

identical to those used for Bluegill. While these sizes are smaller than what many anglers target for Largemouth Bass, their use reflects a realistic scenario with regards to catch-and-release, since small fish of these sizes are often released. Largemouth Bass received a ration of approximately 3% of their body weight of commercial dry pelleted food; this feeding rate was also low as in the Bluegill feeding regime. The water temperatures for bass ranged from 4°C to 6°C, and air temperature ranged from -8°C to 4°C.

After a period of approximately 5 d to recover from draining, all experimental fish were removed from their outdoor tanks, brought inside the laboratory, and randomly placed into 30-L acrylic isolation tanks at a density of two fish per tank. The isolation tanks were divided along their short axes by an opaque partition, preventing the two fish in each section from observing each other or interacting. The temperature of the water in these indoor tanks was maintained between 5°C and 6°C using Teco water chillers, a temperature that closely matched the temperature of the outdoor holding tanks. Ambient air temperature within the lab ranged from 3°C to 8°C throughout the experiment. While indoors, each fish received approximately 48 h of fasting before being assessed to minimize any potential impact of feeding on experimental outcomes (Gingerich et al. 2010; Pang et al. 2010).

Angling simulation.—The experimental protocol for this study involved 5 separate, yet complementary, procedures that were identical for Largemouth Bass and Bluegill. Four of these were treatments preceded by an angling simulation, while the fifth served as a control. All experiments began each day at approximately 0900 hours, after fish had been held for approximately 16 h in isolation. For the experiments described below, 5 Bluegill were run each day (1 per treatment block per day) in experiment 1, 15 Largemouth Bass were run each day (3 per treatment block per day) as part of experiment 2, and a total of 20 Largemouth Bass were biopsied on a single day of assessment (4 per treatment block) for the second portion of experiment 2.

The angling simulation involved quickly netting an individual fish from its isolation container and placing it into a 190-L plastic tote (80 × 65 cm) filled with water at a temperature of 5–6°C. The individual fish was then exercised via tail-pinching, in which a person attempted to grab the tail of the fish, which forces it to burst to escape, a method that has been utilized previously to simulate angling (Suski et al. 2004). During this protocol, fish were exercised for a total of 30 s, a nonexhaustive time course that simulated the short fight times common to ice-angling (Louison et al. 2017b).

Following this exercise protocol, both Largemouth Bass and Bluegill were netted from the tank and subjected to

one of two air exposure durations at one of two different air temperatures for a 2 × 2 full factorial design. Air exposure was carried out for either a “short” period of 30 s or a “long” period of 5 min. These air exposure treatments were based on air exposure times used in previous angling work (Gingerich et al. 2007; Louison et al. 2017b) and are representative of situations in which an angler either handles a fish quickly, or holds the fish out of the water for an extended period for activities such as photographing or measuring to determine if the fish is legal to harvest (Cook et al. 2015; Louison et al. 2017a). Each air exposure treatment was additionally carried out at one of two air temperatures, subfreezing (-7°C) or above-freezing (3–8°C), to represent distinct differences in angling conditions (i.e., a cold winter day versus a warm day, or a day at the beginning or end of the ice-angling season). To create consistent subfreezing temperatures for the air-exposure treatment, fish were first subjected to the chase protocol and then placed inside a snow-filled plastic bin, which was itself placed inside a chest freezer (1.25 × 0.60 × 0.75 m), as maintaining consistent subzero temperature exposures across experimental days would be challenging if conducted outdoors (preliminary assessments of the freezer confirmed that the air temperature during these simulations indeed remained below freezing). The purpose of this design was to replicate a situation where a fish is left on the snow during angling while an angler is searching for a camera, looking for a measuring board, etc. In addition, the use of a bin prevented the fish from contacting the inside of the freezer. For the above-freezing air exposure treatment, the fish was chased as described above, and then immediately netted and held within the net at ambient temperature within the experimental facility (3–8°C), simulating air exposure during mild weather conditions. Fish in the control treatment were directly transferred from the holding tanks without receiving additional air exposure.

Experiment 1: critical swimming speed and oxygen consumption in Bluegill.—Following the angling simulation described above (air exposure time, temperature, or control), each Bluegill was placed within a 30-L Brett-style (Brett 1964) Loligo Systems swim tunnel. Water temperature in the chamber was maintained at 5°C with a chiller. An air stone and Pentair Sweetwater compressor maintained DO saturation above 90%. Upon placement in the swim tunnel, each fish was left for 1 h to acclimate in non-flowing water. After this acclimation period, the water velocity in the swim tunnel was increased to one body length (cm) per second (BL/s), and maintained for 0.5 h as an acclimation period. Following this acclimation, the velocity was increased 0.5 BL/s every 0.5 h until the fish reached exhaustion. For this experiment, exhaustion was defined as the point at which the caudal fin of the fish remained in contact with the rear grate for a period of 20 s.

While this standard is longer than that used for some previous experiments (e.g., Prenosil et al. 2016), the longer defined failure time helped to compensate for the low activity level of fish at 5°C (Alanärä 1994), as fish would often remain motionless for stretches before exhaustion and commencing their swimming again, even at a very low water velocity. At the conclusion of the trial, the critical swimming speed was calculated using the following formula (Brett 1964):

$$U_{\text{crit}} = U_1 + [(t_1/t_2) \times U_2],$$

where U_{crit} = the critical swimming speed, U_1 = the highest speed (BL/s) that a fish had sustained per 30 min step, U_2 = the speed at which failure was reached, t_1 = the amount of time that the fish swam in the failure step, and t_2 = the time of each step (30 min). Only three fish completed the second step (at 1.5 BL/s), and zero fish completed the third step (at 2.0 BL/s).

In addition to swimming performance, the initial 0.5 h at 1 BL/s was used to quantify oxygen consumption (MO_2 ; $\text{mg O}_2 \text{ consumed} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$) based on previously established protocols (Killen et al. 2015; Chabot et al. 2016). The MO_2 is a measurement of the oxygen intake of a fish relative to its body mass, a metric that has previously been shown to influence swimming performance (Gonzalez and McDonald 1992; Reidy et al. 2000). The MO_2 for each Bluegill was calculated from the slope of a regression line that included DO concentration in the swim tunnel as the y -axis, and time as the x -axis. Every second, oxygen concentration was measured using a fiberoptic, Loligo Systems DO probe with individual points based on a 30 s rolling average throughout the first step. The cutoff for acceptable r^2 values from the regression between O_2 concentration and the time for each measurement was set at ≥ 0.9 (Svendsen et al. 2016a, 2016b). Following this swimming challenge, Bluegill were returned to their holding tanks for 48 h to quantify any postprocedure mortality before being stocked into an on-site pond; this monitoring duration is longer than other studies of fish used in ice angling studies (Twardek et al. 2018; Logan et al. 2019). A total of 30 Bluegill were tested for swimming performance and oxygen consumption following angling simulations from January 20 to 26, 2018.

Experiment 2: burst swimming performance in Largemouth Bass.— To quantify the impacts of air exposure temperature and duration on burst swimming performance, 30 Largemouth Bass (15 fish per day; 6 per treatment block) were tested from February 10 to 11, 2018, following previous U_{burst} protocols (Plaut 2001; Raby et al. 2014). The U_{burst} tests were conducted over short durations, and were used to quantify the anaerobic, burst-swimming performance of fish (Plaut 2001). For this experiment, angling simulation treatments were conducted as described above,

and Largemouth Bass were then transferred into the same swim tunnel used in experiment 1 using a net in a manner identical to the methods described above. For U_{burst} assessments, each Largemouth Bass was provided a short acclimation time (10 min) before the start of the swimming challenge. The justification for this short acclimation time was to simulate whether a fish can mount a burst response shortly after capture (for instance, in response to predator threat; Raby et al. 2014) without allowing extended time for recovery. For each U_{burst} assessment, the initial water velocity was set at 1.0 BL/s before being increased by 0.5 BL/s every successive minute; failure for this test was determined to be 5 s of direct contact with the grate. The U_{burst} of Largemouth Bass was calculated using the same formula used to calculate U_{crit} in Bluegill. Once again, fish were monitored for mortality for 48 h following the angling simulation, and were subsequently released into an on-site pond.

Gill damage in Largemouth Bass following the angling simulation.— Processing of Largemouth Bass to examine physical gill damage following the angling simulation took place on February 15, 2018. Gill tissues were chosen for assessment since the secondary (2°) lamellae are the site of oxygen exchange, and they are also likely to be affected during low temperature air exposure as a result of their high surface area and exposure to the environment. For this assessment, 20 Largemouth Bass ($n = 4$ per treatment block) were first subjected to one of the angling and air exposure treatments described above. Following this, Largemouth Bass were immediately euthanized via immersion in an overdose solution ($>400 \text{ mg/L}$) of sodium bicarbonate-buffered MS-222 (tricaine methanesulfonate). Following euthanasia, the lower half of the second gill arch was clipped from each side of the fish. Gill samples were immediately placed into a 10% buffered formalin solution for fixation for a period of 24 h before being transferred to permanent storage in 70% ethyl alcohol (Lillie and Fullmer 1976). Gill samples were then processed at the Histology Laboratory at the School of Veterinary Medicine at the University of Illinois at Urbana–Champaign. Three sections were produced per gill sample, resulting in a thickness of 4–5 μm . All samples were stained with methylene blue to quickly and easily visualize cells and components (Huber et al. 1968).

To quantify damage to the secondary lamellae as a result of the experimental treatments, the median three primary (1°) lamellae were identified from each gill section under a microscope at 4 \times magnification. The length of each selected primary lamella (mm) was measured and the number of extant secondary lamellae were counted on each respective primary lamella. These counts were then averaged together for each gill sample. The total area (mm^2) of these secondary lamellae was then calculated for each sample, based on an average of every fifth lamella, and the calculated areas were then averaged (Gray 1954; Hughes and Morgan 1973).

Statistical analysis.—For each metric (swimming performance and indices of gill damage), an ANCOVA was performed. For each ANCOVA, the response variable of interest was set as the dependent variable (the U_{crit} and MO_2 of Bluegill, and the U_{burst} , primary lamellae length, secondary lamellae count, and secondary lamellae area of Largemouth Bass); treatment block (air exposure time and temperature combination) was set as a fixed effect; and the total length of the fish (cm) was set as a covariate. If a significant effect of the treatment block was found, a post hoc Dunnett's test was performed to compare each treatment block with the control group. Cutoffs for all analyses were set at $P < 0.05$. All analyses were performed using R software (R Core Team, Vienna; version 3.3.2) using the packages “multcomp” (Hothorn et al. 2008), “car” (Fox and Weisberg 2019), and “ggplot2” (Wickham 2016).

RESULTS

The angling simulation, followed by a period of air exposure, resulted in a significant decline in critical swimming speed (U_{crit}) for Bluegill relative to the control

TABLE 1. A summary of all statistical outputs measuring the response to angling simulation, air exposure duration, and air temperature on various swimming and morphological metrics for Largemouth Bass and Bluegill. In each case, treatment blocks were combinations of air exposure durations (long or short) and ambient air temperature (above-freezing or subfreezing). For all metrics taken from swim tunnel testing (Bluegill critical swimming speed [U_{crit}] and oxygen consumption [MO_2]; Largemouth Bass burst swimming [U_{burst}]), an ANCOVA model was run that included total length as a covariate. For Largemouth Bass gill damage assessments (secondary lamellae counts and area), ANCOVAs were performed that only included treatment block as a fixed factor; BL is body length (cm) per second and asterisks denote significant effects.

Metric or factor	df	<i>F</i>	<i>P</i>
Bluegill U_{crit} (BL/s)			
Treatment block	4	3.29*	0.02
Total length (cm)	1	4.08	0.054
Bluegill MO_2 (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$)			
Treatment block	4	0.74	0.57
Total length (cm)	1	34.62*	<0.001
Largemouth Bass U_{burst} (BL/s)			
Treatment block	4	1.44	0.25
Total length (cm)	1	4.68*	0.04
Largemouth Bass 2° lamellae (2° lamellae/1° lamellae)			
Treatment block	4	1.11	0.36
Total length (cm)	1	3.76	0.06
Largemouth Bass 2° lamellae mean area (mm ²)			
Treatment block	4	1.52	0.21
Total length (cm)	1	0.04	0.83
Largemouth Bass 1° lamellae length (mm)			
Treatment block	4	0.77	0.54
Total length (cm)	1	0.03	0.86

treatments, but only when fish were air exposed for a long duration and at subfreezing temperatures (Table 1; Figure 1A; Supplementary Information provided separately in the online version of this article). An angling simulation, followed by either short or long air exposure at warmer air temperatures, did not alter U_{crit} relative to the control treatments (Table 1; Figure 1A). Burst swimming following a 30-s angling simulation in Largemouth Bass was not influenced by either the duration of air exposure or ambient air temperature (Table 1; Figure 1B). However, burst swimming speed was significantly influenced by fish size, with larger fish displaying higher burst swimming speeds independent of treatment block (Table 1). There was no significant effect of any treatment block on MO_2 levels in

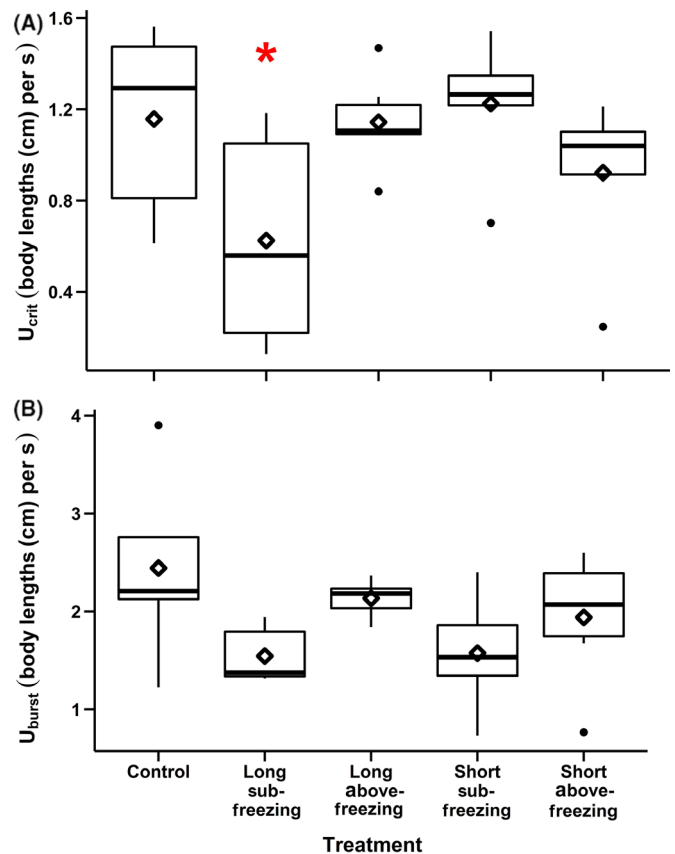


FIGURE 1. (A) Critical swimming speed (U_{crit}) and (B) burst swimming speed (U_{burst}) that was measured in a swim tunnel for Bluegill and Largemouth Bass. Before being placed into the swim tunnel, fish were subjected to one of five different treatments: a control, a long subfreezing treatment, a long above-freezing treatment, a short subfreezing treatment, or a short above-freezing treatment. The U_{crit} for Bluegill in the long subfreezing treatment was significantly lower than for fish in the other treatments. No differences in U_{burst} for Largemouth Bass were detected. The horizontal line in the box plot represents the median for a treatment and the diamond represents the mean. [Color figure can viewed at afsjournals.org.]

Bluegill (Table 1; Figure 2), but there was a negative relationship between fish size and MO_2 for Bluegill (Table 1).

A 30-s angling simulation followed by air exposure at subfreezing or above-freezing temperatures did not affect the average primary lamellae length, average secondary lamellae count, or average secondary lamellae area for Largemouth Bass, nor did fish length affect any of these metrics (Table 1; Figure 3). There were no individual mortalities of either species in their holding tanks during the 48-h monitoring period that was performed following the conclusion of these studies.

DISCUSSION

The aerobic swimming performance of Bluegill was negatively impacted by 5 min of air exposure at -7°C . The U_{crit} of Bluegill in the block that was exposed to this treatment was less than half that of control fish that were not exposed to chasing or air exposure. However, the anaerobic U_{burst} performance in Largemouth Bass was not impacted by any treatment block. Angling has previously been shown to induce a number of physiological disturbances for fish that include increases in ion concentrations in the blood (Arlinghaus et al. 2009), a buildup of lactate in blood and tissues (Ferguson and Tufts 1992), increases in stress hormones (Meka and McCormick 2005), and reduced reflex responsiveness (Raby et al. 2015). These disturbances occur due to a combination of exercise, handling, and air exposure (Arlinghaus et al. 2009), all of

which require oxygen levels to be rectified following the conclusion of the angling event (Suski et al. 2006). Studies at warmer water temperatures have shown that the duration of air exposure for angled fish may be positively correlated with the magnitude of its stress response and recovery time (Cooke et al. 2001; Thompson et al. 2008; Lamansky and Meyer 2016). This relationship between stress and recovery means that extended air exposure may increase the probability of postrelease mortality (Gingerich et al. 2007; Bower et al. 2016) or impair swimming performance (Schreer et al. 2005). During air exposure, the ability of secondary lamellae to perform gas exchange (i.e., uptake of oxygen and excretion of carbon dioxide) may also be impaired, resulting in additional physiological disturbances synergistic with exercise (Ferguson and Tufts 1992), such as a reduction in heart rate (bradycardia; Cooke et al. 2001). Secondary lamellae are able to resume functioning normally and engage in gas exchange when fish are returned to the water (Ferguson and Tufts 1992). In the present study, periods of short air exposure (i.e., 30 s) did not influence U_{crit} in Bluegill relative to a control treatment regardless of air temperature. In addition, at above-freezing temperatures, even 5 min of air exposure did not impact U_{crit} . When exhaustive exercise occurs at low temperatures, many physiological disturbances can be reduced relative to exercise that occurs in warmer water (Wilkie et al. 1997; Davis 2004). This includes angling scenarios where exercise is followed by prolonged air exposure (Louison et al. 2017a; Twardek et al. 2018). The

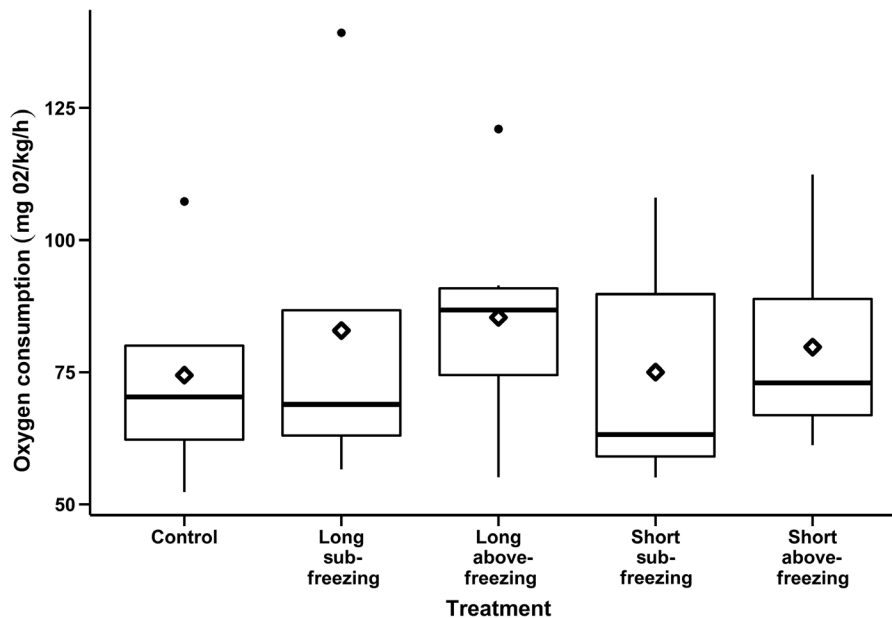


FIGURE 2. Oxygen consumption (MO_2) of Bluegill measured with intermittent flow respirometry following an angling simulation and varying air exposure treatments. Measurements were collected over a 0.5-h period while fish were swimming at a speed of 1 BL/s. The horizontal line in the box plot represents the median for a treatment and the diamond represents the mean.

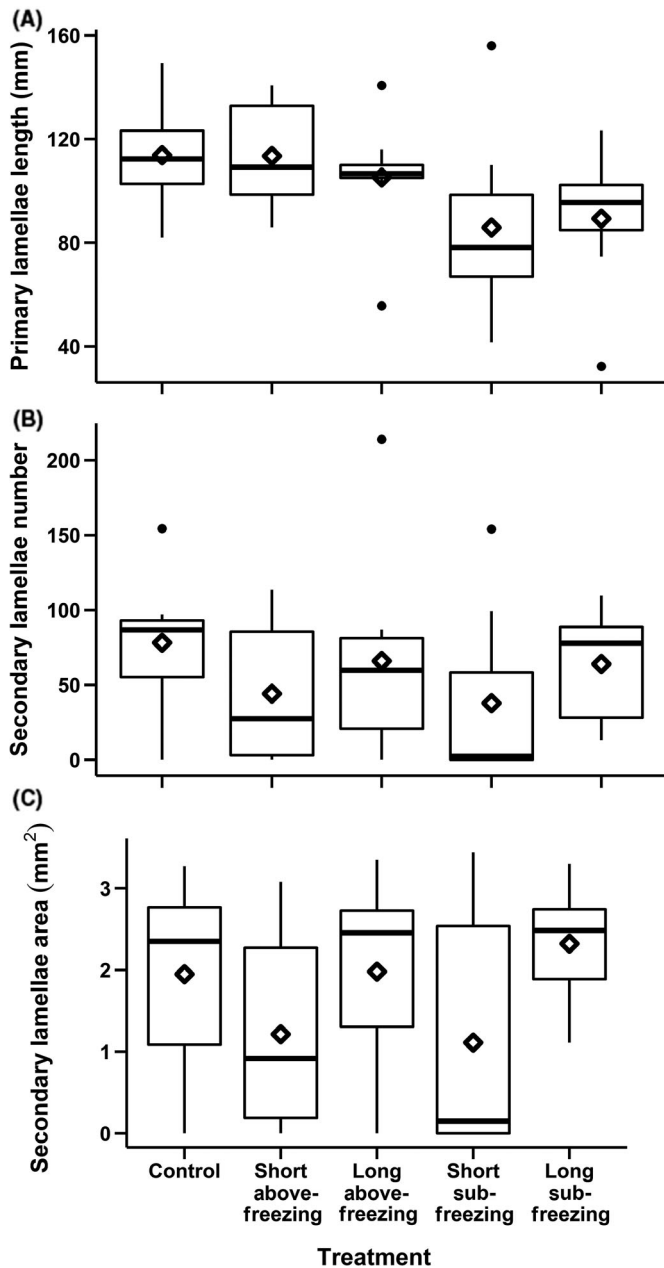


FIGURE 3. (A) Measurements of primary lamellae length, (B) secondary lamellae number, and (C) secondary lamellae area (mm^2) for Largemouth Bass that were subjected to one of five different angling treatments. No differences in gill damage metrics were detected across treatment groups. The horizontal line in the box plot represents the median for a treatment and the diamond represents the mean.

reduced magnitude of physiological disturbances likely explains why there was no impairment of swimming performance of fishes exposed to air for short durations; however, long air exposure at subfreezing temperatures proved to have an impact on critical swimming speed.

The reduced aerobic swimming performance observed in Bluegill following extended air exposure may be due to a variety of impaired physiological functions. For

example, tachycardia (elevated heart rate) occurred following air exposure in Rock Bass *Ambloplites rupestris* (Cooke et al. 2001). The duration of tachycardia correlated positively with the length of air exposure, suggesting that altered cardiac function might be influencing recovery following air exposure (Cooke et al. 2001). Extended exposure to subfreezing temperatures during emersion may also have resulted in cold shock (i.e., physiological changes induced by rapid reductions in temperature), which could have led to a variety of physiological impacts that might impair swimming performance. These impacts of cold shock could include an impaired ability to maintain equilibrium while swimming (Donaldson et al. 2008), a delay in recovery from the physiological stress of the angling simulation (Hyvärinen et al. 2004), a reduction in the replenishment of energy stores (ATP, PCr, etc.) following the simulation event (Galloway and Kieffer 2003; Suski et al. 2006), or a reduction in muscle contractile capacity (Jerrett et al. 1998; Roth et al. 2009). Exposure to cold air may also have damaged aerobic muscular tissue, a process that has been described in harvested marine invertebrates (Warrenchuck and Shirley 2002; van Tameelen 2005). Alternatively, the swimming performance of Bluegill exposed to the long subfreezing treatment could have been impacted by direct damage to the fins. While we did not specifically quantify fin damage as a part of this study, anecdotal records demonstrate that fish subjected to a long subfreezing treatment appeared to suffer a greater degree of fraying of the caudal and pectoral fins compared with other treatments, which could impair swimming (Sinclair et al. 2011; Waldrop et al. 2018). While direct damage to the gills is another possible explanation for the decline in swimming performance due to lack of oxygen availability, this hypothesis was not supported by the data as no difference in gill damage was found between the treatment blocks in Largemouth Bass, and MO_2 (a measure of oxygen uptake) did not differ by treatment block in Bluegill. Regardless of the mechanism, Bluegill that experienced 5 min of air exposure at subfreezing temperatures experienced a significant decline in aerobic swimming performance relative to the control treatments.

Overall, this study provides insights into how fish respond to angler capture and handling at subfreezing winter temperatures, and the management implications of exercise and air exposure of fishes during ice angling. Previous work in the area of winter angling has indicated that fish are resilient to air exposure, with studies demonstrating that the mortality rate of Northern Pike *Esox lucius* angled in winter is less than 1% (Dubois et al. 1994) and the mortality rate of Lake Trout *Salvelinus namaycush* angled in both winter and summer conditions (Dextrase and Ball 1991) is similar. Previous work shows that many fish species are active in the winter (Suski and Ridgway

2009; Suski et al. 2009), and while feeding rates of fishes are typically reduced in winter relative to summer, food capture does indeed occur (Keast 1968), contributing to the overwinter survival of the fish (Fullerton et al. 2000). Fish that are impaired aerobically as a result of angling may be inhibited, at least for short durations, in the ability to feed and carry out other critical activities. Because a primary goal of catch-and-release angling is to ensure that fish are able to survive postcapture (Arlinghaus et al. 2007), our results suggest that managers should recommend to ice-anglers that they minimize air exposure times for fish, especially when conditions are particularly cold. In conclusion of the present study as well as related studies on this issue, short air exposure durations in winter are likely to ensure that fish experience fewer lasting impacts of the capture process, which will help to preserve and enhance valuable recreational fisheries.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.