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An examination of freezing in yellow perch (*Perca flavescens*) following ice fishing using a histological approach

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1 | INTRODUCTION

The process of ice fishing involves fish being hooked, retrieved, and then handled out of water. Landed fish are often held in the air or on ice for a few seconds to several minutes to remove hooks and to take measurements and photos (Lawrence et al., 2022). While fish are frequently harvested, many fish are released back into the water through the hole in the ice for a variety of reasons, including conservation ethics and morals, bycatch, culling, and harvest regulations (Arlinghaus et al., 2007; Cooke & Suski, 2005; Grausgruber et al., 2021). One key assumption of releasing fish after capture is that they continue to survive, reproduce, and are able to be captured again in the future (Brownscombe et al., 2017). However, only a handful of studies have characterized the biological response to ice fishing, making it difficult to confidently define the fate of fish that have been released through the ice. Of the few studies that have been conducted to date on ice fishing, most have largely focused on hooking location and delayed mortality (Althoff et al., 2020; Dextrase & Ball, 1991; DuBois et al., 1994; Persons & Hirsch, 1994; Somers et al., 2021; Twardek et al., 2018), and sub-lethal physiological and behavioural consequences (Bieber et al., 2019; Logan et al., 2019; Louison, Hasler, Fenske, et al., 2017; Louison, Hasler, Raby, et al., 2017; Winter et al., 2018). Generally, findings suggest deeply hooked fish are susceptible to higher rates of delayed mortality, and that stress biomarkers like cortisol, glucose, and lactate are low and/or delayed in comparison to similar studies completed during warmer months (Logan et al., 2019; Louison, Hasler, Fenske, et al., 2017; Louison, Hasler, Raby, et al., 2017).

One possible effect of ice fishing not well characterized in fish is the potential for exposed tissues (e.g., gills, fins, eye, epidermis) to freeze because of sub-zero ice and air temperatures (LaRochelle et al., 2021). During capture and holding, fish may experience sub-zero temperatures when being air exposed, when held in water-filled buckets, or when placed on the ice for photos and measurements. Shown in crabs, but a relevant concern in fish, is that tissues could be injured and hinder important physiological processes, such as metabolism (Haukenes et al., 2009) or cause death (Warrenchuk & Shirley, 2002). To date, only one study has shown surface temperatures of fish cool post-capture, though specific tissues were not assessed (LaRochelle et al., 2021), and only one study has examined exposed tissues following ice fishing related to handling (Bieber et al., 2019). These two studies have demonstrated that fish are freezing and damage may occur; however both did not quantify damage or assess multiple tissues. Thus, it remains unclear if tissue freezing is common in fish caught and handled as a result of ice fishing, and if so, how serious it is.

Our objective was to quantify freezing of tissues in yellow perch (*Perca flavescens*) following ice fishing using a histological approach to define if tissues were compromised, because yellow perch are one of the most popular fish caught during the winter in Canada. We hypothesized that heat loss would occur over a 3-min period when fish were laid on the ice because previous work has shown physiological and behavioural impairments following ice fishing that are consistent with low body temperature (e.g., Louison, Hasler, Fenske, et al., 2017; Louison, Hasler, Raby, et al., 2017). We predicted that if tissues cooled to below 0°C we would observe injuries in sectioned tissues. Should tissue damage be observed, the likelihood that ice fishing results in long-term or lethal consequences could increase as well, meaning delayed mortality resulting from ice fishing may be underestimated.

2 | METHODS

Yellow perch were sampled on March 9, 2019 at Gull Lake, MB, Canada (50.414498°, −96.518582°). Fish were angled through holes in the ice using short rods spooled with 1.8 kg monofilament fishing line. Barbless J-hooks with coloured weighted heads (size 12) were baited with white grubs, dropped down a hole, and then bobbed up and down approximately 50 cm above the lake bottom. Upon capture, the hook was immediately removed and the fish was brought to a central location (no more than 20 m from any hole) for group assignment and processing. Hook removal involved holding the fish with a bare wet hand and using the other hand to dislodge and remove the hook from the fish's jaw (maximum time for hook removal was 5 s). Air temperature during sampling ranged from −5.5°C and −6.4°C and wind chill ranged from −11°C and −7°C (https://climate.weather.gc.ca/, climate identifier = 5032951, 32 km from study site).

Fish were haphazardly assigned to either the control or the treatment group. Fish in the treatment group (n = 8) were measured for total length, weighed to the nearest g, and then placed on the ice for a 3-min ice and air exposure (ice temperature: −3 ± 0.73°C; a 3-min exposure duration is a realistic duration to have fish on the ice prior to release; Lawrence et al., 2022; Grausgruber et al., 2021). Fish were laid on the ice freely and were not gripped or held during the 3-min exposure. The surface temperatures of various parts of the fish (gills, eyes, midbody beneath the dorsal fin, and caudal fin) were recorded using a non-contact, infrared thermometer (FLIR TG165 Imaging IR Thermometer; FLIR Systems, Inc.; Wosnick et al., 2018; basic accuracy = ±1.5%; resolution = 0.1°C). Temperature readings were taken each minute for the air-exposed side of the fish, and at the 3-min mark for the ice-exposed side of the fish. To measure temperature of the gills, the operculum was briefly opened to allow for the thermometer to be pointed directly at the gill filaments. The control group (n = 8) was sampled in the same manner, except these fish were not subjected to the ice and air exposure and instead were held in a cooler containing lake water for several minutes. Temperature readings were measured for the tissues from both sides of the control fish and following the temperature readings, fish were euthanized using cerebral percussion and cervical dislocation. All procedures involving live fish were approved by The University of Winnipeg's animal ethics committee (AE10491).

Immediately following euthanasia, three tissues were excised and fixated for histological analysis. The first gill arch and pectoral fin from both sides of the fish, and a section of the caudal fin were placed in fixative (modified Karnovksy's fixative: 1% paraformaldehyde +2.5% glutaraldehyde in 0.1 M sodium phosphate, pH 7.2 buffer) and stored at room temperature for several weeks. Samples were then dehydrated by rinsing with 70%, 80%, 95% and 100% ethanol at −20°C. The last rinse was allowed to warm up to room temperature, and one final 100% ethanol rinse was then performed for 30 min. Dehydrated tissues were embedded using a Leica Historesin Embedding Kit (7022-18500 Leica Historesin Embedding Kit). Samples were placed in infiltration solution (50 ml Leica Historesin +0.5 g dibenzolperoxide +1.3 ml polyethylene glycol), and the solution was changed twice over a 24 h period while refrigerated. Tissues were then trimmed and placed into molds using embedding solution (15 ml infiltration solution +1 ml hardener). Chucks were placed on top of each mold and left for at least 24 h prior to being cross sectioned using a microtome (Sorvall JB-4 Microtome, Ivan Sorvall, Inc.). Sections (1.5 μm) were then mounted on glass slides and stained with 1% toluidine blue +1% borax stain. Slides were examined using a microscope (CX41 Upright Microscope, Olympus Corporation) and imaged using Infinity Analyze 2-1 (Lumenera Corporation).

Histological samples were assigned identification numbers for each sample so that the assessor did not know the treatment of the fish that the sample came from. Imaged gills were measured for interlamellar cell mass (ILCM; Figure S1) and lamellar length (Figure S1). For lamellar length, ten lengths were randomly measured, as described by Ong et al. (2007) and Blair et al. (2016). Interlamellar cell mass and lamellar length were measured to determine if structural changes or damage within the gills occurred following the ice treatment (Blair et al., 2016; Ong et al., 2007). Pectoral and caudal fins were assessed by measuring the size of mucous cells in the epidermis of the fins (Figure S2). The area of ten randomly selected mucous cells were measured using ImageJ (Schneider et al., 2012) and abnormalities (e.g., aneurysms) were also noted. Mucous cells were assessed because of the protective role they play in producing the outer mucous coat (Zaccone et al., 2001), and the possibility that they may swell if frozen.

Trends were assessed using parametric models. Surface temperatures of the midbody and eye that were exposed to the air throughout the treatment were tested using one-way repeated measures ANOVAs to determine if these temperatures significantly differed throughout the air and ice exposure (left side of fish only). Size was ignored in these models as it was found to be insignificant during preliminary analyses. If statistical significance was found, a post hoc analysis using multiple pairwise paired t-tests was performed to determine significance between the times that the surface temperatures were taken of the air-exposed tissues. The results of the one-way repeated measures ANOVA for the midbody were corrected using the Greenhouse-Geisser correction as these data did not meet the assumption of sphericity. Gill temperatures were analyzed using a linear mixed effects model (Bates et al., 2015) and included total length as a covariate and time point as a fixed effect. Surface temperatures of the caudal fin failed the Shapiro–Wilk test for normality, so a non-parametric Friedman test was performed. The 3-min air-exposed surface temperature reading (left side of the fish) was compared to the 3-min ice-exposed surface temperature reading (right side of the fish) using paired t-tests for each tissue, because the surface temperature of the ice-exposed side was only measured at the end of the treatment. Size of the fish was ignored in the analysis because linear mixed effects models that included total length of the fish as a covariate indicated size was insignificant. Two-way ANOVAs were performed to assess differences in ILCM, lamellar length and ILCM:length (ILCM divided by lamellar length) between control and treatment individuals, as well as between the left and right gill. A binomial logistic regression

was used to assess treatment effects on the presence of aneurysms in the gill, where the presence of aneurysms was the response variable, and both treatment group and gill (left or right) were the fixed effects. Student's *t*-tests were used to assess differences in mucous cell area between control and treatment individuals for the right pectoral fin, left pectoral fin, and the caudal fin. The level of significance was assessed at $\alpha \leq 0.05$ and all statistical analyses were performed using R version 3.6.1 (R Core Team, 2019).

3 | RESULTS

The surface temperature of the air-exposed midbody musculature decreased over the exposure period (Figure 1a, one-way repeated measures ANOVA, $F_{1.51, 10.54} = 24.907$, $p < 0.001$), starting at an average of 1.34°C and decreasing an average of 1.57°C resulting in a mean temperature of −0.23°C at the end of the treatment for the air-exposed midbody. The temperature of the eye, gill, and caudal fin did not differ across the exposure for the air-exposed side of the fish (eye: Figure 1b, one-way repeated measures ANOVA, $F_{3, 21} = 0.537$, $p = 0.662$; gill: Figure 1c, linear mixed effects model, size corrected, $F_{3, 27} = 2.606$, $p = 0.072$; caudal fin: Figure1d, non-parametric Friedman test, $\chi^2 = 4.700$, df = 3, $p = 0.195$). However, all three of these tissues remained below 0°C throughout the entire treatment (Figure 1b–d).

Both the midbody surface temperature and the eye surface temperature significantly differed between the air-exposed side and the ice-exposed side at the end of the treatment period, with the ice-exposed side being colder in both cases (midbody: Figure 2a, paired *t*-test, $t = 4.020$, df = 4, $p = 0.005$; eye: Figure 2b, paired *t*-test, $t = 2.550$, df = 7, $p = 0.038$). The decrease in midbody surface temperature and the eye surface temperature resulted in average surface temperatures of −1.11°C and −2.43°C, respectively, for the ice-exposed side at the end of the treatment. The temperature of the gill and the caudal fin did not decrease between the air-exposed side and the ice-exposed side at the 3-min time point (gill: Figure 2c, paired *t*-test, $t = 0.561$, df = 7, $p = 0.592$; caudal fin: Figure 2d, paired *t*-test, $t = -1.030$, df = 7, $p = 0.337$). However, surface temperature readings were below 0°C for the ice-exposed side at the end of the treatment for all tissues measured (Figure 2).

There was no effect of treatment on any histological metric related to the gills or the fins. Specifically, ILCM (Figure 3a, two-way ANOVA, $F_{1, 29} = 1.151$, $p = 0.292$), lamellar length (Figure 3b, two-way ANOVA, $F_{1, 29} = 1.679$, $p = 0.205$) or ILCM:lamellar length (Figure 3c,

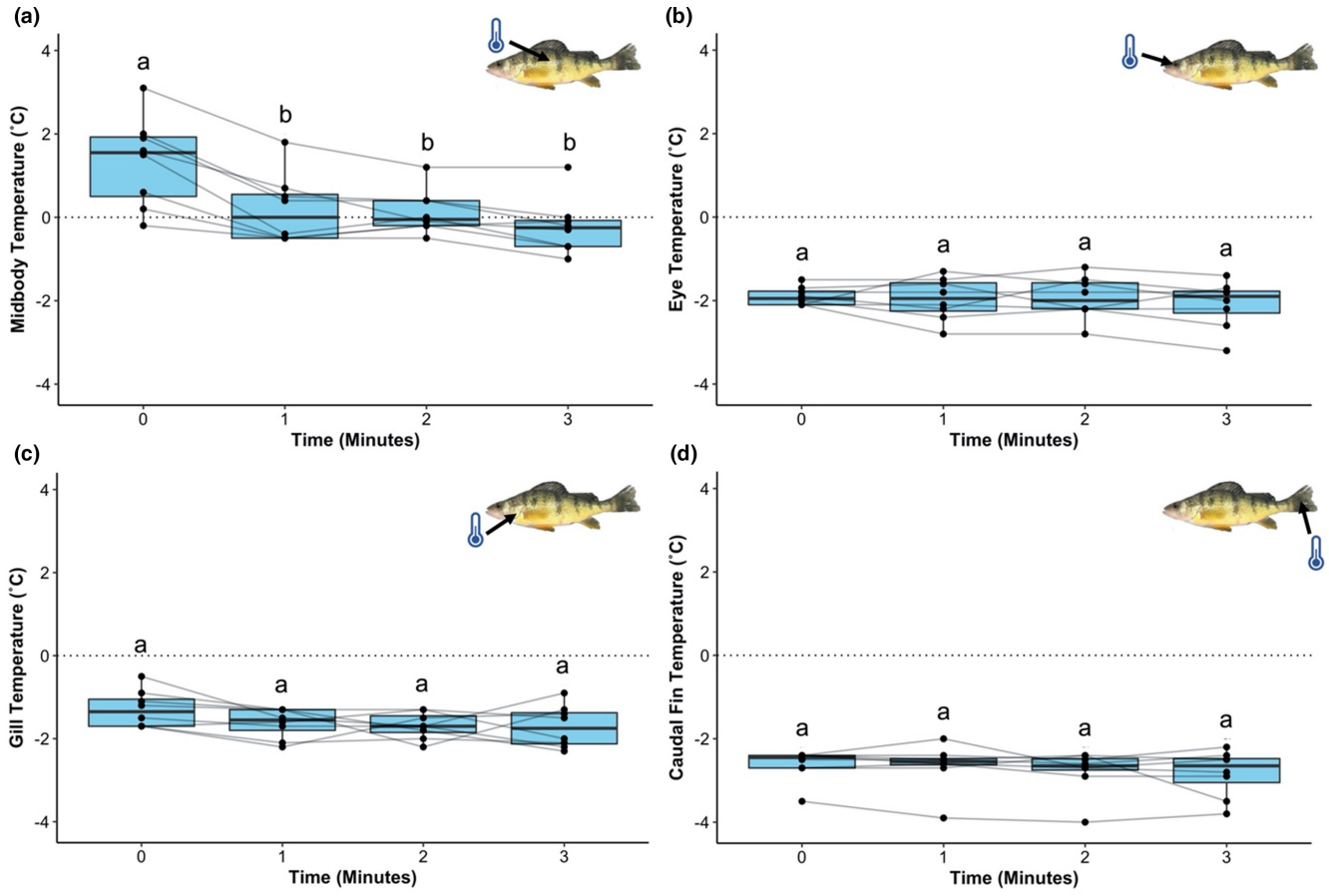

FIGURE 1 Surface temperature of the (a) midbody, (b) eye, (c) gill and (d) caudal fin in yellow perch (*Perca flavescens*) assessed at each minute throughout the 3-min ice- and air-exposure following ice fishing, with significance demonstrated by dissimilar letters using one-way repeated measures ANOVA tests. Statistical significance was assessed at $\alpha < 0.05$

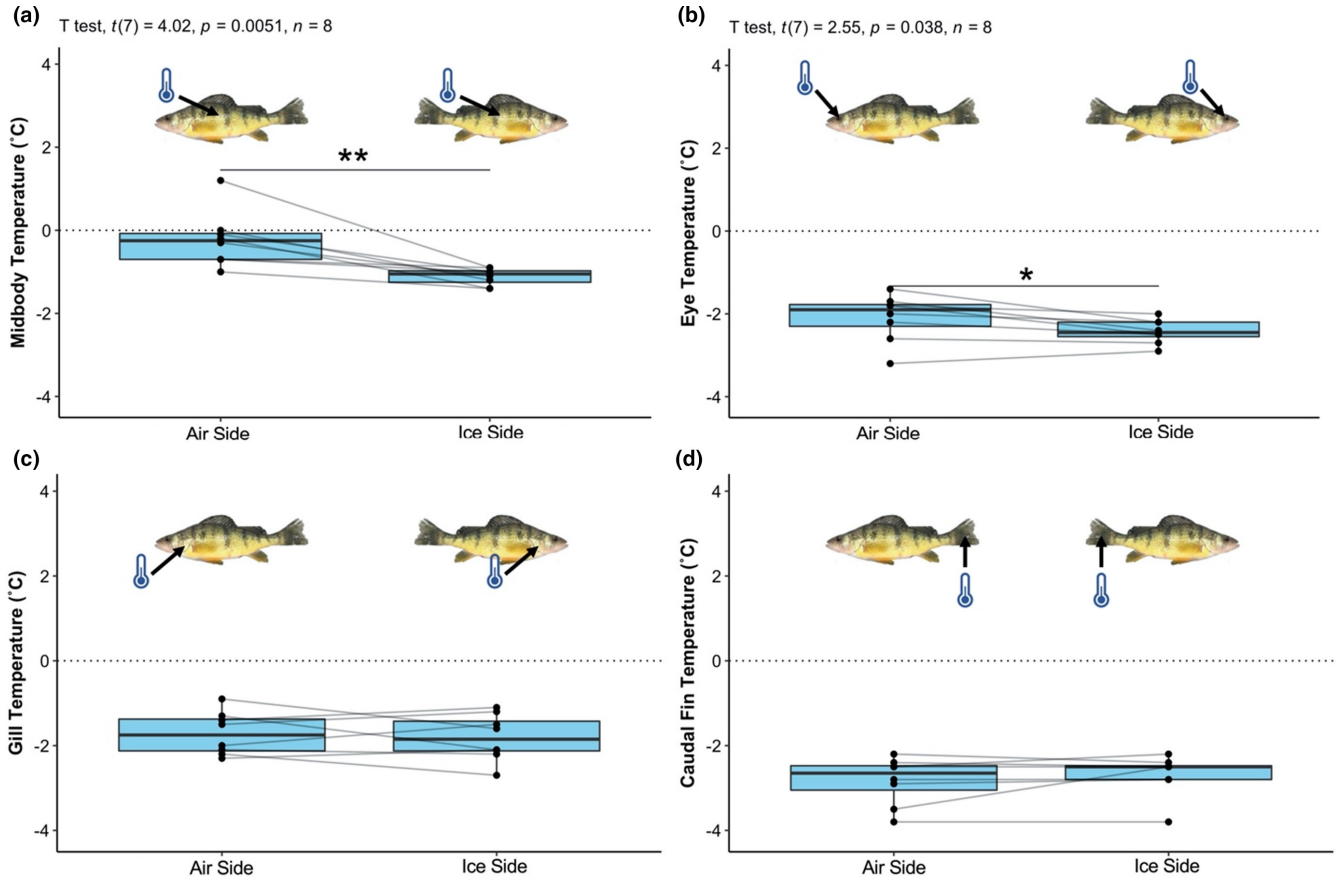

FIGURE 2 Surface temperature of the (a) midbody, (b) eye, (c) gill and (d) caudal fin in yellow perch (*Perca flavescens*) for both the air-exposed side (left) and ice-exposed side (right) at the 3-min time point. Paired *t*-tests were used to assess differences and statistical significance is demonstrated by asterisks, where * represents $\alpha < 0.05$ and ** represents $\alpha < 0.01$

two-way ANOVA, $F_{1, 29} = 0.053$, $p = 0.819$) showed no differences when comparing control and treatment samples. Additionally, there was no treatment effect on gills when samples from air-exposed gills were compared to ice-exposed gills (ILCM: Figure 3a, two-way ANOVA, $F_{1, 29} = 1.789$, $p = 0.192$, lamellar length: Figure 3b, two-way ANOVA, $F_{1, 29} = 0.412$, $p = 0.526$, or ILCM:lamellar length: Figure 3c, two-way ANOVA, $F_{1, 29} = 3.292$, $p = 0.080$). Aneurysms of the secondary lamellae were observed in the gills of both treatment and control individuals (Figure 4), but there were no significant differences in occurrence between treatment groups (binomial logistic regression, $z = -0.734$, $p = 0.463$; Figure S3) or gill side (binomial logistic regression, $z = -1.418$, $p = 0.156$; Figure S3). The area of mucous cells in any of the fins was not statistically different between control and treatment fish (Caudal fin, Student's *t*-test, $t = 0.367$, df = 12, $p = 0.720$; air-exposed left pectoral fin, Student's *t*-test, $t = 0.275$, df = 10, $p = 0.790$; ice-exposed right pectoral fin, Student's *t*-test; $t = -0.684$, df = 9, $p = 0.511$; Figure S4).

4 | DISCUSSION

The surface temperatures of the eye, gill and caudal fin of caught yellow perch were recorded to be below 0°C throughout the monitoring period. The potential for tissue damage as a result of ice fishing has been understudied, though Bieber et al. (2019) noted that secondary lamellae length and numbers did not change based on 5-min exposure to freezing air. Likewise, we found no significant differences between control and treatment groups for gills, pectoral and caudal fins. Therefore we are unsure if freezing resulted in significant injury; however, the number of variables assessed was limited and it is possible that other problems arising from ice crystal formation were not quantified (Kim et al., 2017). Additionally, though we did not use histological techniques to examine the eye, the right eye (exposed to ice) was significantly colder than the left eye (exposed to air) at the end of the treatment. If the freezing of the eye causes any damage to the cornea, both opacity and stromal swelling are possible outcomes (Edelhauser et al., 1968; Smelser, 1962; Ubels & Edelhauser, 1987). Furthermore, one or more of the sampled tissues may have experienced "cold shock", which is characterized as biological impairments induced by rapid decrease in water temperature (Donaldson et al., 2008). Cold shock results in a suite of physiological changes and in extreme cases, death of the organism (Donaldson et al., 2008), though mortality has rarely been reported in ice fishing studies (e.g., Grausgruber et al., 2021; Logan et al., 2019).

Whether ice fishing and air- and ice-exposure influences gill function remains unclear. The primary function of the secondary

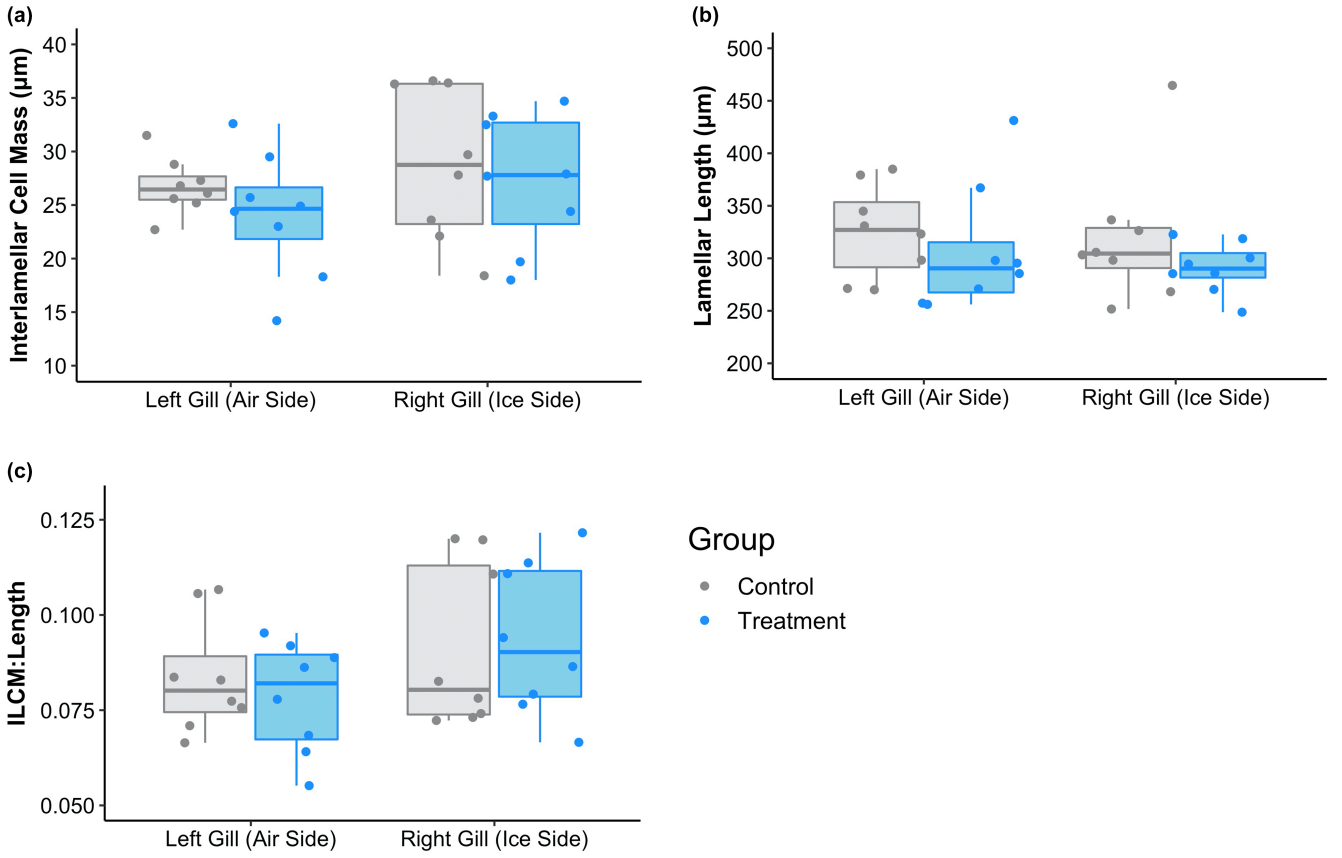

FIGURE 3 Measurements of the (a) interlamellar cell mass, (b) lamellar length, and (c) the ILCM:length for both the left and right gills of yellow perch (*Perca* flavescens) from both control and treatment (ice- and air-exposure for 3-min following ice fishing) groups. No statistically significant differences were found amongst any groups which was assessed using two-way ANOVAs

lamellae in the gills of teleost fish is to facilitate ion and gas transfer into the bloodstream (e.g., oxygen uptake and carbon dioxide release; Ferguson & Tufts, 1992), and their delicate structure provides a large surface area for gas and ion transfer to occur (Wilson & Laurent, 2002). If the gill is damaged or altered as a result of an environmental change, respiratory function and the regulation of internal acid-base status may be impaired (Goss et al., 1992; Jiraungkoorskul et al., 2002). The aneurysms observed in our study are an example of a change within the structure of the secondary lamellae, and were found in over 68% of sampled fish. Aneurysms in the secondary lamellae have been linked to the death of pillar cells that connect the two epithelial sheets of the secondary lamellae to one another, as these pillar cells maintain the structural integrity of the lamellae (Hassaninezhad et al., 2014; Heuvel et al., 2000; Strzyżewska-Worotyńska et al., 2017). If the functionality of pillar cells is lost, the structural integrity of the secondary lamellae will be compromised as these pillar cells regulate blood flow, thus the lamellae will swell and fill with erythrocytes resulting in aneurysm (Hassaninezhad et al., 2014; Heuvel et al., 2000; Strzyżewska-Worotyńska et al., 2017). An aneurysm in the secondary lamellae is considered a severe type of lesion meaning that recovery is possible, but difficult, compared to other changes that may occur in the secondary lamellae such as injury to the epithelial tissue (Hassaninezhad et al., 2014; Mabika & Barson, 2014; Strzyżewska-Worotyńska et al., 2017). It is possible that freezing ruptures pillar cells through crystallization, because pillar cells are composed of collagen columns that exist within the infoldings of the cell membrane (Bettex-Galland & Hughes, 1973), and freezing has been found to destabilize collagen fibrils because of the expansion of intrafibrillar space through ice formation (Ozcelikkale & Han, 2016). Our study is the first to have described aneurysms in the secondary lamellae of teleost fish following an ice-angling event. However, as there were no differences between the control and treatment fish regarding the frequency of aneurysms and surface temperature of the gills was recorded as below 0°C for all fish, we can only speculate that cold temperatures led to the formation of the aneurysms because our study design did not allow us to quantify a 'baseline' aneurysm level (i.e., during warmer temperatures). Therefore, we cannot be certain that the aneurysms were due to freezing temperatures or any other fishing related stressor.

Surface temperature of the midbody of yellow perch decreased to below 0°C during the 3-min air- and ice-exposure. Therefore, fish were losing body heat during the initial handling and exposure periods, a result that is also consistent with a previous study on ice fishing (LaRochelle et al., 2021). A potential outcome of this cooling is the slowing of key physiological processes (e.g., enzyme activity, metabolism, hormone production). Past studies on ice fishing have

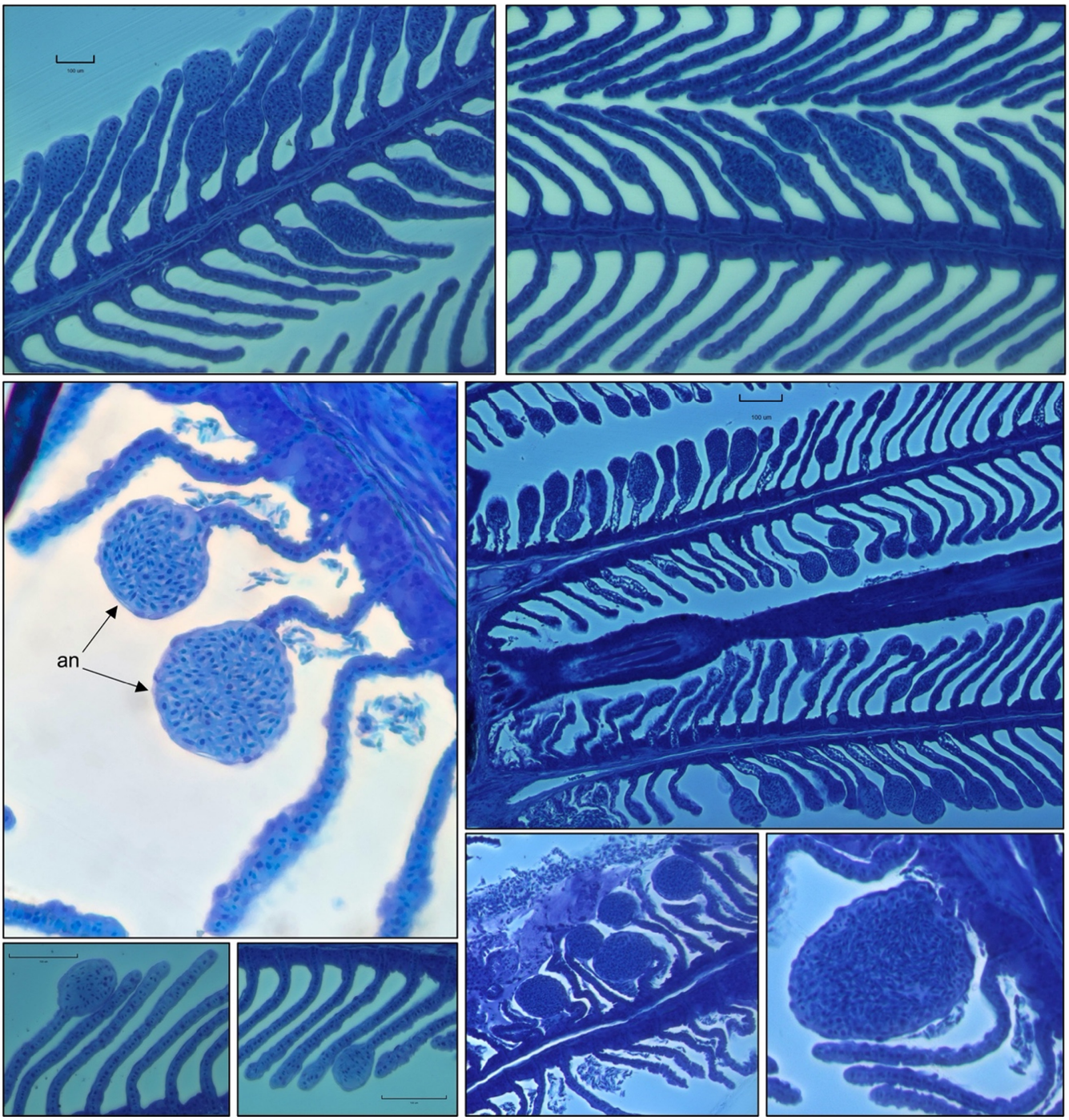

FIGURE 4 Example images of aneurysms (an) occurring in the secondary lamellae of the gills in yellow perch (*Perca flavescens*) following ice fishing. Images are taken from both control and treatment (3-min ice- and air-exposure following ice fishing) fish as aneurysms were found to occur in both groups. Tissues were stained with 1% toluidine blue +1% borax stain and sectioned along the sagittal plane at 1.5 μm thickness. These images were taken at a variety of magnifications and the scale bars in the image, where present, represent 100 μm

shown that metabolic and stress responses (e.g., glucose, lactate, cortisol) are either absent or lower in caught fish in comparison to fish sampled following fishing in warmer time periods, which has been attributed to a slowing of the enzymatic processes needed for the physiological stress response (Grausgruber et al., 2021; Logan et al., 2019; Louison, Hasler, Fenske, et al., 2017; Louison, Hasler, Raby, et al., 2017). The cooling may also contribute to behavioural and locomotory impairment that has also been noted following ice fishing (Bieber et al., 2019; LaRochelle et al., 2021; Logan et al., 2019; Louison et al., 2017a; Louison, Hasler, Raby, et al., 2017), as neuronal activity and forced swimming performance slow at cooler temperatures (Ward et al., 2002; Van den Burg et al., 2015).

The exploratory approach we used poses many questions for future study as the impacts of ice fishing on freshwater fishes in

northern climates is understudied (Lawrence et al., 2022). Our results indicate important tissues are freezing in environments with air temperatures below 0°C following capture, and there may be respiratory consequences for fish as aneurysms were observed within the delicate secondary lamellae of the gills. We recommend that anglers practice a precautionary approach and limit the amount of air-exposure when ice fishing, particularly when the air temperature is below freezing. Additionally, we recommend that anglers release any fish that they do not intend to keep immediately following capture while ice fishing, as this will limit the length of time that tissues are exposed to below 0°C and limit the gradual reduction in body temperature that we also observed. Mitigation measures could also be explored, as simple changes in how fish are handled following ice fishing may lower the likelihood of exposure to freezing temperatures (e.g., placing fish on a mat).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare. All co-authors have seen and agree with the contents of the manuscript and there is no financial interest to report. We certify that the submission is original work and is not under review at any other publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Althoff, A. L., Hasler, C. T., & Louison, M. J. (2020). Impact of retrieval time and hook type on hooking depth in ice-angled northern pike caught on tip-ups. *Fisheries Research*, *225*, 105502. https://doi.org/10.1016/j.fishres.2020.105502

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S. G., & Thorstad, E. B. (2007). Understanding the complexity of catch-and-release in recreational fishing: An integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, *15*, 75–167. https://doi.org/10.1080/10641260601149432

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Bettex-Galland, M., & Hughes, G. M. (1973). Contractile filamentous material in the pillar cells of fish gills. *Journal of Cell Science*, *13*, 359–370. https://doi.org/10.1242/jcs.13.2.359

Bieber, J. F., Louison, M. J., Stein, J. A., & Suski, C. D. (2019). Impact of ice-angling and handling on swimming performance in Bluegill and Largemouth Bass. *North American Journal of Fisheries Management*, *39*, 1301–1310. https://doi.org/10.1002/nafm.10366

Blair, S. D., Matheson, D., He, Y., & Goss, G. G. (2016). Reduced salinity tolerance in the Arctic grayling (*Thymallus arcticus*) is associated with rapid development of a gill interlamellar cell mass: Implications of high-saline spills on native freshwater salmonids. *Conservation. Physiology*, *4*, cow010. https://doi.org/10.1093/conphys/cow010

Brownscombe, J. W., Danylchuk, A. J., Chapman, J. M., Gutowsky, L. F. G., & Cooke, S. J. (2017). Best practices for catch-and-release recreational fisheries—Angling tools and tactics. *Fisheries Research*, *186*, 693–705. https://doi.org/10.1016/j.fishres.2016.04.018

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

Dextrase, A. J., & Ball, H. E. (1991). Hooking mortality of Lake Trout angled through the ice. *North American Journal of Fisheries Management*, *11*, 477–479. https://doi.org/10.1577/1548-8675(1991)011<0477:HMOLTA>2.3.CO;2

Donaldson, M. R., Cooke, S. J., Patterson, D. A., & Macdonald, J. S. (2008). Cold shock and fish. *Journal of Fish Biology*, *73*, 1491–1530. https://doi.org/10.1111/j.1095-8649.2008.02061.x

DuBois, R. B., Margenau, T. L., Stewart, R. S., Cunningham, P. K., & Rasmussen, P. W. (1994). Hooking mortality of Northern Pike angled through ice. *North American Journal of Fisheries Management*, *14*, 769–775. https://doi.org/10.1577/1548-8675(1994)014<0769:HMONPA>2.3.CO;2

Edelhauser, H. F., Hoffert, J. R., & Fromm, P. O. (1968). A comparative study of sodium permeability in lake trout and rabbit corneas. *American Journal of Physiology*, *214*, 389–394. https://doi.org/10.1152/ajplegacy.1968.214.2.389

Ferguson, R. A., & Tufts, B. L. (1992). Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): Implications for "catch and release" fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 1157–1162. https://doi.org/10.1139/f92-129

Goss, G. G., Perry, S. F., Wood, C. M., & Laurent, P. (1992). Mechanisms of ion and acid-base regulation at the gills of freshwater fish. *Journal of Experimental Zoology*, *263*(2), 143–159. https://doi.org/10.1002/jez.1402630205

Grausgruber, S. J., Grausgruber, E. E., & Weber, M. J. (2021). Influence of ice angler culling practices on bluegill physiological stress response and mortality. *North American Journal of Fisheries Management*. https://doi.org/10.1002/nafm.10687

Hassaninezhad, L., Safahieh, A., Salamat, N., Savari, A., & Majd, N. E. (2014). Assessment of gill pathological responses in the tropical fish yellowfin seabream of Persian Gulf under mercury exposure. *Toxicology Reports*, *1*, 621–628. https://doi.org/10.1016/j.toxrep.2014.07.016

Haukenes, A. H., El Mejjati, S. Y., & Buck, C. L. (2009). Effects of emersion temperature on the oxygen consumption rates of male tanner

crabs, *Chionoecetes bairdi*. *Journal of Crustacean Biology*, *29*, 91–95. https://doi.org/10.1651/07-2957.1

Jiraungkoorskul, W., Upatham, E. S., Kruatrachue, M., Sahaphong, S., Vichasri-Grams, S., & Pokethitiyook, P. (2002). Histopathological effects of roundup, a glyphosate herbicide, on Nile tilapia (*Oreochromis niloticus*). *ScienceAsia*, *28*, 121–127. https://doi.org/10.2306/scienceasia1513-1874.2002.28.121

Kim, H. J., Lee, J. H., Hur, Y. B., Lee, C. W., Park, S.-H., & Koo, B.-W. (2017). Marine antifreeze proteins: Structure, function, and application to cryopreservation as a potential cryoprotectant. *Marine Drugs*, *15*, 27. https://doi.org/10.3390/md15020027

LaRochelle, L., Chhor, A. D., Brownscombe, J. W., Zolderdo, A. J., Danylchuk, A. J., & Cooke, S. J. (2021). Ice-fishing handling practices and their effects on the short-term post-release behaviour of Largemouth Bass. *Fisheries Research*. https://doi.org/10.1016/j.fishres.2021.106084

Lawrence, M. J., Jeffries, K. M., Cooke, S. J., Enders, E. C., Hasler, C. T., Somers, C. M., Suski, C. D., & Louison, M. J. (2022). Catch and release ice fishing: Status, issues, and research needs. *Transactions of the American Fisheries Society*. In Press. https://doi.org/10.1002/tafs.10349

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

Louison, M. J., Hasler, C. T., Fenske, M. M., Suski, C. D., & Stein, J. A. (2017). Physiological effects of ice-angling capture and handling on northern pike, *Esox lucius*. *Fisheries Management and Ecology*, *24*, 10–18. https://doi.org/10.1111/fme.12196

Louison, M. J., Hasler, C. T., Raby, G. D., Suski, C. D., & Stein, J. A. (2017). Chill out: Physiological responses to winter ice-angling in two temperate freshwater fishes. *Conservation Physiology*, *5*, 1–11. https://doi.org/10.1093/conphys/cox027

Mabika, N., & Barson, M. (2014). A survey of gill histopathology of thirteen common fish species in the Sanyati Basin, Lake Kariba, Zimbabwe. *Zoologica Poloniae*, *59*, 25–34. https://doi.org/10.2478/zoop-2014-0002

Ong, K. J., Stevens, E. D., & Wright, P. A. (2007). Gill morphology of the mangrove killifish (*Kryptolebias marmoratus*) is plastic and changes in response to terrestrial air exposure. *Journal of Experimental Biology*, *210*, 1109–1115. https://doi.org/10.1242/jeb.002238

Ozcelikkale, A., & Han, B. (2016). Thermal destabilization of collagen matrix hierarchical structure by freeze/thaw. *PLoS One*, *11*, e0146660. https://doi.org/10.1371/journal.pone.0146660

Persons, S. E., & Hirsch, S. A. (1994). Hooking mortality of lake trout angled through ice by jigging and set-lining. *North American Journal of Fisheries Management*, *14*, 664–668. https://doi.org/10.1577/1548-8675(1994)014<0664:HMOLTA>2.3.CO;2

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675. https://doi.org/10.1038/nmeth.2089

Smelser, G. K. (1962). Corneal hydration: Comparative physiology of fish and mammals. *Investigative Ophthalmology*, *1*, 11–32.

Somers, C. M., Goncin, U., Hamilton, S., Chupik, M., & Fisher, R. (2021). Chasing Northern Pike *Esox lucius* under ice: Long-distance movements following catch-and-release ice angling. *North American Journal of Fisheries Management*. https://doi.org/10.1002/nafm.10638

Strzyżewska-Worotyńska, E., Szarek, J., Babińska, I., & Gulda, D. (2017). Gills as morphological biomarkers in extensive and intensive rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) production technologies. *Environmental Monitoring and Assessment*, *189*, 611. https://doi.org/10.1007/s10661-017-6278-7

Twardek, W. M., Lennox, R. J., Lawrence, M. J., Logan, J. M., Szekeres, P., Cooke, S. J., Tremblay, K., Morgan, G. E., & Danylchuk, A. J. (2018). The postrelease survival of walleyes following ice-angling on Lake Nipissing, Ontario. *North American Journal of Fisheries Management*, *38*, 159–169. https://doi.org/10.1002/nafm.10009

Ubels, J. L., & Edelhauser, H. F. (1987). Effects of corneal epithelial abrasion on corneal transparency, aqueous humor composition, and lens of fish. *The Progressive Fish-Culturist*, *49*, 219–224. https://doi.org/10.1577/1548-8640(1987)49<219:EOCEAO>2.0.CO;2

Van den Burg, E. H., Peeters, R. R., Verhoye, M., Meek, J., Flik, G., & Van der Linden, A. (2005). Brain responses to ambient temperature fluctuations in fish: Reduction of blood volume and initiation of a whole-body stress response. *Journal of Neurophysiology*, *93*, 2849–2855. https://doi.org/10.1152/jn.01113.2004

Van den Heuvel, M. R., Power, M., Richards, J., MacKinnon, M., & Dixon, D. G. (2000). Disease and gill lesions in Yellow Perch (*Perca flavescens*) exposed to oil sands mining-associated waters. *Ecotoxicology and Environmental Safety*, *46*, 334–341. https://doi.org/10.1006/eesa.1999.1912

Ward, D. L., Eugene Maughan, O., Bonar, S. A., & Matter, W. J. (2002). Effects of temperature, fish length and exercise on swimming performance of age-0 flannelmouth sucker. *Transactions of the American Fisheries Society*, *131*, 492–497. https://doi.org/10.1577/1548-8659(2002)131<0492:EOTFLA>2.0.CO;2

Warrenchuk, J. J., & Shirley, T. C. (2002). Effects of windchill on the snow crab (*Chionecetes opilio*). *Crabs in Cold Water Regions: Biology, Management*, *19*, 81–96.

Wilson, J. M., & Laurent, P. (2002). Fish gill morphology: Inside out. *Journal of Experimental Zoology*, *293*, 192–213. https://doi.org/10.1002/jez.10124

Winter, H. N., Louison, M. J., Stein, J. A., & Suski, C. D. (2018). Metabolic response of bluegill to exercise at low water temperature: Implications for angling conservation. *Environmental Biology of Fishes*, *101*, 1657–1667. https://doi.org/10.1007/s10641-018-0814-3

Wosnick, N., Navas, C. A., Niella, Y. V., Monteiro-Filho, E. L. A., Freire, C. A., & Hammerschlag, N. (2018). Thermal imaging reveals changes in body surface temperatures of blacktip sharks (*Carcharhinus limbatus*) during air exposure. *Physiological and Biochemical Zoology*, *91*, 1005–1012. https://doi.org/10.1086/699484

Zaccone, G., Kappor, B. G., Fasulo, S., & Ainis, L. (2001). Structural, histochemical and functional aspects of the epidermis of fishes. *Advances in Marine Biology*, *40*, 253–348. https://doi.org/10.1016/S0065-2881(01)40004-6

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