



Short communication

## Post-release locomotor activity of ice-angled Northern Pike

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### ABSTRACT

The study of the stress response and subsequent recovery of angled fish can inform the development of best practices for catch-and-release (C&R) angling. While large bodies of research exist detailing the impacts of C&R during warm periods of the year (i.e., open water), relatively few studies have been conducted during the colder months when sub-freezing temperatures are prominent, and anglers are targeting fish through the ice. Most research on ice angling has focused on conventional physiological stress indicators (i.e., blood cortisol, lactate, glucose) with comparatively little known about potential post-release behavioral impairments. To that end, we evaluated the consequences that ice angling C&R has on the post-release locomotor activity of Northern Pike (*Esox lucius*). Over 7 days of ice-angling, 20 Northern Pike were captured, air exposed for 0, 2, or 5 min and then harnessed with a bilogger (tri-axial accelerometer) prior to release. The post-release locomotor activity of the Northern Pike was then recorded for 30 min before the bilogger was retrieved using a quick release system. It was determined that while overall locomotor activity decreased over time during the post-release monitoring period, there was no difference between air exposure treatment groups in locomotor activity. These data reveal that Northern Pike exhibit similar locomotor activity whether they are air exposed in winter for 0, 2, or 5 min. Nonetheless, there may still be further long-term stresses that were not measured within the time frame of this experiment. Therefore, we recommend anglers fish in a way that minimizes air exposure and as a result reduces the potential for sublethal impairments or mortality.

### 1. Introduction

Anglers, resource managers, and researchers alike aim to create successful fishery systems that are healthy and resilient (Arlinghaus et al., 2009). To accomplish this, managers rely on regulations and best handling practice guidelines, such as catch-and-release (C&R), that are believed to reduce mortality and subsequently support a fishery while maintaining angler satisfaction (Cooke and Schramm, 2007). However, research has shown that this may not always be the case, as released fish may be subjected to numerous sublethal effects that can impair recovery (Cooke and Suski, 2005; Arlinghaus et al., 2009) and lead to other sources of mortality such as predation (Raby et al., 2014). These sublethal effects may be impacted by abiotic conditions at the time of capture, especially water and air temperature, which have been shown to influence the likelihood of mortality (Cooke and Suski, 2005; Gingerich et al., 2007; Gale et al., 2013). It is therefore important to study the response of fish to capture across a range of temperatures in which angling can take place.

Until recently, examinations of the outcomes of angled fish have

disproportionately focused on warmer summer conditions, leaving winter work (i.e., sub-freezing temperatures) underrepresented (Lavery 2015, Lawrence et al., 2022). During the winter, there are numerous changes in the physiology of individual fish as they respond to reduced temperatures, dissolved oxygen, and habitat (Magnuson et al., 1985; Studd et al., 2021) which may alter the resilience of fish to angling. Therefore, there is a need to carefully define the response of fish to ice angling events to tailor the best handling practices specific to this period of the year (Lawrence et al., 2022). Northern Pike (*Esox lucius*) is a popular sportfish and target for ice anglers (Margenau et al., 2003). The response of Northern Pike to angling has been extensively studied in summer, revealing physiological alterations and both short-term and longer-term behavioral impairments, typically reducing movement immediately after release before an increase within approximately 30 min (Klefoth et al., 2008; Arlinghaus et al., 2009). Recently, there has been work done to assess broad-scale movement of Northern Pike following a general ice-angling experience (e.g. no treatment groups). Results indicated no change in movement 7 days post release (Somers et al., 2021). However, other prior work has found evidence of

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physiological responses of Northern Pike to ice angling air exposure, with findings from Louison et al. (2017a) and Louison (2017b) suggesting marginal increases of stress related factors present in blood within 30 min (i.e., cortisol, glucose). Despite these minor physiological alterations, there is reason to believe that ice angling and the subsequent air-exposure may have behavioral impacts such as a reduction in post-release locomotory activity as has been observed for other ice-angled species (Bieber et al., 2019; LaRochelle et al., 2021). Therefore, the goal of the present study was to define the consequences of sub-freezing air exposure on the post-release locomotor activity of Northern Pike. Based on prior work (e.g., Gingerich et al., 2007, Thompson et al., 2008, Arlinghaus et al., 2009, Graves et al., 2016, Bieber et al., 2019), we hypothesized that longer durations of air exposure would negatively influence the locomotor activity of Northern Pike post-release. Together, results from our study have the potential to inform conservation guidelines for winter-angled fish and provide anglers with recommendations that yield positive outcomes for ice angled fish.

## 2. Materials and methods

### 2.1. Study Site

The current study was conducted at Grand Lake, Wisconsin, USA (N 43.689, W 89.121). Grand Lake is a small (98 ha), shallow (~1 m mean depth) flowage of the Grand River (Grand Lake (Millpond)). Angling for Northern Pike took place daily from January 5, 2021, to January 11, 2021, between the hours of 0800–1630. The mean daily air temperature ranged from -6.9 to -2.7° C (measurements taken from a National Oceanic and Atmospheric Administration (NOAA) weather station in Markesan, WI; 43.71°N 89°W) and water temperature directly below the ice and measured once per day ranged from 1.3 to 2.2° C (YSI® ProSolo, Yellow Springs, OH, USA).

### 2.2. Fish capture and accelerometer harnessing

All Northern Pike were captured with tip-ups (in less than 180 s), one of the most common ice angling methods (Lawrence et al., 2022), which were baited with live golden shiner (*Notemigonus crysoleucas*). Between 16 and 20 tip-ups were deployed in a grid pattern each day where each tip up was approximately 15 m from any neighboring one. All capture tip-ups were spooled with 14 kg SpiderWire<sup>(R)</sup> fishing line, attached to a 14 kg Berkley<sup>(R)</sup> 92 black wire leader, and rigged with a size 2 or size 6 Eagle Claw<sup>(R)</sup> 101 treble hook (utilized in a concurrent study). Two tip-ups were devoted for accelerometry (spooled with 27.2 kg line knotted with a swivel clasp) which connected to a removable hook-and-loop harness that held a biologist (Axy-Depth tri-axial accelerometers, TechnoSmArt, Guidonia Montecelio, Italy; 12 × 31 × 11 mm; 7.5 g in air, ~3.5 g in water) which measures acceleration (g) on the X, Y, and Z axis. The biologist was set to collect 5 measurements per second (5 Hz) at an 8-bit resolution with a G-scale at 8. All hook injuries from capture were recorded, and while only a single fish was deep hooked, it was removed from subsequent analysis.

After capture, fish haphazardly received one of three air exposure treatments where they were placed directly on the ice for 0, 2, or 5 min; representing a typical range of time during which an angler unhooks, photographs, measures and/or decides to release their fish, (Louison et al., 2017a). Fish in the 0-minute air exposure treatment were immediately unhooked and measured for total length utilizing a wet, foam lined measuring trough (to the nearest mm) before being harnessed in the same trough (see below) and released as quickly as possible (typically under 30 s after landing). For fish in the 2-minute and 5-minute air exposure groups, timing began immediately after unhooking the fish and laying it on the ice. Fish were measured and harnessed at the end of the treatment period utilizing the identical wet trough as the 0-minute group.

Following air exposure, the accelerometer on the hook-and-loop harness was secured to the ventral side of the Northern Pike behind the pectoral fins (LaRochelle et al., 2021; Chhor et al., 2022) and the harness was then clipped to one of the two tip-ups dedicated to accelerometry prior to being released in the hole they were captured. After 30 min, the researcher returned to the hole, manually retrieved the fish, and removed the accelerometer. Additionally, the risk of recapture was low, as prior work in this system over winter did not recapture any fish (Louison et al., 2017a). In total, 20 ice angled Northern Pike were analyzed for post-release behavior following a 0 (n = 6), 2 (n = 7), or 5 (n = 7) The fish in the study were all similar in size (5-minute = 580 ± SE 2 cm, range = 51–66 cm; 2-minute = 597 ± SE 3 cm, range = 44.5–65.5 cm; 0-minute = 556 ± SE 4 cm, range = 39.5–68 cm).

### 2.3. Data processing

Static acceleration was removed from the acceleration data by passing a 2 s box smoother over each axis using the *rollmean* function in the R package 'zoo' (Zeileis et al., 2005). Dynamic acceleration was calculated by subtracting static acceleration from raw acceleration values directly from the accelerometer. Overall dynamic body action (ODBA) was calculated as the sum of absolute values of the dynamic acceleration of each axis and represents locomotor activity (Brown-scombe et al., 2018; LaRochelle et al., 2021; Chhor et al., 2022; LaRochelle et al., 2022). For subsequent analysis, mean ODBA was grouped into discrete 3-minute bins (i.e., mean ODBA from 0 to 3 min, 3.01–6 min, and so on), providing ten measurements of ODBA within each 30-minute post-release monitoring period.

### 2.4. Statistical Analysis

To quantify the relationship between air exposure and the post-release locomotor activity of Northern Pike, a linear mixed effects model was fitted. The response variable (ODBA) was analyzed along with three main effects (total length, treatment, and minutes post-release), and fish ID as a random effect since multiple data points were collected from each individual fish within the 30 min post-release monitoring period, meaning that each measurement was not independent and potentially correlated (Laird and Ware, 1982; Lindstrom and Bates, 1990). Calculated p-values for fixed factors were derived via a Type III analysis of variance table with Satterthwaite's method. Initially, mixed effects models included all two-way interactions between the three main effects, but these terms were removed when they were found to be non-significant (Harrison et al., 2018) and to not overfit the models. Mixed model analyses were run utilizing the *nlme* (version 3.1.152) package in R (Pinheiro et al., 2013). Post hoc pairwise comparisons of means were conducted utilizing the *emmeans* (version 1.6.0) package in R (Lenth, 2021). All analyses were conducted in R version 4.1.2 (R Core Team 2021).

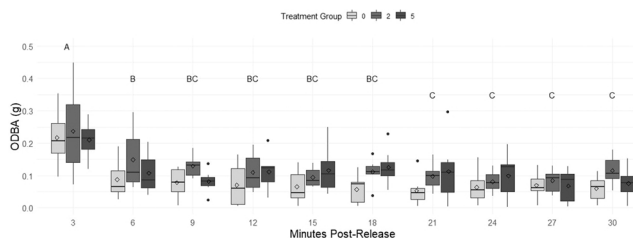
## 3. Results

There was no effect of air exposure treatment on ODBA (Table 1; Fig. 1). The locomotor activity, measured through ODBA, for Northern Pike was highest for all groups within the first 3-minutes bin immediately following release, averaging approximately 0.3 g (Table 1; Fig. 1). Following this initial 3 min, ODBA declined by 50% for all air exposure durations, and remained at this level for the next 12 min post-release (Table 1; Fig. 1). There was an additional decline in ODBA of 20% relative to the six-minute time bin in the final 9 min of monitoring, again with no difference across the 3 air exposure treatments (Fig. 1). Fish size did not influence ODBA (Table 1) and there was no significant differences in fish size between treatment groups (ANOVA,  $F_{2,17} = 0.43$ ,  $p = 0.66$ ) No short-term mortality was observed in this study.

**Table 1**

Output of linear mixed effects models quantifying the effects of treatment (0, 2, or 5 min air exposure after angling), time post-angling (3, 6, 9, 12, 15, 18, 21, 24, 27, or 30 min) and size (TL to nearest mm) on ODBA (overall dynamic body acceleration) of Northern Pike. Significant results are shown in **bold**.  $R^2$  marginal and  $R^2$  conditional for each model are also provided.

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)	$R^2$ m	$R^2$ c
Treatment	0.0057	0.00286	2	16	0.3641	0.7004	0.334	0.560
Length (mm)	0.0066	0.00655	1	16	0.8341	0.3746		
Minutes Post-release	<b>2.041</b>	<b>0.2268</b>	9	171	<b>28.884</b>	<b>&lt; 0.0001</b>		



**Fig. 1.** Overall dynamic body acceleration (ODBA) of Northern Pike that were ice-angled, and air exposed for either 0, 2 or 5 min before being released. Northern Pike were monitored for 30 min post-release with a tri-axial accelerometer, and data are shown grouped into 3-minute bins. The boxes represent the interquartile range of the data. The lines in the boxes represent the median and diamonds represent the mean. The whiskers represent the maximum and minimum values, and dots represent the outliers. Dissimilar letters above boxes denote significant differences across time periods.

#### 4. Discussion

There was no effect of air exposure duration on the post-release locomotor activity of ice-angled Northern Pike during the 30-minute monitoring period. This was somewhat surprising, considering how air exposure has been shown previously to cause numerous behavioral and physiological disturbances in fish including loss of equilibrium and increased recovery time (Ferguson and Tufts, 1992; Gingerich et al., 2007; Thompson et al., 2008; Cook et al., 2015). Summer-angled Northern Pike that had been air exposed for 5 min rested for 30 % longer, took up to 18 min longer to move, and moved an average 65 % less compared to those air exposed 0 s (Arlinghaus et al., 2009). Wintertime presents additional challenges for angled fish such as the potential for gill and cellular damage resulting from freezing (Lawrence et al., 2022) and a concurrent reduction in swimming performance (Bieber et al., 2019) which could lead to a stronger relationship between air exposure and reduced activity, however this is not demonstrated in the present study.

The lack of sub-freezing air exposure effect may be due to one of three possible explanations. First, Northern Pike in the present study could be adversely impacted from the angling experience rather than air exposure as multiple stressors can be synergistic, additive, or antagonistic (Folt et al., 1999; Côté et al., 2016). Second, owing to the low magnitude of disturbance in winter angled fish compared to equal angling stressors in the summer (Louison et al., 2017a; Louison et al., 2017b; Logan et al., 2019) all fish, regardless of air exposure duration, may have experienced equally low levels of impairment from air exposure that did not manifest in altered locomotor activity rates. Lastly, past studies demonstrating movement of fish after release have used acoustic telemetry or radio telemetry (Kobler et al., 2008; Baktoft et al., 2012) which may be better suited for quantifying movement patterns relative to tri-axial accelerometers that yield detailed information on locomotor activity. While air exposure is a demonstrated cause of disturbance in fish across temperatures, results from this study indicate the duration of air exposure during ice angling (in the conditions studied here) for Northern Pike does not influence patterns of ODBA during a 30-minute monitoring period post-release.

Furthermore, Northern Pike exhibited low levels of locomotory

activity throughout the monitoring period. Specifically, the absolute magnitude of ODBA (0.12 g) of Northern Pike after the first 3 min post-release remained low for the duration of the measuring period. While direct quantitative comparisons of ODBA across species and studies is challenging due to differences in accelerometer placement, frequency, and swimming methods (Sato et al., 2007; Halsey et al., 2009), qualitative comparisons of ODBA values can provide interesting insights into locomotor activity. For example, Northern Pike in the present study exhibited a lack of activity resumption within 30 min that has been observed in other similar work (LaRoche et al., 2021; Chhor et al., 2022; LaRoche et al., 2022). The low magnitude of ODBA throughout the 30-minute monitoring period may be due to two possible mechanisms. First, the overall low ODBA of Northern Pike following release may be due to the common angling experience since all fish were captured within a similar timeframe (<180 s). Prior work, in both summer and winter, has shown that capture and the subsequent exercise induces increases in lactate that are correlated with reduced activity (Cooke and Suski, 2005; Arlinghaus et al., 2009; Louison et al., 2017a). Second, the low ODBA values in the present study may reflect the winter foraging ecology of Northern Pike relative to other species, since pike are sit-in-wait predators (Diana, 1980; Baktoft et al., 2012). This may be further exacerbated by the reduced metabolic rate (Gingerich et al., 2007) and muscle function (Wardle, 1980) of fish in winter. In addition, the shallow bathymetry (average depth ~1 m) of the lake in which the present study occurred may facilitate situations where pike quickly find preferred habitat to recover (Klefoth et al., 2008). However, prior work has indicated Northern Pike move similar distances in winter and summer (Somers et al., 2021; Baktoft et al., 2012; Baktoft et al., 2013). Ultimately, the cause of reduced locomotor activity observed in this winter study compared to summer remains unclear due to the inability to collect true “control” data on uncaptured fish. As a result, it cannot be determined whether the comparatively low locomotor activity measured in Northern Pike in this study is the result of generalized activity reduction, recovery from the angling experience, or both.

The results of this study indicate that Northern Pike locomotory activity does not differ with up to 5 min of air exposure following an ice angling experience; however, Northern Pike exhibit lower activity levels when compared to previous studies. Although Northern Pike in this study may indicate resilience to sub-freezing air exposure, there is still further work that must be conducted to fully assess the impacts ice-angling on Northern Pike. For example, future studies may include longer air exposure durations, monitoring periods, assessments of other environmental conditions (i.e. windchill) and inclusion of non-captured controls. Additionally, further work should assess the behavioral impacts of externally attached biologgers on fish. Factors such as type and density of underwater structure, hydrodynamic drag, and weight of the external biologger should be further investigated as they may interact with fish behavior (Chhor et al., 2022). However, in the present study, we do not believe the externally attached biologger created a strong influence on behavior of Northern Pike, as the lake vegetation and structure were observationally low, retrieval effort of the biologger was minimal and consistent across events, and the weight of the biologger and harness was exceedingly low relative to the fish (likely <2% of fish weight). Furthermore, while sample sizes were somewhat low, accelerometers capture high resolution and accurate data with few individuals (Brownscombe et al., 2018), future work should aim to have



more individuals per group. While effects may be muted, fish are still affected by air exposure in the winter (Louison et al., 2017a, Louison, 2017b) and therefore anglers should continue to minimize fight times and air exposure to ensure that likelihood of negative outcomes remain low, and the welfare of angled fish is maintained (Cooke and Suski, 2005; Brownscombe et al., 2017).

### CRedit authorship contribution statement

**John F. Bieber:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft. **Michael J. Louison:** Conceptualization, Methodology, Validation, Investigation, Writing – original draft, Project administration, Funding acquisition. **Cory D. Suski:** Conceptualization, Methodology, Software, Validation, Resources, Data curation, Writing – original draft, Supervision, Funding acquisition. **Steven J. Cooke:** Conceptualization, Methodology, Software, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition. **Luc Larochelle:** Conceptualization, Methodology, Software, Validation, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data Availability

Data will be made available on request.

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### References

- Arlinghaus, R., Klefoth, T., Cooke, S.J., Gingerich, A., Suski, C., 2009. Physiological and behavioural consequences of catch-and-release angling on Northern Pike (*Esox lucius* L.). *Fish. Res.* 97, 223–233.
- Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Jepsen, N., Koed, A., Svendsen, J.C., Skov, C., 2012. Seasonal and diel effects on the activity of Northern Pike studied by high-resolution positional telemetry. *Ecol. Freshw. Fish.* 21, 386–394. <https://doi.org/10.1111/j.1600-0633.2012.00558.x>.
- Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Koed, A., Pedersen, M.W., Svendsen, J.C., Skov, C., 2013. Effects of angling and manual handling on pike behaviour investigated by high-resolution positional telemetry. *Fish. Manag. Ecol.* 20 (6), 518–525.
- 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 Am. J. Fish. Manag.* 39, 1301–1310. <https://doi.org/10.1002/nafm.10366>.
- 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. *Fish. Res.* 186 (3), 693–705.
- Brownscombe, J.W., Lennox, R.J., Danylchuk, A.J., Cooke, S.J., 2018. Estimating fish swimming metrics and metabolic rates with accelerometers: the influence of sampling frequency. *J. Fish. Biol.* 93, 207–214. <https://doi.org/10.1111/jfb.13652>.
- Chhor, A.D., Glassman, D.M., Brownscombe, J.W., Trahan, A.T., Danylchuk, A.J., Cooke, S.J., 2022. Short-term behavioural impacts of air-exposure in three species of recreationally angled freshwater fish. *Fish. Res.* 253, 106342 <https://doi.org/10.1016/j.fishres.2022.106342>.
- Cook, K.V., Lennox, R.J., Hinch, S.G., Cooke, S.J., 2015. Fish out of water: how much air is too much? *Fisheries* 40, 452–461. <https://doi.org/10.1080/03632415.2015.1074570>.
- Cooke, S.J., Schramm, H.L., 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fish. Manag. Ecol.* 14, 73–79. <https://doi.org/10.1111/j.1365-2400.2007.00527.x>.
- 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? *Biodivers. Conserv.* 14, 1195–1209. <https://doi.org/10.1007/s10531-004-7845-0>.
- Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B.* 283, 20152592. <https://doi.org/10.1098/rspb.2015.2592>.
- Diana, J.S., 1980. Diel activity pattern and swimming speeds of Northern Pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Can. J. Fish. Aquat. Sci.* 37, 1454–1458. <https://doi.org/10.1139/f80-187>.
- Ferguson, R.A., Tufts, B.L., 1992. Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for “C&R” fisheries. *Can. J. Fish. Aquat. Sci.* 49, 1157–1162. <https://doi.org/10.1139/f92-129>.
- Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44, 864–877. <https://doi.org/10.4319/lo.1999.44.3.part.2.0864>.
- Gale, M.K., Hinch, S.G., Donaldson, M.R., 2013. The role of temperature in the capture and release of fish. *Fish. Fish.* 14, 1–33. <https://doi.org/10.1111/j.1467-2979.2011.00441.x>.
- Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. *Fish. Res.* 86, 169–178. <https://doi.org/10.1016/j.fishres.2007.06.002>.
- Grand Lake (Millpond) [WWW Document], URL (<https://dnr.wi.gov/lakes/lakepages/LakeDetail.aspx?wbic=161100>) (Accessed 5.16.22).
- Graves, J.E., Marcek, B.J., Goldsmith, W.M., 2016. Effects of air exposure on postrelease mortality rates of White Marlin caught in the US offshore recreational fishery. *North Am. J. Fish. Manag.* 36 (6), 1221–1228.
- Halsey, L.G., Shepard, E.L.C., Quintana, F., Gomez Laich, A., Green, J.A., Wilson, R.P., 2009. The relationship between oxygen consumption and body acceleration in a range of species. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 152, 197–202. <https://doi.org/10.1016/j.cbpa.2008.09.021>.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, 47–94. <https://doi.org/10.7717/peerj.4794>.
- Klefoth, T., Kobler, A., Arlinghaus, R., 2008. The impact of catch-and-release angling on short-term behaviour and habitat choice of Northern Pike (*Esox lucius*). *Hydrobiologia* 601, 99–110.
- Kobler, A., Klefoth, T., Wolter, C., Fredrich, F., Arlinghaus, R., 2008. Contrasting Northern Pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia* 601, 17. <https://doi.org/10.1007/s10750-007-9263-2>.
- Laird, N.M., Ware, J.H., 1982. Random-effects models for longitudinal data. *Biometrics* 38, 963–974.
- 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. *Fish. Res.* 243, 106084 <https://doi.org/10.1016/j.fishres.2021.106084>.
- LaRochelle, L., Trahan, A., Brownscombe, J.W., Danylchuk, A.J., Cooke, S.J., 2022. A comparison of different tournament weigh-in formats on the short-term postrelease behavior of black bass assessed with biologgers. *North Am. J. Fish. Manag.* 42, 250–259. <https://doi.org/10.1002/nafm.10736>.
- Lavery, M., 2015. Winter: the forgotten study season. *The Fisheries Blog*. URL (<https://thefisheriesblog.com/2015/02/09/winter-fieldwork/>) (Accessed 9.1.21).
- 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* n/a. <https://doi.org/10.1002/tafs.10349>.
- Lenth, R.V., Buurkner, P., Herve, M., Love, J., Riebl, H., Singmann, H., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Lindstrom, M.J., Bates, D.M., 1990. Nonlinear mixed effects models for repeated measures data. *Biometrics* 46, 673–687.
- 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. *Fish. Res.* 215, 106–113. <https://doi.org/10.1016/j.fishres.2019.03.014>.
- Louison, M., Hasler, C., Fenske, M., Suski, C., Stein, J., 2017a. Physiological effects of ice-angling capture and handling on Northern Pike, *Esox lucius*. *Fish. Manag. Ecol.* 24, 10–18.
- Louison, M.J., Hasler, C.T., Raby, G.D., Suski, C.D., Stein, J.A., 2017b. Chill out: physiological responses to winter ice-angling in two temperate freshwater fishes. *Conserv. Physiol.* 5. <https://doi.org/10.1093/conphys/cox027>.
- Magnuson, J.J., Beckel, A.L., Mills, K., Brandt, S.B., 1985. Surviving winter hypoxia: behavioural adaptations of fishes in a northern Wisconsin winterkill lake. *Environ. Biol. Fish.* 14, 241–250.
- Margenau, T.L., Gilbert, S.J., Hatzenbeler, G.R., 2003. Angler catch and harvest of Northern Pike in northern Wisconsin lakes. *North Am. J. Fish. Manag.* 23, 307–312.
- Pinheiro, J., Bates, D., Debroy, S., Sarkar, D., 2013. *Nlme: nonlinear mixed-effects models*. R. Package 3.1.
- Raby, G.D., Packer, J.R., Danylchuk, A.J., Cooke, S.J., 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish. Fish.* 15, 489–505. <https://doi.org/10.1111/faf.12033>.

- Sato, K., Watanuki, Y., Takahashi, A., Miller, P.J.O., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T., Watanabe, Y., Mitani, Y., Costa, D.P., Bost, C.-A., Aoki, K., Amano, M., Trathan, P., Shapiro, A., Naito, Y., 2007. Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds, and cetaceans. *Proc. R. Soc. B Biol. Sci.* 274, 471–477. <https://doi.org/10.1098/rspb.2006.0005>.
- Somers, C.M., Goncin, U., Hamilton, S., Chupik, M., Fisher, R., 2021. Chasing Northern Pike under ice: long-distance movements following catch-and-release ice angling. *North Am. J. Fish. Manag.* <https://doi.org/10.1002/nafm.10638>.
- Studd, E.K., Bates, A.E., Bramburger, A.J., Fernandes, T., Hayden, B., Henry, H.A.L., Humphries, M.M., Martin, R., McMeans, B.C., Moise, E.R.D., O'Sullivan, A.M., Sharma, S., Sinclair, B.J., Sutton, A.O., Templer, P.H., Cooke, S.J., 2021. Nine maxims for the ecology of cold-climate winters. *BioScience* 71, 820–830. <https://doi.org/10.1093/biosci/biab032>.
- Thompson, L.A., Cooke, S.J., Donaldson, M.R., Hanson, K.C., Gingerich, A., Klefoth, T., Arlinghaus, R., 2008. Physiology, behavior, and survival of angled and air-exposed largemouth bass. *North Am. J. Fish. Manag.* 28, 1059–1068. <https://doi.org/10.1577/M07-079.1>.
- Wardle, C.S., 1980. Effects of Temperature on the Maximum Swimming Speed of Fishes. In: Ali, M.A. (Ed.), *Environmental Physiology of Fishes*, NATO Advanced Study Institutes Series. Springer, US, Boston, MA, pp. 519–531. [https://doi.org/10.1007/978-1-4899-3659-2\\_20](https://doi.org/10.1007/978-1-4899-3659-2_20).
- Zeileis, A. and Grothendieck, G., 2005. zoo: S3 Infrastructure for Regular and Irregular Time Series. *arXiv:math/0505527*.