Aquatic Diversity and Ecology 1 (2026) 100011

Contents lists available at ScienceDirect

Aquatic Diversity and Ecology

journal homepage: www.keaipublishing.com/ade/

Research Article

Air exposure durations influence post-release swimming activity of Muskellunge (*Esox masquinongy*)

Erin Wilson[a,1], Luc LaRochelle[a,1,*], Andrea Petetta[b], Sean J. Landsman[c], Steven J. Cooke[a,c]

[a] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa K1S 5B6 Canada*
[b] *Institute for Marine Biological Resources and Biotechnology (IRBIM), National Research Council (CNR), Ancona 60125 Italy*
[c] *Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa K1S 5B6 Canada*

ARTICLE INFO

Keywords:
Biologging
Catch-and-release
Fishing
Best practices
Air exposure
Muskellunge

ABSTRACT

Muskellunge (*Esox masquinongy*) are a popular sportfish across their native and introduced range. Recreational fisheries for Muskellunge are intensively regulated, although there is a strong conservation ethic wherein most of the individuals captured by recreational anglers are released. Despite high voluntary release rates, the influence of angling and air exposure on the post-release behaviour of Muskellunge in the wild remains unclear. Here, we captured Muskellunge from waterbodies in eastern Ontario, Canada using conventional Muskellunge angling gear in water temperatures of 19–27 °C and exposed them to air for different durations of time (none: 0 s, medium: 60–94 s, high: 120–160 s). Captured Muskellunge (n = 13) were equipped with a novel pop-off biologging package prior to release. Pop-off biologging packages were used to observe swimming activity, depth and water temperature used by Muskellunge for a 10-h post-release monitoring period. No mortalities occurred during the 10-h monitoring period. Longer air exposure durations resulted in elevated swimming activity during the initial 5-h post-release and returned to the non-air exposed treatment behaviour after 6-h post-release. There were no differences in water temperature or depth used by Muskellunge exposed to air compared to those that were not exposed to air. Anglers should aim to keep air exposure periods $<$ 60 s for Muskellunge that are intended to be released to avoid post-release behavioural alterations that result in increased swimming activity. Increased swimming activity observed once released was presumably a strategy used by Muskellunge to help increase blood flow and clear anaerobic by-products that occured as a result of the fight and air exposure period. Avoiding increased swimming activity during the post-release recovery period is important for reducing excessive energetic expenditures that could influence the fitness of fish (e.g., acquiring food).

1. Introduction

Recreational angling is a common activity practiced globally and provides many cultural, social, economic, psychological, and nutritional benefits (reviewed in Arlinghaus et al., 2007; Arlinghaus et al., 2015). Although some fish are harvested by recreational anglers, many fish are released voluntarily or to comply with regulations (i.e., catch-and-release; Cook et al., 2015; Gaeta et al., 2013). It is generally assumed that a fish released from an angling event survives with minimal effects on their long-term fitness (Cooke and Schram, 2007). However, many studies have documented the sublethal and lethal influences that catch-and-release angling has on a variety of marine and freshwater fishes (reviewed in Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005). Studies investigating factors such as gear type, handling practices, and air exposure have increased, which has ultimately informed fisheries regulations and provided anglers with information on best practices for fish that are intended to be released (see Brownscombe et al., 2017). Although it is possible to identify some general principles associated with catch-and-release that apply across species and contexts, there is also merit in developing species-specific guidelines for more specialized sportfish species (Cooke and Suski, 2005).

Muskellunge (*Esox masquinongy*) are highly sought-after by specialized freshwater anglers due to their size, aggressive behaviour, and low abundance (Casselman, 2007; Kerr, 2006). Muskellunge catch-and-

Peer review under the responsibility of Editorial Office of Aquatic Diversity and Ecology.

* Corresponding author.
E-mail address: larochelle96@gmail.com (L. LaRochelle).
[1] Shared first author

https://doi.org/10.1016/j.ade.2026.100011
Received 31 March 2026; Received in revised form 30 April 2026; Accepted 4 June 2026
Available online 10 June 2026

release angling gained traction in the late 1980s (Gilbert and Sass, 2016) and precluded the establishment of many relatively conservative length- and harvest-based regulations in effect today (e.g., Kerr, 2006). Although the purpose of releasing Muskellunge is to ensure a sustainable population and increase trophy potential (Minnesota Department of Natural Resources, 2025; Simsons, 2012), relatively little is known on the influences that recreational angling may have on the post-release behaviour and survival of Muskellunge in the wild (Shaw et al., 2019). As release rates have increased to almost 100% amongst Muskellunge anglers, the demand for recommendations on proper gear, handling procedures, and landing methods has also increased (Kerr, 2006; Kerr, 2007; Gaeta et al., 2013; Gilbert and Sass, 2016). The implementation of proper catch-and-release angling and handling practices for Muskellunge is somewhat unique. Specialized Muskellunge anglers take it upon themselves to educate and participate in favorable angling, handling, and release procedures, because post-release survival and fitness is of high interest to anglers (Margenau and Petchenik, 2004). As a result, many Muskellunge populations contain limited trophy length individuals that are often recaptured due to these diligent efforts of Muskellunge anglers (Casselman, 2007; Shaw et al., 2019).

The first Muskellunge catch-and-release study was conducted in a laboratory setting where up to a 30% mortality rate was found (Beggs et al., 1980). Subsequent field studies using radiotelemetry to measure broad-scale movement of Muskellunge indicated that contemporary handling procedures likely result in very low angling-related mortality (Landsman et al., 2011). Similarly, high survival (0.99) was noted in Escanaba Lake, Wisconsin post − 1987 during a period characterized by a strong catch-and-release angling ethic among muskellunge anglers. Although angling mortality was generally low (Landsman et al., 2011; Shaw et al., 2019), other studies have suggested that mortality of Muskellunge in their southern range increased when water temperatures were > 25 °C (e.g., Bauerlien et al., 2022; Booth et al., 2023; Jenkins, 2022). However, these studies were largely limited to mortality estimates and did not examine sub-lethal endpoints such as how long the post-release behaviour of Muskellunge was affected by air exposure, or how long it may take for released Muskellunge to recover from capture in the warmest part of the year (e.g., > 20 °C).

Novel pop-off biologging packages equipped with various sensors (e.g., tri-axial acceleration, temperature and pressure) have opened new opportunities for studying the fine-scale post-release behaviour of various fishes in the wild (LaRochelle et al., 2025b). Data collected with pop-off biologging packages can be used to estimate locomotor or swimming activity, depth used, and water temperature occupancy of fish once released. More recently, these metrics have been used in catch-and-release studies to provide anglers with useful best fish handling practices (Bieber et al., 2022; Chhor et al., 2022a; Louison et al., 2023; Madden et al., 2025). Post-release behaviour of angled fish can be evaluated across different treatments that are representative of what fish may experience during an angling event (e.g., capture at different water temperatures, air exposure durations, handling times, and different gear-type) offering beneficial insights on how anglers can improve their handling practices to increase survival of released fish (Brownscombe et al., 2013; LaRochelle et al., 2021; Madden et al., 2024; LaRochelle et al., 2025a). Interactions such as exposure to air or high water temperatures during an angling event often resulted in either increased or decreased locomotor activity that differed across species and environments (Chhor et al., 2022b; LaRochelle et al., 2022; McLean et al., 2019; Qualich and Louison, 2025; Petetta et al., 2025). The alteration of routine swimming behaviour (duration and frequency of movement) can be a good indicator of fish stress and welfare (Schreck, 1990) and a useful metric for addressing these issues. Further, using pop-off tags provides ecological realism as they allow for the assessment of fish in their natural environments, thus removing the potential bias of being held in captivity (Donaldson et al., 2008; LaRochelle et al., 2025b).

The objective of our study was to test the influence of air exposure on the post-release behaviour of Muskellunge following an angling event. Muskellunge were captured with rod and reel, exposed to air for various durations of time and released with a pop-off biologging package. Results from our study will provide Muskellunge anglers with guidance on appropriate air exposure durations while Muskellunge are in their possession (e.g., unhooking, measuring and admiration period) during summertime to benefit fish welfare and survival.

2. Methods

2.1. Fish capture

Muskellunge were captured using specific angling gear including heavy/extra heavy power rods (2.4–2.7 m), large-capacity reels (e.g., 400 size baitcasting reels), 45-kg braided line, and a variety of artificial Muskellunge-specific lures (e.g., topwater, bucktails, crankbaits) with barbed treble hooks. Angling took place during the Muskellunge angling season in southeastern Ontario (in multiple waterbodies within the same ecoregion) from June 11 to September 12, 2024, from a boat. It was necessary to fish multiple waterbodies to achieve reasonable capture rates. Angling effort focused on similar habitats across waterbodies (i.e., shallow water < 4 m deep and characterized by reasonably high densities of aquatic macrophytes). Surface water temperatures ranged from 19 to 27 °C and were recorded for each capture event.

Once a Muskellunge was hooked, fish were brought to the boat as quickly as possible, and landed using a large, knotless, rubber-coated net. Fight time was not recorded to simplify sampling procedures and because Muskellunge often strike boat-side and can be netted within seconds. Hook removal using long-nose pliers occurred with fish in the water while retained in the net. Hook-cutters were used if the unhooking period took longer than approximately 120 s (Landsman et al., 2011). No hooks remained in the Muskellunge when released (i.e., hooks were cut if they were tangled in the net). The total time Muskellunge spent in the net was recorded to the nearest second. In instances where team-based angling was used (i.e., multiple boats on the water), anglers were instructed to begin a stopwatch once fish were in the net, remain in place, and to immediately contact the tagging boat. Once the hooks were removed, Muskellunge were brought into the tagging boat, measured for total length (to the nearest mm) in a foam-lined V-shaped trough, and affixed with a pop-off biologging package (Fig. 1; also see LaRochelle et al., 2023; LaRochelle et al., 2024).

Fish were assigned prior to capture to be exposed to air or not exposed to air. Fish not exposed to air had pop-off biologging packages affixed while submerged in a water filled trough, while fish exposed to air were held out of the water while being affixed with a pop-off biologging package. Air exposure period was classified into three categories: none (n = 4; 0 s), medium (n = 6; 73–94 s) and high (n = 3; 120–160 s). Those that were pre-determined to be exposed to air were then randomly assigned to either the medium or high treatments. Air exposure durations were the sum of the tagging period, length measurements (for air exposed fish, this was done in the aforementioned foam-lined trough drained of water) and a simulated "admiration period" (photos/video, see Landsman et al., 2011). The period that Muskellunge were exposed to air varied because the pop-off biologging package would sometimes dislodge prior to the fish being released resulting in the need to re-attach the biologging package. Based on these observations of Muskellunge anglers, these air exposure categories represented likely air exposure durations that occur during a typical Muskellunge angling event across angler skill levels (i.e., novice to expert) where anglers unhook, measure and take photographs (or release photos only might occur in a no air exposure scenario) with fish. Exposure to air was recorded, to the nearest second, from the time the fish was removed from the water to the time it was released. Once the pop-off biologging package was attached, Muskellunge were released.

2.2. Pop-off biologging package and monitoring period

Floating pop-off biologging packages were made from a hard foam (Smooth-on Feather Lite™; Smooth-on, Inc., Macungie, Pennsylvania,

Fig. 1. Pop-off biologging package placed on the ventral side between, but posterior to, the pectoral fins of a Muskellunge (*Esox masquinongy*).

USA) dyed orange (50 × 30 × 15 mm; 11 g; casing alone). The pop-off biologging packages were equipped with a radio transmitter used for relocation (BD − 2 Holohil, Carp, Ontario, Canada; 1.2 g in air) and an AXY − 5XS biologger that recorded tri-axial acceleration, water temperature and depth (TechnoSmArt, Guidonia Montecelio, Italy; 20 × 10 × 6 mm; 2.5 gr in air). Biologgers recorded acceleration in all three axes at a rate of 25 Hz with an 8-bit resolution (Brownscombe et al., 2018). The temperature and pressure (depth) sensor recorded at a rate of 1 Hz with a resolution of ± 0.1 °C and ± 5 cm, respectively. Pop-off biologging packages were positioned on the ventral side between the pelvic fins of Muskellunge (Fig. 1). To secure the pop-off biologging packages to Muskellunge, two self-locking straps were connected with approximately 3-cm of 3–0 plain catgut suture to create a dissolvable link (550B, Ethicon, Sommerville, New Jersey, United States). The self-locking straps were then placed into a receptacle on either side of the pop-off biologging package and tightened. Once the dissolvable link broke, or the tensile strength was lost, the pop-off biologging package would float to the surface to be retrieved.

Post-release swimming activity of Muskellunge was assessed using overall dynamic body acceleration (ODBA) which is a good proxy for locomotor activity and energy expenditure (Wilson et al., 2006; Gleiss et al., 2011; Wright et al., 2014). The ODBA of Muskellunge was calculated by summing the acceleration in all three axes (Halsey et al., 2011) and then removing the static acceleration (i.e., force of gravity) from the dynamic acceleration using a 2-s box smoother (Shepard et al., 2008). For each fish, the total ODBA for each minute post-release was calculated, and then the mean ODBA for each hour during post-release monitoring period was calculated. Mean depth and water temperature used during the post-release monitoring period was also calculated for each hour. Muskellunge were observed for 10-h once released. Individuals that did not retain their tags for at least 10-h were excluded from the analyses.

2.3. Statistical analysis

All statistical analyses were done in R version 4.5.1 (R Core Team, 2025) via R studio (v2025.05.1.153; Posit team, 2025). Figures were created using *ggplot2* (version 4.0.0; Wickham, 2016). A Spearman correlation test was used to test for a relationship between the total length of Muskellunge and the time spent in the net. Given the small sample size and the non-normal distribution of time spent in the net and surface water temperature, Kruskal-Wallis (χ^2) tests were used to test whether there was a difference in those variables across the air exposure categories. This was then followed up with a Dunn test using the *dunnTest* function (*FSA*, version 0.10.0; Ogle et al., 2025) with the Bonferroni method (corrected $\alpha = 0.017$) to test for differences among the air exposure categories.

Post-release swimming activity, depth used and water temperature occupied were modeled using generalized linear mixed models with the *glmmTMB* function and package (version 1.1.11; Brooks et al., 2017). Gaussian family with identity link was used for the generalized linear mixed models. All models were fit with fish ID as a random variable to account for the repeated measures across individuals. Each model was fit with the interaction of time post-release (i.e., monitoring period) with air exposure category, surface water temperature at the time of capture, net time and location of capture as predictor variables. Net time was used for modelling instead of total length because it is easier for anglers to change and control the time fish spend in the net compared to size of fish being captured. Pairwise comparisons were made to test for differences in the response variables across significant predictors using the *emmeans* and *pairs* function from the *emmeans* package (version 1.11.1; Lenth, 2025). Significance was determined at $\alpha = 0.05$ for all models.

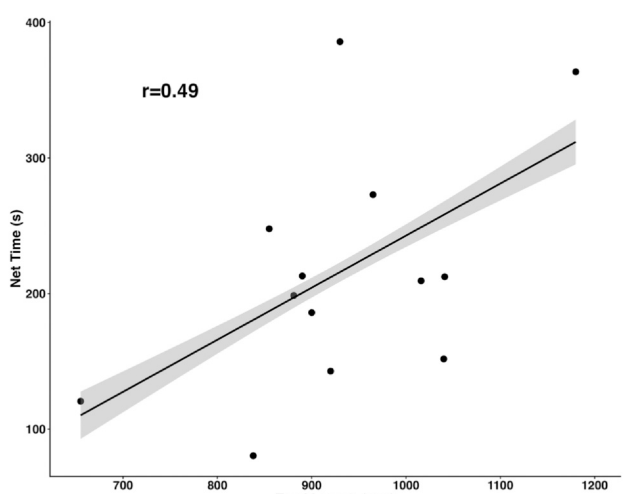

Fig. 2. Relationship between the total length of Muskellunge (*Esox masquinongy*) and the time spent in the net prior to release.

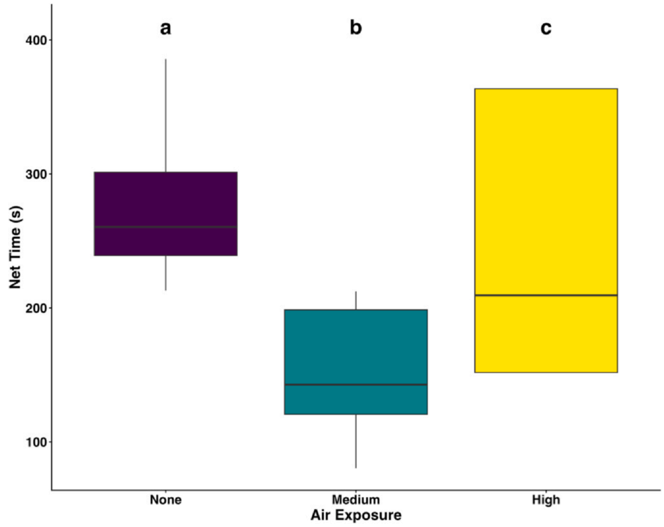

Fig. 3. Time spent in the net by Muskellunge (*Esox masquinongy*) across three different air exposure categories. Dissimilar letters represent significant differences between groups. Horizontal lines represent medians, upper and low bounds of each box represent the lower and upper quartiles, and the lower and upper ends of the vertical lines represent the minimum and maximum values, respectively.

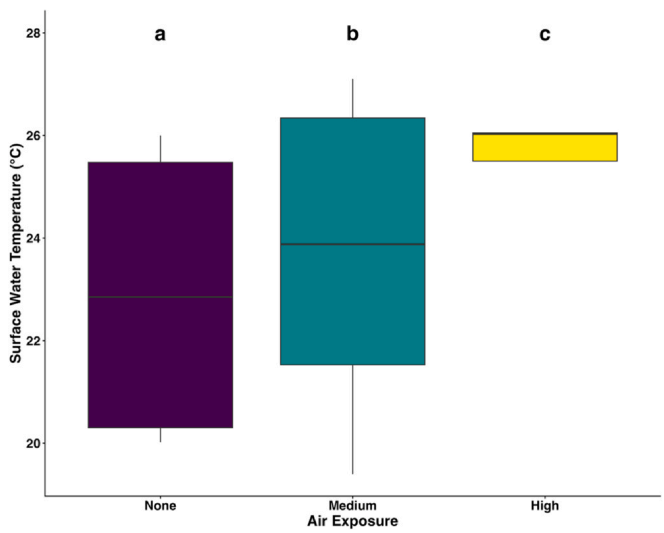

Fig. 4. Surface water temperature that Muskellunge (*Esox masquinongy*) were caught from across the different exposure to air categories. Dissimilar letters represent significant differences between groups. Horizontal lines represent medians, upper and low bounds of each box represent the lower and upper quartiles, and the lower and upper ends of the vertical lines represent the minimum and maximum values, respectively.

3. Results

Of the 18 successfully tagged Muskellunge, 13 retained their tags for the 10-h minimum threshold (i.e., 5 were excluded from analyses). Of these individuals, there was a significant correlation between the total length of Muskellunge ($n = 13$; mean ± = 926 ± 122 mm, range = 655–1180 mm) and the time spent in the net. The time spent in the net increased with total length of Muskellunge ($r = 0.486$, $p < 0.001$; Fig. 2). Net time ($\chi^2 = 228.820$, $p < 0.001$) and surface water temperature ($\chi^2 = 79.514$, $p < 0.001$) varied significantly between air exposure categories. Muskellunge not exposed to air spent a median time of 260 s in the net which was significantly longer than the medium (143 s; $z = 14.945$, $p < 0.001$) and high (209 s; $z = 5.386$, $p < 0.001$) exposure to air periods (Fig. 3). Muskellunge exposed to air for the medium treatment period spent a median time of 143 s in the net, which was significantly less (66 s less) than the high exposure to air period (209 s; $z = -7.979$, $p < 0.001$). Surface water temperature at the time of capture for the high exposure to air period was 26 °C which was significantly warmer than the 23 °C surface water temperature for the Muskellunge not exposed to air ($z = 8.865$, $p < 0.001$) or the Muskellunge caught from 24 °C waters in the medium air exposure period ($z = 4.605$, $p < 0.001$). Muskellunge exposed to air for the medium period were caught from significantly warmer water temperatures than the Muskellunge that were not exposed to air ($z = 5.237$, $p < 0.001$; Fig. 4).

Surface water temperature ($\chi^2 = 0.527$, $p = 0.468$), time spent in the net ($\chi^2 = 0.749$, $p = 0.387$) and location of capture ($\chi^2 = 0.989$, $p = 0.320$) did not influence post-release activity (i.e., ODBA values) of Muskellunge. Swimming activity of Muskellunge was significantly influenced by air exposure category and time during the post-release monitoring period ($\chi^2 = 37.486$, $p < 0.001$). Swimming activity of Muskellunge exposed to air for the longest period of time was elevated for the first 5-h post-release compared to Muskellunge that were not exposed to air (Fig. 5; Table 1; Table S1). The swimming activity of Muskellunge in the highest air exposure period declined to levels similar to Muskellunge from the non-air exposed treatment at 6-h post-

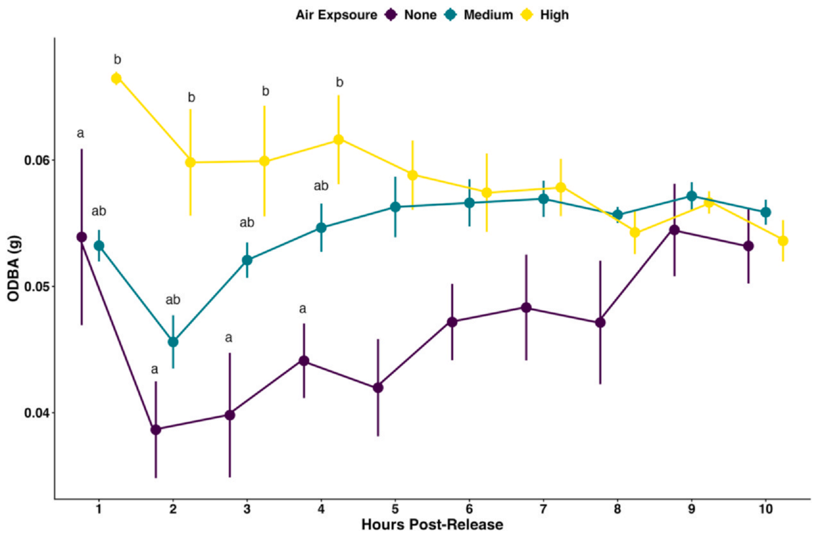

Fig. 5. Mean (points) overall dynamic body acceleration (ODBA – proxy for estimating swimming activity) of Muskellunge (*Esox masquinongy*) during a 10-h post-release monitoring period. Vertical lines represent the standard error around the mean depth used for each hour. Data were collected with a pop-off biologging package. Dissimilar letters represent significant differences in mean ODBA across periods exposed to air within the respective hour. No letters or similar letters represent no differences in ODBA across air exposures.

release. Muskellunge exposed to air for the medium duration did not differ from the non-air exposed or highest air exposed Muskellunge during the post-release monitoring period.

Post-release depth used was not influenced by surface water temperature ($\chi^2 = 3.014, p = 0.083$), by time spent in the net ($\chi^2 = 2.220$, $p = 0.136$) or by the location of capture ($\chi^2 = 1.667, p = 0.197$). The interaction of air exposure period with time in the post-release period had a statistically significant influence on post-release depth used (Fig. 6; $\chi^2 = 8.452$, $p = 0.015$). However, post-hoc tests did not identify significant differences in depth used across the air exposure treatments for each hour post-release (Table S2).

Water temperature used by Muskellunge during the post-release monitoring period was not influenced by time spent in the net ($\chi^2 = 3.081$, $p = 0.079$). Surface water temperature had a significant influence on the water temperature used during the post-release monitoring period ($\chi^2 = 35.152$, $p < 0.001$), where fish captured in warmer surface water temperatures spent more time in warmer water temperatures during the 10-h post-release monitoring period ($z = 1.137$, $p < 0.001$). Post-release water temperature used by Muskellunge was also significantly influenced by the location of capture ($\chi^2 = 9.681$, $p = 0.002$), where fish caught in the Kawartha system were in warmer waters (median 23 °C) compared to Muskellunge in the Rideau system (median 22 °C) ($t = 3.111$, $p = 0.002$). The interaction of air exposure period with time post-release had a statistically significant influence on the water temperature used by Muskellunge ($\chi^2 = 16.508, p < 0.001$; Fig. 7). However, post-hoc tests did not identify significant differences in water temperature used between the air exposure treatments for each hour post-release (Table S3).

4. Discussion

This study provided evidence that exposing Muskellunge to air led to short-term behavioural alterations. The swimming activity of Muskellunge exposed to air for the longest duration of time (120–160 s) was elevated compared to Muskellunge that were not exposed to air during the initial 5-h post-release monitoring period. Recovery of all Muskellunge seemed to occur roughly 9-h into the post-release monitoring period when swimming activity was equivalent for all Muskellunge in the study. Muskellunge that were in the medium air exposure period showed no differences in post-release swimming activity or temperature used compared to the Muskellunge that were not exposed to air. In a previous study by Landsman et al. (2011), Muskellunge exposed to air for 90 s showed no differences in movement rates shortly after release, but did exhibit slightly increased swimming activity relative to fish not exposed to air for up to an hour post-release. Our results further support that Muskellunge are relatively robust to some exposure to air and can endure exposure to air for periods of < 90 s (Landsman et al., 2011), but anglers should still exercise precautions to reduce the overall amount of exposure to air as much as possible when handling Muskellunge.

It was unclear why Muskellunge exposed to air for the longest period engaged in increased swimming activity during the initial hours of post-release relative to Muskellunge that were not exposed to air. This type of behaviour has previously been reported in fish that were transported in a live well and released in a new location (LaRochelle et al., 2022). Such behaviour could be a strategy that fish use to escape from an area of perceived danger or as a tactic used to search for suitable habitat to recover in, all of which are potential adaptive responses that could aid fish in the recovery from the stress event (Brownscombe et al., 2013). Without detailed positions of Muskellunge during the post-release monitoring period and habitat maps, it was hard to identify if this elevated swimming activity was related to seeking appropriate habitat for recovery. Alternatively, it was possible that Muskellunge exposed to air for the longest period were spending more time in the warm water, likely because stress (e.g., exhaustion) can manifest in short-term erosion of the cognitive capacity of fish (Flink et al., 2025).

Although our study did not assess physiological parameters, behaviour is often tightly linked to the physiological state of animals (Huntingford et al., 2012). Angling can lead to a cascade of physiological changes in fish that arise when white muscle energy storage is used during the fight (Kieffer, 2000) and from hypoxic conditions during air exposure (see Cook et al., 2015). For example, the build-up of anaerobic by-products such as lactate can occur during exposure to air (i.e., hypoxia; Cook et al., 2015; Gustaveson et al., 1991; Suski et al., 2004). Muskellunge exposed to air for the longest period may have been using increased swimming activity to metabolize by-products that occurred because of the exposure to air. Fish may increase movement to enhance oxygen exchange across gill lamellae, which stimulates circulatory functions and promotes the conversion of lactate to pyruvate which is metabolized aerobically (Dando, 1969; Gleeson, 1996; Kieffer, 2000; LaRochelle et al., 2025a; Milligan, 1996).

Engaging in elevated swimming activity once released could be an important recovery strategy used by Muskellunge, although there could be fitness related consequences by expending extra energy to recover. Using warmer water also increases metabolic rate which ultimately increases energy expenditure (Prystay et al., 2017) and oxygen demand to sustain basic life functions (Brett, 1971), which possibly makes

Table 1
Marginal means for the swimming activity (i.e., overall dynamic body acceleration) of Muskellunge (*Esox masquinongy*) for each hour post-release across the different exposure to air periods.

Hour Post-Release	Air Exposure	Emmean	S.E.	Lower C.I.	Upper C.I.
1					
	None	0.042	0.004	0.034	0.051
	Medium	0.051	0.004	0.044	0.058
	High	0.068	0.007	0.055	0.081
2					
	None	0.043	0.004	0.035	0.052
	Medium	0.051	0.004	0.044	0.058
	High	0.067	0.007	0.054	0.080
3					
	None	0.044	0.004	0.036	0.052
	Medium	0.052	0.004	0.045	0.060
	High	0.066	0.007	0.053	0.077
4					
	None	0.045	0.004	0.037	0.053
	Medium	0.053	0.004	0.046	0.060
	High	0.065	0.006	0.052	0.078
5					
	None	0.046	0.004	0.038	0.054
	Medium	0.054	0.004	0.047	0.060
	High	0.064	0.006	0.051	0.076
6					
	None	0.047	0.004	0.039	0.055
	Medium	0.054	0.004	0.047	0.061
	High	0.063	0.006	0.050	0.075
7					
	None	0.048	0.004	0.040	0.056
	Medium	0.055	0.004	0.048	0.062
	High	0.062	0.006	0.049	0.074
8					
	None	0.049	0.004	0.041	0.057
	Medium	0.056	0.004	0.049	0.063
	High	0.061	0.007	0.048	0.073
9					
	None	0.050	0.004	0.042	0.058
	Medium	0.056	0.004	0.049	0.063
	High	0.059	0.007	0.047	0.072
10					
	None	0.051	0.004	0.043	0.059
	Medium	0.057	0.004	0.050	0.064
	High	0.058	0.007	0.046	0.071

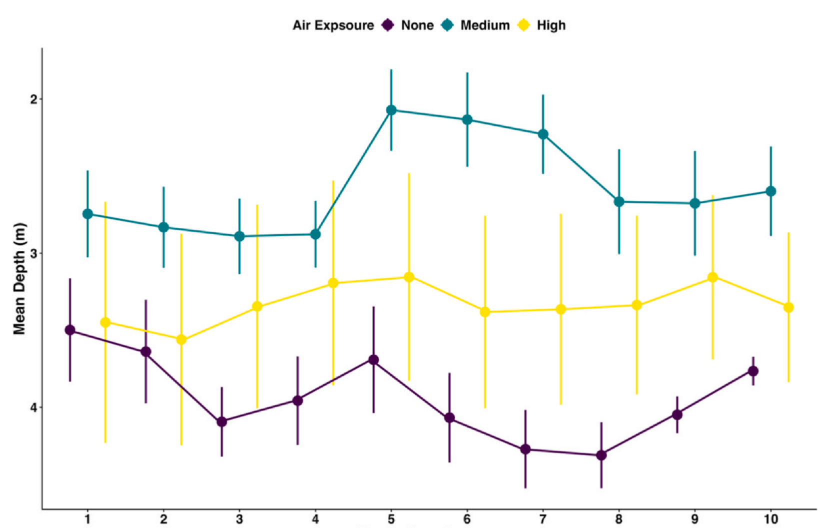

Fig. 6. Mean depth (points) used by Muskellunge (*Esox masquinongy*) during a 10-h post-release monitoring period. Vertical lines represent the standard error around the mean depth used for each hour. Data were collected with a pop-off biologging package.

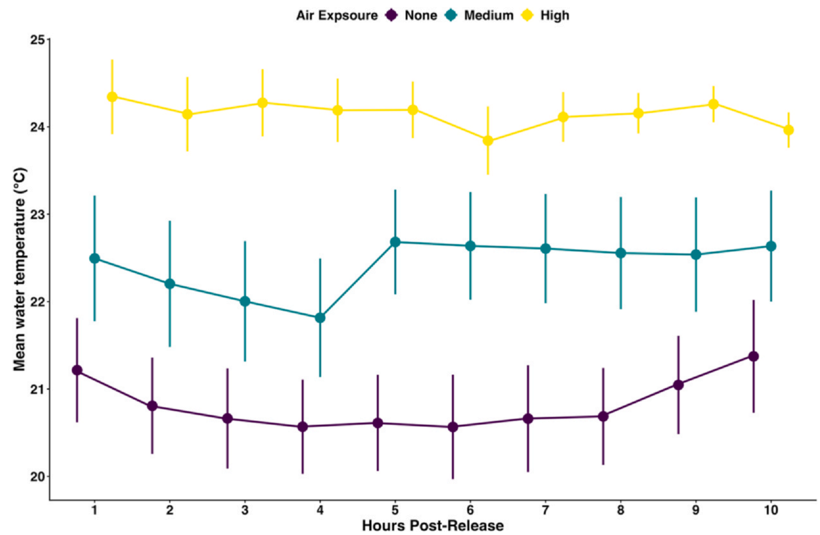

Fig. 7. Mean water temperature (points) used by Muskellunge (*Esox masquinongy*) during a 10-h post-release monitoring period. Vertical lines represent the standard error around the mean depth used for each hour. Data were collected with a pop-off biologging package.

recovery more challenging for Muskellunge and fish in general (e.g., less dissolved oxygen in warmer water; Gale et al., 2013). Regardless of the reason that Muskellunge engaged in this increased swimming activity post-release, anglers should aim to avoid factors that lead to this type of behaviour, such as extended periods of air exposure.

There were some limitations to our study given the small sample size ($n = 13$) that are worth noting. It is possible that a greater sample size could have increased the power to detect differences in swimming activity between the medium air exposure and the non-air exposed fish. To maintain reasonable catch rates, we angled in locations that maximized capture opportunities, resulting in not all fish being captured from the same waterbody. We attempted to mitigate that by limiting our efforts to the same ecoregion and focusing our angling efforts on similar habitats (i.e., shallow, abundant macrophytes). We acknowledge that local adaptation can contribute to population-specific variation in fish physiology (e.g., Fraser et al., 2011) but that typically occurs across latitudes or ecoregions, whereas our fishing effort was restricted to a relatively narrow geographic range and in a single ecoregion. Another key limitation was the short duration of time (10-h) used for the post-release monitoring period. Although no mortality events occurred during our 10-h post-release monitoring period, it is possible—though unlikely (see Shaw et al., 2019)—that mortality could have occurred in the following days (up to 14 days post-release; Booth et al., 2023). However, we speculate that mortality was unlikely to occur given the thermal refuge that was available to the Muskellunge at the time of release (Hartman et al., 2024) and the fact that swimming activity for all air exposure treatments returned to similar values at about 9-h post-release.

This was the first study to our knowledge that showed indications of a short-term post-release (10-h) behavioural alterations for air-exposed Muskellunge captured during the summer. Although Muskellunge appear resilient to modern handling practices (Landsman et al., 2011; Shaw et al., 2019), recent research indicates an increased risk of mortality at water temperatures above 25 °C when fish were held out-of-water (Bauerlien et al., 2022). Our findings provide important thresholds for exposure to air (no more than 60 s) that can be used by Muskellunge anglers when practicing catch-and-release. Minimizing the exposure to air for Muskellunge can reduce the duration for behavioural recovery. Overall, Muskellunge anglers should aim to reduce periods exposed to air as much as possible to avoid behavioural alterations once released that could lead to excessive energy expenditure and thus compromise recovery.

5. Conclusion

Exposure to air greater than 60 s increased the post-release swimming activity of captured Muskellunge, but not the depth or water temperature used. The swimming activity air exposed for the longest period (> 120 s) remained elevated for 6-h post-release relative to the control. Anglers should strive to keep air exposure period to less than 60 s if possible. By doing so, anglers can reduce the behavioural alterations that occur from being exposed to air.

Ethics statement

All tagging procedures were in accordance with Canadian Council of Animal Care approved by Carleton University (AUP #110723).

Funding

Hugh C. Becker Foundation and Muskies Canada, Inc. (National and Kawartha Lakes Chapter) provided funding for this study. Additional support was provided by the Natural Sciences and Engineering Research Council of Canada.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Sean Landsman reports financial support was provided by Muskies Canada Inc. Sean Landsman reports financial support was provided by Hugh C. Becker Foundation. The other authors, declare no competing financial interests or personal relationships that could have influenced the work reported in this paper.

Acknowledgments

We thank Christopher Zepf from CSMZ Inc. for creating the mold used to manufacture the pop-off biologging packages. We also thank Ezoko Fishing (Montreal, Canada) and Shimano for providing tackle and gear to support fish capture for this project. Research was conducted in accordance with ethical guidelines.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ade.2026.100011.

References

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C.D., 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. Rev. Fish. Sci. 15 (1–2), 75–167.

Arlinghaus, R., Tillner, R., Bork, M., 2015. Explaining participation rates in recreational fishing across industrialised countries. Fish. Manag. Ecol. 22 (1), 45–55.

Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish. Biol. Fish. 15 (1–2), 129–154.

Bauerlien, C.J., Crane, D.P., Smith, S., Palmer, G., Young, T., Goetz, D.B., Hartman, K., 2022. Low catchability limits the effect of warm-water catch-and-release mortality on muskellunge. Fish. Res. 254, 106434.

Beggs, G.L., Holeton, G.F., Grossman, E.J., 1980. Some physiological consequences of angling stress in muskellunge, *Esox masquinongy* Mitchill. J. Fish. Biol. 17 (6), 649–659.

Bieber, J.F., LaRochelle, L., Cooke, S.J., Suski, C.D., Louison, M.J., 2022. Post-release locomotor activity of ice-angled Northern Pike. Fish. Res. 256, 106481.

Booth, I.T., Hartman, K.J., Crane, D., Hansbarger, J., Weeks, J., Henesy, J., Walsh, H., Williams, J., 2023. Evaluating muskellunge catch-and-release mortality at elevated summer water temperature. Trans. Am. Fish. Soc. 152 (5), 577–593.

Brett, J.R., 1971. Energetic responses of Salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of Sockey Salmon (*Oncorhynchus nerkd*). Integr. Comp. Biol. 11 (1), 99–113.

Brooks, M.E., Kristensen, K., van, Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9 (2), 378–400.

Brownscombe, J.W., Thiem, J.D., Hatry, C., Cull, F., Haak, C.R., Danylchuk, A.J., Cooke, S.J., 2013. Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (Albula spp.) following exposure to angling-related stressors. J. Exp. Mar. Biol. Ecol. 440, 207–215.

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.

Casselman, J.M., 2007. Determining minimum ultimate size, setting size limits, and developing trophy standards and indices of comparable size for maintaining quality muskellunge (*Esox masquinongy*) populations and sports fisheries. Environ. Biol. Fish. 79 (1–2), 137–154.

Chhor, A.D., Glassman, D.M., Brownscombe, J.W., Trahan, A.T., Danylchuk, A.J., Cooke, S.J., 2022a. Short-term behavioral impacts of air-exposure in three species of recreationally angled freshwater fish. Fish. Res. 253, 106432.

Chhor, A.D., Reid, J.L., Holder, P.E., Nowell, L.B., Brownscombe, J.W., Danylchuk, A.J., Cooke, S.J., 2022b. Temporary retention in cold water reduces postrelease behavioral impairment in angled rainbow trout. N. Am. J. Fish. Manag. 42 (1), 140–150.

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 (9), 452–461.

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.

R. Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Dando, P.R., 1969. Lactate Metabolism in Fish. J. Mar. Biol. Assoc. U.K. 49 (1), 209–223.

Donaldson, M.R., Arlinghaus, R., Hanson, K.C., Cooke, S.J., 2008. Enhancing catch-and-release science with biotelemetry. Fish Fish 9 (1), 79–105.

Flink, H., Berge, A., Leggieri, F., Kolm, N., Tibblin, P., 2025. Transient cognitive impacts of oxygen deprivation caused by catch-and-release angling. Biol. Lett. 21, 20240527.

Fraser, D.J., Weir, L.K., Bernatchez, L., Hansen, M.M., Taylor, E.B., 2011. Extend and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity 106 (3), 404–420.

Gaeta, J.W., Beardmore, B., Latzka, A.W., Provencher, B., Carpenter, S.R., 2013. Catch-and-release rates of sport fishes in Northern Wisconsin from and angler diary survey. N. Am. J. Fish. Manag. 33 (3), 606–614.

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), 1–33.

Gilbert, S.J., Sass, G.G., 2016. Trends in northern Wisconsin muskellunge fishery: Results from a countrywide angling contest, 1964-2010. Fish. Manag. Ecol. 23 (2), 172–176.

Gleeson, T.T., 1996. Post-exercise lactate metabolism: a comparative review of sites, pathways, and regulation. Annu. Rev. Phsyiol. 58, 565–581.

Gleiss, A.C., Wilson, R.P., Shepard, E.L.C., 2011. Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. Methods Ecol. Evol. 2, 23–33.

Gustaveson, A.W., Wydoski, R.S., Wedemeyer, G.A., 1991. Physiological Response of Largemouth Bass to Angling Stress. Trans. Am. Fish. Soc. 120 (5), 629–636.

Halsey, L.G., Shepard, E.L.C., Wilson, R.P., 2011. Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 158, 305–314.

Hartman, K.J., Bauerlien, C.J., Jenkins, P.I., Crane, D.P., Hansbarger, J., 2024. Stratification mitigates population-level effects of warmwater catch and release of Muskellunge in a southern reservoir. Trans. Am. Fish. Soci. 153 (6), 697–713.

Jenkins, P.I., 2022. Summer habitat use, home range, and effect of catch and release mortality on the trophy potential of Muskellunge, Esox masquinongy, Mitchill, 1824, in a southern reservoir population. West Virginia University.

Huntingford, F., Tamilselvan, P., Jenjan, H., 2012. Why do some fish fight more than others? Physiol. Biochem. Zool. 85 (6), 585–593.

Kerr, S.J., 2006. Characteristics of Ontario Muskellunge fisheries based on volunteer angler diary information. In: Diana, J.S., Margenau, T.L. (Eds.), The Muskellunge Symposium: A Memorial Tribute to E.J. Crossman. Environ. Biol. Fish 26. pp. 61–69.

Kerr, S.J., 2007. Characteristics of Ontario Muskellunge (*Esox masquinongy*) fisheries based on volunteer angler diary information. Environ. Biol. Fish. 79, 61–69.

Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 126 (2), 161–179.

Landsman, S.J., Wachelka, H.J., Suski, C.D., Cooke, S.J., 2011. Evaluation of the physiology, behavior, and survival of adult muskellunge (*Esox masquinongy*) captured and released by specialized anglers. Fish. Res. 110 (2), 377–386.

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 post-release behavior of black bass assessed with biologgers. N. Am. J. Fish. Manag. 42 (2), 250–259.

LaRochelle, L., Burton, D., Madden, J.C., Clark, S., Danylchuk, J., Cooke, S.J., Danylchuk, A.J., 2023. Using a novel biologging approach to assess how different handling practices influence the post-release behavior of northern pike across a wide range of body sizes. Aquat. Living Resour. 3, 2.

LaRochelle, L., Haniford, L., Burton, D., Bieber, J.F., Robichaud, J.A., Suski, C.D., Danylchuk, A.J., Cooke, S.J., 2024. Do live-well additives influence the physiological and behavioral recovery of Largemouth Bass? N. Am. J. Fish. Manag. 44 (1) 289-203.

LaRochelle, L., Bernardi, J., Madden, J.C., Brownscombe, J.W., Goodenough, A.M., Danylchuk, A.J., Cooke, S.J., 2025a. Effects of recreational fishing gear type on reflex impairment and post-release swimming activity of smallmouth bass. Fish. Manag. Ecolo 32 (2), e12776.

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.

LaRochelle, L., Griffin, L.P., Brownscombe, J.W., Elvidge, C.K., Hasler, C.T., Robichaud, J.A., Madden, J.C., Landsman, S.J., Raoult, V., Danylchuk, A.J., et al., 2025b. On the behavior of fish released following fisheries capture: methods, endpoints, and consequences. Revi. Fish. Sci. Aquac. 33 (4), 629–656.

Lenth R. 2025. _emmeans: Estimated Marginal Means, aka Least-Squares Means_.

Louison, M.J., LaRochelle, L., Cooke, S.J., 2023. Effectiveness of barotrauma mitigation methods in ice-angled bluegill and black crappie. Fish. Manag. Ecol. 30 (3), 229–239.

Madden, J.C., LaRochelle, L., Burton, D., Danylchuk, S.C., Danylchuk, A.J., Cooke, S.J., 2024. Biologgers reveal unanticipated issues with descending angled walleye with barotrauma symptoms. Can. J. Fish. Aquat. Sci. 81 (2), 212–222.

Madden, J.C., LaRochelle, L., Goodenough, A.M., Danylchuk, A.J., Cooke, S.J., 2025. Free falling: fizzing wild-caught smallmouth bass results in the inability to control buoyancy in deep water. Fish. Manag. Ecol. 32 (4), 41–49.

Margenau, T.L., Petchenik, J.B., 2004. Social aspects of Muskellunge management in Wisconsin. N. Am. J. Fish. Manag. 24 (1), 82–93.

McLean, M.F., Litvak, M.K., Cooke, S.J., Hanson, K.C., Patterson, D.A., Hinch, S.G., Crossin, G.T., 2019. Immediate physiological and behavioral response from catch-and-release of wild white sturgeon (*Acipenser transmontanus* Richardson, 1836). Fish. Res. 214, 65–75.

Minnesota Department of Natural Resources. 2025. Long range plan for muskellunge through 2040. Minnesota Department of Natural Resources, Division of Fish and Wildlife.

Ogle, D.H., Doll, J.C., Dinno, A., 2025. _FSA: Simple Fisheries Stock Assessment Methods_. R package version 0.10.0.

Milligan, C.L., 1996. Metabolic recovery from exhaustive exercise in rainbow trout. Comp. Biochem. Physiol. A. Physiol. 113 (1), 51–60.

Petetta, A., Li Veli, D., La Mesa, M., Grati, F., Bolognini, L., 2025. Catch, release and second chances: exploring the impact of angling on two coastal fish species. Front. Mari. Sci. 12, 1638216.

Prystay, T.S., Eliason, E.J., Lawrence, M.J., Dick, M., Brownscombe, J.W., Patterson, D.A., Crossin, G.T., Hinch, S.G., Cooke, S.J., 2017. The influence of water temperature on sockeye salmon heart rate following simulated fisheries interactions. Conserv. Physiol. 5 (1) cox050.

Qualich, J.M., Louison, M.J., 2025. Effects of temperature, air exposure time, and bleeding on post-release movement of angled channel catfish. Fish. Manag. Ecol. 32 (5), 320–329.

Schreck, C.B., 1990. Physiological, behavioural, and performance indicators of stress. Page Status and use of bioindicators for evaluating effects of chronic stress of fish. Bethesda, Maryland.

Shaw, S.L., Sass, G.G., Eslinger, L.D., 2019. Effects of angler harvest on adult Muskellunge growth and survival in Escanaba Lake, Wisconsin, 1956-2016. N. Am. J. Fish. Manag. 39 (1), 124–134.

Shepard, E.L.C., Wilson, R.P., Halsey, L.G., Quintana, F., Gómez Laich, A., Gleiss, A.C., Liebsch, N., Myers, A.E., Norman, B., 2008. Derivation of body motion via appropriate smoothing of acceleration data. Aquat. Biol. 4, 235–241.

Simsons, T., 2012. Muskellunge Management Update. Wisconsin Department of Natural Resources. Publication FH-508–2012.

Posit team, 2025. RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, Massachusetts.

Wickham, H., 2016. Ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

Suski, C.D., Killen, S.S., Cooke, S.J., Kieffer, J.D., Philipp, D.P., Tufts, B.L., 2004. Physiological Significance of the Weigh-In during Live-Release Angling Tournaments for Largemouth Bass. Trans. Am. Fish. Soc. 133 (6), 1291–1303.

Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Nikolai, L., Graham, M.R., Butler, P.J., 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J. Anim. Ecol. 75, 1081–1090.

Wright, S., Metcalfe, J.D., Hetherington, S., Wilson, R., 2014. Estimating activity-specific energy expenditures in a teleost fish, using accelerometer loggers. Mar. Ecol. Prog. Ser. 496, 19–32.