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Short-term behavioural impacts of air-exposure in three species of recreationally angled freshwater fish

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ABSTRACT

Fish captured and released by recreational anglers are often exposed to air to enable hook removal and for admiration (e.g., photography). It is necessary to identify thresholds for air exposure that minimize sublethal alterations to inform best practice guidelines yet doing so in ecological-relevant field settings is challenging. We developed a novel attachment method for tri-axial accelerometer and depth biologgers to quantify short-term post-release behaviour in recreationally angled northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*) following a range of air exposure treatments (i.e., 0, 15, 30, 60, and 180 s). The biologgers were attached to the fish using a quick-release Velcro® harnesses that facilitated easy retrieval of the device from free-swimming fish without the need to recapture the individual. For this study, biologgers were retrieved after a 10 min observational period. Overall dynamic body acceleration (ODBA) was calculated from accelerometric data to estimate post-release swimming activity. Clustering of ODBA via k-means was used to classify distinct movement patterns: resting, steady-state swimming, and high intensity swimming occurrences. In northern pike, ODBA in the first minute after release was significantly higher in the 0 s air exposure treatment compared to the 15 s, 30 s, 60 s, and 180 s treatments, however the same patterns were not observed for smallmouth bass or walleye. We did not observe differences in the time spent resting, time spent steady-state swimming, or the number of high intensity swimming occurrences among air exposure treatments across all study species. This proof-of-concept study demonstrated the utility of this non-invasive bio-logger approach for the short-term study of catch-and-release and also revealed that for the species and context (e.g., water temperatures of 17–25 °C) studied here, air exposure had relatively little negative short-term impact on behaviour or reflex impairment. Nonetheless, we encourage air exposure to be minimized as longer fight times or higher water temperatures may interact with air exposure to increase behaviour impairments and negatively impact survival.

1. Introduction

Catch and release angling (C&R) is practiced worldwide and is an important tool for the conservation of fish stocks whether to comply with regulations or because of angler conservation ethic (Cooke and Schramm, 2007). Given that the number of fish released annually by anglers is in the billions (Cooke and Cowx, 2004) there is great interest in ensuring that released fish survive and recover from injuries and stress experienced during the process. Indeed, cryptic mortality arising from C&R can complicate management (Coggins et al., 2007) and undermines the value of C&R as a management tool (Wydoski, 1977; Cooke and Schramm, 2007). Even when fish survive, injuries and stress have the potential to reduce fitness (Arlinghaus et al., 2009) and diminish the welfare status of angled fish (Cooke and Sneddon, 2007). As such, there have been great efforts to identify the factors that influence mortality, injury and stress in order to inform best fishing practices (see Brownscombe et al., 2017).

One of the factors that is regarded as important in influencing outcomes for angled fish is the duration of air exposure (Cook et al., 2015). Although results vary among species and contexts, it is reasonable to conclude that air exposure is not of benefit to fish and that beyond a threshold it can lead to mortality (Cook et al., 2015). What is unclear is

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how air exposure thresholds translate to post-release behaviour impairments in the field. Such information would be useful for overcoming some of the criticisms of existing research that has been largely restricted to laboratory environments (e.g., Ferguson & Tufts 2001; Cooke et al., 2001; White et al., 2008).

Behaviour can serve as an important biomarker for physiological changes associated with stress (Schreck et al., 1997), as fish alter their behaviour to avoid or tolerate stressors that could potentially negatively impact fitness. Such behaviours can include predator avoidance and temperature selection (Beitinger, 1990). Assays of these behaviours, among others, serve as qualitative indicators of stress and can help to form hypotheses regarding survival, growth, and reproduction (Beitinger, 1990). Extreme deviations from normal behaviour can indicate an increased likelihood of mortality. In fish, stress associated mortality can be predicted by evaluating reflex action mortality predictors (RAMP) such as righting response, body flex upon restraint, and vestibular-ocular response (Davis, 2010). The exact physiological basis for fish reflex impairment associated with air exposure is unclear (Davis, 2010) but presumably reflects neuro-motor control alterations that arise from severe exhaustion and fish experiencing extreme anaerobiosis (Cooke et al., 2014). For instance, in bonefish (*Albula vulpes*), air exposure was strongly associated with the loss of equilibrium, and fish that were released without equilibrium were six times more likely to experience post-release predation in the short term. (Danylchuk et al., 2007). Air exposed fish have also been observed to take longer to leave the release site (Thompson et al., 2008) and generally exhibit greater deviations from normal behaviour (Davis, 2005). Stress can also alter reproductive behaviour, potentially resulting in individual fitness consequences and population health if a high proportion of individuals are affected (Cooke et al., 2002). In nest-guarding black bass (*Micropterus* spp.), air exposure has been associated decreased parental care (Suski et al., 2003) and increased nest abandonment (Cooke et al., 2000). In Atlantic Salmon (*Salmo salar*) air exposure associated with catch-and-release angling has been shown to impact upstream migration by increasing downstream resting periods and altering movement patterns (Mäkinen et al., 2000; Thorstad et al., 2007; Lennox et al., 2015; Havn et al., 2015). As such, behaviour has the potential to be used to understand the consequences of C&R (Donaldson et al., 2008) and to identify thresholds for different aspects of a C&R event such as air exposure duration.

Tri-axial accelerometer biologgers have been widely used in a variety of taxa including fish to remotely observe animals in their natural environment (Brownscombe et al., 2014; Cooke et al., 2016). They record acceleration in three axes (pitch, roll, yaw) and can be equipped with temperature and depth sensors. Studying free-ranging animals removes potential stressors associated with captivity and thus can give a more accurate depiction of natural behaviour (Rutz and Hays, 2009). Recently, advances in data processing have allowed for the classification of specific behaviours from tri-axial acceleration data. In the aquatic realm, fine-scale behaviours such as foraging, air breathing, and high intensity swimming have been classified in a number of aquatic species (Føre et al., 2011; Brownscombe et al., 2014; Lennox et al., 2018). When compared to visual observations, the analysis of acceleration data has been shown to be able to predict such behaviours in fish with a high degree of accuracy (Brownscombe et al., 2014).

The objective of our study was to determine if short-term post-release behaviours serve as a sensitive sub-lethal indicator of the impacts of different fisheries handling treatments. To do so, we assessed the short-term post-release behaviour in angled freshwater gamefish exposed to various durations of air exposure. We did not quantitively conduct inter-specific comparisons as fish were captured from different lakes in a variety of environmental conditions, potentially influencing behaviour. Included in our study were northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*). Northern pike is a recreationally important freshwater gamefish found throughout the Northern Hemisphere in North America and Europe. In North America, the incidence of C&R practices for northern pike is relatively high with the majority of fish being released (Pierce et al., 1995). Previous studies on northern pike suggest that C&R events induce some level of physiological and behavioural impairment, however such impairments are short-term and reversible (Arlinghaus et al., 2009; Klefoth et al., 2008). Smallmouth bass is also an important freshwater gamefish and is one of the two black bass species (*Micropterus spp.*) that are highly prized by anglers (Quinn and Paukert, 2009). There is a strong conservation ethic among bass anglers such that release rates are quite high even when harvest regulations are in effect. Walleye are managed through mandatory/voluntary C&R programs however regulations tend to include smaller bag limits and the extensive use of size regulations given their popularity as a food item (Goeman, 2002). By focusing on these species, the outcome of our study aims to contribute to the improvement of fish handling practices which benefit the welfare and survival of fish that are released. Moreover, this study will also allow us to assess a novel approach for studying sub-lethal behavioural impairments of free-swimming fish in the wild.

2. Material and methods

2.1. Study sites

Northern pike were angled on Opinicon Lake, located in South Frontenac, Ontario (44.558784 −76.328816) between June 3rd and June 7th, 2019. Sample sizes for each air exposure treatment were n = 11 for the 0 s treatment, n = 10 for the 15 s treatment, n = 9 for the 30 s treatment, n = 8 for the 60 s treatment, and n = 10 for the 180 s treatment. The lake is relatively shallow (average depth 2.5 m), and moderately developed (CRCA, 2017).

Smallmouth bass were angled on Big Rideau Lake in Lanark County, Ontario (44.729426 −76.239921) between July 10th and July 24th, 2019. Sample sizes for each air exposure treatment were n = 10 for the 0 s treatment, n = 9 for the 15 s treatment, n = 6 for the 30 s treatment, n = 10 for the 60 s treatment, and n = 9 for the 180 s treatment. The lake is deep (max depth 109 m) and is arguably one of the most developed lakes in the Rideau system and as a result experiences heavy multi-species angling pressure.

Walleye were angled on Mississippi Lake, located in Carleton Place, Ontario (45.030765 −76.202722) between August 7th and August 27th, 2019. Sample sizes for each air exposure treatment were n = 7 for the 0 s treatment, n = 6 for the 15 s treatment, n = 6 for the 30 s treatment, n = 5 for the 60 s treatment, and n = 5 for the 180 s treatment. Mississippi Lake is a natural lake situated between two stretches of the Mississippi River and is relatively shallow (max depth 9 m) and relatively developed (MVCA, 2014). The lake is a productive recreational fishery for black bass, walleye, and northern pike and experiences significant fishing pressure both in the summer and winter as a consequence of its proximity to metropolitan areas.

2.2. Fish capture

All three fish species were captured using spinning or baitcasting rods spooled with 13.6 kg break-strength braided line and equipped with artificial lures (crank baits, soft plastics), 1.7–3.5 g jigs tipped with live bait (leeches, worms, small baitfish), or by trolling 14 g bottom bouncers rigged with crawler harnesses. For each species, we attempted to conduct angling in relatively similar habitat and depths within the lake, however this was not always possible due to environmental factors and catch rates. Generally, northern pike were angled along deep channels (3 – 4.5 m) with defined weed edges, smallmouth bass were angled along rocky points and drop-offs (4.5 – 6 m), and walleye were angled off underwater humps and large flats (5 – 7 m). Northern pike and smallmouth bass were primarily caught by casting-retrieving, while walleye were primarily caught trolling. Both treble and single hooks were used, and all hooks were barbed. Fish were fought for no longer than 30 sec from initial hookset to landing, and all fish were landed in a rubber net to minimize mucus loss (Barthel et al., 2003; Lizeé et al., 2018). Fish were quickly transferred to a cooler filled with fresh lake water, and the water was changed between fish to ensure adequate oxygen levels. Once in the cooler, the hook was removed with pliers, while the fish remained submerged. Dehooking took no longer than 1 min and fish that were deeply hooked or exceeded the 1 min dehooking threshold were excluded from the study. Total length (mm), surface water temperature (Cº), water depth at the release site (m), and presence/absence of major reflex action mortality predictors were assessed prior to the air exposure treatment. Reflex action mortality predictors (RAMP) are behaviours that can indicate increased risk of mortality in fish which include equilibrium, startle response, mouth clamping, fin erection, body flex upon restraint, and vestibular ocular response (Davis et al., 2010). For the purposes of this study, we assessed three such behaviours (equilibrium, startle response, operculum/eye activity) as they were able to be evaluated without requiring restraint of the fish (i.e., body flex, mouth clamping, gag response). To evaluate post-release behaviour, we attached biologgers around the mid-body of the fish (Description: 7.5 g in air, ~ 3.5 g in water, 12 ×31×11 mm, Technosmart Axy-Depth, Rome, Italy; Sampling rate: tri-axial acceleration = 25 Hz, temperature/depth = 1 Hz; Resolution: tri-axial acceleration = 8 bit, temperature = 0.1 ° C, depth = 5 cm, G scale = 8) using a custom made harness which consisted of the logger epoxied to a plexiglass plate and threaded through a length of Velcro® tape (3 M Scotch Fasteners, Saint Paul, USA, length = 20 – 25 cm, width = 1.5 cm) (Fig. 1). Harnesses of various lengths were used to accommodate fish of different girths. Attachment of the harness took no longer than 30 s. While fish were submerged in the water filled cooler, a biologger harness was affixed by wrapping the length of Velcro® around the mid-body and positioning the accelerometer centred on the ventral side between the pelvic fins (Fig. 2). Care was taken to ensure that the Velcro straps were not hindering the normal range of motion for both the pelvic and pectoral fins in order to reduce the impact of the package on the swimming performance of the fish. In smallmouth bass and walleye, attaching the package required the compression of the dorsal spines against the body. Through analysis of underwater videos and snorkel surveys, we noticed little to no dorsal spine flexion in both smallmouth bass and walleye during normal swimming behaviour, suggesting limited use for propulsion or directional movement. The biologger harness was then connected to a fishing rod and reel spooled with 27 kg braided spectra line by clipping a small snap swivel through a reinforced hole in one end of the Velcro® strap. The air exposure treatment was then conducted, and the fish was again assessed for equilibrium, startle response, and opercular/eye activity at the moment of release. Fish were released by hand at the side of the boat and the bail on the reel was opened, allowing the fish to swim freely without drag. The observation period lasted 10 min and movement of the boat was minimized. In areas with abundant underwater structure (i.e., submerged trees, large marcophyte stands), care was taken to release fish in open water areas that were within the near (~ 50 m radius) vicinity of the capture site in order to limit entanglement of the line. At the end of the observation period, the package was retrieved by tugging the line which subsequently detached the Velcro® and allowed the harness to be reeled in. Before reeling the package in, the presence of the fish on the end of the line was confirmed by feeling for motion and weight before tugging the line.

Fig. 1. A Velcro® harness (black) containing the accelerometer biologger (white). The biologgers were secured to a small plexiglass plate using marine epoxy and the Velcro® was threaded through small slits on each end of the plate.

Fig. 2. Placement of a Velcro® harness on a smallmouth bass (left) and walleye (right). The biologger (in white) was positioned on the underside of the fish, with the small plexiglass plate pressed against the belly between the two pelvic fins.

2.3. Air exposure treatment

After attaching the accelerometer package, air exposure was conducted by lifting the fish by hand out of the water filled cooler, placing it in a dry measuring trough, and holding it firmly to reduce the likelihood of accidentally removing the accelerometer package. Air exposure was divided into five treatments, 0 s, 15 s, 30 s, 60 s, and 180 s. Our minimum air exposure treatment of 0 s constitutes a best-case scenario and can be easily accomplished by having a water filled container ready before landing or removing the hook without removing the fish from the water (e.g., by leaning over the side of the boat or kneeling down on shore). These intervals were determined using a combination of personal observation of online angling videos and time-to-dehook data collected from Trahan et al. (In progress). While we are aware of efforts to surreptitiously observe anglers to generate real measure of air exposure duration (Chiaromonte et al., 2018), our evidence suggests that a maximum air exposure treatment of 180 s represents a worst-case scenario and could occur with inexperienced anglers or when fish are deeply hooked by multiple treble hooks, while 0 s of air exposure is aligned with emerging social norms in the recreational angling community, as well as fundamental knowledge of fish respiration.

2.4. Data processing

Data processing and analysis was conducted using R version 4.0.5 (R core team, 2021) We converted accelerometer logger data to units of *g* (9.8 m s $^{-1}$) by dividing pitch (x axis), roll (y axis), and yaw (z axis) by 2048, the standard conversion factor for the biologger (Brownscombe et al., 2013; Lennox et al., 2018). Static acceleration was calculated by passing a 2 s box smoother over each axis using the rollmean function in the R package zoo (Zeileis and Grothendeick, 2005) and converted to degrees by multiplying values by 180/π. Pitch (x axis) and roll (y axis) were calculated from these values (Brownscombe et al., 2013; Lennox et al., 2018). Dynamic acceleration was calculated by subtracting static acceleration from raw acceleration values for each axis. Overall dynamic body action (ODBA) was calculated as the absolute sum of the dynamic acceleration of each axis. We summarized acceleration data by each second as the resolution of raw data initially gathered by the tag (25/s) was too high for realistic estimates of behaviour. Data was then trimmed to include only the first 10 min of each trial to remove the period of time of which the accelerometer was retrieved. K-means clustering with $k = 3$ was used to cluster ODBA values into three distinct behaviours: resting, steady-state swimming, and high intensity swimming. Rest was defined as the cluster with the lowest ODBA values, steady-state swimming was the intermediate cluster, and high intensity swimming was the highest cluster (Chhor 2022a; Chhor 2022b). Number of high intensity swimming occurrences was determined by producing a scatterplot of ODBA vs. time in seconds with clusters as a coloured variable. High intensity swimming occurrences were defined as clusters of the highest ODBA values which contained at least three data points. The *length* function was also used to determine the duration of time the fish spent at the surface, when depth values were less than 10 cm. Mean depth was calculated as the mean of 600 (1/second) absolute depth values collected by the biologger during the 10 min trial.

2.5. Statistical analysis

Linear models were used to analyze ODBA, time spent resting (s), time spent steady-state swimming (s), mean depth (m), or time spent at the surface (s), with air exposure as the predictor variable. We chose to exclude fish total length as a predictor as it did not vary significantly among air exposure treatments (ANOVA, pike: mean = 524 mm, +/- 7 mm, p = 0.844, smallmouth: mean = 327 mm +/- 9 mm, p = 0.912, walleye: mean = 388 mm +/−13 mm, p = 0.948). We ensured assumptions were met by analyzing plots of standardized residuals vs. theoretical quartiles (Q-Q), residuals vs. fitted values, square root of standardized residuals vs. fitted values (scale-location) and examined outliers by calculating Cook's distance.

To analyze the number of high intensity swimming occurrences and RAMP scores, we developed Poisson-distributed generalized linear models (GLM's) with air exposure treatment as the predictor. All pairwise comparisons were conducted using the false discovery rate (FDR) (Benjamini and Hochberg, 1995). Linear models were also used to fit ODBA in the 1st minute, 5th minute, and 10th minute after release with air exposure as the predictor.

3. Results

3.1. Angling statistics and field observations

A total of 144 fish were angled, consisting of 59 northern pike, 55 smallmouth bass, and 30 walleye. Surface water temperature fluctuated between 16 °C – 18 °C during northern pike angling, 24 °C – 26 °C during smallmouth bass angling, and 22 °C – 24 °C during walleye angling. After accounting for tag malfunctions and harnesses that slipped off before the trial could finish, data for 48 northern pike, 44 for smallmouth bass, and 29 for walleye were used for the analysis (successful deployment rate of 86%, 80%, and 97%, respectively). Compared to northern pike and walleye, the wider girth and more uneven body shape of smallmouth bass was likely the cause of most premature detachments. Upon release, we observed two general behaviours; some fish immediately burst away from the boat and continued swimming, while others slowly descended to the bottom and remained motionless for the rest of the trial. One mortality was observed; a walleye in the 15 s treatment that was unable to regain equilibrium immediately after release. We also noted qualitative differences in behaviour among species, with smallmouth generally being the most active of the three species, and northern pike being the least active. Across species, most individuals spent the majority of their time at rest. The majority of northern pike immediately descended to the bottom and remained motionless for the rest of the trial. Nonetheless, quantitative comparisons among species are not informative due to significant variation between study sites, stress responses in species, and angling contexts, therefore no formal interspecific analyses were conducted.

3.2. Post-release activity and behaviour

For northern pike, mean ODBA for the entirety of the trial was significantly influenced by air exposure (ANOVA, df = 4, F = 2.955, p = 0.028) and was highest in the 0 s treatment however the pairwise differences were not statistically significant (Fig. 3). In the first minute after release, ODBA was influenced by air exposure (ANOVA, df = 4, F = 7.511, p < 0.01) and was significantly higher in the 0 s treatment compared to the 30 s, 60 s treatment, and 180 s treatments (FDR, p < 0.01) (Fig. 4). ODBA in the first minute was also significantly higher in the 15 s treatment compared to the 30 s and 60 s treatments (FDR, p = 0.03). Mean depth varied significantly among treatments (ANOVA, df = 4, F = 10.232, p < 0.01) and was significantly higher (deeper) in the 30 s treatment compared to the 0 s, 15 s, and 180 s treatments (Fig. 5). Mean depth was also significantly higher (deeper) in the 60 s treatment compared to the 0 s, 15 s, and 180 s treatments. Air exposure marginally influenced time spent on the surface (ANOVA, df = 4, F = 2.449, p = 0.059), but did not influence time spent resting (ANOVA, df = 4, F = 1.697, p = 0.166), time spent steady-state swimming (ANOVA, df = 4, F = 1.867, p = 0.133), or the number of high intensity swimming occurrences (ANOVA, df = 4, LR = 0.6332, p = 0.96). Total RAMP (sum of scores for equilibrium, startle response, operculum/eye activity) was also not influenced by air exposure (ANOVA, df = 4, LR = 0.089, p = 0.99).

For smallmouth bass, mean ODBA for the entirety of the trial was not influenced by air exposure (ANOVA, df = 4, F = 1.037, p = 0.399) (Fig. 3). ODBA 1 min, 5 min, and 10 min post-release was also not significantly influenced by air exposure (Fig. 4). Mean depth varied significantly among treatments (ANOVA, df = 4, F = 11.866, p < 0.01) and was significantly higher (deeper) in the 60 s treatment compared to all other treatments (FDR, p < 0.01) (Fig. 5). Mean depth was also significantly lower (shallower) in the 0 s treatment compared to the 15 s and 30 s treatments. Time spent at the surface varied slightly among air exposure treatments (ANOVA, df = 4, F = 2.112, p = 0.095), but did not influence time spent resting (ANOVA, df = 4, F = 1.538, p = 0.207), time spent steady-state swimming (ANOVA, df = 4, F = 1.591, p = 0.194, the number of high intensity swimming occurrences (ANOVA, df = 4, LR = 4.137, p = 0.388)), or total RAMP (ANOVA, df = 4, LR = 2.841, p = 0.585).

For walleye, mean ODBA for the entirety of the trial was not influenced by air exposure (ANOVA, df = 4, F = 1.132, p = 0.364,) (Fig. 3). ODBA in the first minute post-release was marginally influenced by air exposure (ANOVA, df = 4, F = 2.297, p = 0.087), however no significant differences were revealed in pairwise comparisons (Fig. 4). Mean depth varied significantly among treatments (ANOVA, df = 4, F = 12.138, p < 0.01) and was significantly higher (deeper) in the 30 s treatment compared to the 0 s and 15 s treatments (FDR, p < 0.01) (Fig. 5). Mean depth was also significantly lower (shallower) in the 15 s treatment compared to all other treatments (FDR, p < 0.01). Air exposure did not influence time spent on the surface (ANOVA, df = 4, F = 0.773, p = 0.555), time spent resting (ANOVA, df = 4, F = 0.775, p = 0.553,), time spent steady-state swimming (ANOVA, F = 0.449, p = 0.772), number of high intensity swimming occurrences (ANOVA, LR = 4.530, p = 0.339), or total RAMP (ANOVA, LR = 1.374, p = 0.849).

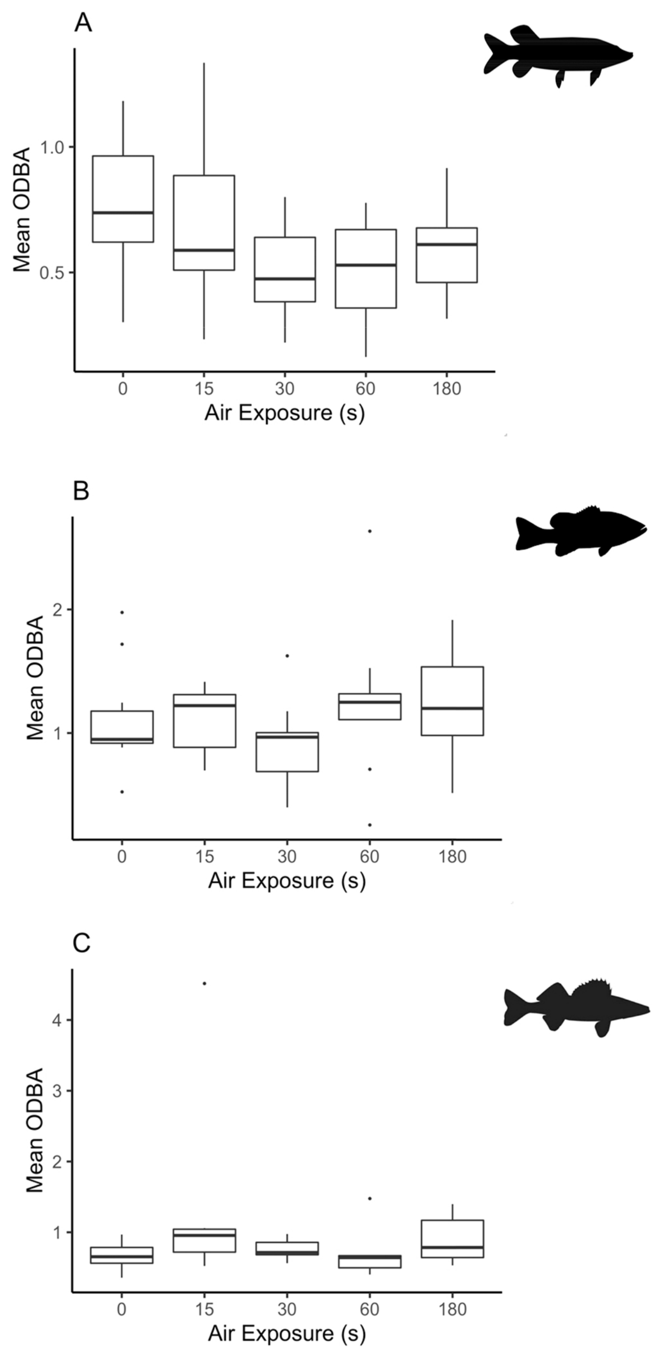

Fig. 3. Mean Overall Dynamic Body Acceleration (ODBA) over 10 trials for 0 s, 15 s, 30 s, 60 s, and 180 s of air exposure in northern pike (A), smallmouth bass (B), and walleye (C).

4. Discussion

4.1. Swimming activity

Our study found minimal impacts of angling stressors on the short-term swimming activity of northern pike, smallmouth bass, and walleye. In northern pike, ODBA values varied significantly among air exposure treatments however no significant differences were observed between treatments, and no linear relationships between ODBA and air exposure duration were observed. In smallmouth bass and walleye, we observed similar 10 min ODBA values among air exposure treatments. In northern pike, differences in swimming activity being only apparent in the first minute after release, with ODBA values in fish that were not air exposed were 2–3x greater than values in fish that received 15 s, 30 s, or 180 s of air exposure. Similar swimming activity for the rest of the trial and the lack of differences in reflex action mortality predictors (RAMP) among treatments suggest that cognitive impairment, rather than locomotor impairment (i.e., impaired swimming activity), caused the reductions in swimming activity observed in the first minute after release. Previous experiments have suggested that fish may be disoriented or "dazed" immediately following an angling event and exhibit cognitive impairment. For example, spanish flag snapper (*Lutjanus carponotatus*) took significantly longer to inspect and enter a refuge when they had been angled and exposed to air (Cooke et al., 2014). Raby et al. (2018) also found a similar effect, with exhausted and air exposed fish spending more time in a vulnerable position while apparently having full locomotory capacity. Cognitive impairment, especially immediately after release, could conceivably increase predation risk if fish are unable to seek adequate refuge. It is important to note that our experiment was conducted at relatively cool ambient water temperatures (16–18 °C for northern pike, 22–24 °C for smallmouth bass and walleye). This could explain the lack of behavioural impairments observed in our study species. Elevated water temperatures can compound angling stressors and lead to increased behavioural impairments or mortality (Gingerich et al., 2007; Boyd et al., 2010; Wilde et al., 2000). Lastly, our experiment focused on relatively short-term (10 min) behaviour, which may have limited our ability to distinguish behavioural impacts that occur over broader time scales. For example, Algera et al. (2017) observed decreased swimming behaviour in experimentally stressed smallmouth bass (using cortisol injections), however these differences only became apparent after ~ 30 min and differences in swimming activity were present for the entirety of the 64-h observational period. Increasing the observational period or changing the data gathering resolution of the biologgers may help future studies discern potential differences in behaviour over longer time scales that mirror longer term physiological disturbances and recovery dynamics.

For all three species, depth usage varied significantly among treatments. After 60 s of air exposure, northern pike and smallmouth bass tended to spend more time deeper in the water column compared to those that were not air exposed. Additionally, fish that were not air exposed had similar depth usage compared to fish in the 180 s treatment. However, these differences were at most 0.5 m for northern pike and 1 m for smallmouth bass. In walleye, fish air exposed for 15 s tended to spend more time ~ 2 m shallower than fish that received 30, 60, and 180 s of air exposure, while fish that were not air exposed had similar depth usage (within 1 m). The lack of a linear relationship between air exposure duration and depth usage suggests that other factors, such as variability in aquatic habitat, may be the primary drivers. Habitat metrics such as substrate type, macrophyte height, and proximity to cover may have led some fish to swim deeper to reach adequate refuge. Variation in depth usage could also be due to differences in temperature and dissolved oxygen throughout the water column. Some migratory fish have been observed to seek cool, deep water to facilitate recovery following thermal stress (Keefer et al., 2019; Mathes et al.; 2010), however further research is needed to determine if fish exhibit similar behaviour following angling events. While we attempted to standardize the depth of release sites, there is a potential that variation in total depth at the site of release may have influenced our results.

No significant differences were observed for time spent resting, time spent steady-state swimming, or the number of high intensity swimming occurrences. Anecdotally, smallmouth bass were observed to swim greater distances and pull more line compared to walleye and northern pike, however these could be due to intraspecific variation in physiology and behaviour as well as environmental factors such as water temperature, aquatic habitat, and other lake effects. As we used a relatively short 10 min observational period, we may have overlooked broader behavioural impacts that occur over longer periods of time, as previous studies have noted significant behavioural impairment in northern pike

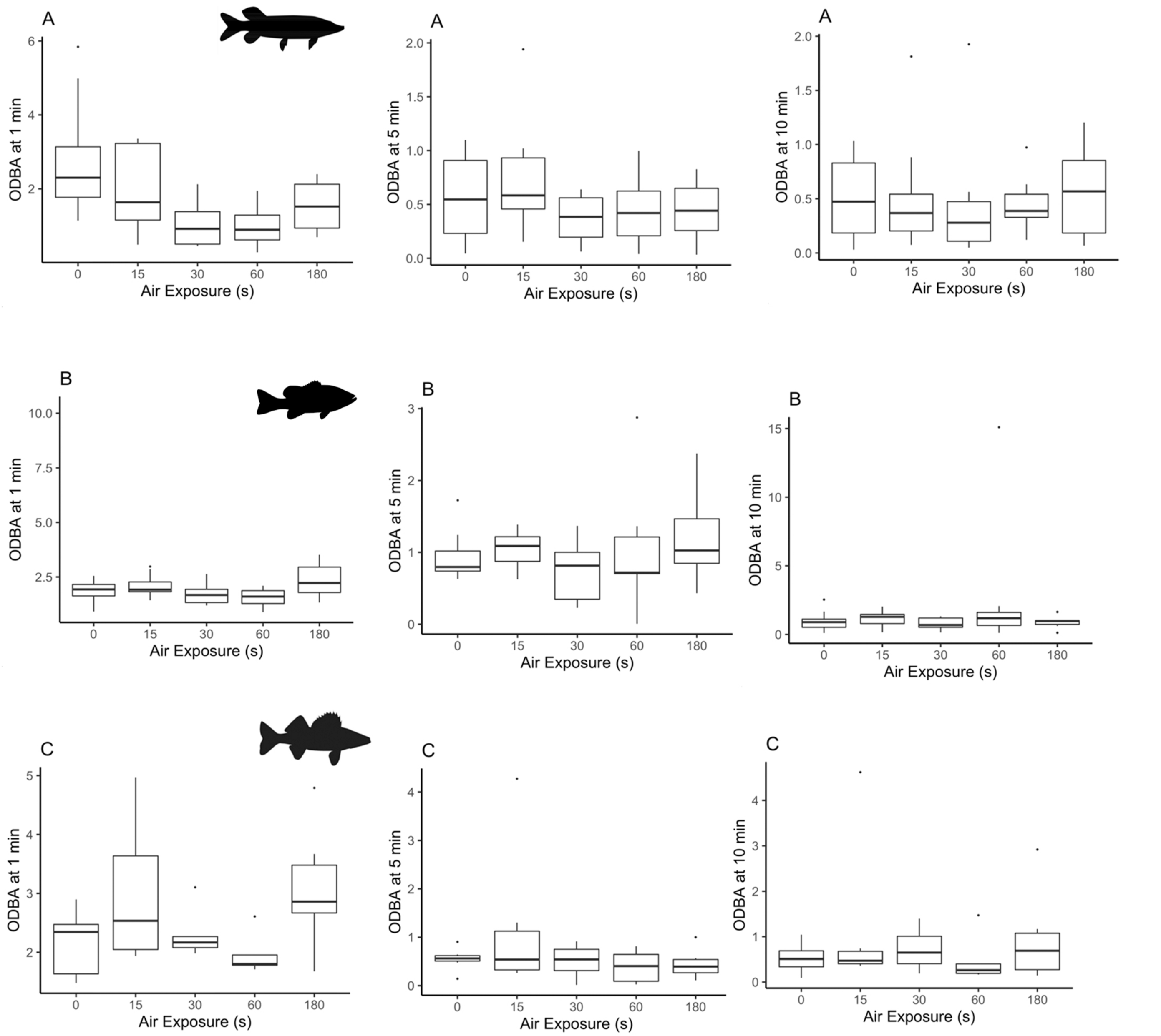

Fig. 4. ODBA 1 min, 5 min, and 10 min after release for 0 s, 15 s, 30 s, 60 s, and 180 s of air exposure in northern pike (A), smallmouth bass (B), and walleye (C).

over the course of one hour (Arlinghaus et al., 2009), however impairments were only observed when air exposure duration reached 300 s (5 min). Besides angling stressors, differences in post-release behaviour can also be attributed to environmental factors. In bonefish (*Albula vulpes*), Cooke and Philipp (2004) observed greater periods of rest in fish released in a high predation environment compared to a low predation environment, however these differences were noted over a 1-hour monitoring period. Our data also suggest that air exposure may have increased the time spent at the surface in northern pike and smallmouth bass. Based on visual observations, we believe that this difference was mainly driven by equilibrium impairment (i.e., impaired righting response) immediately following release. In northern pike, median time spent at the surface was greatest in the 0 s treatment compared to other air exposure treatments, however the difference between the 0 s treatment and the 180 s treatment was less than 1 s. Equilibrium impaired northern pike were observed to recover and swim away within 5–10 s, indicating relatively short recovery periods for equilibrium impaired fish. In comparison, time spent at the surface was highest in the 180 s treatment for smallmouth bass, with fish taking on average 20–30 s to swim away. In both species, there was wide variation in the recovery period, with some individuals swimming away immediately and others taking 30–40 s. Previous studies have highlighted the effects of air exposure on equilibrium status of released fish, most suggesting that increased air exposure increases the probability of equilibrium loss (Thompson et al., 2008; Cooke and Philipp, 2004; White et al., 2008). Air exposure can also have interactive effects with other stressors such as exhaustive exercise (Ferguson and Tufts, 1992) and water temperature (Gingerich et al., 2007) which may further exacerbate equilibrium impairment. Equilibrium status can be an important predictor of later mortality, as Danylchuk et al. (2007) observed increased predation of equilibrium impaired bonefish by sharks compared to fish who swam away strongly. In the context of our study species, predators such as large birds of prey, otters, or other large fish pose similar threats to impaired fish, however there is little evidence supporting actual predation rates in freshwater environments.

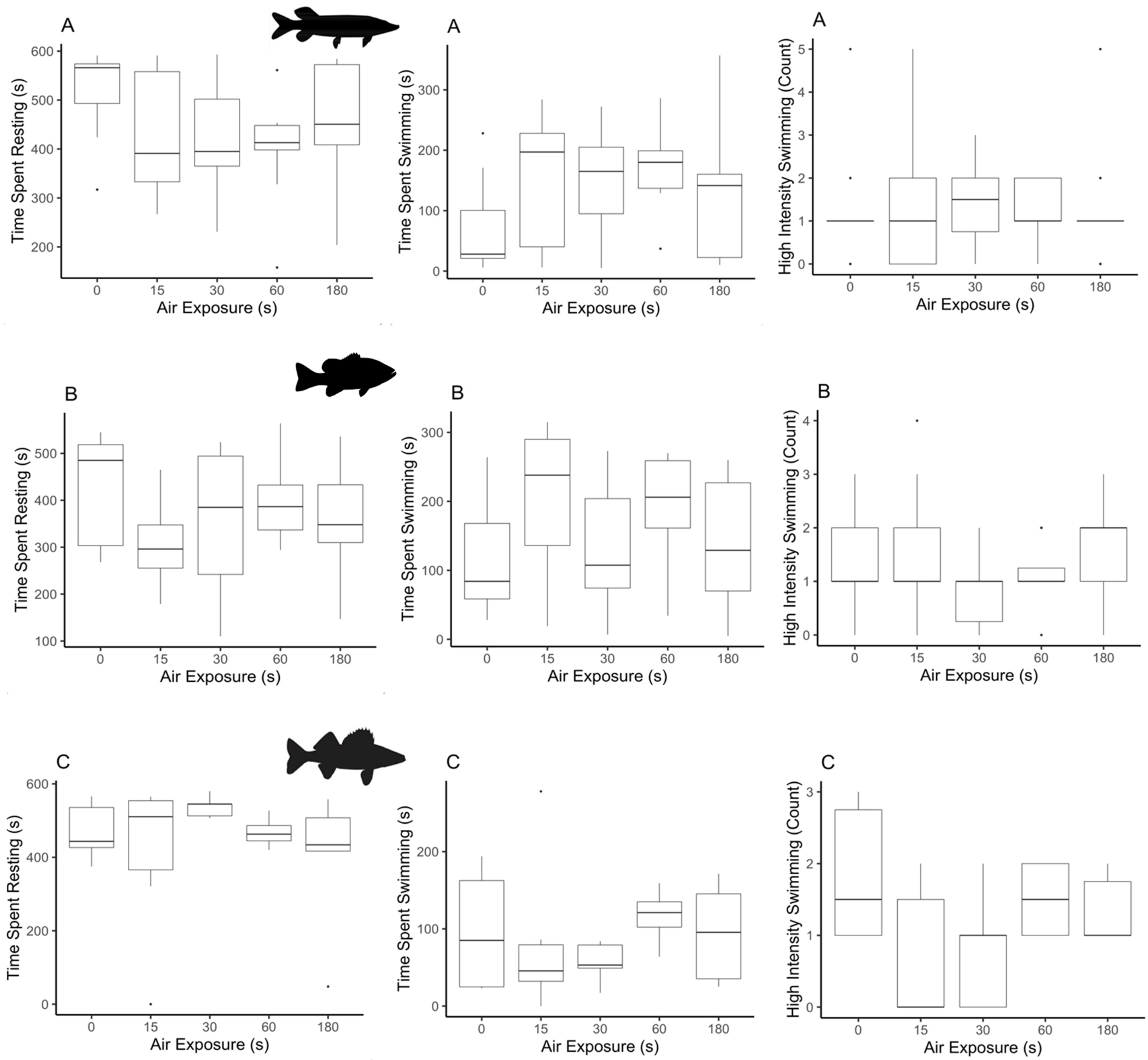

Fig. 5. Time spent resting (s), time spent steady-state swimming (s), and number of high intensity swimming occurrences after 0, 15, 30, and 180 s of air exposure in northern pike (A), smallmouth bass (B), and walleye (C).

4.2. Non-invasive biologging

In conservation research there is an inherent struggle to obtain data on study organisms yet do so without causing undue harm to animals being studied (Putman, 1995; McMahon et al., 2012). This is especially true for field-based tracking studies, where attachment of biologgers can have a variety of negative effects on study animals. In aquatic species, externally attached biologgers can increase hydrodynamic drag or impede swimming mechanics, leading to increased energetic costs (Rosen et al., 2017; Jepsen et al., 2015). Additionally, devices that require insertion into musculature can create open wounds susceptible to infection (Jepsen et al., 2015). In the case of imperiled species, minimizing the negative impacts of conservation research is especially important (McMahon et al., 2012). In most cases, biologging tags that are physically attached to study species need to be retrieved after the observational period to download the data. Retrieval can result in additional stress/injury to study species as animals may need to be recaptured for removal of the bio-logger. In marine environments, one solution is the use of pop-up satellite archival transmitters (PSATs) which automatically detach from the animal and float to the surface for retrieval. However, development of freshwater PSATs has not yet occurred as current “pop-up” mechanisms rely on saline environments to corrode links (Cooke et al., 2013) and current PSAT devices are too large for most freshwater fish species. Devices that record fine-scale activity, such as accelerometers, almost always require retrieval for the collection of data given the vast quantities of data that are generated. Using Velcro® tape for our attachment method proved to be a simple, minimally invasive method for the attachment of biologgers on wild fish in their natural environments. We based the quick-release design on a similar method detailed in Lennox et al. (2018) where biologgers were attached to Arapaima using elastic bands. The nature of our design allowed us to reduce handling time during attachment of the accelerometer to < 30 sonds with the animal submerged in a water filled trough and completely eliminated the need for recapture of the animal for retrieval of data. It should be noted that while minimally invasive, our attachment method still involved additional handling time compared to typical C&R scenarios. The process of attaching the biologger took anywhere between 15 s and 60 s and involved physically handling the fish while it struggled, albeit always while in the water. Regardless of air exposure, fight duration, and other angling treatments, handling time has been found to be a significant predictor of post-release behaviour and survival (Teffer, 2018; Chapman et al., 2020). Our attachment method also likely increased hydrodynamic drag on the fish, and the combination of increased handling and other tagging effects may have prevented this study from observing truly natural swimming activity. Finally, the Velcro® harnesses used in this study may not be as effective in environments that are abundant in underwater structure or with high flows which could cause entanglement of the line. More research is needed to develop minimally invasive biologger attachment methods that are more applicable to complex and dynamic environments. Nonetheless, the usage of Velcro® to externally attach a biologger to fish likely resulted in lessened stress and injury experienced by the fish compared to other methods of attachment that involve surgery. Developing ways to measure swimming distance would also provide an additional metric related to post-release behaviour. Overall, attachment and monitoring methods that minimize stress and injury will allow researchers to observe the most natural behaviour possible while simultaneously maximizing the welfare of study individuals. Nonetheless, we acknowledge that there are other emerging approaches for studying the post-release behaviour of fish (e.g., use of underwater drones; Raoult et al., 2019).

5. Conclusion

Tri-axial accelerometer and depth biologgers were an effective means for monitoring post-release behaviour in free-swimming fish and the use of Velcro® proved to be a simple and effective method for monitoring fine-scale post-release behaviour in freshwater gamefish. Our novel accelerometer attachment method allowed us to quantify fine-scale post-release behaviour in free swimming fish while eliminating the need to recapture study species. This allowed us to minimize stress and possibly reduce experiment-related mortality. As we begin to understand the negative impacts of biologger attachment on study animals, methods that are minimally invasive and eliminate the need for recapture will help to reduce research related stressors and allow researchers to better understand the behaviour of wild, free-swimming fish.

Our results suggest that air exposure had minimal effects on the post-release behaviour of northern pike, smallmouth bass, and walleye. Nonetheless, we encourage air exposure to be minimized as longer fight times or higher water temperatures may interact with air exposure to increase behavioural impairments and negatively impact survival. The water temperatures (i.e., 17–25 °C) studied here are moderate and well within the thermal tolerances of these species. Moreover, fight times were short. There is a growing body of literature that has revealed that context is highly important for considering the biological consequences of catch-and-release (Cooke & Suski 2005; Raby et al., 2015).

CRediT authorship contribution statement

Auston Chhor: Conceptualization, Methodology, Formal analysis, Software, Investigation, Writing – original draft. **Daniel Glassman:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Jacob Brownscombe:** Formal analysis, Software, Writing – review & editing. **Alexandria Trahan:** Investigation, Writing – review & editing. **Andy J. Danylchuk:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Steven J. Cooke:** Conceptualization, Methodology, Writing – review & editing, Supervision.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106342.

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