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Consequences of oral lure retention on the physiology and behaviour of adult northern pike (*Esox lucius* L.)☆

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ABSTRACT

After a fish snaps an angler's line, the hook(s) still embedded in its mouth, the question arises: what will the encounter cost the fish? The consequences of retained gear on the physiology and behaviour of fish is not well understood. This study aimed to quantify the impact of prolonged exposure to a retained lure (simulated break off in recreational angling) to the physiology and behaviour of northern pike (*Esox lucius*) was studiedin a laboratory setting. A combination of blood-based physiological metrics and metabolic rate measurements were used to provide a comprehensive overview of the physiological consequences of lure retention in this species using two different treble hook sizes on metal casting spoons in three different hooking locations. Fine-scale video observations of pike following simulated break off were collected to assess pike interaction with a retained lure and to quantify activity patterns. We found that the retention of a lure did not significantly affect metabolic rate, blood physiology or locomotor activity of pike. However, gill ventilation rate was found to be elevated in pike hooked deeply in the throat suggesting that lures in obstructive locations may somewhat challenge recovery from exercise. Elevated cortisol levels in these fish compared to wild controls suggests that confinement produced prolonged stress in all treatments that may have affected the physiological and behaviour responses that we observed. Our findings provide important observations about the interpretation of stress-oriented laboratory studies using northern pike and the extrapolation of these results to the wild. Despite our negative findings in relation to lure impacts on pike physiology and behaviour, avoiding break offs would still be advisable for fish welfare reasons.

1. Introduction

'Break off' occurs when, during an angling event, fish break away from the line with gear (e.g., hooks or lures) still embedded in the mouth (Arlinghaus et al., 2008; Henry et al., 2009). Lure loss can occur for a variety of reasons including line entanglement, gear failure or angler error, or as a result of the behaviour of certain fish species. In the case of fish with sharp dentition such as northern pike (*Esox Lucius*), muskellunge (*Esox masquinongy*) or barracuda (*Sphyraena barracuda*), lines can be cut after coming in contact with the teeth of the fish. In some fisheries such as targeted bass angling, tackle selection (e.g., lightweight tackle, non-steel leaders) increases the risk of break off by northern pike, which share similar habitat to bass. The extent to which lure loss occurs for individual fish species is largely anecdotal as data are limited. Although some research has determined tackle loss by creel surveys (Radomski et al., 2006), little formal attention has been paid to the cost of break off to the fish, despite being identified as a research priority to inform our understanding of the consequences of catch-and-release fisheries (Arlinghaus et al., 2007).

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Catch-and-release (C&R) angling is associated with stressors such as exhaustion, injury, and air exposure that induce a physiological stress response in the fish (reviewed in Cooke and Suski, 2005; Cooke et al., 2013). During a stress response in teleost fish, the release of cortisol mobilizes energy resources (i.e. glucose) and promotes the ability of fish to cope with and recover from the stressor in the short term (Barton, 2002). However, if the stressor is severe or sustained, this physiological response can have a negative effect on the fish's well-being, behaviour, and ultimate survival, as metabolic energy is redirected from growth and reproduction in an effort to maintain homeostasis (Barton, 2002). Specifically, cortisol release causes secondary responses including increases in ion and water flux, metabolic rate, gluconeogenesis (increasing plasma glucose levels), respiratory rate, oxygen consumption and hematocrit, and a decrease in liver carbohydrate reserves (Mommsen et al., 1999; Wendelaar Bonga, 1997). Sustained release of cortisol caused by chronic stressors also results in tertiary responses such as inhibition of growth, reduction of appetite, suppression of the immune system and negative effects on reproduction (reviewed in Wendelaar Bonga, 1997). Exhaustive exercise (e.g. simulating a C&R angling event) typically causes changes in plasma and muscle lactate, changes in plasma ionic status (increased potassium and sodium along with decreased chloride), decreases in energy resources (ATP and PCr) and decreases in blood pH (with associated decreased plasma HCO_3^- and increased PCO_2) (Kieffer, 2000). The rate of recovery from the stress response and exhaustive exercise depends on the species of fish, its life history and physiological requirements (Kieffer, 2000; Barton, 2002), the recovery environment (Milligan, 1996; Suski et al., 2006), the duration and intensity of the stressor (Kieffer, 2000) and the physiological variable being measured (Donaldson et al., 2010; Cooke et al., 2013). Although the fish may recover from the initial challenge, prolonged or repeated stress responses can have sublethal effects on fish behaviour, fitness and survival (Schreck et al., 1997; Barton, 2002). A retained lure is presumably an example of such a sustained stressor, and thus may have long-term sub-lethal or lethal consequences for fishes.

The impact of retained gear on fish physiology and behaviour is generally not well understood. In the break off scenario, some of the variables affecting stress responses are similar to those that occur during C&R angling (e.g. exhaustive exercise), while other elements are minimized or eliminated (e.g. effects of handling and air exposure) (Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Suski et al., 2007) as the fish is typically not removed from the water. Henry et al. (2009) examined lure retention in nesting smallmouth bass (*Micropterus dolomieu*) and demonstrated that short-term lure retention (24 h) produced elevations in blood glucose levels but little change in lactate concentrations and hematocrit relative to controls. Arlinghaus et al. (2008) using telemetry, provided preliminary insight into the behavioural response of pike after post-release with artificial lures to simulate break off. Lure retention caused short-term behavioural changes (initially lack of movement and then a bout of hyperactivity), but typical behavioural patterns resumed as quickly as 24 h post release. A recent laboratory study by Eckroth et al. (2014) similarly failed to identify significant physiological or behavioural effects of retained hooks in Atlantic cod (*Gadus morhua*). However, retaining a lure in the mouth has the potential to impact feeding and respiration, which could in turn have fitness consequences. Evaluation of both physiological and behavioural indicators over the duration that the lure is retained is needed to provide important information about how a fish adapts to or is affected by break off. A laboratory environment enables the collection of detailed information that would assist in interpreting past (e.g. Arlinghaus et al., 2008) and future field studies.

The objective of this study was to quantify the physiological and behavioural consequences to northern pike of prolonged exposure to a retained lure (simulated break off) in a laboratory setting. We anticipated that retained gear would impact fish at a physiological level manifesting as increased stress response and increased metabolism in addition to changes in short term behaviour, specifically increased activity to rid the obstruction. Northern pike were chosen for the study as these fish are in heavy demand by recreational anglers across the northern hemisphere (e.g. Arlinghaus and Mehner, 2004; Arlinghaus et al., 2010; Pierce, 2010), particularly in the trophy class where large mature fish are targeted and are prone to gear break off (Arlinghaus et al., 2008) due to their sharp dentition. To evaluate physiological aspects of lure retention, we used a combination of blood-based physiological metrics (Experiment 1) and metabolic rate measurements (Experiment 2) to provide a comprehensive overview of the physiological consequences of lure retention in this species using two different hook types in three different hooking locations. To assess behavioural aspects, lure retention and ventilation (Experiment 3) we also collected direct, video observations of pike following simulated break off with a retained lure in the laboratory to assess pike interaction with the lure and to quantify their locomotory and ventilatory activity patterns.

2. Materials and methods

2.1. Study site and study animals

This study was conducted at the Queens University Biological Station (QUBS) in eastern Ontario, Canada, (44°31′N, 76°22′W) in May and June 2008. Northern pike were collected from Lake Opinicon, which has an abundant natural pike population, by conventional hook-and-line angling from a variety of locations throughout the lake. Angling gear consisted of medium action spinning rods and reels spooled with 15–20 pound test line. Lures, consisting of spoons and artificial fish imitations (crank baits), were attached to the line with wire leaders and swivels. Angling involved casting and trolling with a target of collecting eight fish per day. On a given day, a number of locations were sampled to ensure that fish were not collected from the same area. Barbless hooks were used to minimize injury and to increase ease of hook removal (Alós et al., 2008). Upon capture, fish were immediately brought to the boat and netted keeping angling time shorter than 60 s. Fish that were angled for longer periods of time or to exhaustion were not included in the study. Following collection and hook removal, fish were visually assessed. Fish in good condition (i.e. no visible signs of excessive injury or bleeding) were retained and transported to the QUBS wet lab facility in an onboard live-well that was regularly refreshed with lake water.

At the QUBS wet lab, pike were held in three 1200 L (152 cm diameter) shaded flow-through holding tanks for 24 h to allow the fish to return to a baseline resting state, following methods similar to Suski et al. (2007). Fish were distributed among the three tanks to minimize density effects (no more than 5 fish per tank at any time). After a 24 h holding period, the fish were carefully netted from their tank and randomly allocated to control or treatment groups. The one variation on this approach was the lake controls which were captured and sampled for blood immediately upon netting into the boat. An individual fish was only used once.

2.2. Experiment 1: effect of lure retention on recovery after exercise

2.2.1. Exercise and hooking treatment groups

To quantify the effects of lure retention on recovery after exhaustive exercise, we used a conventional chasing protocol to induce physiological disturbances and thereby simulate a C&R event. Pike were removed from the 24 h holding tanks and then

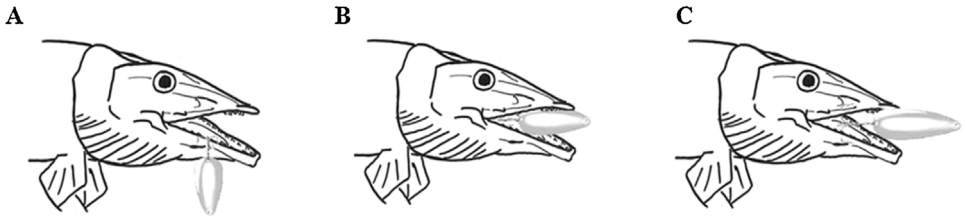

Fig. 1. Hooking locations for lure treatments. (A) Hook through lower jaw; (B) Hook in throat (through soft tissue at the base of the tongue); (C) Upper and lower jaw hooking, one hook each through the tissue of the upper and lower jaw. Both small (5 cm blade length) and large (12 cm blade length) spoons were used in each location.

exercised for 60 s using tail pinches (Suski et al., 2007; Arlinghaus et al., 2009) in a circular (92 cm diameter) tank half-full of lake water. Following exhaustive exercise, pike in all treatment groups were netted, transferred to a foam-padded v-shaped trough filled with fresh lake water and a lure treatment was applied. Six groups of treatment fish were differentiated: (1) a small spoon (5 cm blade length [bl], #6 Mustad barbed treble hook) hooked in the lower jaw; (2) a small spoon hooked into the throat (tissue at the base of the tongue); (3) a small spoon hooked in both the upper and lower jaw; (4) a large spoon (12 cm bl, #3/0 Mustad barbed treble hook) hooked in the lower jaw; (5) a large spoon hooked into the throat; and (6) a large spoon hooked in both the upper and lower jaw (Fig. 1). Hooks were placed into position using pliers and pushed through the tissues with a direct unidirectional application of force to simulate hooking that would occur during an angling event.

To date, the most accurate method to establish baseline physiological parameters in fishes is to measure values in individuals captured and sampled quickly (i.e. wild controls) before physiological changes due to angling can occur (Cooke et al., 2013). For this reason, a wild control group of fish were captured, and sampled for blood immediately in the study lake (i.e. less than 3 min after hooking). For this procedure, pike were held supine in a padded v-shaped trough filled with fresh lake water. A blood sample was then drawn from each fish using caudal puncture with a 3.8 cm, 21-gauge needle and a 2 mL heparinized vacutainer (lithium heparin, Becton-Dickson, NJ, USA). Fish were then released back into the lake. In addition to the wild controls, pike were assigned to three additional laboratory control groups: (1) exercise only, fish were handled identically to the fish described above and received the exhaustive exercise treatment, but did not receive a lure; (2) no treatment, fish did not receive either the exhaustive exercise or the lure treatments; and (3) C&R simulation, fish received the exhaustive exercise, and a small spoon was placed in the jaw and then removed to simulate a C&R event. Samples size, mean fork length and a description of hooking and exercise treatments for all groups of fish is summarized in Table 1.

2.2.2. Physiological sampling

Immediately following the lure attachment and exercise protocol described above, fish were non-lethally sampled for blood as described above. Each fish was then transferred to an isolation box. Each 79 cm × 15 cm × 15 cm (length × width × height) box was constructed from black, 6 mm acrylic sheet with a total volume of 16.5 L. Ten boxes were placed on racks over two 152 cm × 61 cm × 61 cm fiberglass tanks continually supplied with lake water. Oxygenated lake water was pumped to a header pipe and then directed to each chamber through a hole in the removable lid into a small overflow chamber where the flow was dissipated and then overflowed into the main raceway where the fish were held. Fish were oriented into the flow with water passing over them to the drain. The drain end consisted of a false back which created a weir over which the water flowed into the small overflow chamber and through a drain hole set in the end. The overflow served to maintain water level and further block ambient light that may have entered through the drain hole. To eliminate the risk of the fish dislodging the lids, each lid was inset and held in place with webbing straps secured with plastic cam lock buckles. Flow into the chambers was set to average 0.87 L per min for a turnover rate of 14.36 L per hour.

One hour post exercise, fish were removed from the isolation box and quickly transferred to the sampling trough filled with fresh lake water, resampled for blood, and then returned to the box as quickly as possible to avoid air exposure. After 24 h, fish were again removed from the isolation chamber, resampled for blood, and then transferred to a cooler filled with lake water in which they were transported to the lake and released. The few fish that showed loss of equilibrium or other behavioural impairments were held until they resumed normal activity and then released.

2.2.3. Physiological assays

A portion of whole blood was used to quantify hematocrit (the percentage of red blood cells within the total volume of blood) using microhematocrit capillary tubes centrifuged for 5 min (using a CritSpin-Micro-Hematocrit Centrifuge). The remaining whole blood was stored in ice slurry for up to 1 h until it could be processed. Blood was centrifuged at 10,000*g* for 5 min (Clay Adams Compact II Centrifuge) and lactate and glucose concentrations were quantified from plasma using hand-held lactate (Lactate Pro LT-1710 portable lactate analyser; Arkray Inc., Kyoto, Japan) and glucose (ACCU-CHEK glucose meter; Roche Diagnostics, Basel, Switzerland) meters. The devices have previously been calibrated for use on fish (Cooke et al., 2008; Stoot et al., 2014). Plasma was then placed in a dewar and transported to Carleton University where it was held in a −80 °C ultracold freezer until analysis. As an indicator of possible tissue damage serum activity of aspartate transaminase (AST) was determined. Plasma AST and ion assays (sodium, potassium, chloride) were completed using a Roche-Hitachi 917 analyzer (Basal, Switzerland) and based upon the International Federation of Clinical Chemistry and Laboratory Medicine (IFCC). To ensure that the integrity of the analysis was maintained, laboratory personnel followed the Veterinary Laboratory Association Quality Assurance Program, New York State Department of Health, College of American Pathologists, and the Canadian Food Inspection Agency External Proficiency Panel guidelines.

Plasma cortisol was determined in a single assay using a commercial kit (ImmunoChem Cortisol ^{125}I RIA kit; MP Biomedicals, Orangeburg, NY) and a Cobra Auto-Gammer (Hewlett-Packard Inc., Palo Alto, CA) following the methods outlined in Gamperl et al. (1994). Intra-assay variability (% CV) was 10.45%.

2.3. Experiment 2: effect of lure retention on metabolic rate

2.3.1. Hooking treatment groups

To quantify the effect of hooking treatment on metabolic rate, a 12 h static respirometry assessment was completed using pike assigned to a set of treatment and control conditions similar to

Table 1
Sample size, mean fork length and description of hooking and exercise treatments given to ten groups of northern pike for Experiment 1 (to assess the effect of retaining a small or large lure in three different hooking locations on blood physiology over 24 h). Physiological sampling times following hooking and exercise are given for each group.

Treatment			Physiological sampling				Sample size	Fork length (mean ± SD)
Hooking Location/Lure Size		Exercise	At capture	0 h	1 h	24 h		
	small spoon	60 s	×	×	√	√	8	504 ± 62 mm
	small spoon	60 s	×	×	√	√	9	489 ± 51 mm
	small spoon	60 s	×	×	√	√	8	497 ± 62 mm
	large spoon	60 s	×	×	√	√	8	534 ± 57 mm
	large spoon	60 s	×	×	√	√	8	553 ± 26 mm
	large spoon	60 s	×	×	√	√	9	499 ± 59 mm
Wild control	no hooking	angling only	√	×	×	×	9	466 ± 56 mm
Exercise only	no hooking	60 s	×	×	√	√	10	490 ± 39 mm
Simulated C&R	lower jaw & then hook removed	60 s	×	√	√	√	7	505 ± 58 mm
No treatment	no hooking	no exercise	×	×	×	√	9	481 ± 35 mm

those used in Experiment 1. For this portion of the study, pike were subjected to one of the following three treatments: (1) a small spoon hooked in the lower jaw (n = 5; mean fork length 467 ± 24 mm); (2) a small spoon hooked in both the upper and lower jaw (n = 7; mean fork length 502 ± 49 mm); (3) a large spoon hooked in both the upper and lower jaw (n = 4; mean fork length 517 ± 38 mm); and a control, where the fish received no lure (n = 13; mean fork length 483 ± 48 mm).

2.3.2. Metabolic rate measurements

Standard metabolic rate (SMR) was determined using computerized, intermittent-flow respirometry (Loligo Systems, Hobro, Denmark) (Steffensen, 1989). During each experimental cycle (12 h overnight tests), 4 fish individuals were used: 3 fish that received one the hooking treatments and 1 control fish.

To calibrate the equipment prior to metabolic rate measurements, each fish (netted from the 24 h holding tank) was placed in a water-filled displacement tube from which water was expelled into a calibrated flask to determine volume that was used to calculate mass. After the hook treatment was applied as described above, fish were transferred to a glass chamber (746 mm length × 140 mm wide) outfitted with fiber optic oxygen probes. The tubes were split between two tanks (152 cm × 61 cm × 61 cm) filled to a depth of approximately 24 cm with lake water at ambient temperatures (over the course of the experiment, temperature ranged from 19 °C to 25 °C; within each experimental cycle, temperature varied by no more than 2 °C). Water was circulated between the two tanks to ensure all fish were subjected to the same water mix and two large air stones from the laboratory's central air system oxygenated each tank. The water was exchanged between tests to prevent build-up of wastes.

Each glass chamber (holding one fish) was connected to two aquarium pumps; one pump recirculated water through the chamber, and the other flushed ambient, oxygenated water into the chamber. The total volume per set up, including the glass chamber, pumps, and all associated tubing was 11.48 L. Oxygen consumption in each individual chamber was quantified within 15 min cycles that consisted of an 8 min measurement phase, a 4 min flush period to replace water in each chamber, and a 3 min wait period that followed each flushing prior to commencing measurements. Water from the chambers was continually circulated over the fiber optic oxygen probes to ensure adequate mixing during each measurement cycle. The change in oxygen concentration (α) for each chamber was calculated as a slope (ΔO_2saturation/Δt) and used to estimate the mass-specific oxygen consumption rate (MO_2, mg O_2 kg^{-1} h^{-1}) for each fish as:

$$MO_2 = \alpha Vresp \beta {M_b}^{-1},$$

where Vresp is the volume of each glass chamber minus the volume of the fish (L), β is oxygen solubility (adjusted daily for both temperature and barometric pressure), and M_b is the fish mass (kg) calculated before being placed in the respirometer chamber. All calculated dissolved oxygen values were corrected for background oxygen consumptions generated for each specific fish and chamber prior to commencing experiments. Regular calibration of the fiber optic oxygen probes occurred with oxygen-free water and fully saturated water through the experiments. Data were recorded with AutoResp software Version 1.4 (Schurmann and Steffensen, 1997; Steffensen, 1989). SMR values were calculated as the average of six lowest values recorded between 2000 and 0600 as very minimal human disturbance occurred in the laboratory during these hours (Schurmann and Steffensen, 1997; Gingerich et al., 2010).

2.4. Experiment 3: effect of lure retention on pike – videographic observations

2.4.1. Exercise and hooking treatment groups

Similar to Experiment 1, after the 24 h hold time, a new group of pike were exercised for 60 s using tail pinching, and then transferred to a padded trough with fresh lake water, and randomly assigned to a treatment group. For this experiment, treatment groups were: (1) a large spoon hooked in the lower jaw (n = 10;

mean fork length 496 ± 63 mm); (2) a large spoon hooked into the throat (n = 9; mean fork length 499 ± 107 mm; (3) a large spoon hooked in both the upper and lower jaw(n = 10; mean fork length 545 ± 45 mm); and (4) control fish that received an exhaustive exercise treatment, but no lure treatment (n = 10; mean fork length 496 ± 63 mm).

2.4.2. Videography methods

After the prescribed treatment, fish were immediately transferred to one of two 60 cm by 76 cm observation tanks with a 56 cm by 38 cm glass viewing window. The bottom of each tank was covered with a sheet of white plastic lattice to raise the bottom of the tank while maintaining good water circulation so that fish could be viewed even if they rested on the bottom of the tank. A wood frame was attached to the front of each observation tank that was covered in black plastic sheet. At the apex of the cone, approximately 60 cm from the viewing pane, a small observation hole was created where the lens of a video camera (Sony HDD 2000) was placed at a suitable focal length for collecting video footage. This minimized disturbance to the fish in the tank. The same video camera was used for both tanks and moved during each 24 h observation period. The top of each tank was covered with a screened cover to limit the possibility of pike jumping from the tank. Each tank was connected to the laboratory's lake water system and was continuously supplied with fresh lake water. In addition, air stones were added to the tank to ensure adequate oxygenation. Strict use of tank and laboratory isolation, frequent turnover of tank water with fresh lake water, and supplemental aeration were done to ameliorate some of the confounding influences of captivity on the pike.

Data were collected during five minute digital video observation periods at 5, 20, 35 and 50 min and then again at 6, 12 and 24 h. Observations of 2 fish were completed in each 24 h period. The videos were transferred to a computer and visually analyzed every 10 s over the course of each 5 min observation period. Behavioural data collected included: swimming within the tank water column, darting (sudden burst movements about the tank), jumping in an attempt to clear the water, rubbing against the tank, head shaking, resting and/or exploring (probing the water surface). Physical data collected included: injury severity (e.g. lacerations), evidence of bleeding, change in lure location and opercular pumping (ventilation). All video data were analyzed by the same independent observer.

2.5. Statistical analyses

For experiment 1, two-way repeated measure analysis of variance (ANOVA) models were used to quantify the interaction between treatment (lure retention) and sampling time post-exercise (1 h and 24 h) for all physiological variables. All physiological data were log-transformed or arc-sine transformed (hematocrit only) to improve normality and heteroscedasticity. Levene's tests were used to determine homogeneity of variances across treatment groups. Given the relatively small sample size in each treatment during each time period, it was not possible to test the assumption of normality in all cases; however, the aforementioned transformation was used to correct issues associated with unequal variance. For experiment 2, a one-way ANOVA was used to quantify differences in metabolic rate between control and treatment groups. Finally, for Experiment 3, principal component analysis was used as a data-reduction method to integrate the 7 behavioural metrics into a single score represented by the first principal component (PC-1). Two-way repeated measure ANOVAs were used to compare tank behaviours (PC-1) and opercular rate among treatment groups, with treatment group, time post-hooking and their interaction as independent variables.

Where ANOVA determined statistical significance, Tukey's honestly significant difference (HSD) tests were used to determine which treatment groups differed. All analyses were conducted using JMP v10 (SAS Institute, Cary, NC). Data are expressed as mean ± standard deviation and significance was evaluated at $\alpha < 0.05$.

3. Results

3.1. Experiment 1: effect of lure retention on recovery after exercise

3.1.1. Mortality and lure retention

Of the 104 fish used for this experiment, four fish (4%) died. Because mortalities were rare and equally spread across treatment and controls, there was no impact of lure retention on mortality. Over the course of the experiment, 15 (18%) fish were able to expel their lures in the isolation chambers. Of these, 3 lures (20%) were expelled at 1 h and 11 lures (80%) expelled at 24 h. All fish that expelled lures were hooked shallowly; four (27%) small spoon/lower jaw fish; four (27%) small spoon/upper and lower jaw fish, four large spoon/lower jaw fish (27%) and three (19%) large spoon/upper and lower jaw fish, indicating no differential effects of spoon size or location on the loss of lures when fish were shallowly hooked. By contrast, no fish hooked in the throat (small or large spoons) expelled lures over the duration of one day. Fish that died or expelled the lure during the experiment were not analyzed further for physiological effects, and were replaced by new fish.

3.1.2. Baseline physiological values

To assess the physiological effect of holding pike in our laboratory, blood physiology of wild controls (fish that were sampled directly after angling from the lake) was compared to that of two groups of confined control pike; the results are summarized in Table 2. Wild control fish had significantly lower levels of glucose (ANOVA, $F_{(2)} = 40.7$, $p < 0.0001$) and cortisol (ANOVA, $F_{(2)} = 85.8$, $p < 0.0001$) than either confined control groups (fish that experienced simulated C&R angling or those that were held in a holding tank and then confined in isolation). Lactate (ANOVA, $F_{(2)} = 28.9$, $p < 0.0001$) was significantly higher in control fish that experienced simulated C&R angling than in either control fish that were not exercised or in wild controls. The only other differences seen between control groups were aspartate transaminase (ANOVA, $F_{(2)} = 16.0$, $p < 0.0001$) that was higher and plasma chloride (ANOVA, $F_{(2)} = 7.10$, $p = 0.004$) that was lower in confined pike that were not exercised compared with wild controls. Overall, data revealed that both exhaustive exercise and the confinement in laboratory conditions were stressful for pike as indicated by alteration of physiological variables compared to the situation in the wild immediately after capture.

3.1.3. Effects of lure retention on blood physiology post exercise

To assess the physiological effects of retained lures on recovery from exercise, the post exercise blood physiology of pike with two different lure types in three different hooking locations as well as control pike with no lure under otherwise similar conditions was compared (results summarized in Tables 3 and 4).

Statistical analysis showed no significant interactions between treatment and time post exercise on plasma levels of glucose, cortisol, AST, sodium, potassium or chloride or in hematocrit. There was a significant interaction between treatment and time post-exercise on lactate levels.

All pike that were exercised (with and without lure treatment) showed recovery of plasma levels of lactate, glucose, sodium and potassium and in hematocrit which, at 24 h post exercise, were

Table 2
Comparison of blood physiology among three control groups of northern pike: fish sampled immediately after angling (wild controls), fish that were held for 24 h and then experienced exhaustive exercise (simulated C&R angling) and fish that were held in a holding tank for 24 h and then confined in isolation in a black tube for an additional 24 h without being exercised (no treatment) to assess the effect of confinement on physiological parameters. Values are presented as mean ± SD. Levels with dissimilar letters are significantly different. (HCT, hematocrit; AST, aspartate transaminase; Na^+, sodium; K^+, potassium; Cl^-, chloride).

Treatment	Sample Time	Physiological variable							
		Lactate (mmol l^{-1})	Glucose (mmol l^{-1})	Cortisol (ng ml^{-1})	HCT (%PVC)	AST (IU L^{-1})	Na^+ (mmol l^{-1})	K^+ (mmol l^{-1})	Cl^- (mmol l^{-1})
Wild control	At capture	0.8 ± 0.3^a	3.1 ± 1.2^a	1.4 ± 1.5^a	18 ± 2.8	750 ± 261^a	141 ± 4.3	3.9 ± 2.1	124 ± 3.3^a
Simulated C&R	0 h	6.9 ± 2.9^b	6.8 ± 0.9^b	589 ± 239^b	24 ± 3.3	1725 ± 804^{ab}	149 ± 4.4	4.0 ± 0.6	126 ± 4.2^a
No treatment	24 h	1.7 ± 1.1^a	6.5 ± 0.9^b	435 ± 295^b	18 ± 4.6	2867 ± 2240^b	136 ± 8.6	4.9 ± 3.4	117 ± 5.7^b

significantly lower than levels measured 1 h post exercise. In addition, plasma levels of these variables measured 24 h after exercise were not different from those levels measured in control pike that had been confined in isolation for 24 h but had not been exercised (ANOVA, lactate, $F_{(8)} = 2.474$, $p = 0.022$; glucose, $F_{(8)} = 0.1.609$, $p = 0.139$; sodium, $F_{(8)} = 1.5648$, $p = 0.153$; potassium, $F_{(8)} = 1.4146$, $p = 0.208$; hematocrit, $F_{(8)} = 1.893$, $p = 0.076$). Twenty-four hours after exercise, plasma levels of cortisol and chloride were not significantly different from levels measured at 1 h post exercise and were also not different from levels in control pike that had not been exercised (cortisol, $F_{(8)} = 0.5804$, $p = 0.790$; chloride, $F_{(8)} = 2.0128$, $p = 0.058$). Plasma levels of AST 24 h post exercise were significantly greater than those measured 1 h post exercise but were not different from control pike that had been confined for the same length of time but not exercised ($F_{(8)} = 0.584$, $p = 0.788$).

No significant differences in levels of any of the physiological variables (lactate, glucose, cortisol, hematocrit, AST, sodium, potassium or chloride) were detected between any of the eight groups of fish (with or without lure treatment) 1 h post exercise indicating no effect of lure retention, hooking location or size of lure on these physiological responses to recovery from exercise at this time (Table 4).

At 24 h post exercise, no differences in plasma levels of glucose, cortisol, AST, sodium, potassium, chloride and hematocrit were detected between control pike who did not receive a lure treatment but were exercised and any of the groups of pike that received a lure treatment indicating that lure retention has no effect on responses of these physiological variables to exercise. The only significant difference observed between control pike and any treatment groups at the 24 h time period was lactate concentrations which were significantly higher in control fish than in fish with a small spoon hooked in the lower jaw (Tukey's HSD, $p = 0.022$) or those with a small spoon hooked in the upper & lower jaw (Tukey's HSD, $p = 0.005$). Statistical differences in three variables were also detected between specific pairs of treatment groups at the 24 h time period: (1) deeply hooked/small spoon fish had lactate levels significantly higher than lower jaw/small spoon fish (Tukey's HSD, $p = 0.024$); (2) plasma chloride was significantly higher in upper & lower jaw/small spoon fish than in lower jaw/small spoon fish and (3) hematocrit was significantly greater in upper & lower jaw/large spoon pike than in lower jaw/large spoon pike.

3.2. Experiment 2: effect of lure retention on metabolic rate

The standard metabolic rate of control pike (without a lure) was not significantly different from metabolic rates calculated for pike with any of the 3 lure treatments tested, indicating that lure retention has no effect on metabolic rate (ANOVA, $F_{(4)} = 1.006$, $p = 0.418$). The mean metabolic rate for control pike with no lure treatment was 126 ± 21 mgO_2 kg^{-1} h^{-1}. Mean metabolic rates for treatment fish were comparable at 128 ± 16 mgO_2 kg^{-1} h^{-1} (lower jaw/small spoon treatment), 122 ± 25 mgO_2kg^{-1} h^{-1} (upper & lower jaw/small spoon treatment) and 117 ± 19 mgO_2 kg^{-1} h^{-1} (upper & lower jaw/large spoon treatment).

3.3. Experiment 3: video observations

3.3.1. Mortality and lure retention

Of the 43 pike that were used for this experiment, 4 mortalities occurred (9%) and were not included in the analysis: one lower jaw/large spoon fish, two upper & lower jaw/large spoon fish and one control fish (without a lure treatment). Because mortalities were rare and spread across treatment and controls, there was no impact of lure retention on mortality. Seven of the 29 fish with a lure treatment (24%) shed the lure during the 24 h observation period. The incidence of lure loss was also evenly distributed across treatments (3 lower jaw/large spoon fish; 2 deeply hooked/large spoon fish; and 2 upper & lower jaw/large spoon fish).

3.3.2. Effects of lure retention on behaviour

PC-1 (eigenvalue = 2.38) was positively associated with all behavioural metrics (Table 5) and explained 34.0% of the variance within the data. There was no difference in PC-1 behaviour among treatments (ANOVA, $F_{(3)} = 0.37$, $p = 0.777$) or among time periods (ANOVA, $F_{(6)} = 1.50$, $p = 0.179$) and there was no significant interactions between these two terms (ANOVA, $F_{(18)} = 0.767$, $p = 0.738$). Generally, fish remained in a resting position on the bottom of the tanks with little activity recorded. Fish made little or no effort to actively dislodge their lures. Momentary (<5 s) bursts of hyperactivity were observed; however, this type of activity was infrequent and consistent across treatment groups. Occasionally, a fish would be observed either actively hovering or exploring the surface of the tank; however, while still noteworthy, none of these activities were sustained.

3.3.3. Effects of lure retention on ventilation

There was no significant interaction between treatment and time post-hooking on opercular pumping rate (ANOVA, $F_{(18)} = 0.36$, $p = 0.992$); however, independently, treatment and time post-hooking had significant effects on opercular pumping rate (i.e. ventilation rate; ANOVA, $F_{(3)} = 9.48$, $p < 0.0001$ and $F_{(6)} = 6.89$, $p < 0.0001$, respectively). For all fish (both treatment and control), ventilation rate peaked between 20 and 50 min post hooking and declined steadily thereafter with significant differences noted between the first hour (50 min) of observation (59 ± 2 beats per minute [bpm]) and at 24 h (47 ± 27 bpm; Tukey HSD, $p = 0.001$; Fig. 2). Fish with deep hooking in the esophogeal passage showed significantly higher opercular pumping rates throughout the 24 h observation period than those of fish in the other two treatment groups or in fish with no hooking treatment (Tukey HSD, $p < 0.03$).

4. Discussion

In our laboratory-based study, retention of a lure failed to significantly impact the physiological or behavioural ability of pike to recover from exhaustive exercise (i.e. simulated angling). These results agree with a previous field study by Arlinghaus et al. (2008) who revealed limited impacts on field behaviour of northern pike post release and with a recent study on the physiology and

Table 3
Comparison of blood physiology among pike receiving one of 6 different hooking treatments or control groups sampled 1 h and 24 h after exhaustive exercise. Values are presented as mean ± SD.

Sample time	Treatment	Physiological variable							
		Lactate (mmol l^{-1})	Glucose (mmol l^{-1})	Cortisol (ng ml^{-1})	HCT (%PVC)	AST (IU L^{-1})	Na^+ (mmol l^{-1})	K^+ (mmol l^{-1})	Cl^- (mmol l^{-1})
1hr	 SS	9.7 ± 3.0*	9.6 ± 2.5*	408 ± 308	19 ± 2.7*	1836 ± 942*	135 ± 11*	3.8 ± 1.7*	106 ± 7.7
	 SS	11 ± 1.3*	12 ± 3.6*	493 ± 269	19 ± 2.8*	1275 ± 587*	137 ± 7.6*	5.1 ± 3.4*	109 ± 8.0
	 SS	11 ± 0.9*	10 ± 2.3*	400 ± 139	21 ± 1.3*	2038 ± 1424*	140 ± 6.7*	5.6 ± 3.7*	113 ± 2.8
	 LS	10 ± 1.7*	12 ± 3.1*	447 ± 343	19 ± 6.7*	1527 ± 579*	141 ± 9.1*	6.2 ± 4.0*	113 ± 8.8
	 LS	11 ± 1.9*	13 ± 4.4*	568 ± 264	22 ± 3.5*	1251 ± 602*	139 ± 11*	5.8 ± 1.7*	110 ± 9.9
	 LS	11 ± 0.9*	11 ± 2.8*	306 ± 190	23 ± 4.6*	1664 ± 954*	144 ± 8.9*	4.2 ± 1.2*	112 ± 4.5
	Exercise only	11 ± 2.1*	9.8 ± 2.0*	356 ± 184	19 ± 3.5*	1526 ± 670*	137 ± 6.6*	4.7 ± 2.8*	110 ± 9.5
	Simulated C&R	12 ± 0.7*	12 ± 2.4*	475 ± 166	18 ± 1.6*	1489 ± 798*	144 ± 12*	4.7 ± 1.7*	112 ± 6.7
24hr	 SS	1.5 ± 0.6[a]	5.4 ± 2.1	565 ± 439	15 ± 1.9	3977 ± 3302	127 ± 8.3	5.2 ± 2.7	102 ± 16[a]
	 SS	1.6 ± 0.8[bc]	6.8 ± 2.2	444 ± 576	16 ± 5.6	2211 ± 805	128 ± 14	3.7 ± 2.1	109 ± 13
	 SS	0.8 ± 0. 5[ab]	5.8 ± 0.7	447 ± 423	15 ± 3.8	3636 ± 2872	139 ± 3.9	3.4 ± 1.8	119 ± 5.6[b]
	 LS	0.6 ± 0.4	6.8 ± 1.5	440 ± 231	14 ± 4.1[a]	3382 ± 1862	135 ± 14	2.9 ± 1.5	113 ± 13
	 LS	1.6 ± 0.7	7.8 ± 2.4	420 ± 261	16 ± 3.6	2968 ± 2292	128 ± 11	3.4 ± 1.0	109 ± 12
	 LS	1.5 ± 1.3	5.6 ± 1.8	233 ± 161	18 ± 2.4[b]	5162 ± 5042	133 ± 5.8	5.1 ± 3.2	114 ± 4.8
	Exercise only	2.6 ± 2.8[c]	6.0 ± 2.0	451 ± 355	14 ± 3.1	2941 ± 2843	132 ± 8.3	3.7 ± 1.2	110 ± 8.0
	Simulated C&R	1.9 ± 1.7	5.9 ± 1.4	435 ± 329	13 ± 2.0	3230 ± 1839	134 ± 2.2	2.5 ± 0.6	114 ± 3.5
	No treatment	1.7 ± 1.1c	6.5 ± 0.9[a]	435 ± 295a	18 ± 4.6[b]	2867 ± 2240a	136 ± 8.6[a]	4.9 ± 3.4a	117 ± 5.7[bc]

Dissimilar letters shows significant differences of variables between treatment groups. HCT, hematocrit; AST, aspartate transaminase; Na^+, sodium; K^+, potassium; Cl^-, chloride; SS, small spoon; LS, large spoon.
* Shows significant difference between 1 h compared with 24 h for the same treatment group.

Table 4
Results of two-way repeated measure analysis of variance (ANOVA) quantifying the interaction between treatment (lure retention) and sampling time post-exercise (1 h and 24 h) for eight blood-based physiological variables. Significant values are bolded.

Physiological variable	Interaction		Time (1 hr and 24 hr post-exercise) comparison		Treatment comparison	
	F-ratio ($F_{(7)}$)	p-value	F-ratio ($F_{(1)}$)	p-value	F-ratio ($F_{(7)}$)	p-value
Lactate (mmol l^{-1})	**2.356**	**0.029**	*			
Glucose (mmol l^{-1})	0.317	0.945	**129.14**	**<0.001**	2.06	0.056
Cortisol (ng ml^{-1})	0.543	0.801	2.424	0.122	1.124	0.352
Hematocrit (%PVC)	0.311	0.948	32.19	<0.001	**3.02**	**0.006**
AST (IU L^{-1})	0.197	0.986	**43.783**	**<0.001**	1.132	0.348
Na^+ (mmol l^{-1})	0.5709	0.778	**20.748**	**<0.001**	2.096	0.049**
K^+ (mmol l^{-1})	1.903	0.075	**12.082**	**0.001**	0.559	0.788
Cl^- (mmol l^{-1})	0.4166	0.890	0.0195	0.889	**2.512**	**0.019**

* Because of significant interaction, Tukey's HSD was used to compare treatment pairs (p values for significant results are included in the body of the text).
** No post-hoc differences.

Table 5
Comparison between control and treatment groups of pike showing mean proportion of time spent engaged resting or in 7 different activities during the 24 h observation period. Values expressed as mean ± SD. Eigenvectors for PC-1 analysis provided for each activity.

Behaviour	Control (no hooking)	 LS	 LS	 LS	PC-1 Eigenvector
Resting	0.910 ± 0.23	0.83 ± 0.33	0.91 ± 0.25	0.91 ± 0.24	*
Exploring	0.007 ± 0.05	0	0.0043 ± 0.017	0.0076 ± 0.033	0.46283
Swimming	0.023 ± 0.076	0.039 ± 0.11	0.015 ± 0.036	0.017 ± 0.046	0.37085
Hovering	0.041 ± 0.16	0.094 ± 0.24	0.058 ± 0.21	0.042 ± 0.19	0.27956
Darting	0.008 ± 0.032	0.0096 ± 0.023	0.0061 ± 0.02	0.0033 ± 0.013	0.36499
Jumping	0.008 ± 0.050	0.0038 ± 0.014	0.0051 ± 0.014	0.012 ± 0.046	0.51650
Rubbing	0.001 ± 0.008	0.002 ± 0.0094	0.0024 ± 0.008	0.0015 ± 0.0062	0.23227
Head Shaking	0.0013 ± 0.0059	0.018 ± 0.039	0.0084 ± 0.025	0.0044 ± 0.018	0.34083

* Resting was not used in the PC analysis. No differences in activity were detected between any of the groups. LS = large spoon.

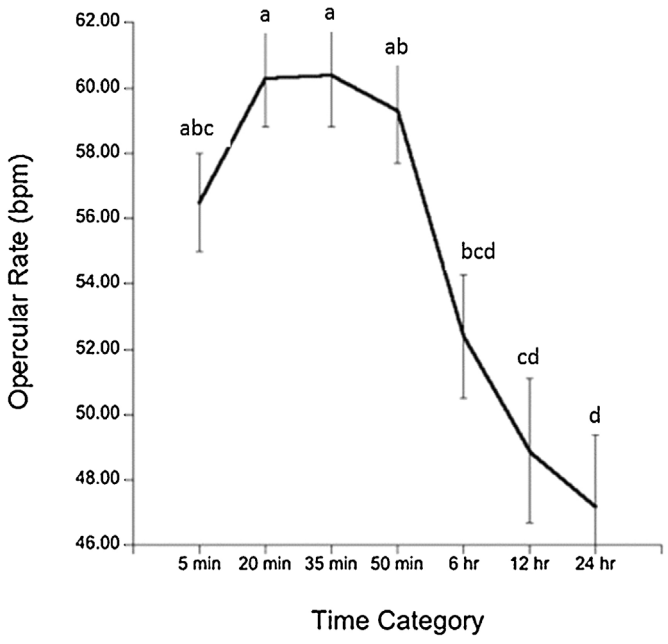

Fig. 2. Comparison of mean (±SD) opercular rate (beats per minute, bpm) measured over time (minutes, min; hours, hr) following treatment for all fish (combined treatment groups and controls, n = 35). Opercular rate peaked at 35 min and declined over the course of the observation period for all groups. Dissimilar letters indicate statistically different opercular rates measured at different times.

behaviour of retained hooks in Atlantic cod (Eckroth et al., 2014). This finding is still somewhat remarkable given that the presence of a foreign object in the mouth of an animal must surely compromise the animal in some way. Whatever the consequences are on pike, they were not readily detectable using the comprehensive endpoints studied here.

4.1. Blood-based physiological responses of pike to lure retention

Based upon the blood-based physiological variables that we tested, we saw no differences in the ability of pike with retained lures to recover from exhaustive exercise compared to control pike that did not have a retained lure. Lure retention has caused changes in some blood-based parameters in other fish species. For example, nesting smallmouth bass with a retained lure have shown elevated blood glucose concentrations relative to controls, but no changes in hematocrit or blood lactate (Henry et al., 2009). It is possible that pike are a particularly resilient species and that they recover more easily from multiple stressors (i.e. exhaustive exercise and lure retention) than other species. Support for this idea is provided by Arlinghaus et al. (2009), in which air exposure had little effect on the physiological response to exercise in pike which recovered rapidly from the exercise within just a couple of hours.

The resampling of physiological indicators over the course of 24 h allowed us to examine recovery dynamics in pike complementing a previous study by Arlinghaus et al. (2009). All pike that were exercised showed recovery of plasma levels of lactate, glucose, sodium and in hematocrit which, at 24 h post exercise, were lower than levels measured in the same fish 1 h post exercise and that were the same as levels measured in fish that had been confined in isolation for 24 h but had not been exercised (all of which was unaffected by lure treatment). Interestingly, we did not see the rapid recovery of lactate that was previously reported by Arlinghaus et al. (2009) for pike, where full recovery of muscle lactate occurred within 1 h post-exercise. In our study, blood lactate and glucose recovered more slowly in agreement with Schwalme and Mackay (1985). Because pike are able to remove lactate without conversion to glucose (Schwalme and Mackay, 1985), the elevations in glucose may be attributed to the stress response and mobilization of energy stores rather than as a result of lactate clearance. Together, our results indicate that the retention of a lure in the mouth of pike does not result in any significant physiological impairment to the

timeline for recovery and that the recovery dynamics we observed were in broad agreement with most previous work on the species.

4.2. Confinement stress

It is important to note that our results were obtained from pike in a laboratory setting and physiological responses in both control and treatment fish may have been impacted by the effect of confinement in this particular species. Plasma cortisol and glucose concentrations in our study were significantly higher in pike that were contained in a holding tank than in pike that were sampled immediately after angling (wild controls); these elevated values persisted throughout the study period indicating that confinement produced significant stress even after a "rest" period of 24 h and, in one group of control fish, after an additional 24 h period in an isolation chamber. In addition, plasma cortisol levels in fish that were exercised were not greater than those in fish that were not exercised indicating that cortisol did not increase in response to exhaustive exercise as expected. The failure to see any response of cortisol to or after exercise could indicate that the stress of confinement had maximized cortisol release and further increases were not physiologically possible even with additional stress caused by a lure. Although we were able to see some physiological responses to exercise (i.e., disturbances in lactate, glucose and ions), it is possible that even these responses were attenuated because cortisol release was at a maximal level and that any additional effect of the lure in the mouth was masked. Previous studies have observed that the stress response in some fish species is altered by artificial elevation of cortisol and these fish are less able to meet challenges of additional physiological stressors (O'Connor et al., 2010; McConnachie et al., 2012).

The measurement of hematocrit can be used as an indicator of blood loss and overall condition for a fish as well as an indicator of stress as a result of erythrotic swelling, fluid shifts or splenic contractions (Barton, 2002). In our study, hematocrit levels in fish that were confined were higher than those in wild controls again likely indicating a stress response to confinement. Although hematocrit levels decreased over 24 h, they did not fall below those of wild controls; therefore, the decreases in hematocrit are likely due to a recovery from stress and not due to deterioration of the fish. Aspartate transaminase (AST) levels did increase over the study period in all fish (both with and without a lure) similar to confinement effects in other fish species (Rapp et al., 2012, 2014). Although plasma levels of AST 24 h post exercise were significantly greater than those measured 1 h post exercise, they were not different from pike that had been confined for the same length of time but not exercised and were not affected by lure retention.

Although many species of fish adapt to laboratory conditions, it appears that pike do experience significant stress related to confinement. Indeed, Edeline et al. (2010) showed that doubling pike density (increased social stress) in large (5 m diameter) ponds caused a neuroendocrine stress response but no further increases in plasma cortisol. Interestingly, cortisol values recorded by Edeline et al. (2010) were higher than the levels that we measured in wild controls indicating that even in large ponds confinement likely produces stress in pike (Edeline et al., 2010). Our findings raise a cautionary note about interpreting results of laboratory studies using wild northern pike, particularly large adults of the species. The stress of confinement may make it difficult to obtain appropriate baseline physiological controls in the laboratory setting. This limitation complicates our ability to assess the effects of additional stressors and makes it challenging to extrapolate the results to circumstances in the wild. For example, Arlinghaus et al. (2009) reported that air exposure does not impact the physiological recovery to exercise in pike. However, as fish in that study had blood glucose concentrations similar to those obtained in our confined fish, high stress levels may have masked the additional effect of air exposure in their study.

4.3. Metabolic responses of pike to lure retention

Remarkably, the standard metabolic rate was not elevated in fish that had a retained lure relative to appropriate controls. We predicted that a change in metabolism would not have been unexpected as a retained lure could cause difficulty with respiration such that metabolism would be reduced, or possibly stress or attempts to expel the lure (i.e. higher physical activity) could have elevated metabolic demands. The lack of a metabolic response to a retained lure is consistent with our observations of a lack of physiological changes seen in the blood of pike. Cumulatively, these findings strongly support the idea that pike are able to compensate for the challenge of a retained lure. It is still possible that lure retention may affect respiration under natural conditions when fish are recovering from an oxygen debt after actively swimming or after burst exercise, an effect that our static respirometry study would not have identified. Metabolic rates for pike have varied across studies, but the metabolic rate of pike in our study falls within the range reported in previous studies (reviewed in Armstrong and Hawkins, 2008). Our results suggest that pike are able to respire normally even with a retained lure in the mouth.

4.4. Behavioural responses of pike to lure retention

In our laboratory setting, retention of a lure in the mouth did not impact activity levels or other behaviour in pike in the short term (within 24 h of a hooking event). Specifically, no differences in movement or behaviour between fish with and without a retained lure were observed, but all pike (both treatment and control) showed limited activity within the 24 h study period, similar to those reported under field conditions (Arlinghaus et al., 2009). Other field studies have also shown short term reduced activity levels in pike that underwent a catch and release angling event (Klefoth et al., 2008, 2011; Baktoft et al., 2013). Our results did not agree with those of Arlinghaus et al. (2008) who, in a field study, observed that pike with a retained lure had significantly lower movement in the first hour post release compared to fish with no lure. Although their observations were of pike in a natural setting, the study design by Arlinghaus et al. (2008) did not allow for direct observation of the fish to quantify fine scale behaviour that occurred within this time period.

Contrary to our expectations, pike spent little time trying to disengage the retained lure. These observations are similar to those made by Henry et al. (2009) of nesting male smallmouth bass released with retained lures following simulated break off. The authors of that study observed that while fish with buoyant type lures appeared to actively attempt to remove the lure, fish with neutrally buoyant lures, such as soft plastics and jig heads, were less active or disturbed by the presence of the lure. The lures used in our study were negatively buoyant spoons and also appeared to not elicit significant responses.

4.5. Ventilation

Interestingly, ventilation rates of pike gradually declined over the 24 h study period. This gradual decrease in opercular pumping could indicate a recovery from exhaustive exercise similar to the recovery in other physiological variables after exercise that we observed. Alternatively, the decreases in ventilation rate could also signal acclimatization of pike to the observation tank (Gibson and Mathis, 2006). Increased opercular movement occurs in response to stress and has been used as an indicator of stress in fish (Gibson and Mathis, 2006; Eckroth et al., 2014). For example, exposing

fish to external stimuli (Huuskonen and Karjalainen, 1997), application of electrical current to water (Jansen and Green, 1970) or application of chemical stimulants to water (Gibson and Mathis, 2006; James et al., 2003; Thomas and Rice, 1975) will all increase ventilation rate. In our study, although all fish experienced a similar ventilation response to exercise, mean ventilation rates in fish that were hooked deeply were significantly greater than those in other fish. The increased ventilation rates in these fish were not likely a compensatory mechanism to hypoxic water as dissolved oxygen levels were adequate in all tanks. Interruptions in ventilator strokes (opercular pumping) occur when a fish creates brief reversals of flow that appear as coughs (Moyle and Cech, 2004) to the observer. Fish use this action to clear foreign matter and mucosa from the gills. Toxicology studies in brook trout (*Salvelinus fontinalis*) showed that cough frequency increased when fish were challenged with excessive concentrations of copper in the water and that cough frequency can be used as a sub lethal indicator of stress (Drummond et al., 1973). While coughing was not quantified, the deeply hooked pike may have been inhibited in their ability to "cough" and to clear the gill area on a regular basis. They may therefore have increased their ventilation rate to compensate for their inability to clear foreign matter and mucosa from the gills.

5. Conclusion

In conclusion, we have demonstrated that lure retention in northern pike had little effect on either physiological recovery to exhaustive exercise or resting metabolic rate in the laboratory setting. Further, behavioural observations suggest that lure retention had no effect on movement or behaviour of pike in the short term. Our results also suggest that wild northern pike are highly sensitive to captivity, which may affect the ability to test stress responses in a laboratory setting in this species and that these types of studies must be designed to minimize the effects of confinement. In order to interpret laboratory results, plasma cortisol should be measured and referenced to values obtained by quick capture and sampling of wild fish. Finally, to get a true understanding of the effects of lure retention on northern pike, laboratory studies must be complemented by field studies in the wild where fish must engage in locomotory activity to forage and avoid predators. Although our results indicate that pike are relatively resilient to lure retention, accounting for lure loss and the potential impact on fish should remain an important consideration in managing fisheries and for informing angling practices. In this context, to maximize the welfare of fish, recommendations should be made for improving angling practices that minimize break off (e.g., using appropriate gear strength and wire leaders) and increase the likelihood that the fish can successfully expel a retained lure in as short a time as possible, (e.g. using barbless hooks).

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