Fisheries Research xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.)

Robert Arlinghaus[a,b,*], Thomas Klefoth[a], Steven J. Cooke[c], Andrew Gingerich[c,d], Cory Suski[d]

[a] *Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany*
[b] *Inland Fisheries Management Laboratory, Institute of Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-University of Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany*
[c] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, Ont. K1S 5B6, Canada*
[d] *Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 S. Goodwin Avenue, Urbana, IL 61801, USA*

ARTICLE INFO

Article history:
Received 20 November 2008
Received in revised form 9 February 2009
Accepted 10 February 2009

Keywords:
Air exposure
Angling
Exhaustive exercise
Fish welfare
Recreational fishing
Radio telemetry

ABSTRACT

We examined the physiological and behavioural consequences of, and recovery from, catch-and-release related stressors using a combined laboratory and field study in northern pike (*Esox lucius* L.). A laboratory experiment was conducted to investigate the recovery dynamics of physiological indicators of stress resulting from a simulated angling event resulting in exhaustion, with and without additional air exposure of 300 s. In addition, a field study using a combination of physiological and behavioural assessment was conducted to assess the long-term consequences of exhaustive exercise and various air exposure durations. Exhaustive exercise for 60 s led to increased muscle lactate, decreased tissue energy stores, and alterations in plasma ionic status. Recovery from physiological disturbance was rapid with all physiological variables except plasma glucose returning to baseline levels after 6 h. The recovery profile was largely unaffected by air exposure of 300 s that simulated extended de-hooking time. The field component of our study verified the impact of exhaustive exercise on blood lactate values, but did not detect any impact of air exposure varying between 0 s and 300 s on physiological stress indicators. However, pike exposed to air for 300 s were behaviourally impaired in the first hour post-release indicating that despite limited effects on physiological status air exposure resulted in significant impairment of organismal performance. Behavioural patterns returned to normal within several hours. In a three-week post-release monitoring period no mortality occurred. Our results emphasize that angling-induced stressors result in physiological and behavioural disturbances, but that recovery is quick. This suggests that pike are relatively resilient to catch-and-release related stressors but air exposure durations should be kept <300 s to minimize behavioural impairment.

1. Introduction

Catch-and-release (C&R) angling, total or partial, is a critical component of most harvest regulations and a practice voluntarily conducted by many recreational anglers worldwide (Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007a). The impacts of C&R angling on fish can range from lethal (coined immediate or delayed hooking mortality, Muoneke and Childress, 1994) to sub-lethal endpoints (Cooke et al., 2002; Arlinghaus et al., 2007a). Contingent on the life history of a species, C&R-induced mortality can have negative consequences for exploited populations (Pine et al., 2008). However, the population might also be impacted if the fish survives the C&R event because this practice may induce various sub-lethal physiological and behavioural disturbances in response to C&R-related stressors (e.g., exhaustive exercise, injury, air exposure) and affect fitness (Cooke et al., 2002; Arlinghaus et al., 2007a). To reduce undesirable impacts associated with C&R angling, there is a need to provide species-specific information on handling procedures and terminal gear configurations that minimize injury, air exposure and other potentially detrimental impacts on the fish (Cooke and Suski, 2005; Cooke and Schramm, 2007; Arlinghaus et al., 2007a, 2008a).

In freshwater fisheries, C&R rates are particularly high for specialized fisheries such as largemouth bass (*Micropterus salmoides*) (Myers et al., 2008), common carp (*Cyprinus carpio*) Arlinghaus, 2007), muskellunge (*Esox masquinongy*) (Fayram, 2003) and northern pike (hereafter termed pike, *Esox lucius*, Pierce et al., 1995). It is the latter species that is of interest in the present paper. The conservation of pike through mandatory and/or voluntary C&R angling

* Corresponding author at: Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany. Tel.: +49 3064181 653; fax: +49 3064181 750.
E-mail address: arlinghaus@igb-berlin.de (R. Arlinghaus).

0165-7836/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2009.02.005

is an important fishery management objective in many regions of the world because this species is a popular target of recreational anglers (Paukert et al., 2001; Arlinghaus and Mehner, 2004). Various authors have reported that recreational fishing of pike results in pronounced changes in the size and age structure of the population (Mosindy et al., 1987; Pierce et al., 1995) indicating vulnerability to overexploitation (Post et al., 2002). To develop effective conservation measures for pike, there is a need to provide baseline information on the lethal and sub-lethal impacts of C&R angling (Arlinghaus et al., 2008a; Klefoth et al., 2008).

There is some information available on hooking mortality levels in pike and their determinants such as hooking-related injuries (reviewed in Arlinghaus et al., 2008a), but little is known about sub-lethal impacts and the factors influencing the physiological and behavioural responses to a C&R event (Klefoth et al., 2008). Pike are of particular concern as unhooking can be expected to take relatively long periods since anglers may fear personal injury from this toothy predator (Newman and Storck, 1986). The amount of air exposure that a fish is subjected to is one of the most challenging aspects of any C&R event (Cooke and Suski, 2005). While out of water, gill lamellae can collapse and inhibit gas exchange (Ferguson and Tufts, 1992), thereby inducing substantial physiological and biochemical disturbances through consumption of energy stores, production of lactate, and osmotic alterations (Schwalme and Mackay, 1985b; Suski et al., 2006, 2007; Killen et al., 2006). More importantly, these physiological disturbances have the potential of increasing the likelihood of mortality (Ferguson and Tufts, 1992), or negatively impacting post-release behaviours (e.g., reduced ability to avoid predators, Schreer et al., 2005; Klefoth et al., 2008). Longer air exposure tends to result in larger adverse physiological and behavioural impacts and longer recovery periods (e.g., Ferguson and Tufts, 1992; Cooke et al., 2001; Davis and Parker, 2004; Schreer et al., 2005), and DuBois et al. (1994) found that handling time was a significant predictor of hooking mortality in pike. Nothing is known, however, about the impact of different air exposure durations on sub-lethal physiological responses and post-release behaviour in esocid species including pike. Systematically varying air exposure duration and assessing its impact on C&R endpoints (physiological disturbances, behaviour, mortality) is necessary to determine air exposure thresholds for a particular species to subsequently use these results to inform anglers about appropriate angling techniques (Schreer et al., 2005).

The physiological disturbances that occur during exhaustive exercise and other stressors such as handling take approximately 8–12 h to fully recover for most fish species (Kieffer, 2000), including pike (Soivio and Oikari, 1976; Schwalme and Mackay, 1985a,b). Any primary and secondary physiological response to C&R angling may, however, alter behaviour of a fish post release (i.e., lead to a tertiary stress response; Cooke et al., 2002; Arlinghaus et al., 2007a). Indeed, behavioural measures constitute sensitive indicators of the complex biochemical and physiological changes that occur in response to stress (Schreck et al., 1997) and thus are particularly suitable as an integrative measure to study the sub-lethal impacts of C&R angling (Donaldson et al., 2008). Klefoth et al. (2008), for example, reported that pike reduced swimming activity and chose safer habitat after being captured and released by angling. However, Klefoth et al. (2008), using radio-telemetry, tracked released pike only once a week; assessment of behaviour post release was therefore relatively coarse. It is unclear if and how the behaviour of pike is altered immediately following capture and when resumption of normal behaviour occurs. Another limitation from previous studies on physiological disturbance and recovery in pike is that they all focused solely on exercise (Soivio and Oikari, 1976; Beggs et al., 1980; Schwalme and Mackay, 1985b), and only the study by Schwalme and Mackay (1985a) actually involved a real angling event. It is unclear the degree to which the pike's physiological disturbances to angling-related stressors in laboratory setting are also expressed in real life angling situations in field settings.

Using a combined laboratory and field experiment, the objective of the present study was to comprehensively assess the physiological and behavioural alterations and recovery dynamics from C&R angling in pike. Specifically, we were interested in quantifying the impact of different air exposure durations on physiological and behavioural endpoints of C&R. By using biotelemetry techniques, we coupled individual physiological condition at release with the individual's behavioural reactions post release. Furthermore, our post-release observation period extended three weeks, thereby enabling us to quantify both behavioural reactions and survival (i.e., fate) post-release. A laboratory component was added to this study to assess recovery dynamics of various physiological indicators of the secondary stress response in pike following simulated angling. We hypothesized that exposing pike to air would result in physiological disturbance and altered behaviour post release, with longer air exposure corresponding to more extreme biological responses.

2. Methods

2.1. Study area and pike angling

The study was carried out between May 3 and June 1, 2006 at Lake Opinicon, a shallow (mean depth = 4.5 m, size 787 ha), dimictic, mesotrophic natural lake in eastern Ontario, Canada (N 44°33′56.0″ W 76°19′23.6″). The laboratory component of this study used facilities at the Queen's Biology Station at Lake Opinicon using fresh lake water. Pike used in the study were captured by angling from a boat in Lake Opinicon using medium-action spinning rods and multifilament line (16.3 kg test). Angling was conducted by actively casting or trolling a variety of artificial lures, and all lures were fished with at least one treble hook (see Arlinghaus et al., 2008a for details). Upon hooking, captured pike were landed in a rubber net to minimize handling related injuries (Barthel et al., 2003). Playing time was standardized to 60 s, which constitutes an average playing time for smaller-sized pike allowing safe landing and handling (Schwalme and Mackay, 1985a; DuBois et al., 1994).

2.2. Laboratory experiment

A laboratory experiment was conducted to assess the recovery dynamics of physiological variables in pike following exercise, and to assess if this recovery profile was significantly altered by a 300 s period of air exposure. This air exposure duration was chosen as it represents the worst-case scenario of air exposure that could be experienced by pike during an angling event (DuBois et al., 1994). Pike used for the laboratory experiment were captured in Lake Opinicon as explained above. Unhooking was done under water within a cooler filled with fresh lake water to avoid air exposure, and fish were transported alive into the laboratory. In the laboratory, pike were stocked into darkened fibreglass holding aquaria (153 cm × 62 cm × 57 cm; water exchanged twice per hour) supplied with fresh, fully oxygenated Lake Opinicon water for 48 h prior to experimentation. During the experiments, water quality was measured daily every three hours and was as follows: mean oxygen concentration ±SD: 8.5 ± 0.5 mg l^{-1} (range 7.5–9.5 mg l^{-1}); mean water temperature ±SD: 18.6 ± 2.7 °C (range 15.1–22.9 °C).

To generate control (resting) physiological values, individual pike were netted from the holding tank and transferred for 48 h to darkened, individual Perspex holding chambers (volume of approximately 12 l) continuously supplied with fresh lake water. After 48 h, the water supply to the chambers was terminated. To euthanize the individual pike, clove oil (250 ppm) was added to the

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

chambers. Following cessation of ventilation, a blood sample and a white muscle sample was taken. Blood samples were collected using the caudal venipuncture technique (Houston, 1990). For this, a vacutainer syringe (38 mm, 21.5 gauge, lithium heparin) was used to draw 3 ml of blood from the caudal vessels (Cooke et al., 2005). Blood samples were briefly held in an ice–water slurry until they were centrifuged to obtain plasma within 10 min. Afterwards, they were placed in liquid nitrogen for later analysis (see below). Further, a white muscle sample (approximately 10 g of tissue from an elongate piece that ran laterally along the body of the fish) was taken from the epaxial musculature below the dorsal fin and above the lateral line using a scalpel immediately after the blood sample was obtained. This sample was transferred into vials and immediately placed in liquid nitrogen.

To generate a treatment of exhaustive exercise that replicated an angling event, pike were individually netted from their holding tank and chased by tail pinching for 60 s as described in Suski et al. (2006) in a rectangular treatment tank (62 cm × 62 cm × 57 cm) filled with fresh lake water. After 60 s all pike failed to react to the stimulus indicating exhaustion. To assess the immediate physiological response to this exhaustive exercise, a group of fish was immediately sampled for blood (see below) and white muscle (see above). To determine the time required for recovery from physiological disturbances induced by exercise, fish were exercised for 60 s as described above, and then transferred to darkened Perspex boxes continuously supplied with fresh aerated lake water. After either 1, 3 or 6 h of recovery, pike were sampled for blood and white muscle after adding clove oil (250 ppm) to the chambers to euthanize the fish. The same procedure was applied to fish exhaustively exercised by tail pinching for 60 s that were exposed to air for 300 s before being placed individually into Perspex holding chambers. This rather extreme air exposure duration was chosen to simulate a worst-case situation. While appearing unrealistic such air exposure levels can still occur in real pike fisheries, particularly when fish are handled by inexperienced anglers (Robert Arlinghaus, personal observation). In each treatment and for each recovery period $N = 8$ different pike were used in the treatment groups and $N = 10$ laboratory control fish, i.e., every pike was used only once. Total length of all fish used in the laboratory experiment was on average 491 ± 51 mm (SD) and 607 ± 194 (SD) g wet body mass, and these variables did not differ significantly between treatment groups (total length: $F = 0.963$, df = 70, $p = 0.473$; body mass: $F = 1.147$, df = 70, $p = 0.346$).

2.3. Field experiment

The field component of the study involved assessing the impact of different air exposure durations on physiological indicators in the blood of angled pike, as well as monitoring post-release behaviour from a common release site (N 44°33′56″, W 133 76°19′24″) and survival in a natural lake environment. Post-release behaviour was monitored using two complimentary techniques: long-term observations that continued for three weeks after release using radio telemetry, and fine spatial scale observations within 1 h following release using surface floats. A common release site was chosen to confront all pike with the same release environment and to avoid site-specific post-release behaviours within a supposed home range of individual pike (Kobler et al., 2008a) at the location of capture. Average ± SD distance between capture point and the release site was 858 ± 462 m, and there were no significant differences in distance to release point among treatment groups (ANOVA, $F = 0.468$, df = 3, $p = 0.706$). Thus, there was an equal spread of pike sampled from various distances to the release site among treatments, which controlled for the potential effect of site fidelity behaviour of pike.

All pike used in the field experiment were collected by angling as described above from locations in Lake Opinicon. To determine physiological status after angling, a field control group was immediately non-lethally sampled for blood without the use of anesthetic by holding the fish under water following a standardized fight time of 60 s as described above. All other fish were blood sampled without the use of anesthetic (Cooke et al., 2005) after first attaching a radio transmitter externally to the fish (see below) and randomly applying one of the following air exposure treatments: 0 s, 60 s, 180 s or 300 s. We chose to attach the radio transmitter prior to exposing fish to air to be able to unambiguously link the physiological response to the additional air exposure. The 0 s air exposure treatment served as a control group of the transmitter attachment procedure. Sample size per air exposure treatment was $N = 10$ but $N = 22$ field control fish were sampled to yield precise post-exercise values of physiological parameters. Average size (±SD) of pike used in the field component of this study was 500 ± 45 mm in total length, and size of pike did not differ between treatments ($F = 1.296$, df = 59, $p = 0.319$). Water temperature at time of capture averaged 15.7 ± 1.0 °C and ranged from 14.0 °C to 17.2 °C. There were no significant differences in water temperature at time of sampling between treatments ($F = 2.45$, df = 56, $p > 0.05$).

For monitoring movement activity during the first three weeks post release, pike of the air exposure treatments were outfitted with external radio telemetry tags (Model PD-2, Holohil Systems Inc., Ontario, Canada; weight in air = 3.7 g, 25 mm × 13 mm × 6 mm, battery life 6 months, 120 mm antenna wire). For external transmitter attachment, angled pike were placed ventral side down in a V-shaped foam lined trough filled with water where they were measured for total length. A neoprene backing plate was placed on two 22 gauge hypodermic needles mounted on 3 ml syringes and was pushed through the dorsal back musculature, ventral to the junction of the dorsal fin. From the opposite side, the transmitter attachment wires (surgical stainless steel, 20 gauge) that had already been threaded through the transmitter were inserted into the lumen of the needles. The wires were pulled out on the opposite side of the fish, and when the needles were removed, the neoprene backing plate was left in place to protect the body of the fish. The wires were twisted carefully and trimmed to minimize potential of fouling by vegetation (Cooke, 2003). Air exposure as the treatment variable was applied to the fish after attachment of the external transmitter and a blood sample was taken as described above. The only difference to the laboratory protocol was that here fish were held in a water filled trough for bleeding and we only removed 1.5 ml of blood (as per Cooke et al., 2005). Fish were released back into the lake following a standardized time of 10 min in a cooler filled with fresh lake water.

All fish were released at the same point (the littoral zone of a small bay) within a predefined observation area close to the Queen's Biology Station. The release bay was 2.7 ha and corresponded to the maximum detection range of radio-transmitters from the boat docks of the research station. Defining this somewhat artificial observation area allowed the research team to rapidly assess the presence of the pike in the vicinity of the release point. Although there were concerns that an area of 2.7 ha would be too large for a species such as pike that is often assumed to be inactive and sedentary when undisturbed by anglers (Kobler et al., 2008b), it became quickly obvious that movement of pike was extensive in Lake Opinicon. This rendered the approach to define a relatively extended observation area useful.

For monitoring the post-release behaviour of pike at a fine spatial scale within the first hour post release, fish were fitted with a small, coloured Styrofoam float attached to the superficial tissue at the posterior to the origin of the dorsal fin via a size eight J-type hook and monofilament nylon line (2.5 m long, 1.7 kg test line) (as per the approach of Cooke and Philipp, 2004). During the

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

first hour after release, detailed notes on the behaviour of the fish were recorded using float movement as an indicator of spatial activity. Observations were conducted from boat docks several m away from the pike, so that the fish would not see the observing person. Stopwatches and maps were used to estimate the time until first movement post release, rates of movement and distance travelled during the initial 1 h period. The duration within the first hour post release that the fish was stationary (resting time in % of first hour) was also determined. After 60 min, the float and the hook were removed by approaching the float by boat and gently tugging on the float and leaving the fish unrestrained. Because the hook associated with the float was placed in minimally vascularized fin tissue, bleeding and injury was likely negligible (Cooke and Philipp, 2004).

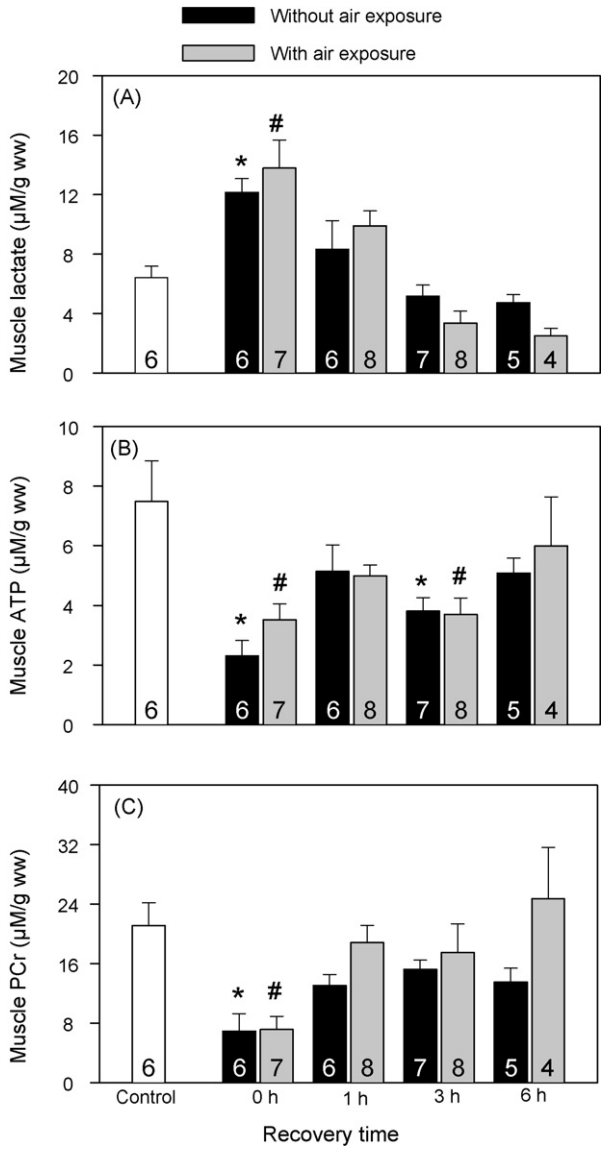

Fig. 1. Recovery profiles of variables in the muscle for pike with and without air exposure of 300 s after exhaustive exercise compared to resting control fish. Results of ANOVAs for fish not exposed to air were: muscle lactate ($F = 7.25$, df = 29, $p = 0.001$); muscle ATP ($F = 5.49$, df = 29, $p = 0.003$); muscle PCr ($F = 5.91$, df = 29, $p = 0.002$). Results of ANOVAs for pike exposed to air for 300 s were: muscle lactate ($F = 14.92$, df = 32, $p < 0.001$); muscle ATP ($F = 3.86$, df = 32, $p = 0.013$); muscle PCr ($F = 3.43$, df = 32, $p = 0.021$). *Significant differences for pike not exposed to air compared to laboratory controls; #significant differences for pike exposed to air compared to laboratory controls. Numbers in bars represent sample size.

In the first days and weeks post release, radio telemetry was used to assess distances moved for the first three days and more irregularly for three weeks post release for all air exposure treatments. Radio tracking was performed manually from a 9.9 horse powered outboard boat using a handheld receiver (Lotek SRX 400 Telemetry Receiver, Lotek, Ontario, Canada) and a three element Yagi antenna. This method has proved to generate acceptable location data because pike can be approached within about 2 m before eliciting a flight response (Kobler et al., 2008b; Klefoth et al., 2008). Each fish was tracked once a day for the first three days after release. Once a fish was located, its position was taken by a handheld global positioning system (Garmin, etrex summit, Kansas, USA; UTM coordinates) with a precision of ±5 m. Minimally moved distances were standardized to 12 h and determined as the straight line between successive locations (e.g., release point to location outside the observation area) and/or the nearest water distance between tracking points if a fish swam around a bay or an island. For the next three weeks, longer time intervals between successive locations were chosen and the moved distances were standardized to minimally moved distances per three days. Also, the distance to the release point in the days following release was calculated to analyze displacement patterns.

2.4. Biochemical analysis

Lactate and glucose levels were measured *in situ* on whole blood by adding 10 µl of blood into handheld glucose (Accu-check glucose meter, Roche diagnostics Corp., 150 Indianapolis, IN) and lactate (Lactate Pro LT-1710 portable lactate analyzer, Arkray Inc., Kyoto, Japan) meters. Appropriate standards and calibrations were used with meters prior to analysis as per the manufacturer guidelines. These field meters have been shown to produce results that are comparable to laboratory values for fish and other animals (e.g., Morgan and Iwama, 1997; Wells and Pankhurst, 1999) and even if minor deviations in values from laboratory assays exist, the relative differences among treatments are useful (Morgan and Iwama, 1997; Venn Beecham et al., 2006). After measuring the whole blood concentration of lactate and glucose, the blood sample was transferred to a centrifuge (Clay Adams Compact II Centrifuge, NY) and immediately spun at 10,000 × *g* for 5 min. Plasma was then removed using a pipette, placed in vials, and then stored in a liquid nitrogen dewar. Vials remained in liquid nitrogen until transferred to an ultracold (−80 °C) freezer. Laboratory processing occurred within 6 months after sample collection. Unfortunately, some vials failed, which reduced sample size for some treatments. Laboratory

Table 1
Results of a two-way-analysis of variance on the influence of recovery time and air exposure of 300 s on muscle tissue variables in pike: water content, muscle lactate, muscle ATP and muscle PCr. Significant factors are indicated in bold.

	Type III sum of squares	*F*	df	*p*-value
Water content (overall model)	18.08	1.27	7	0.287
Recovery time	1.837	0.303	3	0.823
Air exposure	0.001	0.001	1	0.980
Recovery × air exposure	15.942	2.627	3	0.064
Muscle lactate (overall model)	764.58	11.32	7	**<0.001**
Recovery time	708.41	24.48	3	**<0.001**
Air exposure	0.527	0.055	1	0.816
Recovery × air exposure	40.372	1.395	3	0.257
Muscle ATP (overall model)	54.29	2.90	7	**0.014**
Recovery time	49.94	6.233	3	**0.001**
Air exposure	2.652	0.993	1	0.325
Recovery × air exposure	4.722	1.574	3	0.625
Muscle PCR (overall model)	1383.46	3.817	7	**0.003**
Recovery time	989.93	6.273	3	**0.001**
Air exposure	287.82	5.558	1	**0.023**
Recovery × air exposure	181.88	1.171	3	0.332

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

analyses were conducted to determine plasma ion concentrations (Na^+, K^+, Ca^{++}, Cl^-) using a Roche Hitachi 917 analyzer (Basel, Switzerland) with the relevant Roche reagents. Analyses were based on the International Federation of Clinical Chemistry and Laboratory Medicine (IFCC) standard reference model. Excised muscle samples were also stored in vials at −80 °C until being processed. Tissue lactate, phosphocreatine (PCr), and adenosine triphosphate (ATP) concentrations were measured following the enzymatic methods of Lowry and Passonneau (1972) after processing the muscle according to the procedure described in Booth et al. (1995). Water content in white muscle was determined by drying pre weighed frozen tissue in an 80 °C oven for approximately 48 h until a constant mass was obtained.

2.5. Statistical analyses

Continuous variables (e.g., physiological variables, distance moved, and distance to release point) were compared between the treatment groups and control values using parametric tests (one-way-ANOVAs). Each ANOVA was followed by the conservative Tukey's *post hoc* tests to assess differences between treatment groups when variances were homogenous, and Dunnet T-3 post hoc tests were used when variances were heterogeneous was assessed by Levene's tests. In the laboratory experiment, differences between treatment groups were analyzed relative to resting control values, and two separate one-way-ANOVAs were calculated for fish that were and were not exposed to air. To analyze whether air exposure affected the recovery profile of the physiological variables in the laboratory, a two-way-ANOVA was applied with recovery period and air exposure and their interaction as factors. In case of deviations from the underlying assumptions of parametric tests (normality, variance homogeneity, $p < 0.05$), continuous data were $\log_e$-transformed. After transformation, all dependent variables met the assumptions for parametric tests ($p > 0.05$ in all cases). For all comparisons the significance was assessed at $\alpha = 0.05$. Sample size in the different analyses varied due to vial malfunction, partial failure to track all fish on all occasions or entanglement of the float in shoreline vegetation or other structures within the first hour post release. In the latter case, the data were analyzed until the time when the float detached from the pike. All statistical tests were conducted using SPSS version 14.0. Data are presented as means ±1SE unless otherwise noted.

3. Results

3.1. Recovery from exercise in the laboratory

One minute of exhaustive exercise significantly affected muscle metabolite concentrations in pike. Specifically, 60 s of exercise caused muscle lactate concentrations to double relative to control values, and this concentration was not significantly influenced by an additional 300 s of air exposure (Fig. 1A; Table 1). Following this exercise and air exposure duration, muscle lactate concentrations returned to control values with 1 h recovery time (Fig. 1A; Table 1).

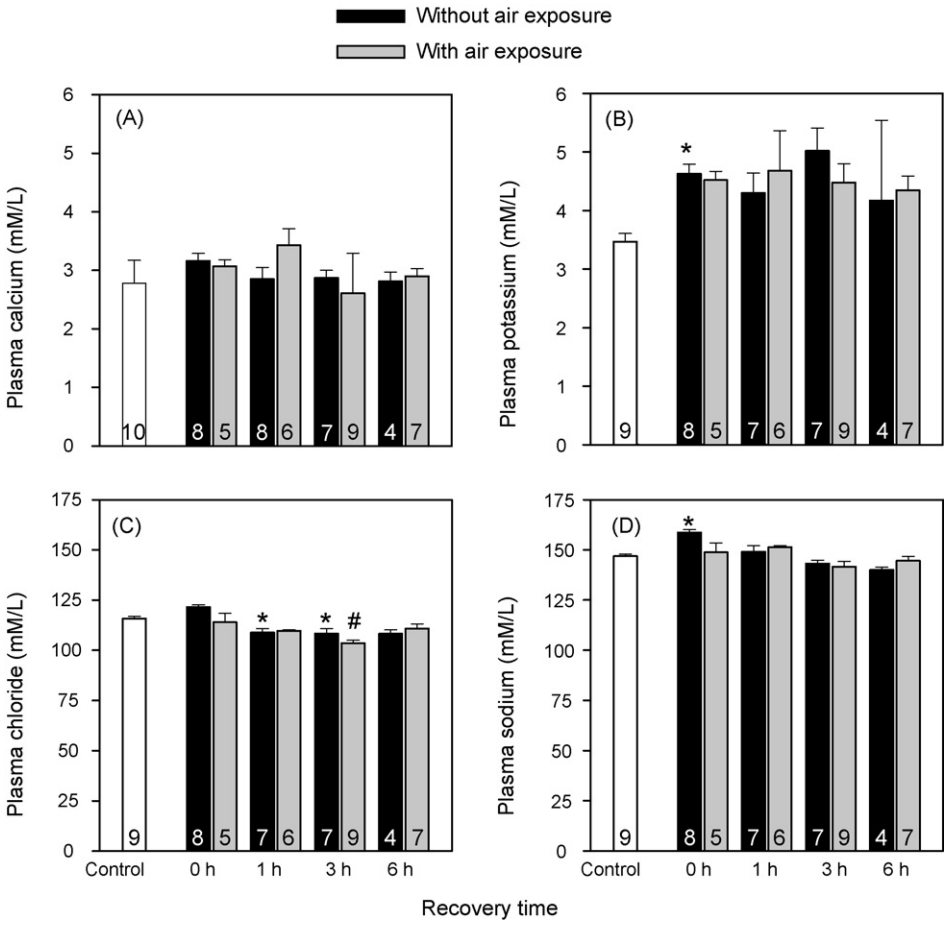

Fig. 2. Recovery profiles of plasma ions for pike with and without air exposure of 300 s after exhaustive exercise compared to resting control fish. Results of ANOVAs for fish not exposed to air were: calcium ($F = 1.34$, df = 36, $p = 0.274$); chloride ($F = 12.00$, df = 34, $p < 0.001$); potassium ($F = 4.50$, df = 30, $p = 0.006$); sodium ($F = 13.40$, df = 30, $p < 0.001$). Results of ANOVAs for pike exposed to air for 300 s were: calcium ($F = 3.83$, df = 36, $p = 0.012$; Dunnett-T3-post hoc test did not reveal any differences between treatments); chloride ($F = 6.84$, df = 35, $p < 0.001$); potassium ($F = 2.20$, df = 35, $p = 0.090$); sodium ($F = 2.48$, df = 35, $p = 0.064$). *Significant differences for pike not exposed to air compared to laboratory controls; #significant differences for pike exposed to air compared to laboratory controls. Numbers in bars represent sample size.

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

In pike exercised but not exposed to air, muscle ATP and PCr levels declined by approximately 70% and 66%, respectively, compared to control values (Fig. 1B and C), while muscle ATP and PCr levels declined by approximately 50% and 66%, respectively, compared to resting control values in fish exposed to air for 300 s. Full recovery of muscle PCr was achieved after 1 h regardless of air exposure duration, but required 6 h in ATP (Fig. 1B and C). A two-way-ANOVA showed that recovery profiles were similar for fish with and without air exposure for tissue lactate, ATP and PCr as indicated by the lack of significant recovery time × air exposure interaction term (Table 1). However, muscle PCr values were significantly affected by air exposure (Table 1). Water content in muscle was stable across all recovery periods and did not vary with either exercise, recovery or air exposure duration (Table 1).

Similarly, one minute of exhaustive exercise induced ionic disturbances in pike. Specifically, pike that had been exercised for 60 s without additional air exposure experienced a significant elevation in plasma potassium and sodium relative to control values (Fig. 2); these disturbances were corrected following 1 h of recovery and were not present in pike that received an additional 300 s air exposure treatment. In addition, in fish with and without air exposure plasma chloride levels significantly dropped at 1 h and 3 h of recovery, respectively, relative to baseline values, but these disturbances were corrected following 6 h recovery (Fig. 2). A two-way-ANOVA with recovery time and air exposure as factors showed that plasma chloride and sodium levels significantly differed across recovery periods but plasma calcium and potassium levels were stable. It is noteworthy to note that air exposure of 300 s was unrelated to all plasma ion levels and all interactions terms between air exposure × recovery time were not statistically significant (Table 2). This indicated that air exposure of 300 s did not magnify osmotic disturbances nor altered the recovery profile.

Exhaustive exercise with and without additional air exposure resulted in significantly elevated plasma glucose levels in pike compared to control values (Fig. 3). For pike that were air exposed for 300 s following exercise, plasma glucose concentrations at 1 h post exercise were approximately double control values, but this disturbance returned to resting levels after 3 h of recovery. Similarly, pike that were exercised but did not receive additional air exposure exhibited plasma glucose concentrations that were approximately 50% greater than control values at 6 h post exercise. A two-way-ANOVA with recovery time and air exposure and their interactions as factors revealed that air exposure of 300 s did not significantly alter the recovery profile of plasma glucose (Table 2).

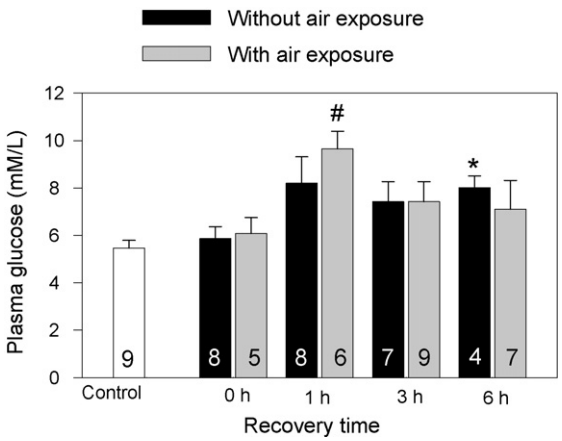

Fig. 3. Recovery profiles of plasma glucose for pike with and without air exposure of 300 s after exhaustive exercise compared to resting control fish. Result of ANOVA for fish not exposed to air was $F = 2.949$, df = 35, $p = 0.036$ and for fish exposed to air $F = 3.467$, df = 35, $p = 0.019$. *Significant differences for pike not exposed to air compared to laboratory controls; #significant differences for pike exposed to air compared to laboratory controls. Numbers in bars represent sample size.

Table 2
Results of a two-way-analysis of variance on the influence of recovery time and air exposure of 300 s on plasma ions and glucose in pike. Significant factors are indicated in bold.

	Type III sum of squares	*F*	df	*p*-value
Calcium (Ca^{++}) (overall model)	3.065	2.064	7	0.067
Recovery time	1.614	2.535	3	0.068
Air exposure	0.086	0.405	1	0.528
Recovery × air exposure	1.398	2.197	3	0.101
Potassium (K^+) (overall model)	3.066	0.483	7	0.841
Recovery time	1.561	0.574	3	0.635
Air exposure	0.007	0.007	1	0.933
Recovery × air exposure	1.700	0.626	3	0.602
Chloride (Cl^-) (overall model)	1541.42	7.561	7	**<0.001**
Recovery time	1004.71	11.43	3	**<0.001**
Air exposure	60.62	2.071	1	0.157
Recovery × air exposure	198.26	2.257	3	0.095
Sodium (Na^+) (overall model)	1821.12	6.468	7	**<0.001**
Recovery time	1238.34	10.26	3	**<0.001**
Air exposure	17.10	0.425	1	0.518
Recovery × air exposure	351.00	2.909	3	**0.045**
Glucose (overall model)	65.273	1.621	7	0.153
Recovery time	56.67	3.285	3	0.029
Air exposure	0.496	0.86	1	0.770
Recovery × air exposure	8.6	0.499	3	0.685

3.2. Influence of air exposure on physiological status in the field

Exposing angled pike to air for different durations up to 300 s significantly increased blood lactate concentrations relative to control values (Fig. 4A) but not blood glucose levels (Fig. 4B) or plasma ions (Fig. 5). Compared to field control fish, all air exposure treatments raised blood lactate concentrations approximately two-fold (Fig. 4A). However, blood lactate concentrations did not correlate positively with air exposure duration (Fig. 4A). In contrast, air exposure durations of 60 s, 180 s or 300 s did not result in significant changes to blood glucose (Fig. 4B), plasma chloride, plasma sodium, plasma calcium or plasma potassium (Fig. 5).

3.3. Influence of air exposure on post-release behaviour and fate in the field

Behaviour of released pike within the first hour post release was significantly related to air exposure duration (Fig. 6). Specifically, pike exposed to air for 300 s spend a larger fraction time resting (rather than actively swimming) during the first hour post release than fish not exposed to air (Fig. 6A). Similarly, pike exposed to the longest air exposure duration required significantly longer (on average more than 15 min) to initiate the first movement post release compared to fish exposed to 0 s or 60 s of air exposure (Fig. 6B). There was also a trend for reduced swimming activity with increasing air exposure duration (Fig. 6C) but this relationship was not statistically significant due to high inter-individual differences in moved distances. Overall, pike were rather sedentary in the first hour post release moving on average less than 50 m in all air exposure treatments.

Pike behaviour in the first days post release was unrelated to air exposure duration (Table 3). For all movement metrics examined (minimally moved distance per 12 h in the first three days post release, distance to release point) no statistical differences in behavioural patterns were found among air exposure treatment fish. The general movement pattern of all treatment groups involved minimally moved distances of between 100 m and 250 m per 12 h in the first three days post release. Within the first three weeks post release minimally moved distances were smaller than those exhibited during the first three days post release (Table 3).

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

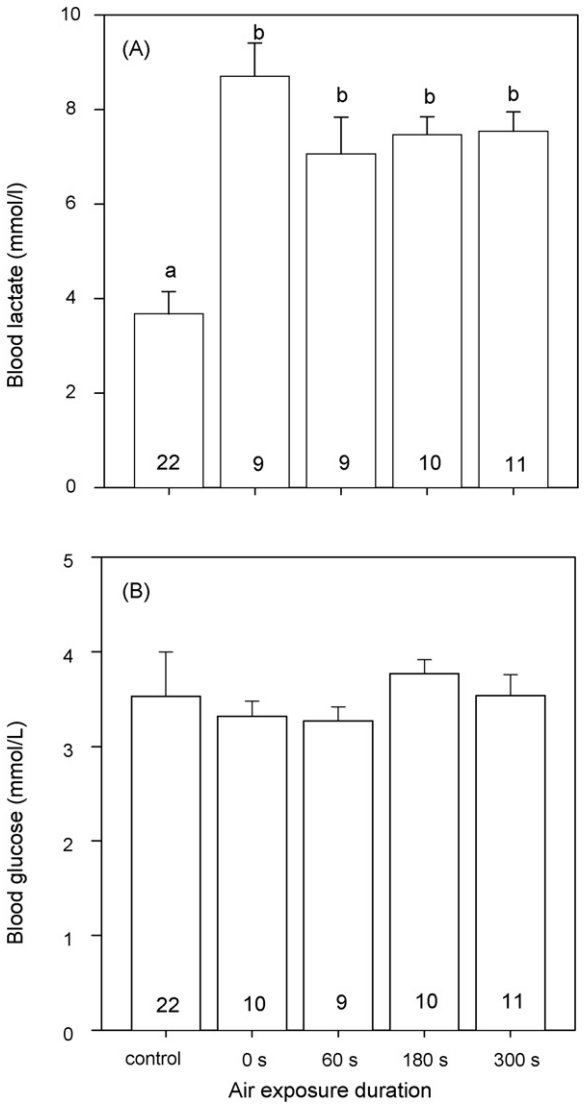

Fig. 4. Impact of air exposure duration on blood lactate and glucose for pike compared to field control fish. Results of ANOVAs were: lactate $F = 15.73$, df = 60, $p < 0.001$; glucose $F = 2.028$, df = 61, $p = 0.942$. Bars sharing the same letter are not significantly different. Numbers in bars represent sample size.

Average distances moved per three days ranged between 56 m and 443 m in the treatment groups, and were thus substantially smaller than the movement exhibited during the first three days post release. Displacement away from the common release site was moderate within the first day post release for all treatment groups exhibiting displaced distances of less than 250 m on average (with the 60 s treatment group as an exception). A consistently large displacement movement away from the release site took place after day one post release. After 48 h at the end of day two, all pike from all treatment groups were located between 1.5 km and 2.5 km away from the release site (Table 3). After this peak, displacement was less pronounced in a three-week post-release monitoring period. In fact, many pike moved closer to the release site again after day two post release (Table 3). The maximum displacement after three weeks was 3.8 km and the lowest value was only 212 m.

Within a three-week post-release monitoring period no pike died as inferred from substantial movement of the tagged pike and in fact several fish were recaptured by anglers and reported to the research team indicating active feeding of the released fish.

4. Discussion

We found partial support for our hypothesis that exposing pike to air results in physiological alterations and modified behaviour post release, with longer air exposure elevating these adaptive responses. While we indeed found a strong, yet statistically not significant trend, for longer air exposure duration reducing swimming activity of pike, air exposure of 300 s did significantly influence only some physiological variables and the recovery profiles in our laboratory study, and there were no relations between air exposure duration and stress physiology indicators in the field. It appeared that physiological disruption in pike was mainly related to exhaustive exercise. However, the significantly impaired behaviour of pike exposed to air for 300 s relative to other air exposure treatments indicated that despite lack of clear signals in the blood physiology values, prolonged air exposure was detrimental to organismal performance.

We reported three novel insights on the physiological and behavioural dynamics of pike in response to C&R related stressors. First, recovery of pike from exhaustive exercise designed to simulate an angling event was found to be more rapid than previously reported; most physiological variables examined returned to baseline levels within the first hour of recovery, and full recovery was completed within 6 h for all examined physiological parameters except for glucose. Second, the recovery profile of most physiological variables was largely unaffected by an extreme period of air exposure (300 s); the field component of this study verified this

Table 3
Long-term movement and displacement of pike exposed to different air exposure durations (0 s, 60 s, 180 s or 300 s, sample size in parentheses). Note different units for first three days compared to thereafter resulting from inconsistent tracking intervals (with more effort devoted to the first three days). There were no significant differences among treatments, which is why results of statistical tests are not presented.

Movement variable	0 s	60 s	180 s	300 s
Minimal movement rate post release				
Day 1 (m 12 h^{-1})	98 ± 25 (10)	254 ± 97 (8)	177 ± 82 (10)	140 ± 56 (8)
Day 2 (m 12 h^{-1})	211 ± 55(10)	221 ± 43 (7)	156 ± 39 (10)	225 ± 98 (10)
Day 3 (m 12 h^{-1})	119 ± 51 (10)	144 ± 55 (7)	156 ± 58 (10)	130 ± 62 (9)
1st week (m 3 $days^{-1}$)	232 ± 63 (9)	253 ± 77 (8)	443 ± 159 (8)	222 ± 124 (8)
2nd week (m 3 $days^{-1}$)	70 ± 32 (9)	60 ± 37 (9)	251 ± 81 (7)	134 ± 45 (6)
3rd week (m 3 $days^{-1}$)	195 ± 64 (7)	238 ± 101 (7)	65 ± 23 (8)	56 ± 26 (8)
Distance to release point				
Day 1 (m)	105 ± 32.1 (10)	610 ± 251 (9)	230 ± 121 (10)	246 ± 99 (11)
Day 2 (m)	1819 ± 526 (8)	2093 ± 886 (7)	1559 ± 282 (9)	2570 ± 666 (8)
Day 3 (m)	1881 ± 503 (9)	2303 ± 933 (7)	1946 ± 361 (7)	1541 ± 572 (8)
Day 7 (m)	1089 ± 197 (9)	1246 ± 255 (8)	1025 ± 155 (8)	732 ± 194 (8)
Day 14 (m)	1133 ± 198 (9)	1197 ± 248 (9)	708 ± 182 (7)	842 ± 168 (8)
Day 21 (m)	899 ± 198 (7)	998 ± 308 (7)	670 ± 145 (8)	1138 ± 407 (8)

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

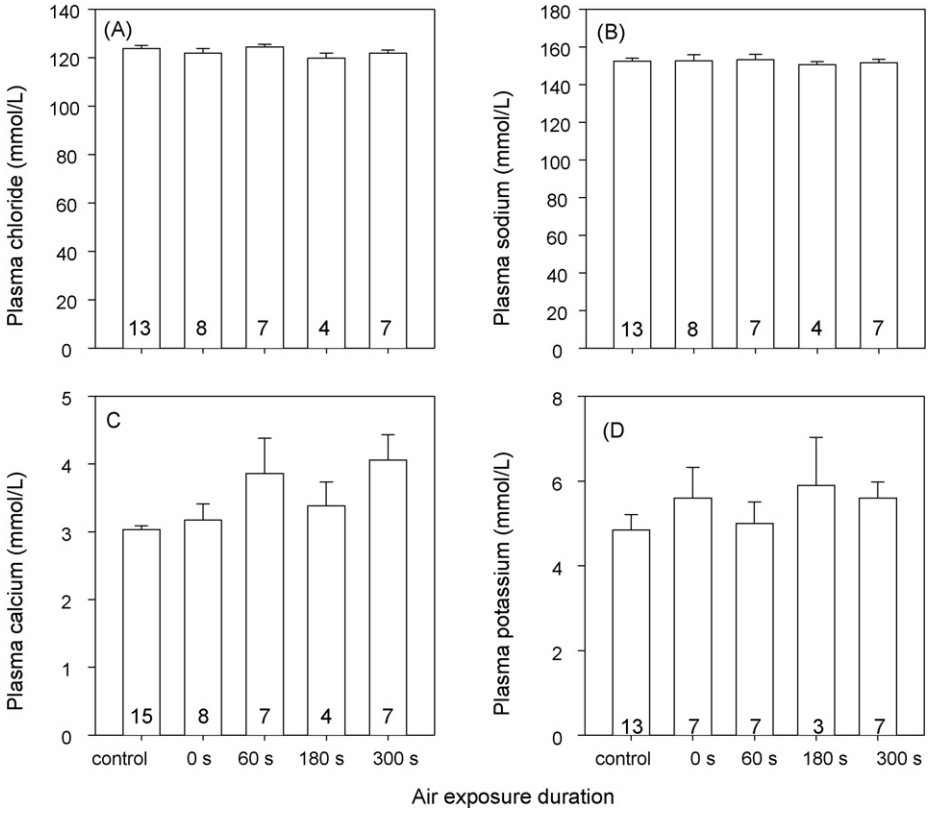

Fig. 5. Impact of air exposure duration on plasma ions for pike compared to field control fish. Results of ANOVAs were: chloride (plot A, $F = 1.081$, df = 38, $p = 0.381$); sodium (plot B, $F = 0.145$, df = 38, $p = 0.964$); calcium (plot C, $F = 2.780$, df = 40, $p = 0.041$; Dunnett-T3-post hoc test did not reveal any differences between treatments); potassium (plot D, $F = 0.680$, df = 35, $p = 0.611$). Numbers in bars represent sample size.

findings by showing that most physiological variables did not vary with air exposure duration ranging from 0 s to the maximum of 300 s, and maximum response of physiological variables occurred through exhaustive exercise in the process of playing the fish for 60 s. Third, we found that exhaustively exercised fish that experience air exposure are behaviourally impaired, but only in the short term within the first hour post release, which conformed with rapid physiological recovery observed in the laboratory.

It is worth noting that air exposure and exhaustive exercise did not lead to post-release mortality in a three-week monitoring period. This finding contrasted with the study of DuBois et al. (1994) who reported a positive relation between short air exposure (termed handling time by the authors) and post-release mortality in pike. However, there was a significant interaction between study-lake and hooking location on handling times (i.e., air exposure) in the study by DuBois et al. (1994). The authors were thus unable to disentangle the impacts of air exposure and hooking location on hooking mortality in pike. Our study indicates that exhaustive exercise coupled with air exposure up to 300 s does not lead to post-release mortality but we constrained our study to pike that were not hooked deeply and appeared healthy. However, there is the limitation that tagged pike in our study might have been predated upon by cannibals or other predators as we inferred survival indirectly based on movement propensity. However, since there are few large pike and no other large predators in the study-lake, it is unlikely that a substantial fraction of pike released with transmitters were predated suggesting robustness of our findings. Irrespective, understanding the interactive effects of different C&R related stressors (e.g., level of injury, condition of fish, air exposure duration and water temperature) on post-release mortality including predation by predators constitutes a promising avenue for future studies in pike and other species (Gingerich et al., 2007).

Our results on the recovery dynamics from physiological disruption after exhaustive exercise in pike agree well with previous work on this species. In the laboratory component of our study, muscle lactate, as well as the energy fuels ATP and PCr, all changed significantly following a simulated angling event. Recovery from physiological disturbances such as angling varies across the indicator used, but full recovery was previously reported to occur within the first 12 h in pike (Soivio and Oikari, 1976; Armstrong et al., 1989; Schwalme and Mackay, 1985a,b). We presented evidence that recovery of physiological disruption is even more rapid in this species. Angling-induced stressors are identical to that of exhaustive exercise, and typically result in decreases in white muscle energy stores (i.e., PCr and ATP) and accumulation of lactate (e.g., Wood, 1991; Suski et al., 2003, 2004, 2006, 2007). The same patterns were observed in our study.

The abrupt increase of muscle lactate in pike shortly after exhaustive exercise was expected given the fast-start nature of this species (Harper and Blake, 1991), which is well adapted to rapid attack bursts of short duration (Schwalme and Mackay, 1985a,b). The maximum concentration of muscle lactate post exercise observed in the present study conformed with maximum values published by Suski et al. (2006) for exhaustively exercised largemouth bass, but were lower than maximum values reported by Schwalme and Mackay (1985a) for pike (44.8 μmol/g). Intraspecific differences are likely related to the type and degree of exercise/handling/stress applied across the two different studies. For example, Schwalme and Mackay (1985a) angled pike for an average of 1.4 min at slightly higher average water temperature (19 °C) than was the case in the present study (1 min exercise at 18.6 °C). Moreover, Schwalme and Mackay (1985a) sampled fish 7 min after being angled, while we sampled pike immediately after angling simulation in the laboratory. These divergent treatments

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

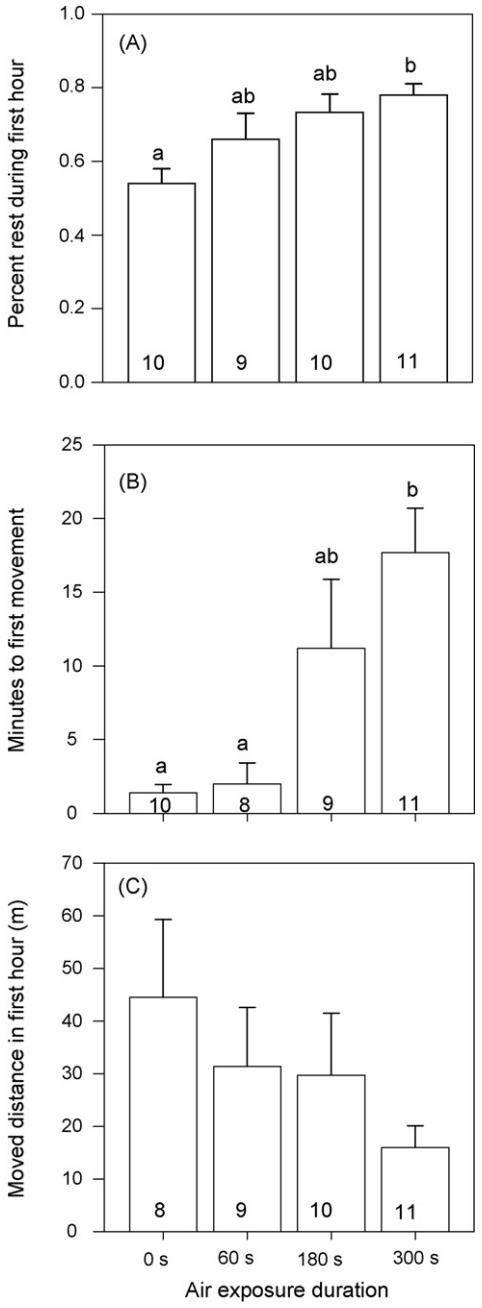

Fig. 6. Impacts of air exposure duration on short-term behavioural patterns within the first hour post release in pike. Results of ANOVAs were: percent resting within the first hour (plot A, $F = 4.522$, df = 39, $p = 0.009$); minutes to first movement (plot B, $F = 7.665$, df = 37, $p < 0.001$); total movement (m) in first hour (plot C, $F = 1.205$, df = 37, $p = 0.323$). Bars sharing the same letter are not significantly different. Numbers in bars represent sample size.

and environmental conditions as well as different analytical techniques make the direct comparison of absolute lactate values across studies difficult. However, the recovery dynamics after stress were similar in both studies. Clearance of lactate from the muscle and restoration of anaerobic fuels was quick in the present study and concentrations returned to control values after only 1 h.

Schwalme and Mackay (1985a) found that pike are able to clear their lactate load from the blood without conversion into glucose. Elevated glucose levels in the blood of pike are therefore not a consequence of lactate removal but constitute a true indicator of a secondary stress response (energy mobilization). Indeed, we found that plasma glucose was the only physiological indicator of the secondary stress response in fish that remained elevated even after 6 h in exhaustively exercised pike. This may indicate some level of stress from holding fish in captivity unrelated to the actual treatment (Schwalme and Mackay, 1985a; Wendelaar Boga, 1997; Mommsen et al., 1999). Indeed previous work in pike has shown that glucose levels remained elevated for as long as 96 h post release in confined situations (Soivio and Oikari, 1976; Schwalme and Mackay, 1985a).

The assumption that pike experienced some level of captivity stress in laboratory environments is also supported by the counterintuitive short-term increases in potassium and sodium levels observed immediately after the simulated angling in the laboratory. Often, plasma ions tend to decrease following the onset of a stressor for freshwater fish (Wendelaar Bonga, 1997) as was evident for chloride in the present study. Interestingly, however, Soivio and Oikari (1976) reported increases (rather than decreases) in potassium concentrations in stressed pike in the laboratory, which agrees with our findings. Because we did not find any changes in water muscle content in response to exhaustive exercise and air exposure, changes in plasma electrolytes are likely not a result of "haemoconcentration" resulting from water shifts from the blood into the white muscle. Wang et al. (1994) noted that increases in electrolytes in rainbow trout (*Onchorhynchus mykiss*) directly after exhaustive exercise that were likely related to fluid shits into red blood cells, and perhaps tissues other than white muscle, as well as ionic movements at the gills. While increased sodium update from the water in exchange for protons (Holeton et al., 1983) was one likely explanation for the short-term increase in this variable in our study, the delayed fall of calcium concentrations we observed was probably due to losses of this ion across the gills over time following decreased Cl^-/HCO_3^- exchange for acid-based regulation (Holeton et al., 1983). In terms of potassium, gill tissue and adrenergically stimulated and swollen red blood cells remain likely sources (Wang et al., 1994) that might explain the short-term elevation of potassium in the present study. Irrespective of these ionic alterations, all plasma ions returned to baseline values within 6 h indicating rapid recovery of osmotic balance, and no impact of air exposure on plasma ions was detected in the field component of our study. This indicates that osmotic disturbances in pike in response to exhaustive exercise and air exposure exist only in the short term (laboratory study) if at all (field study).

In the field component of our study, playing pike for 60 s revealed elevated blood lactate values in all air exposure treatment groups compared to field controls, but air exposure did not significantly alter either blood glucose or plasma ion concentrations. The increased lactate concentrations from pike in the 0 s air exposure treatment group compared to control fish is related to the timing of the blood sample. In all treatment groups the blood sample was taken after an external transmitter was attached. Despite rapid attachment of transmitters within 3 min after capture, the time between sampling blood differed between field control fish (sampled immediately after a 60 s fight) and all air exposure treatment fish, including the 0 s air exposure level. This difference in sampling time likely allowed lactate produced during angling to leak into the blood while fish were being equipped with their external transmitter (Milligan and Wood, 1986). This explains the significantly elevated blood lactate concentrations in all treatment groups compared to control fish and, particularly, the significant differences between 0 s of air exposure and field control fish. What is important to note, however, is the lack of relation between blood lactate values and air exposure duration in pike, which does not confirm with studies on other freshwater fish species, most of which document a positive correlation between stressor duration and lactate concentration (Gustaveson et al., 1991; Davis and Schreck, 2005; Killen et al., 2006). This discrepancy is likely related to the physiological characteristics and metabolism of pike. The pike's muscle predominantly is comprised of white (i.e., anaerobic)

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

fibres (Schwalme and Mackay, 1985a). Thus, after an extended angling bout, the anaerobic capacity of the muscle in fast start sprinter species such as pike seems to be already at maximum response such that additional anaerobic challenges related to air exposure do not further increase lactate values.

Despite the lack of a relationship between air exposure duration and most physiological variables, the behavioural portion of our study revealed important insights into the sub-lethal impacts of air exposure on organismal performance. Pike exposed to air for 300 s were significantly less mobile in the first hour post release compared to control fish, and there was a strong, albeit not significant, trend for reduced swimming activity with increasing air exposure duration. It is difficult to unambiguously relate this reduced swimming activity of to a single physiological variable. For example, the laboratory study revealed that PCr levels in the muscle and chloride levels in the plasma were significantly related to air exposure of 300 s, while there was no impact of this air exposure level of blood lactate and glucose in the field. It is entirely possible that unmeasured variables played a crucial role in reducing the swimming activity after long durations of air exposure, and other authors have also noted a lack of concordance between physiological responses to stress and various organismal endpoints in fish (Davis et al., 2001; Davis and Schreck, 2005; Thompson et al., 2008). Indeed, behavioural measures in response to stressors integrate a multitude of biochemical and physiological changes that occur in response to stress (Schreck et al., 1997) such as the reduction in swimming activity to extended air exposure in our study is likely to constitute a cumulative response to various physiological changes. Irrespective of the exact physiological mechanism, our study showed that air exposure duration of 300 s combined with exhaustive exercise resulted in a marked tertiary stress response as indicated by reduced movement activity shortly after release. This air exposure duration thus constitutes an upper air exposure threshold in pike if the intention is to avoid behavioural impairments in terms of swimming activity post release, but this threshold potentially only holds for rather moderate water temperatures and may be lower at higher water temperatures (Gingerich et al., 2007). Indeed, air exposures of this duration have been shown to also reduce swimming ability in other freshwater fish species post release (Mitton and McDonald, 1994; Schreer et al., 2005), including pike (Klefoth et al., 2008), confirming the short-term behavioural changes observed in the present study.

Our laboratory study has shown that recovery of physiological homeostasis is rapid in pike. With few exceptions such as glucose, all variables returned to baseline levels within a period of 6 h of post-release recovery and we also found that air exposure did not substantially affect the recovery profile in pike. Thus, we would not expect any differences among air exposure treatments in their post-release behaviour once physiological recovery is completed. Consistent with this idea, no significant differences in movement metrics (e.g., minimally moved distances or displaced distances away from a common release site) were detected between air exposure treatments in the present study after the first hour post release. This corroborated the rapid recovery of normal behavioural patterns, but this statement must be interpreted with caution as we did not record the behaviour of pike before they were captured and handled. This is a general limitation of telemetry studies in a C&R context that depend on fish to be captured in the first place (Donaldson et al., 2008). However, lacking a control group that was not angled in our study does not affect the validity of our findings as our results were generated relative to appropriate (i.e., equally handled) treatment groups that differed only in the duration of air exposure. In addition, Klefoth et al. (2008) compared the behaviour of pike post release with pre capture behaviour and also reported decreased swimming activity post release. The authors showed that resubmission of pre-capture behavioural patterns can be expected within the first week post release in pike but pike were located at large temporal intervals of several days. The results in the present paper suggest that recovery of normal behavioural patterns occurs much sooner than previously reported within the first 24 h post release.

Results of our study indicate that C&R related stressors result in disruption of physiological homeostasis and impairment of behaviour. However, since recovery of these variables was found to be rapid, our study also indicates a high level of resiliency of pike against C&R related air exposure. However, we did not assess other variables of the tertiary stress response to C&R related stressors such as growth depression (Siepker et al., 2006) and we can only speculate about potential population-level consequences such that the last statement shall be viewed with caution. In addition, one final concern has to be raised if one subjects to a fish welfare perspective (Arlinghaus et al., 2007b). When taking this perspective, any secondary and tertiary stress response to C&R should be minimized whenever possible. With behavioural impairment being a sensitive aggregate indicator of the welfare status of a fish (Arlinghaus et al., 2007b; Arlinghaus et al., 2008b), the short-term behavioural changes observed in the present study in response to extended air exposure of 300 s support the recommendation that anglers should expose pike to less than 300 s of air to maintain the welfare status of the fish post release.

Acknowledgements

We thank the staff of Queen's Biological Station for facilitating this research activity in Canada. Work was approved by the Canadian Council on Animal Care through the Carleton University Animal Care Committee (Application B06-04). We also thank the Ontario Ministry of Natural Resources for kindly providing scientific collection permits. Funding for this project was provided by the German Academic Exchange Service (DAAD) through an international master of science grant to TK, the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, the Leibniz-Community within the Adaptfish-project to RA (www.adaptfish.igb-berlin.de), the Canadian Foundation for Innovation, the Natural Sciences and Engineering Research Council, the Rainy Lake Fisheries Charity Trust, and Carleton University. We thank Mike Donaldson, Kyle Hanson and the students of the Cooke lab for help with the field work and Martin Bork for editorial assistance. Josh Sherwood provided valuable assistance with laboratory analyses. Two anonymous reviewers provided positive comments on a previous version of this paper, which is gratefully acknowledged.

References

Arlinghaus, R., 2007. Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp (*Cyprinius carpio*) angling in Germany. Fish. Manage. Ecol. 14, 161–171.

Arlinghaus, R., Mehner, T., 2004. A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). Environ. Manage. 33, 331–344.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., Thorstad, E.B., 2007a. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev. Fish. Sci. 15, 75–167.

Arlinghaus, R., Cooke, S.J., Schwab, A., Cowx, I.G., 2007b. Fish welfare: a challenge to the feelings-based approach, with implications for recreational fishing. Fish Fish. 8, 57–71.

Arlinghaus, R., Klefoth, T., Kobler, A., Cooke, S.J., 2008a. Size-selectivity, capture efficiency, injury, handling time and determinants of initial hooking mortality of angled northern pike (*Esox lucius* L.): the influence of bait type and size. N. Am. J. Fish. Manage. 28, 123–134.

Arlinghaus, R., Klefoth, T., Gingerich, A.J., Donaldson, M.R., Hanson, K.C., Cooke, S.J., 2008b. Behaviour and survival of pike, *Esox lucius*, with a retained lure in the lower jaw. Fish. Manage. Ecol. 15, 459–466.

Armstrong, J.D., Lucas, M.C., Priede, I.G., de Vera, L., 1989. An acoustic telemetry system for monitoring the heart rate of pike (*Esox lucius* L.) and other fish in their natural environment. J. Exp. Biol. 143, 549–552.

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005

Barthel, B.L., Cooke, S.J., Suski, S.D., Philipp, D.P., 2003. Effects of landing net mesh type on injury and mortality in a freshwater recreational fishery. Fish. Res. 63, 275–282.
Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. 15, 129–154.
Beggs, G.L., Holeston, G.F., Crossman, E.J., 1980. Some physiological consequences of angling stress in muskellunge (*Esox masquinongy* Mitchell). J. Fish Biol. 17, 649–659.
Booth, R.K., Kieffer, J.D., Davidson, K., Bielak, A.T., Tufts, B.L., 1995. Effects of late-season catch and release angling on anaerobic metabolism, acid-based status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 52, 283–290.
Cooke, S.J., 2003. Externally attached radio transmitters do not affect the parental care behaviour of rock bass. J. Fish Biol. 62, 965–970.
Cooke, S.J., Philipp, D.P., 2004. Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. Biol. Conserv. 118, 599–607.
Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodiv. Conserv. 14, 1195–1209.
Cooke, S.J., Schramm, H.L., 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. Fish. Manage. Ecol. 14, 73–79.
Cooke, S.J., Schreer, J.F., Dunmall, K.M., Philipp, D.P., 2002. Strategies for quantifying sublethal effects of marine catch-and-release angling—insights from novel freshwater applications. Am. Fish. Soc. Sym. 30, 121–134.
Cooke, S.J., Philipp, D.P., Dunmall, K.M., Schreer, J.F., 2001. The influence of terminal tackle on injury, handling time, and cardiac disturbance of rock bass. N. Am. J. Fish. Manage. 21, 333–342.
Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., Alexander, R.F., Healey, M.C., van der Kraak, G., Farrell, A.P., 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. J. Fish Biol. 67, 1342–1358.
Davis, M.W., Parker, S.J., 2004. Fish size and exposure to air: potential effects on behavioural impairment and mortality rates in discarded sablefish. N. Am. J. Fish. Manage. 24, 518–524.
Davis, M.W., Schreck, C.B., 2005. Response by Pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality. Trans. Am. Fish. Soc. 134, 991–998.
Davis, M.W., Olla, B.L., Schreck, C.B., 2001. Stress induced by hooking, net towing, elevated sea water temperature and air in sable fish: lack of concordance between mortality and physiological measures of stress. J. Fish Biol. 58, 1–15.
Donaldson, M.R., Arlinghaus, R., Hanson, K.C., Cooke, S.J., 2008. Enhancing catch-and-release science with biotelemetry. Fish Fish. 9, 79–105.
DuBois, R.B., Margenau, T.L., Stewart, R.S., Cunningham, P.K., Rasmussen, R.W., 1994. Hooking mortality of northern pike angled through ice. N. Am. J. Fish. Manage. 14, 769–775.
Fayram, A.H., 2003. A comparison of regulatory and voluntary release of muskellunge and walleyes in northern Wisconsin. N. Am. J. Fish. Manage. 23, 619–624.
Ferguson, R.A., Tufts, B.L., 1992. Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for "catch and release" fisheries. Can. J. Fish. Aquat. Sci. 49, 1157–1162.
Gingerich, A.J., Cooke, S.J., Hansen, K.C., Donaldson, M.R., Hasler, C., Suski, C., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. Fish. Res. 86, 169–178.
Gustaveson, A.W., Wydoski, R.S., Wedemeyer, G.A., 1991. Physiological response of largemouth bass to angling stress. Trans. Am. Fish. Soc. 120, 629–636.
Harper, D.G., Blake, R.W., 1991. Prey capture and the fast-start performance of northern pike (*Esox lucius*). J. Exp. Biol. 155, 175–192.
Holeton, G.F., Neuman, P., Heisler, N., 1983. Branchial ion exchange and acid–base regulation after strenuous exercise in rainbow trout (*Salmo gairdneri*). Respir. Physiol. 51, 303–318.
Houston, A.H., 1990. Blood and circulation. In: Schreck, C.B., Moyle, P.B. (Eds.), Methods for Fish Biology. Am. Fish. Soc., Bethesda, Maryland, pp. 273–334.
Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. Part A 126, 161–179.
Killen, S.S., Suski, C.D., Cooke, S.J., Philipp, D.P., Tufts, B.L., 2006. Factors contributing to the physiological disturbance in walleyes during live-release angling tournaments. Trans. Am. Fish. Soc. 135, 557–569.
Klefoth, T., Kobler, A., Arlinghaus, R., 2008. The impact of catch-and-release on short term behaviour and habitat choice of northern pike (*Esox lucius* L.). Hydrobiologia 601, 99–110.
Kobler, A., Klefoth, T., Arlinghaus, R., 2008a. Activity and seasonal changes in activity centre size between summer and winter in female pike. J. Fish Biol. 73, 584–596.
Kobler, A., Klefoth, T., Wolter, C., Fredrich, F., Arlinghaus, R., 2008b. Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. Hydrobiologia 601, 17–27.
Lowry, O.H., Passonneau, J.V., 1972. A Flexible System of Enzymatic Analysis. Academic Press, New York.
Milligan, L.C., Wood, C.M., 1986. Tissue intracellular acid–base status and the fate of lactate after exhaustive exercise in the rainbow trout. J. Exp. Biol. 123, 123–144.
Mitton, C.J.A., McDonald, D.G., 1994. Effects of electroshock, air exposure, and forced exercise on swim performance in rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. 51, 1799–1803.
Mommsen, T.P., Vijayan, M.M., Moon, T.W., 1999. Cortisol in teleosts: dynamics, mechanism of action, and metabolic regulation. Rev. Fish Biol. Fish. 9, 211–268.
Morgan, J.D., Iwama, G.K., 1997. Measurements of stressed states in the field. Soc. Exp. Biol. Sem. Ser. 62, 247–268.
Mosindy, T.E., Momot, W.T., Colby, P.J., 1987. Impact of angling on the production and yield of mature walleyes and northern pike in a small boreal lake in Ontario. N. Am. J. Fish. Manage. 7, 493–501.
Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. 2, 123–156.
Myers, R., Taylor, J., Allen, M., Bonvechio, T.F., 2008. Temporal trends in voluntary release of largemouth bass. N. Am. J. Fish. Manage. 28, 428–433.
Newman, D.L., Storck, T.W., 1986. Angler catch, growth, and hooking mortality in small centrarchid-dominated impoundments. Am. Fish. Soc. Spec. Publ. 15, 346–351.
Paukert, C.P., Klammer, J.A., Pierce, R.B., Simonson, T.D., 2001. An overview of northern pike regulations in North America. Fisheries 26 (6), 6–13.
Pierce, R.B., Tomcko, C.M., Schupp, D.H., 1995. Exploitation of northern pike in seven small North-Central Minnesota lakes. N. Am. J. Fish. Manage. 15, 601–609.
Pine III, W.E., Martell, S.J.D., Jensen, O.P., Walters, C.J., Kitchell, J.F., 2008. Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design. Can. J. Fish. Aquat. Sci. 65, 975–988.
Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., Shuter, B.J., 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27 (1), 6–15.
Schreck, C.B., Olla, B.L., Davis, M.W., 1997. Behavioural responses to stress. In: Iwama, G.K., Pickering, A.D., Sumpter, J.P., Schreck, C.B. (Eds.), Fish Stress and Health in Aquaculture. Cambridge University Press, Cambridge, pp. 145–170.
Schreer, J.F., Resch, D.M., Gately, M.L., Cooke, S.J., 2005. Swimming performance of brook trout after simulated catch-and-release angling: looking for air exposure thresholds. N. Am. J. Fish. Manage. 24, 1513–1517.
Schwalme, K., Mackay, W.C., 1985a. The influence of angling-induced exercise on the carbohydrate metabolism of northern pike (*Esox lucius* L.). J. Comp. Physiol. B 156, 67–75.
Schwalme, K., Mackay, W.C., 1985b. The influence of exercise-handling stress on blood lactate, acid–base, and plasma glucose status of northern pike (*Esox lucius* L.). Can. J. Zool. 63, 1125–1129.
Siepker, M.J., Ostrand, K.G., Wahl, D.H., 2006. Effects of angling on feeding by largemouth bass. J. Fish Biol. 69, 783–793.
Soivio, A., Oikari, A., 1976. Haematological effects of stress on a teleost (*Esox lucius* L.). J. Fish Biol. 8, 397–411.
Suski, C.D., Killen, S.S., Morrissey, M., Lund, S.G., Tufts, B.L., 2003. Physiological changes in largemouth bass caused by live-release angling tournaments in southeastern Ontario. N. Am. J. Fish. Manage. 23, 760–769.
Suski, C.D., Killen, S.S., Cooke, S.J., Kieffer, J.D., Philipp, D.P., Tufts, B.L., 2004. Physiological significance of the weigh-in during life-release angling tournaments for largemouth bass. Trans. Am. Fish. Soc. 133, 1291–1303.
Suski, C.D., Killen, S.S., Kieffer, J.D., Tufts, B.L., 2006. The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live-release angling tournaments. J. Fish Biol. 68, 120–136.
Suski, C.D., Cooke, S.J., Danylchuk, A.J., O'Connor, C.M., Gravel, M.-A., Redpath, T., Hanson, K.C., Gingerich, A.J., Murchie, K.J., Danylchuk, S.E., Koppelman, J.B., Goldberg, T.L., 2007. Physiological disturbance and recovery dynamics of bonefish (*Albula vulpes*), a tropical marine fish, in response to variable exercise and exposure to air. Comp. Biochem. Physiol. Part A 148, 664–673.
Thompson, L.A., Donaldson, M.R., Hanson, K.C., Arlinghaus, R., Cooke, S.J., 2008. Physiology, behavior and survival of angled and air exposed largemouth bass. N. Am. J. Fish. Manage. 28, 1059–1068.
Venn Beecham, R., Small, B.C., Minchew, C.D., 2006. Using portable lactate and glucose meters for catfish research: acceptable alternatives to established laboratory methods? N. Am. J. Aquat. 68, 291–295.
Wang, Y., Heigenhauser, G.J.F., Wood, C.M., 1994. Integrated responses to exhaustive exercise and recovery in rainbow trout white muscle: acid-based, phosphogen, carbohydrate, lipid, ammonia, fluid volume and electrolyte metabolism. J. Exp. Biol. 195, 227–258.
Wells, R.M.G., Pankhurst, N.W., 1999. Evaluation of simple instruments for the measurement of blood glucose and lactate, and plasma protein as stress indicators in fish. J. World Aquat. Soc. 30, 276–284.
Wendelaar Bonga, S.E., 1997. The stress response in fish. Physiol. Rev. 77, 591–625.
Wood, C.M., 1991. Acid–base and ion balance, metabolism, and their interactions after exhaustive exercise in fish. J. Exp. Biol. 160, 285–308.

Please cite this article in press as: Arlinghaus, R., et al., Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. (2009), doi:10.1016/j.fishres.2009.02.005