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Physiological and behavioural consequences of capture and retention in carp sacks on common carp (*Cyprinus carpio* L.), with implications for catch-and-release recreational fishing

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ABSTRACT

Common carp (*Cyprinus carpio* L.) captured by specialised carp anglers are often retained in so-called "carp sacks" and released after substantial retention periods of several hours duration. Little is known about the lethal and sub-lethal (e.g., physiological disturbances, behavioural impairments) consequences associated with this practice. In this study, the effects of capture and retention in carp sacks on the physiological status of small hatchery-reared carp were examined at two moderate water temperatures (12 °C and 22 °C) in a laboratory setting, where water quality changes in carp sacks were also studied. A complementary field approach was used to examine the effects of carp sack retention on physiology, tissue damage, short-term behaviour and long-term fate of large feral carp in Dow's Lake, a lentic section of the Rideau Canal in Ottawa, Ontario, Canada. During retention for up to 9 h, decreasing plasma lactate levels suggested recovery from initial capture stress, yet there was evidence of pronounced primary and secondary physiological stress responses resulting from the combined capture and retention in carp sacks in both the laboratory and the field. In addition, there was evidence of tissue damage in carp retained in carp sacks for long periods. The moderate water temperatures studied did not strongly affect the stress response in carp, and changes in water quality parameters within carp sacks were minor and likely not of biological relevance. Physiological changes were associated with impaired post-release behaviour reflecting a tertiary stress response, but recovery was rapid within a couple of hours post-release. No mortalities occurred in a two month observation period. Our findings indicate that despite being sub-lethally affected by capture and retention, carp are able to recover rapidly with negligible mortality from retention in carp sacks like those used in the present study.

1. Introduction

Angling constitutes one of the physically most demanding forms of exercise fish for fish during natural conditions (Wood, 1991). It can cause alterations in neuro-endocrine functions (primary stress response) and will usually also result in subsequent changes in tissue biochemistry (secondary stress response in blood and muscle; reviewed in Cooke and Suski, 2005; Arlinghaus et al., 2007). Biochemical and physiological demands that exceed a threshold can affect the whole-animal performance (tertiary stress response; Wendelaar Bonga, 1997; Barton et al., 2002). Previous catch-and-release studies have indeed revealed behavioural alterations (reviewed in Donaldson et al., 2008) and other organismal endpoints, such as reduced reproductive output (Ostrand et al., 2004) or altered feeding behaviour potentially reducing growth and condition (Clapp and Clark, 1989; Diodati and Richards, 1996; Siepker et al., 2006; Klefoth et al., 2011). In addition to stress responses at various levels, angling can cause further sub-lethal effects to fish, including the appearance of cytoplasmatic enzymes in the blood stream that are indicative of angling-induced tissue damage, as the function of these enzymes is restricted to intracellular spaces and they are only released upon cell defects or death (Morrissey et al., 2005; Moyes et al., 2006; Butcher et al., 2011). Severe injuries and levels of stress experienced during a catch-and-release event can ultimately result in either immediate or delayed mortalities (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Arlinghaus et al., 2007).

Environmental conditions are among the main determinants that influence the level of stress response and affect survival of fish

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that are caught and released (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Arlinghaus et al., 2007). In particular, the effect of high water temperature is noteworthy, which can result in elevated physiological disturbances, extended recovery periods and increased mortality rates across many stenotherm cold-water fish species such as salmonids (reviewed in Gale et al., in press), but this may also be applicable to low water temperatures in warm water-adapted fish species (Arlinghaus et al., 2007). Specifically for carp (*Cyprinus carpio* L.) as a eurytherm species that prefers warm water (Blanck et al., 2007) little is known about the effects of temperature on the stress response and survival in a catch-and-release angling context. Pottinger (1998) observed differences in cortisol dynamics between trials in carp angling experiments conducted at temperatures of 4 °C and 15 °C. In this study, cortisol continued to rise for a longer time period after the onset of a stressor in trials conducted at the low water temperature compared to the high water temperature (Pottinger, 1998). These findings indicate that the effect of water temperature on catch-and-release effects in carp demand further study.

Post-capture handling procedures can constitute further stressors to the fish (Cooke and Suski, 2005; Arlinghaus et al., 2007), and it has been shown that these stressors can be cumulative and interactive, intensifying biochemical, physiological and behavioural changes (Killen et al., 2003; Suski et al., 2003), which may delay or inhibit recovery (Cooke et al., 2002a; Suski et al., 2004; Gingerich et al., 2007). Similar to capture itself, the effects of subsequent handling-related stressors on physiology, behaviour and survival can be influenced by environmental conditions such as water temperature (Davis and Schreck, 2005; Gingerich et al., 2007). In specialised carp angling, extended post-capture retention prior to release is one of the most pronounced and long-lasting handling practices. Carp anglers value photographic memories of their catch (Arlinghaus and Mehner, 2003) and in particular trophy-sized fish are often retained when captured during adverse light conditions for photography (i.e., during night) in order to take pictures when conditions have improved to obtain quality photographs (i.e., during daylight). To this end, so-called "carp sacks", which are collapsible, dark, and knotless mesh bags made of synthetic fibre cloth, are widely used to temporarily retain fish in specialised carp angling. Despite their frequent use, no information is available on the effects of carp sack retention on fish.

Previous research on net retention gear in recreational fisheries has focused on keepnets (Raat et al., 1997; Pottinger, 1997, 1998; Cooke and Hogle, 2000; Schreckenbach and Wedekind, 2000; Gallardo et al., 2010; Butcher et al., 2011), which technically differ from carp sacks in that they have a rigid structure which supports the mesh. Moreover, the net mesh in keepnets is typically rigid and mesh sizes larger compared to carp sacks. Studies with various cyprinid species showed that the effects of keepnet retention on the physiological status are generally minor and often do not exacerbate the physiological stress response induced by capture alone (Pottinger, 1998; Schreckenbach and Wedekind, 2000; Gallardo et al., 2010). Moreover, Pottinger (1998) demonstrated that carp recover from capture during keepnet retention. This was also reported for other retention gear used in recreational angling in other species (e.g., largemouth bass, *Micropterus salmoides*, and walleye, *Sander vitreus*, retention in live-wells) provided that appropriate water quality is maintained (Suski et al., 2004; Killen et al., 2006). In addition, previous studies found no evidence that keepnet retention results in increased mortality rates or long-term consequences for growth in various cyprinid fish species, including carp (Raat et al., 1997; Schreckenbach and Wedekind, 2000). Until now, it is unknown whether the same applies to retention in carp sacks, which, as explained above, differ in shape and design from keepnets. Therefore, it is not appropriate to transfer research results from keepnets to carp sacks without careful evaluation.

The objectives of the present study were to assess whether and to what degree a specialised carp angling event that includes post-capture retention in carp sacks results in a primary, secondary or tertiary stress response, or stress-induced tissue damage. Moreover, our study aimed at studying the effects of a high and low water temperature on the stress response of carp retained in carp sacks after capture. These questions were addressed using complementary laboratory and field approaches. The laboratory experiments were used to evaluate the effects of carp sack retention on the physiological status of small hatchery-reared carp at two different water temperatures (12 °C and 22 °C), and in addition were used to examine changes in water quality parameters during retention in carp sacks as a possible contributor to the stress response in retained fish. The field component was used to assess the effects of retention in carp sacks on fish physiology, tissue damage, short-term behaviour, and long-term fate of large feral carp as they are targeted by specialised carp anglers.

2. Methods

2.1. Assessment of carp sack retention on the physiological status of carp in the laboratory

Two hundred 2-year old mirror common carp (mean total length ± SD: 27.7 ± 2.7 cm) were obtained on 16 October 2007 from the commercial pond aquaculture facility Peitz (Schlepzig, Germany; N52°01′45.25″, E13°53′43.60″) and equally distributed in 4 holding aquaria (~2000 l, 50 fish per tank) in a temperature-controlled laboratory at Humboldt-Universität zu Berlin, Germany. Initial water temperature was 18 °C. During the first 2 weeks, water temperature in the holding aquaria was gradually changed (by a max. of 0.5 °C d^{-1}) to 12 °C and 22 °C in each of two aquaria. The experimental water temperatures were chosen to reflect typical temperatures during spring summer and fall, which are the main seasons for specialised carp angling in central Europe. Carp were acclimated to laboratory conditions over a period of 6 weeks and were fed a commercial diet (Kraftfutter Beskow GmbH, Beeskow, Germany, KM 28/08) twice per day at 2% body weight per feeding.

To assess the effects of capture and retention in carp sacks on the physiological state of the study animals, 10 individual carp from each water temperature treatment (12 °C and 22 °C) were randomly allocated to either a control group, a group that was subjected to simulated capture resulting in physical exhaustion only or one of four different retention treatment groups of 0.5 h, 3 h, 6 h or 9 h after physical exhaustion (N = 120, mean total length ± SD: 27.9 ± 2.7 cm). The 0.5 h retention treatment mimicked short-term retention, e.g., when carp anglers take photographs shortly after capture. The 3 h, 6 h, and 9 h retention treatments correspond to short-, medium-, and long-term retention in carp sacks in a typical specialised carp angling event, e.g., when fish are captured during late evening hours, night or early morning hours and are retained until the next morning when light conditions for photography have improved.

Maximum one fish was netted from an individual holding tank to avoid an influence of sequential sampling on physiological status (Pickering et al., 1982). Control fish experienced no further treatment. Fish in the simulated capture and retention treatment groups were individually transferred into a 200 l tank with identical water temperature as the respective holding tank from which they were netted and subjected to a simulation of capture (i.e., the physical activity associated with the capture process of a hooked fish) by tail pinching the fish for 3 min (e.g., Suski et al., 2004; Killen et al., 2006; Arlinghaus et al., 2009). Fish in all retention treatment groups were

then individually transferred into a black polyester carp sack with knotless 3 × 2 mm mesh (Daiwa Inc., Germany, model: Cormoran Karpfensack "De Luxe"). Carp sacks were reduced in size to a dimension of 45 × 25 cm to account for the small body size of experimental carp used in the laboratory. Carp sacks were closed by an incorporated zip cord and placed into a 900 l tank. The tank was equipped with a filter system and additionally supplied with 30 l tempered fresh water per hour (either 12 °C or 22 °C according to the treatment). Fish were left undisturbed during the retention period.

Blood samples were taken directly following the treatments (or netting from the holding tank in the control group) by caudal venipuncture approaching the caudal vasculature below the lateral line (Dyer and Cervasio, 2008). An assistant held the carp in place while blood samples were taken with heparinized syringes (23 gauge, 31.8 mm; syringe: 1 ml, Omnifix-F1). Six ml of blood were withdrawn per fish, and the sampling time was limited to 3 min. If blood sampling was not finished after this period, the fish was excluded and replaced by a new individual. Four ml of blood were centrifuged to separate the plasma from the blood constituents (5000 × *g*, 10 min). Plasma samples were immediately frozen in liquid nitrogen and then transferred to an ultra-cold freezer (−80 °C) until analysed for cortisol as a primary stress hormone, and indicators of the secondary stress response including glucose as an indicator of metabolic changes during stress, plasma lactate as an indicator of anaerobiosis and recovery thereof, as well as osmolality and plasma ions (sodium, chloride, and potassium) as indicators of osmotic and ionic disturbances. Two 1 ml vials of blood were not processed and used for blood-pH and haematocrit analyses. Blood-pH was measured within a 30 min time period to assess acid–base disturbances and haematocrit was assessed directly following blood sampling to assess haematological changes (see below for details).

2.2. Assessment of water quality changes within carp sacks during retention in the laboratory

Water quality changes during carp sack retention were assessed in a second set of experiments. A pipe (length: 5 cm, diameter: 3 cm) was permanently attached to the opening of a carp sack to allow taking water samples without disturbing confined fish. Carp were subjected to simulated capture prior to retention as described above. One fish at a time was retained in a carp sack which was then placed in a 900 l tank ($N = 8$). Water parameters tested included ammonia, dissolved oxygen and pH. Water parameters were measured in the tank at 0 h and were then monitored after 0.5 h, 3 h, 6 h, and 9 h inside the carp sack and in the ambient water. Water samples for ammonia measurements inside the carp sacks were taken with a syringe via the pipe, and concentrations were assessed photometrically as described in Zwirnmann et al. (1999). Handheld devices were used to measure dissolved oxygen (WTW, Weilheim, Germany, model: CellOx 325) and pH (WTW, Weilheim, Germany, model: Multi 320i), and probes were inserted directly into the carp sack through the pipe.

2.3. Assessment of carp sack retention on the physiological status, tissue damage, post-release behaviour and survival of carp in the field

The field experiment on a feral population of common carp was conducted across 18 fishing days between 9 September and 3 October 2007 at Dow's Lake, a lentic section of the Rideau Canal in Ottawa, Ontario, Canada (N45°23′46.14″, W75°42′03.09″). Water temperature and dissolved oxygen were measured daily at 8 am and ranged from 18.3 °C to 23.1 °C (mean ± SD: 20.3 ± 1.3 °C) and 8.4 mg/l to 12.8 mg/l (mean ± SD: 10.4 ± 1.5 mg/l). All angling was conducted from shore and took place at the same fishing site by the same angler to control the influence of angler experience (Dunmall et al., 2001). The angling method conformed to a standard bottom fishing technique in specialised carp angling with a fixed lead sinker and a short leader as described in detail in Rapp et al. (2008). This set-up contributes to a shallow hooking depth, completely avoiding hooking in critical (i.e., deep) locations (Rapp et al., 2008) and thus facilitating rapid unhooking which minimises the influence of additional handling after capture. Playing during capture was standardised to 3 min—consistent with the laboratory experiment described before. If the fish was exhausted within a shorter time period, it was played near the shore until the 3 min time limit was reached. If the fish could not be landed within 3 min it was excluded from the study. To account for the relatively short playing period, considering the size of captured fish, breaking strength of the hooklink (Rapala VMC Corporation, Helsinki, Finland, brand: Sufix Camo Skin, test: 11.3 kg) and the mainline (Shimano Inc., Osaka, Japan, brand: Power Pro, test: 18.1 kg) were chosen accordingly. Carp were landed with a knotless landing net that minimises injury to the fish (Barthel et al., 2003). Following landing, the fish were immediately transferred into a water-filled trough to avoid air exposure during unhooking and enable fish size (total length) to be recorded to the nearest 1 cm (mean ± SD: 68.3 ± 8.16 cm).

Individual carp were randomly allocated to a baseline group, which was captured by rod and reel, but experienced no further treatment, and three different retention treatment groups of 3 h, 6 h or 9 h, consistent with the retention periods used in the laboratory ($N = 10$ per treatment). No unharmed control group was included in the field experiment as all capture methods cause stress in fish. Wild fish held in captivity do often not react in the same manner compared to when in their natural environment and thus do not provide an appropriate control (Cooke et al., 2002b). However, many physiological stress indicators require several minutes or more to reach the blood stream and increase to maximum levels (e.g., cortisol and glucose; e.g., Pickering et al., 1982; McDonald and Milligan, 1997; Ruane et al., 2001), and thus the fish's physiological state at landing after a 3 min capture period served as a baseline to which the retention periods were compared (Hanson et al., 2009; Butcher et al., 2011). Following unhooking, the fish was immediately transferred into a carp sack using the same model as in the laboratory experiment. As a result of to the large body size of carp used in the field experiment, carp sacks were not scaled down and used in their original dimension of 140 × 120 cm. Every fish was confined individually as described before. The carp sacks were placed into the lake, and the incorporated zip cord was attached to a metal pole on shore to avoid drifting. Fish were then left undisturbed during the retention period.

Blood samples were taken immediately following the treatments or following capture in the baseline group. Fish were placed into a water-filled trough to avoid air exposure and an assistant held the fish while a 3 ml blood sample was taken using vacutainer syringes (Becton-Dickinson, Inc., Franklin Lakes, New Jersey, U.S.A.; needle: 21 gauge, 38.1 mm; vacutainer: 3 ml, lithium heparin anticoagulant). Blood was collected as described before, and blood sampling was limited to 1 min. Any fish that required more than 1 min for sampling was excluded from the study. Plasma was separated by centrifugation (10,000 × *g*, 5 min), frozen in liquid nitrogen until the field sampling period was terminated and stored in an ultra-cold freezer (−80 °C) until analysed. Plasma samples were analysed for the same primary and secondary stress indicators as in the laboratory experiment with the exception of blood-pH and haematocrit, which could not be assessed in the field experiment. In addition, lactate dehydrogenase (LDH) and aspartate transaminase (AST) were analysed in the plasma and served as indicators of tissue cell damage.

Radio tracking was then used to monitor carp behaviour post-release. External transmitters were attached immediately

following blood sampling in the water-filled trough avoiding air exposure (Cooke et al., 2005). An assistant held the fish in place during this procedure. Transmitters (Holohil Systems Inc., Ontario, Canada, model: PD-2 transmitters, weight in air: 3.8 g, battery life: 6 month, dimensions: $L \times W \times H$ (mm): $23 \times 12 \times 7$) were attached externally below the dorsal fin as described by Cooke (2003). No anaesthetic was used as this may have altered post-release behaviour of the fish (Cooke et al., 2005). Due to ongoing carp fishing by other anglers in the study lake, an anchor tag (Floy Manufacturing Inc., Seattle, Washington, U.S.A.) with an individual identity number and a phone number was inserted into the dorsal musculature. No carp was reported as recaptured by local anglers, and also the authors did not recapture any fish.

Tracking was initially conducted manually from shore using a handheld radio receiver (Lotek Wireless, Newmarket, Ontario, Canada, model: SRX 400) and a three element Yagi antenna. The reception range with different gain settings was evaluated by attaching a line to a transmitter, which was subsequently positioned in different water depths and distances to the tracker. Fish movement was observed constantly for the first 30 min post-release using successive gain reductions (i.e., zero-point tracking; Gravel and Cooke, 2008; Gillis et al., 2010). Shoreline positions were quantified by detailed descriptions of the shoreline on basis of characteristic landmarks (Curry et al., 2007) and GPS data points (accuracy: 5–10 m depending on satellite reception; Garmin International Inc., Olathe, Kansas, U.S.A., model: eTrex Summit). Distance from shore was estimated using the previously assessed reception ranges. Upon release, all fish swam in close distance to the shoreline where water depth was shallow and did not vary decisively. Thus, it was assumed that influence of water-depth on signal reception was negligible and the reception ranges established during tracking calibrations were valid. The coordinates of each fish position were assessed with an electronic GIS map based on the shoreline GPS position and shoreline descriptions coupled with the estimated distance of the fish from shore. Distance moved within the first 30 min, time required to leaving the release site, and time rested within 30 min post-release were calculated as behavioural indicators.

Further tracking points were taken from each fish at 1 h, 12 h, 24 h, 36 h, 48 h, 60 h, and 72 h post-release using a combination of zero-point tracking (Gravel and Cooke, 2008; Gillis et al., 2010) and triangulation (Mech, 1983) to generate minimum displacement between successive locations. Minimum displacement was assessed as a straight line and/or the nearest water distance between tracking points if a fish swam around a point (Arlinghaus et al., 2009). Less frequent tracking was conducted for a period of two months post-release to assess long-term mortality. Fish that moved between tracking dates were assumed to be alive because predation of carp was not possible due to the absence of predators in the ecosystem that were large enough to prey on these fish.

2.4. Biochemical blood analyses

Plasma cortisol analysis was conducted with an enzyme-linked immunoabsorbent assay (ELISA) kit (IBL International GmbH, Hamburg, Germany, test: RE 52611) according to the manufacturers protocol. Optical density was measured at 450 nm using a microplate reader (Tecan, Maennedorf, Switzerland, model: Spectrafluor Plus). Plasma glucose from the laboratory experiment and plasma lactate were analysed using standard assay kits (glucose: Diasys Diagnostic Systems GmbH, Holzheim, Germany, test: GOD FS; lactate: Trinity Biotech plc, Bray, Ireland, test: 735-10) according to the manufacturers protocols and absorbance was measured at 500 nm (glucose) and 540 nm (lactate) using a plate reader (Tecan, Maennedorf, Switzerland, model: Genios). Blood-pH was assessed potentiometrically using an open salt-bridge microelectrode (Radiometer, Copenhagen, Denmark, model: BMS 2 Mk 2) connected to an acid–base analyser (Radiometer, Copenhagen, Denmark, model: PHM 72). For haematocrit analysis well mixed blood was drawn into microhaematocrit tubes (Brand GmbH & Co. KG, Wertheim, Germany, size: 75×1.15 mm), centrifuged ($12{,}000 \times g$, 10 min) and haematocrit was analysed using a micro haematocrit reader. Plasma osmolality was analysed with a freezing point osmometer (Gonotec GmbH, Berlin, Germany, model: Osmomat 030). All plasma ion analyses of the laboratory samples followed the protocols outlined in Zwirnmann et al. (1999).

Plasma cortisol, lactate and osmolality from the field samples were analysed using the same protocol as described before for the laboratory experiments. Plasma glucose, sodium, chloride, potassium, lactate dehydrogenase (LDH) and aspartate transaminase (AST) were analysed using an autoanalyser with appropriate reagents according to the manufacturer protocol (Roche Hitachi, Basal, Switzerland, model: Roche/Hitachi 917). These analyses were based upon the International Federation of Clinical Chemistry and Laboratory Medicine Standard Reference Model.

2.5. Statistical analyses

In the laboratory trials, mean total fish length did not differ significantly between treatment groups and was therefore not included in the analysis (two-way ANOVA: retention factor: $F = 0.598$, df = 5, $P = 0.701$; temperature factor: $F = 2.289$, df = 1, $P = 0.950$). Physiological variables were compared between the treatment groups as a function of the factors retention time and water temperature (two levels) using two-way-ANOVAs after verifying that data met underlying assumptions for parametric tests. Normality was tested using a Kolmogorov-Smirnov test ($P < 0.05$), and homogeneity of variances was tested using Levene's test ($P < 0.05$). In case of violation of these assumptions, data were subjected to a logarithmic transformation [ln ($x + 1$)]. Transformation resulted in normal distribution for all dependent variables in the laboratory experiment. In models with significant effects of retention time on physiological variables a Tukey's *post hoc* test was used for variance homogenous data to assess differences among retention periods. In case of variance heterogeneity non-transformed data were used and a Dunnett-T3 *post hoc* test was applied. In models with a significant temperature effect on physiological variables a t-test comparing high and low water temperature levels within each retention level was applied and the significance level was adjusted using a Bonferroni-Holm correction (Holm, 1979).

Changes of water parameters in carp sacks during retention in the laboratory were compared using linear mixed models for repeated measures after verifying that the data meet the assumptions for parametric test as described above. Factors were retention time and sampling site (inside the carp sack and ambient water). In significant models, a Bonferroni *post hoc* test was used to assess which samples differed from each other.

In the field experiment, plasma samples of 6 fish showed signs of haemolysis, icterus or lipemia, which can interfere with analysis of plasma constituents and cause errors in test results (Bellamy and Olexson, 2000). Consequently, these fish were excluded from statistical analysis of haematological variables, and sample sizes deviate slightly from the initially reported sample sizes. Analysis of behavioural parameters included all fish. Environmental variables (i.e., water temperature and dissolved oxygen) that could not be controlled in the field but might influence haematological variables, behaviour or survival of carp in response to capture and retention did not differ significantly between treatment groups (all P-values > 0.05, for each water parameter during all investigations) indicating that carp in each treatment group experienced similar environmental conditions. Mean total fish length differed significantly between treatment groups in the field study (physiology: ANOVA, $F = 3.563$, df = 3, $P = 0.026$; behaviour: ANOVA, $F = 3.952$,

df = 3, $P = 0.016$). Subsequent ANCOVAs and generalised linear models (for data not meeting assumptions of parametric tests) revealed no significant influence of total fish length as a covariate on haematological variables and the behavioural parameter of distance moved, time rested, and minimum displacement ($P > 0.05$ for all parameters). Similarly, a Cox regression model revealed no significant influence of total fish length as a covariate on time required to leave the release site ($P > 0.05$). Therefore, fish length was not included in the final analyses. Continuous variables (i.e., haematological variables, distance moved, time rested and minimum displacement) were compared between treatment groups using one-way ANOVAs and Tukey's *post hoc* tests after verifying that data meet the assumptions for parametric tests as described before. In case of deviations from underlying assumptions a logarithmic transformation [$\ln(x+1)$] was applied. If the transformation did not result in normal distribution the non-parametric Kruskal-Wallis-H test was used to compare treatment groups. To identify which treatment groups differed from each other in significant models, multiple comparisons were conducted by non-parametric Nemenyi *post hoc* tests (i.e., sample size independent Nemenyi *post hoc* tests for comparisons of haematological data, and sample size dependent Nemenyi *post hoc* tests for comparisons of behavioural data; Sachs and Hedderich, 2006). If the logarithmic transformation did not result in variance homogeneity non-transformed data were used and differences between treatments groups were tested by one-way ANOVAs, and an appropriate *post hoc* test for heterogeneous variances (Dunnett-T3) was applied. The behavioural parameter time required to leave the release site was compared among treatment groups using a Kaplan-Meier analysis. Analyses were conducted using the software package SPSS (SPSS Inc., Chicago, Illinois, U.S.A., Version: 15.0) and significance was judged at $P < 0.05$. Results are presented as mean ± SE. All results are presented as non-transformed values to facilitate interpretation.

3. Results

3.1. Influence of retention in carp sacks on the physiological status of carp in the laboratory

Capture and retention in carp sacks significantly affected the cortisol concentrations in the blood of carp as indicated by a significant treatment effect in the two-way ANOVA (Table 1). Specifically, plasma cortisol concentrations of retained carp peaked after carp sack retention for a brief period of 0.5 h and decreased thereafter reaching baseline values of captured fish after 6 and 9 h of retention (Table 2). While differences in cortisol concentration between retained carp for 6 and 9 h of duration and individuals tail pinched only were not statistically significant, cortisol concentration remained elevated relative to undisturbed control fish (Table 2). Similarly, plasma glucose increased during simulated capture and was significantly higher in all retention treatment groups relative to undisturbed controls, and carp retained for 9 h showed significantly elevated glucose values relative to the baseline group, which was subjected to simulated capture but not retained in carp sacks (Table 2).

There were significant effects of carp sack retention with respect to plasma lactate, blood-pH, osmolality along with various plasma ions, whereas haematocrit was unaffected by retention (Table 1). Plasma lactate increased significantly during simulated capture, peaked after retention for 0.5 h, and decreased thereafter at which control levels were reached within a retention period of 6 h (Table 2). Blood-pH decreased significantly during capture and remained below resting levels for a period of 0.5 h (Table 2). Thereafter, it increased above resting levels at which the acid-base equilibrium was not fully restored after a retention period of 9 h. Simulated capture was also associated with osmotic and ionic changes in the blood plasma as indicated by elevated osmolality, and decreased sodium concentrations, but all parameters returned to control levels during retention (Table 2).

The water temperature significantly affected plasma glucose, haematocrit, and all plasma ion concentrations (as evidenced by significant temperature effects in the two-way ANOVAs, Table 1), but pairwise comparisons between high and low water temperature in a given treatment level only revealed a few significant differences for plasma glucose, osmolality and plasma potassium. Significantly higher plasma levels were observed in control and baseline fish for glucose and in control fish for potassium and significantly lower levels were observed for osmolality in fish that were held in carp sacks for 9 h at the high temperature treatment compared to the low water temperature treatment (Table 2). Generally, water temperature did not affect the magnitude and dynamics of the physiological stress response as indicated by the lack of interactive effects between the treatments and water temperature in all two-way ANOVAs (Table 1).

3.2. Changes of water quality during retention in the laboratory

Dissolved oxygen decreased after 0.5 h of retention in the carp sack and in the ambient water and stabilised thereafter at this level throughout the entire retention period of 9 h (Fig. 1A). The oxygen concentration tended to be lower in the carp sack relative to the surrounding water; however, these differences were not significant (Fig. 1A). Similarly, pH decreased in the carp sack and in the ambient water and was significantly lower after retention for 6 h, but pH inside the carp sack and in the ambient water were similar (Fig. 1B). Ammonia concentrations were stable in both ambient water and the carp sack across the entire retention period of 9 h (Fig. 1C).

3.3. Influence of retention in carp sacks on the physiological status and tissue damage of carp in the field

All carp retained in carp sacks in the field exhibited a significant increase in plasma cortisol concentrations relative to baseline fish, and the cortisol concentration was found to increase with retention duration (Table 3). Also, plasma glucose increased with retention duration, and glucose levels were significantly higher following retention for 9 h relative to baseline fish (Table 3). Plasma lactate concentrations were lower in fish retained for 9 h relative to carp directly after exhaustive capture and were also lower compared to carp retained for 3 h, indicating physical recovery from angling during carp sack retention (Table 3). While plasma osmolality did not differ between treatment groups in the field, analysis of individual plasma electrolyte concentrations revealed mild ionic disturbances (Table 3). Specifically, carp retained for 6 h and 9 h in carp sacks exhibited a decrease in plasma sodium concentrations relative to baseline fish, and similarly plasma chloride concentrations dropped significantly in carp retained for 3 h relative to baseline fish (Table 3). By contrast, plasma potassium concentration was higher in fish retained for 6 h relative to baseline fish (Table 3). In terms of indicators of tissue damage, plasma LDH and AST concentrations were found significantly higher in fish retained in carp sacks for 9 h relative to baseline fish (Table 3).

3.4. Influence of retention in carp sacks on the post-release behaviour and survival

The distances moved by carp after release in Dow's Lake did not vary among retention treatment groups within 30 min post-release (Fig. 2A), and no differences in patterns leaving the release site were observed (Fig. 3). However, fish retained for long periods (i.e., 9 h) were found to spend significantly more time resting within the first

Table 1
Test statistics of the two-way analysis of variance on the influence of carp sack retention and water temperature on physiological parameters of juvenile carp in the laboratory. Bold fonts in the first column indicate haematological variables, and bold fonts in the last column indicate significant effects.

Variable	Typ III sum of squares	*F*	df	*P*-value
Plasma cortisol	453106.807	8.549	11	**<0.001**
Treatment	429498.264	17.829	5	**<0.001**
Water temperature	1979.380	0.411	1	0.523
Treatment × water temperature	21450.545	0.890	5	0.490
Plasma glucose	283.430	8.275	11	**<0.001**
Treatment	201.280	12.928	5	**<0.001**
Water temperature	43.239	13.885	1	**<0.001**
Treatment × water temperature	34.133	2.192	5	0.060
Plasma lactate	1257.111	36.889	11	**<0.001**
Treatment	1235.087	79.734	5	**<0.001**
Water temperature	4.954	1.599	1	0.209
Treatment × water temperature	21.455	1.385	5	0.236
Blood pH	3.471	31.226	11	**<0.001**
Treatment	3.430	67.896	5	**<0.001**
Water temperature	0.001	0.066	1	0.798
Treatment × water temperature	0.063	1.254	5	0.289
Haematocrit	115.602	1.340	11	0.213
Treatment	50.698	1.293	5	0.272
Water temperature	37.879	4.829	1	**0.030**
Treatment × water temperature	26.598	0.678	5	0.641
Osmolality	7196.165	4.094	11	**<0.001**
Treatment	4792.615	5.999	5	**<0.001**
Water temperature	1653.833	10.350	1	**0.002**
Treatment × water temperature	772.684	0.967	5	0.441
Sodium	4659.371	2.637	11	**0.005**
Treatment	2958.014	3.683	5	**0.004**
Water temperature	1558.493	9.702	1	**0.002**
Treatment × water temperature	60.507	0.075	5	0.996
Chloride	1825.974	1.524	11	0.133
Treatment	215.851	0.396	5	0.850
Water temperature	1132.789	10.401	1	**0.002**
Treatment × water temperature	461.400	0.847	5	0.519
Potassium	46.516	11.382	11	**<0.001**
Treatment	40.738	21.930	5	**<0.001**
Water temperature	4.550	12.248	1	**0.001**
Treatment × water temperature	1.267	0.682	5	0.638

Table 2
Mean blood biochemistry and haematology values ± SE in control fish, carp subjected to exhaustive exercise of 3 min (simulated capture) and individuals exhausted and retained in carp sacks for up to 9 h in the laboratory. Different letters indicate significant differences between treatment groups in the overall means across both water temperature (for statistical results, see Table 1). Bold fonts indicate significant differences between water temperatures within a given retention level).

Variable		Control	Baseline (capture)	Retention 0.5 h	Retention 3 h	Retention 6 h	Retention 9 h
Plasma cortisol (ng/ml)	22 °C	46.3 ± 27.9	63.5 ± 31.2	235.6 ± 120.4	124.3 ± 62.1	99.2 ± 57.8	133.3 ± 80.7
	12 °C	31.6 ± 38.7	68.4 ± 28.7	214.5 ± 128.7	163.9 ± 69.6	90.2 ± 47.4	85.0 ± 41.8
	Total	39.0 ± 33.7^{a}	66.1 ± 29.1^{ab}	224.8 ± 121.8^{d}	144.1 ± 67.3^{c}	94.5 ± 51.3^{abc}	109.2 ± 67.3^{bc}
Plasma glucose (mmol/l)	22 °C	**3.9 ± 1.2**	**5.5 ± 1.6**	6.4 ± 1.5	8.3 ± 4.0	6.1 ± 1.5	6.3 ± 1.4
	12 °C	**2.5 ± 0.4**	**3.4 ± 0.4**	5.1 ± 1.1	5.6 ± 1.6	5.6 ± 1.2	7.0 ± 2.4
	Total	3.2 ± 1.1^{a}	4.4 ± 1.5^{ab}	5.8 ± 1.4^{b}	7.0 ± 3.3^{c}	5.9 ± 1.3^{bc}	6.7 ± 1.9^{c}
Plasma lactate (mmol/l)	22 °C	1.2 ± 0.4	7.4 ± 1.8	8.6 ± 2.5	3.1 ± 2.8	1.3 ± 0.5	1.0 ± 0.4
	12 °C	1.5 ± 1.3	6.7 ± 1.9	10.6 ± 2.9	3.0 ± 2.1	2.1 ± 1.0	1.3 ± 0.6
	Total	1.3 ± 0.9^{a}	7.0 ± 1.8^{b}	9.5 ± 2.8^{c}	3.1 ± 2.4^{d}	1.7 ± 0.9^{ad}	1.2 ± 0.5^{a}
Blood-pH	22 °C	7.6 ± 0.1	7.3 ± 0.1	7.4 ± 0.2	7.7 ± 0.1	7.7 ± 0.1	7.7 ± 0.1
	12 °C	7.6 ± 0.1	7.4 ± 0.1	7.4 ± 0.1	7.7 ± 0.04	7.7 ± 0.1	7.7 ± 0.1
	Total	7.6 ± 0.1^{a}	7.3 ± 0.1^{b}	7.4 ± 0.1^{b}	7.7 ± 0.1^{c}	7.7 ± 0.1^{c}	7.7 ± 0.1^{c}
Haematocrit (%)	22 °C	25.4 ± 2.8	26.3 ± 3.8	26.6 ± 2.8	25.5 ± 3.1	25.1 ± 2.8	26.0 ± 2.1
	12 °C	22.9 ± 2.9	24.5 ± 3.3	25.5 ± 2.3	26.1 ± 2.6	24.2 ± 2.7	24.9 ± 1.7
	Total	24.2 ± 3.1	25.3 ± 3.6	26.1 ± 2.6	25.8 ± 2.8	24.6 ± 2.7	25.5 ± 1.9
Osmolality (mOsmol/kg)	22 °C	272.4 ± 15.7	290.5 ± 11.0	293.5 ± 8.9	273.2 ± 6.7	273.0 ± 10.1	**277.3 ± 9.1**
	12 °C	280.5 ± 14.4	292.6 ± 13.3	292.7 ± 20.9	285.5 ± 13.0	285.9 ± 14.6	**287.4 ± 5.4**
	Total	276.5 ± 15.2^{a}	291.7 ± 12.1^{b}	293.1 ± 15.6^{b}	279.4 ± 11.9^{a}	279.8 ± 14.0^{a}	282.4 ± 8.9^{ab}
Sodium (mmol/l)	22 °C	133.9 ± 8.1	135.9 ± 16.3	133.1 ± 13.4	122.0 ± 20.1	128.9 ± 12.2	129.1 ± 13.2
	12 °C	142.1 ± 16.9	143.4 ± 11.1	139.9 ± 8.1	127.0 ± 9.4	135.3 ± 7.0	138.6 ± 8.1
	Total	138.0 ± 13.5^{a}	140.0 ± 13.8^{a}	136.5 ± 11.3^{a}	124.5 ± 16.0^{b}	132.2 ± 10.0^{a}	133.8 ± 11.7^{a}
Chloride (mmol/l)	22 °C	105.4 ± 4.5	100.9 ± 24.7	105.7 ± 7.1	101.4 ± 11.8	98.41 ± 16.09	100.55 ± 9.81
	12 °C	106.8 ± 1.4	112.9 ± 6.5	106.7 ± 3.9	107.7 ± 10.4	107.68 ± 4.74	107.51 ± 4.78
	Total	106.1 ± 3.3	107.5 ± 17.8	106.2 ± 5.6	104.5 ± 11.3	103.3 ± 12.2	104.0 ± 8.3
Potassium (mmol/l)	22 °C	**3.5 ± 0.5**	4.4 ± 0.6	3.1 ± 0.5	2 ± 0.8	3.0 ± 0.8	2.8 ± 0.5
	12 °C	**2.8 ± 0.4**	4.2 ± 0.8	2.8 ± 0.5	2.7 ± 0.6	2.4 ± 0.6	2.4 ± 0.5
	Total	3.1 ± 0.6^{a}	4.3 ± 0.7^{b}	2.9 ± 0.5^{a}	2.8 ± 0.7^{a}	2.7 ± 0.7^{a}	2.6 ± 0.5^{a}

Table 3
Mean biochemistry and haematology values ± SE in baseline fish and carp retained in carp sacks for up to 9 h after the capture in the field. *F*-values refer to ANOVA results, while Chi^2-values refer to non-parametric Kruskal-Wallis-*H* test results. Different letters indicate significant differences between treatment groups.

Variable	Baseline (capture)	Retention 3 h	Retention 6 h	Retention 9 h	*F*-value/Chi^2-value; df; *P*-value
Cortisol (ng/ml)	33.5 (±25.0)[a]	120.5 (±17.1)[b]	142.1 (±21.6)[b]	188.7 (±40.7)[b]	$F = 19.782$, df = 3, $P < 0.001$
Glucose (mmol/l)	4.2 (±0.7)[a]	7.3 (±1.4)[ab]	8.3 (±1.2)[ab]	8.6 (±0.8)[b]	$F = 3.554$, df = 3, $P = 0.026$
Lactate (mmol/l)	9.0 (±1.1)[ab]	12.0 (±0.8)[b]	5.8 (±1.2)[ac]	4.8 (±0.9)[c]	$F = 10.468$, df = 3, $P < 0.001$
Osmolality (mOsmol/kg)	318.6 (±4.0)	313.6 (±3.9)	308.0 (±11.5)	311.0 (±6.4)	$Chi^2 = 0.291$, df = 3, $P = 0.962$
Sodium (mmol/l)	158.3 (±1.9)[a]	156.6 (±2.6)[ab]	148.6 (±0.6)[b]	149.9 (±1.0)[b]	$F = 7.284$, df = 3, $P = 0.001$
Chloride (mmol/l)	117.8 (±1.0)[a]	113.6 (±1.0)[b]	114.0 (±1.1)[ab]	116.0 (±1.2)[ab]	$Chi^2 = 8.735$, df = 3, $P = 0.033$
Potassium (mmol/l)	2.7 (±0.4)[a]	3.2 (±0.2)[ab]	3.9 (±0.2)[b]	3.2 (±0.3)[ab]	$F = 3.271$, df = 3, $P = 0.035$
LDH (U/l)	382.0 (±114.8)[a]	528.0 (±105.5)[ab]	447.3 (±112.9)[ab]	1087.1 (±358.6)[b]	$F = 3.495$, df = 3, $P = 0.028$
AST (U/l)	111.4 (±17.5)[a]	125.7 (±14.6)[ab]	148.3 (±19.0)[ab]	230.0 (±39.7)[b]	$F = 4.834$, df = 3, $P = 0.007$

half hour post-release relative to fish retained for short periods of only 3 h (Fig. 2B). From 31 min to 60 min post-release, fish retained for 9 h moved significantly less relative to baseline fish (Fig. 2C). Short- and medium-term retention did not result in significantly reduced minimum displacement, but also carp retained for these periods tend to move less relative to the baseline group (Fig. 2C). Minimum displacement of carp during subsequent tracking intervals after the first hour post-release did not differ significantly between treatment groups, and no initial or delayed mortality was observed during an observation period of 2 months (Table 4).

4. Discussion

The present study revealed that capture and confinement of carp in carp sacks is associated with a primary, secondary and tertiary stress response, indicated by physiological alterations and behavioural impairments (Wendelaar Bonga, 1997; Barton et al., 2002). However, with regard to physiological stress indicators, the pattern differed quantitatively and qualitatively between the laboratory and the field experiment. Plasma cortisol levels in the laboratory after simulated capture (baseline levels) and maximum levels during retention were slightly higher than those in the field. Those quantitative differences in stress responsiveness, especially evident in the endocrine responses, are frequently reported and can originate from a variety of intrinsic and extrinsic factors (Barton et al., 2002). The observed control levels in the laboratory are however within the range of previously reported basal levels (Pottinger, 1998; Tanck et al., 2000; Ruane et al., 2001), and significant holding stress in the tanks therefore seems to be unlikely.

With regard to qualitative differences, plasma cortisol peaked in the laboratory following retention for 0.5 h and decreased thereafter, but remained higher relative to the unstressed control fish. Plasma glucose, in contrast, increased during retention and remained on the same high levels for the entire retention period. Hyperglycaemia is a frequently observed response to an acute stressor through hormonal stimulation of glycogenolysis and gluconeogenesis (Wendelaar Bonga, 1997; Barton et al., 2002). The decline of cortisol during retention after the initial peak contradicted the field study where cortisol and glucose rose continuously with increasing retention duration. The conflicting findings in terms of a lack of pronounced cortisol increase in the laboratory and a clear increase in cortisol in carp retained in carp sacks in the field might be explained by the different origin of experimental animals. Fish used in the laboratory setting were obtained from a hatchery, while fish captured in the field originated from a feral carp population. In an earlier study with carp in a keepnet retention context, Pottinger (1998) also used hatchery-reared fish and reported that physiological changes in keepnets were minor and carp were rather tolerant towards keepnet retention. Fish reared in aquaculture settings may be selected for stress resistance and recovery from stressors, as these traits confer obvious benefits to aquaculturists in terms of growth and disease resistance (Fevolden et al., 1993; Weil et al., 2001; Øverli et al., 2006). Furthermore, repeated brief stressors during hatchery operation (e.g., netting and transfer of fish) can reduce the stress response in fish through habituation (Rush and Umminger, 1978; Barton et al., 1987; Auperin and Geslin, 2008). Thus, hatchery-reared fish used in the laboratory may not have reacted to carp sack retention in the same manner as the naturalized carp that were exposed to retention in the field experiment. In agreement with this argument, Woodward and Strange (1987) noted greater physiological changes during confinement in wild rainbow trout (*Oncorhynchus mykiss*) compared to similarly treated hatchery-reared fish. There is also evidence that physiological changes in response to exercise and capture can differ with fish size and several authors found greater physiological alterations in larger fish (Wydoski et al., 1976; Meka and McCormick, 2005; Gingerich and Suski, in press). Because both the origin of fish (hatchery versus wild) as well as their size (small fish in laboratory study versus large fish in the field) varied and not all environmental variables could be fully controlled in the field, it is suggested that a combination of factors can be brought forward as an explanation for the observed differences in cortisol dynamics when comparing the laboratory and field components. However, the main findings remain unaffected by this uncertainty in that there was a clear effect of capture and retention in carp sacks on the primary and secondary stress response in carp.

The laboratory and the field setting revealed similar results with respect to physical recovery from capture during carp sacks retention. Metabolic demands for the fish increased during capture, which was reflected in the accumulation of lactate as the end product of anaerobic consumption of adenosine triphosphate, phosphocreatine and glycogen during the exhaustive exercise (Kieffer, 2000). Lactate subsequently decreased in the bloodstream

Table 4
Mean minimum displacement (MDP) (m) ± SE 12–72 h post-release in baseline fish and carp retained in carp sacks for up to 9 h after capture. *F*-values refer to ANOVA results, while Chi^2-values refer to non-parametric Kruskal-Wallis-*H* test results.

Time post-release—range (h)	Mean MDP (m) Baseline (capture)	Mean MDP (m) 3 h	Mean MDP (m) 6 h	Mean MDP (m) 9 h	*F*-value/Chi^2-value; df; *P*-value
1–12	346.6 (±60.3)	301.5 (±41.6)	198.0 (±61.6)	278. 6 (±53.8)	$Chi^2 = 3.120$; df = 3; $P = 0.373$
12–24	287.9 (±91.6)	349.9 (±95.4)	237.2 (±54.0)	271.8 (±48.3)	$F = 0.138$; df = 3; $P = 0.936$
24–36	220.6 (±55.6)	172.6 (±47.6)	183.0 (±37.6)	305.4 (±62.2)	$F = 1.386$; df = 3; $P = 0.267$
36–48	158.7 (±27.0)	228.1 (±65.1)	155.3 (±41.2)	248.4 (±42.8)	$F = 1.090$; df = 3; $P = 0.369$
48–60	306.1 (±65.4)	244.2 (±52.1)	253.4 (±70.7)	201.9 (±65.6)	$F = 0.458$; df = 3; $P = 0.714$
60–72	265.1 (±59.3)	177.8 (±43.7)	190.1 (±57.7)	201.8 (±77.5)	$F = 0.410$; df = 3; $P = 0.747$

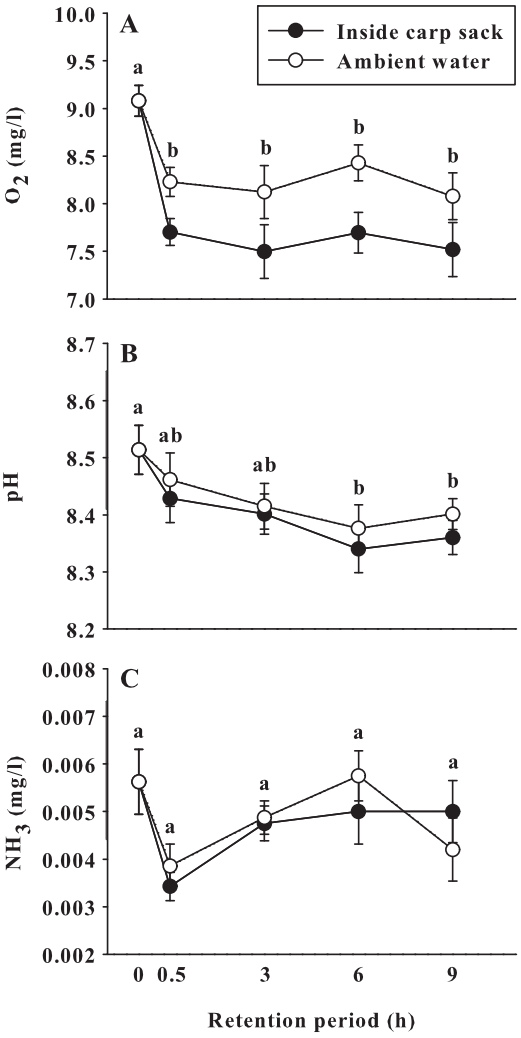

Fig. 1. Mean dissolved oxygen ± SE (mg/l; linear mixed model, retention time: $F = 15.619$, $df_1 = 4$, $df_2 = 52.619$, $P < 0.001$, Bonferroni *post hoc* test; point of measurement: $F = 3.918$, $df_1 = 1$, $df_2 = 18.320$, $P = 0.063$; panel A), mean water pH ± SE (linear mixed model, retention time: $F = 5.165$, $df_1 = 4$, $df_2 = 52.105$, $P = 0.001$, Bonferroni *post hoc* test; point of measurement: $F = 0.393$, $df_1 = 1$, $df_2 = 17.805$, $P = 0.538$; panel B), and mean ammonia ± SE (mg/l; linear mixed model, retention time: $F = 1.409$, $df_1 = 4$, $df_2 = 44.095$, $P = 0.247$; point of measurement: $F = 0.041$, $df_1 = 1$, $df_2 = 23.876$, $P = 0.841$; panel C) inside the carp sack and in the ambient water. Different letters indicate significant differences at differing times; there were no differences between ambient water and water inside the carp sacks.

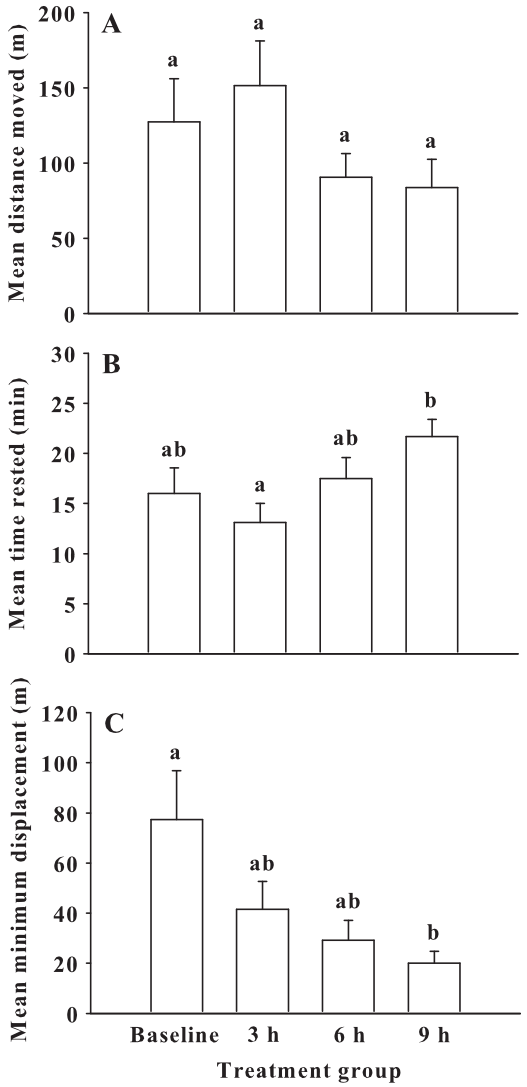

Fig. 2. Mean distance moved ± SE (m; ANOVA, $F = 1.750$, df = 3, $P = 0.174$; panel A) and mean time rested ± SE (min; Kruskal-Wallis-H, $Chi^2 = 8.225$, df = 3, $P = 0.042$, Nemenyi *post hoc* test; panel B) from 0 to 30 min post-release in baseline fish and carp retained in carp sacks for up to 9 h after capture. Mean minimum displacement ± SE (m; ANOVA, 3.438, df = 3, $P = 0.027$, Tukey *post hoc* test, panel C) from 31 to 60 min post-release in control fish and carp retained in carp sacks for up to 9 h after capture. Different letters indicate significant differences between treatment groups.

and approached pre-capture levels in the laboratory setting during medium and long-term retention in carp sacks indicating physical recovery. This finding is consistent with previous studies that examined lactate changes during retention in various gear types used in recreational fisheries (e.g., keepnets, live-wells) for various fish species given adequate water quality (Pottinger, 1998; Suski et al., 2004; Killen et al., 2006). The lactate peak observed during short-term retention in both the laboratory (at 0.5 h) and the field (at 3 h) likely resulted from capture and was unrelated to retention, as the release of lactate from the muscle into the bloodstream is relatively slow and the blood lactate peak occurs temporarily delayed (Holeton et al., 1983; Wood et al., 1983; Wang et al., 1994). In addition, acid–base disturbances were observed as a result from capture indicated by a mild acidosis, with a subsequent alkalosis. The alkalosis persisted throughout the entire retention period indicating that the acid–base equilibrium was not fully restored and recovery from exercise was not entirely completed after 9 h. By contrast, capture and subsequent retention in carp sacks did not result in

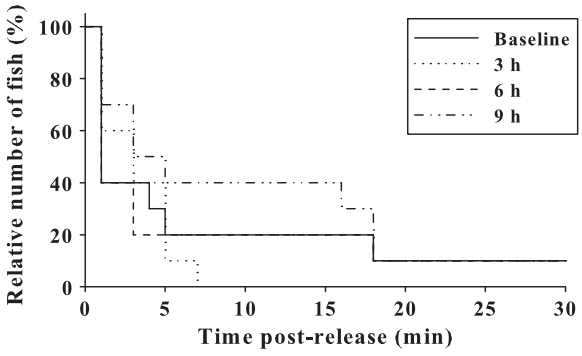

Fig. 3. Relative number of fish at the release site (%) plotted against the time post-release (min) for baseline fish and carp retained in carp sack for up to 9 h after capture. Differences were not significant (Kaplan-Meier, $Chi^2 = 2.14$, df = 3, $P = 0.543$).

significant changes of haematocrit, which is a common indicator to reflect physiological adaptations to increased oxygen demand through increased numbers of circulating erythrocytes or erythrocyte swelling. The lack of haematocrit changes during retention supported the notion that fish likely did not experience hypoxia while retained in carp sacks (Ruane et al., 1999, 2001). This is in agreement with our results from the assessment of water quality changes in carp sacks during retention as discussed below. Moreover, Suski et al. (2006) observed an inhibition of lactate clearance during recovery under hypoxic conditions, therefore our data, that revealed a lactate decrease to pre-capture levels, indicate sufficient oxygen conditions during carp sack retention.

While several plasma electrolytes were found to be significantly different from control and baseline levels during selected retention periods in both the laboratory and the field, most parameters returned to control or baseline levels within 9 h of retention, suggesting recovery of the plasma ion equilibrium. Previous studies on the stress response in fish revealed that plasma ions tend to decrease during confinement stress due to ion loss via the gills, haemodilution due to net influx of water through the gills and diuretic ion loss (McDonald and Milligan, 1997; Wendelaar Bonga, 1997; Barton et al., 2002). However, in the present study plasma ion changes differed from this pattern as there was an decrease in sodium and chloride, but an increase in potassium, which was similarly reported earlier in fish that were subjected to exercise, including capture by rod and reel, and recovery thereof (Holeton et al., 1983; Wood et al., 1983; Wang et al., 1994; Arlinghaus et al., 2009). As such, it seems likely that the observed osmotic and ionic disturbances resulted from capture rather than from retention in carp sacks. Moreover, all plasma ion changes were only of low magnitude in both the laboratory and the field, and, except for potassium in the field experiment, within the range of commonly observed plasma ion changes of 10% during stress in fish (Barton et al., 2002). Although relatively higher, the absolute plasma potassium ion changes in the field experiment were only of low magnitude and concentrations were well below those that cause heart failure in mammals suggesting that the experimental animals were probably well able to cope with the ionic disturbances and it is unlikely that they were of significance for the fish's viability (Wood et al., 1983).

Besides a physiological stress response and metabolic changes resulting from angling, the field component revealed that a specialised carp angling event including post-capture retention is associated with an increase of the intracellular enzymes LDH and AST in the plasma indicating cell damage. This agrees with a recent study by Butcher et al. (2011) who observed elevated AST concentrations in the plasma of keepnet-confined luderick (*Girella tricuspidata*) although absolute concentrations of AST were considerably lower than in the present study. It is difficult to specify the affected tissue and the degree of tissue damage, due to the occurrence of these indicators in multiple tissues and differences in enzyme activity between tissues (Johnston, 1977; Morrissey et al., 2005; Moyes et al., 2006). The increase in intracellular enzymes in the bloodstream might be due to muscle tissue damage occurring from struggle during capture and handling as assumed by others (Moyes et al., 2006; Butcher et al., 2011) or it might be due to stress-induced cell damage or increased cell membrane permeability (Pearl et al., 1966; Arakawa et al., 1997; Sánchez et al., 2002). In the present study both LDH and AST increased with retention duration, in which AST is predominantly active in heart and liver cells (Morrissey et al., 2005). Thus, a stress-induced enzyme leakage seems to be more plausible than white muscle damages caused by extensive exercise or struggling.

High water temperature affected the stress response of carp as evidenced by some plasma variables (in particular plasma glucose, osmolality and potassium), but effects were similar across retention treatments as indicated by non-significant interaction terms between temperature and retention period. Most importantly, no mortalities were observed at either of the two temperatures examined (i.e., 12 °C and 22 °C). Because many plasma variables were not significantly affected by high water temperature, our findings suggested only subtle temperature effects on the carp's stress response in the laboratory. This disagree with other studies that reported pronounced temperature-dependent stress responses and survival as a result of catch-and-release angling in various fish species (reviewed in Cooke and Suski, 2005; Arlinghaus et al., 2007; Gale et al., in press). Differences in study findings may result from species-specific temperature tolerance ranges or be explained by the fact that, in the study species carp, the water temperature range in the present experiment was moderate and not reaching extreme (e.g., very low or very high) levels. Indeed, the majority of studies that observed increased physiological changes and increased mortality were conducted with stenotherm cold-water fish species (Gale et al., in press), which are very sensitive to elevated water temperatures beyond certain thresholds. Carp, in contrast, are eurythermal with a preference for warm water temperatures (Blanck et al., 2007) and an overall wide range of temperature tolerance (4–35 °C; Plumb and Hanson, 2010). To explain the impact of water temperature on fish performance, it was suggested that temperature tolerance is linked to the performance of the oxygen supply chain (Pörtner, 2001, 2002). In this context, at high temperature, a high metabolic rate challenges higher aerobic ATP generation, which may, however, be limited at high temperatures leading to a decrease in aerobic scope (Pörtner, 2001, 2002). At low temperatures, by contrast, limited muscular performance may lead to a pronounced decrease in external (gill) and probably internal (heart) ventilatory capacity and similarly decrease the aerobic scope (Pörtner, 2002). However, previous studies revealed that carp are able to maintain aerobic metabolism over a wide range of temperatures from at least 5 °C to 25 °C by increasing respiratory and cardiovascular functions at higher temperatures (Ott et al., 1980; Hughes et al., 1983; Glass et al., 1990; Stecyk and Farrell, 2006). These data suggest that the tested water temperatures in our experiment, which are typical for water bodies in central Europe during spring, summer and fall, did not exceed critical thresholds, although the same water temperature may already be problematic for other species, e.g., cold-water adapted salmonids. However, it cannot be ruled out that lower (Pottinger, 1998) or higher water temperatures than included in the laboratory experiment may alter impacts of catch-and-release angling on carp. Further studies on the stress response in carp that use a wider temperature range are recommended.

The combined physiological disturbances associated with retention in carp sacks were reflected in a tertiary stress response as indicated by behavioural alterations in particularly by fish retained for 9 h. These fish were found to rest for a significantly longer time period within the first half hour post-release compared to short-term retained fish, and their swimming activity (i.e., minimum displacement) between 31 min and 60 min post-release was found to be substantially lower compared to fish that were captured, but not retained in carp sacks. Both, baseline fish and fish retained for 3 h had lower plasma levels of physiological stress indicators (i.e., cortisol, glucose) compared to long-term retained fish, but the long-term retained fish seemed to be physically recovered from capture. Thus, the behavioural impairment can be interpreted as indication of a response to retention-induced stress unrelated to physical recovery. Impaired swimming performance following confinement was previously demonstrated for dip net retained striped bass (*Morone saxatilis*) and may reflect the increased metabolic demands arising from confinement stress and the reduced metabolic capacity for activity (Strange and Cech, 1992). Behavioural alterations

resulting from retention in carp sacks were largely reversed within 12 h post-release as indicated by similar minimum displacement in all treatment groups. This rapid recovery period from angling-induced stress is consistent with a number of other studies with various fish species (Cooke et al., 2000; Arlinghaus et al., 2008, 2009). However, the present study did not include a non-angled control in the behavioural component, and potentially longer lasting effects on fish behaviour compared to a pre-angled state, such as altered feeding behaviour and reduced growth, are at least theoretically possible. It can largely be ruled out that retention in carp sacks will result in significant mortalities, however, as all carp were alive after a two month observation period. This is in accordance with previous studies reporting only low or even zero catch-and-release mortalities in carp (Beukema, 1970; Raat, 1985), and no lethal consequences of keepnet retention in various cyprinid species (Raat et al., 1997; Schreckenbach and Wedekind, 2000).

The impacts of retention are particularly harmful for fish if water quality in the retention gear approaches critical levels. In the present study no evidence was found that this applies to carp sacks as during a 9 h retention period water parameters inside the carp sack did not differ from the ambient water and they remained within a suitable range for carp (Schreckenbach, 2002). Thus, the changes of the examined water quality parameters during retention were likely not of biological significance. Indeed, the findings that many plasma variables indicative of physical exhaustion and recovery thereof returned to control levels during retention suggest that the fish did not suffer from oxygen deprivation in the carp sacks, and water quality changes inside the carp sacks likely did not influence the physiological stress response shown by the experimental fish. This is consistent with the results of a previous study that examined water quality changes within keepnets (Pottinger, 1997). However, in a natural setting there might be environmental conditions during which carp sack retention may negatively affect carp. For example, shoreline areas in eutrophic lakes can be subjected to large daytime oxygen fluctuations during summer and suffer from low oxygen levels during night due to oxygen consuming processes (Schwoerbel and Brendelberger, 2005). Carp sack retention is typically conducted in shallow water, and under the described circumstances critical oxygen levels could be approached in the carp sacks and may negatively affect the fish's welfare and ultimately its viability. In fact, there is anecdotal evidence of mortalities during over-night carp sack retention, which may originate from insufficient oxygen levels combined with elevated temperatures or from poor water quality at the fishing site. As carp are, however, very tolerant to low oxygen and diurnal changes in oxygen levels (Lykkeboe and Weber, 1978) such incidences should not be attributed to carp sack retention itself (as the present study revealed), but rather to the inappropriate usage of this retention gear, i.e., if retention is conducted during unsuitable environmental conditions or in unsuitable areas.

To conclude, the results of the present study revealed that a specialised carp angling event including post-capture retention in carp sacks that are characterised by a knotless, fine mesh fabric and the lack of a rigid frame is associated with a primary, secondary and tertiary stress response as well as tissue damage. However, recovery of the physiological state and behavioural patterns are reasonably rapid (within several hours), and no significant mortalities are to be expected. From a fish population management and conservation perspective, which mainly focuses on survival endpoints, the results suggest that the impacts of capture and subsequent retention in carp sacks are of minor concern due to rapid recovery dynamics and high survival of released fish. However, if one takes an individual-based fish welfare perspective (Arlinghaus et al., 2007), which aims at minimising any adverse effects on fish, the physiological stress responses, tissue damage and behavioural impairments associated with capture and retention in carp sacks suggest that the use of carp sacks is to be discouraged and the fish should be photographed and released directly after capture when legally allowed.

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References

Arakawa, H., Kodama, H., Matsuoka, N., Yamaguchi, I., 1997. Stress increases enzyme activity in rats: differential effects of adrenergic and cholinergic blockades. J. Pharmacol. Exp. Ther. 280, 1296–1303.

Arlinghaus, R., Mehner, T., 2003. Socio-economic characterisation of specialised common carp (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries management and eutrophication control. Fish. Res. 61, 19–33.

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

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

Arlinghaus, R., Klefoth, T., Cooke, S.J., Gingerich, A., Suski, C., 2009. Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. 97, 223–233.

Auperin, B., Geslin, M., 2008. Plasma cortisol response to stress in juvenile rainbow trout is influenced by their life history during early development and by egg cortisol content. Gen. Comp. Endocrinol. 158, 234–239.

Barthel, B.L., Cooke, S.J., Suski, C.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.

Barton, B.A., Schreck, C.B., Barton, L.D., 1987. Effects of chronic cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. Dis. Aquat. Organ. 2, 173–185.

Barton, B.A., Morgan, J.D., Vijayan, M.M., 2002. Physiological and condition-related indicators of environmental stress in fish. In: Adams, S.M. (Ed.), Biological Indicators of Aquatic Ecosystem Stress. American Fisheries Society, Bethesda, MD, pp. 111–148.

Bellamy, J.E.C., Olexson, D.W., 2000. Quality Assurance Handbook for Veterinary Laboratories. Iowa State University Press, Ames, IA, p. 101.

Beukema, J.J., 1970. Angling experiments with carp (*Cyprinus carpio* L.). II. Decreasing catchability through one-trial learning. Neth. J. Zool. 20, 81–92.

Blanck, A., Tedesco, P.A., Lamouroux, N., 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. Freshw. Biol. 52, 843–859.

Butcher, P.A., Broadhurst, M.K., Hall, K.C., Cooke, S.J., 2011. Post-release survival and physiology of angled luderick (*Girella tricuspidata*) after confinement in keeper nets in an Australian estuary. ICES J. Mar. Sci. 68, 572–579.

Clapp, D.F., Clark Jr., R.D., 1989. Hooking mortality of smallmouth bass caught on live minnows and artificial spinners. N. Am. J. Fish. Manage. 9, 81–85.

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., Hogle, W.J., 2000. Effects of retention gear on the injury and short-term mortality of adult smallmouth bass. N. Am. J. Fish. Manage. 20, 1033–1039.

Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodivers. Conserv. 14, 1195–1209.

Cooke, S.J., Philipp, D.P., Schreer, J.F., McKinley, R.S., 2000. Locomotory impairment of nesting male largemouth bass following catch-and-release angling. N. Am. J. Fish. Manage. 20, 968–977.

Cooke, S.J., Schreer, J.F., Wahl, D.H., Philipp, D.P., 2002a. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Am. Fish. Soc. Symp. 31, 489–512.
Cooke, S.J., Schreer, J.F., Dunmall, K.M., Philipp, D.P., 2002b. Strategies for quantifying sub-lethal effects of marine catch-and-release angling: insights from novel freshwater applications. Am. Fish. Soc. Symp. 30, 121–134.
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.
Curry, R.A., Doherty, C.A., Jardine, T.D., Currie, S.L., 2007. Using movements and diet analyses to assess effects of introduced muskellunge (*Esox masquinongy*) on Atlantic salmon (*Salmo salar*) in the Saint John River, New Brunswick. Environ. Biol. Fish. 79, 49–60.
Davis, M.W., Schreck, C.B., 2005. Responses by pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality. Trans. Am. Fish. Soc. 134, 991–998.
Diodati, P.J., Richards, R.A., 1996. Mortality of striped bass hooked and released in salt water. Trans. Am. Fish. Soc. 125, 300–307.
Donaldson, M.R., Arlinghaus, R., Hanson, K.C., Cooke, S.J., 2008. Enhancing catch-and-release science with biotelemetry. Fish Fish. 9, 79–105.
Dunmall, K.M., Cooke, S.J., Schreer, J.F., McKinley, R.S., 2001. The effect of scented lures on the hooking injury and mortality of smallmouth bass caught by novice and experienced anglers. N. Am. J. Fish. Manage. 21, 242–248.
Dyer, S.M., Cervasio, E.L., 2008. An overview of restraint and blood collection techniques in exotic pet practice. Vet. Clin. North Am. Exot. Anim. Pract. 11, 423–443.
Fevolden, S.E., Nordmo, R., Refstie, T., Røed, K.H., 1993. Disease resistance in Atlantic salmon (*Salmo salar*) selected for high or low responses to stress. Aquaculture 109, 215–224.
Gale, M.K., Hinch, S.G., Donaldson, M.R. The role of temperature in the capture and release of fish. Fish Fish., in press.
Gallardo, J.M., Alavi, S.M.H., Adámek, Z., Drozd, B., 2010. External damage and changes in blood parameters in female tench, *Tinca tinca* (L.) retained in anglers' keepnets. Rev. Fish Biol. Fish. 20, 403–408.
Gillis, N.C., Rapp, T., Hasler, C.T., Wachelka, H., Cooke, S.J., 2010. Spatial ecology of adult muskellunge (*Esox masquinongy*) in the urban Ottawa reach of the historic Rideau Canal, Canada. Aquat. Living Resour. 23, 225–230.
Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. Fish. Res. 86, 169–178.
Gingerich, A.J., Suski, C.D. The effect of body size on post-exercise physiology in largemouth bass. Fish Physiol. Biochem., in press.
Glass, M.L., Andersen, N.A., Kruhoffer, M., Williams, E.M., Heisler, N., 1990. Combined effects of environmental P_{o2} and temperature on ventilation and blood gases in the carp *Cyprinus carpio* L. J. Exp. Biol. 148, 1–17.
Gravel, M.-A., Cooke, S.J., 2008. Severity of barotrauma influences the physiological status, postrelease behavior, and fate of tournament-caught smallmouth bass. N. Am. J. Fish. Manage. 28, 607–617.
Hanson, K.C., O'Connor, C.M., Van Der Kraak, G., Cooke, S.J., 2009. The relative roles of parental investment and organismal condition in parental aggression in smallmouth bass. Horm. Behav. 55, 495–499.
Holeton, G.F., Neumann, P., Heisler, N., 1983. Branchial ion exchange and acid-base regulation after strenuous exercise in rainbow trout (*Salmo gairdneri*). Respir. Physiol. 51, 303–318.
Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6, 65–70.
Hughes, G.M., Albers, C., Muster, D., Gotz, K.H., 1983. Respiration of the carp, *Cyprinus carpio* L., at 10 °C and 20 °C and the effects of hypoxia. J. Fish Biol. 22, 613–628.
Johnston, I.A., 1977. A comparative study of glycolysis in red and white muscles of the trout (*Salmo gairdneri*) and mirror carp (*Cyprinus carpio*). J. Fish Biol. 11, 575–588.
Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A 126, 161–179.
Killen, S.S., Suski, C.D., Morrissey, M.B., Dyment, P., Furimsky, M., Tufts, B.L., 2003. Physiological responses of walleyes to live-release angling tournaments. N. Am. J. Fish. Manage. 23, 1238–1246.
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 simulated live-release angling tournaments. Trans. Am. Fish. Soc. 135, 557–569.
Klefoth, T., Kobler, A., Arlinghaus, R., 2011. Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius*) fishery. Knowl. Manage. Aquat. Ecosyst. 403, doi:10.1051/kmae/2011072, 11p1–11p18.
Lykkeboe, G., Weber, R.E., 1978. Changes in respiratory properties of blood in the carp, *Cyprinus carpio*, induced by diurnal variation in ambient oxygen tension. J. Comp. Physiol. 128, 117–125.
McDonald, G., Milligan, L., 1997. Ionic, osmotic and acid-base regulation in 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. 119–144.
Mech, L.D., 1983. (Ed.). Handbook of Animal Radio-Tracking. University of Minnesota Press, Minneapolis, MN, p. 107.
Meka, J.M., McCormick, S.D., 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. Fish. Res. 72, 311–322.
Morrissey, M.B., Suski, C.D., Esseltine, K.R., Tufts, B.L., 2005. Incidence and physiological consequences of decompression in smallmouth bass after live-release angling tournaments. Trans. Am. Fish. Soc. 134, 1038–1047.
Moyes, C.D., Fragoso, N., Musyl, M.K., Brill, R.W., 2006. Predicting postrelease survival and large pelagic fish. Trans. Am. Fish. Soc. 135, 1389–1397.
Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. 2, 123–156.
Ostrand, K.G., Cooke, S.J., Wahl, D.H., 2004. Effects of stress on largemouth bass reproduction. N. Am. J. Fish. Manage. 24, 1038–1045.
Ott, M.E., Heisler, N., Ultsch, G.R., 1980. A re-evaluation of the relationship between temperature and the critical oxygen-tension in freshwater fishes. Comp. Biochem. Physiol. A 67, 337–340.
Øverli, O., Sørensen, C., Kiessling, A., Pottinger, T.G., Gjøen, H.M., 2006. Selection for improved stress tolerance in rainbow trout (*Oncorhynchus mykiss*) leads to reduced feed waste. Aquaculture 261, 776–781.
Pearl, W., Balasz, T., Buyske, D.A., 1966. The effects of stress on serum transaminase activity in the rat. Life Sci. 5, 67–74.
Pickering, A.D., Pottinger, T.G., Christie, P., 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time-course study. J. Fish Biol. 20, 229–244.
Plumb, J.A., Hanson, L.A., 2010. Health Maintenance and Principal Microbial Diseases of Cultured Fishes, 3rd edition. Wiley-Blackwell, Ames, IA, p. 400.
Pörtner, H.O., 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88, 137–146.
Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp. Biochem. Physiol. A 132, 739–761.
Pottinger, T.G., 1997. Changes in water quality within anglers' keepnets during the confinement of fish. Fish. Manage. Ecol. 4, 341–354.
Pottinger, T.G., 1998. Changes in blood cortisol, glucose and lactate in carp retained in anglers' keepnets. J. Fish Biol. 53, 728–742.
Raat, A.J.P., 1985. Analysis of angling vulnerability of common carp, *Cyprinus carpio* L., in catch-and-release angling in ponds. Aquacult. Fish. Manage. 16, 171–187.
Raat, A.J.P., Klein Breteler, J.G.P., Jansen, S.A.W., 1997. Effects on growth and survival of retention of rod-caught cyprinids in large keepnets. Fish. Manage. Ecol. 4, 355–368.
Rapp, T., Cooke, S.J., Arlinghaus, R., 2008. Exploitation of specialised fisheries resources: the importance of hook size in recreational angling for large common carp (*Cyprinus carpio* L.). Fish. Res. 94, 79–83.
Ruane, N.M., Wendelaar Bonga, S.E., Balm, P.H.M., 1999. Differences between rainbow trout and brown trout in the regulation of the pituitary-interrenal axis and physiological performance during confinement. Gen. Comp. Endocrinol. 115, 210–219.
Ruane, N.M., Huisman, E.A., Komen, J., 2001. Plasma cortisol and metabolite level profiles in two isogenic strains of common carp during confinement. J. Fish Biol. 59, 1–12.
Rush, S.B., Umminger, B.L., 1978. Elimination of stress-induced changes in carbohydrate metabolism of goldfish (*Carassius auratus*) by training. Comp. Biochem. Physiol. A 60, 69–73.
Sachs, L., Hedderich, J., 2006. Angewandte Statistik: Methodensammlung mit R. Springer-Verlag, Berlin, p. 701.
Sánchez, O., Arnau, A., Pareja, M., Poch, E., Ramírez, I., Soley, M., 2002. Acute stress-induced tissue injury in mice: differences between emotional and social stress. Cell Stress Chaperones 7, 36–46.
Schreckenbach, K., 2002. Einfluss von Umweltbedingungen auf Karpfen. Fischer und Teichwirt 53, 207–208.
Schreckenbach, K., Wedekind, H., 2000. Einfluss der Angelfischerei und der Behandlung nach dem Fang auf die Stressreaktionen und die Fleischqualität von Regenbogenforellen (*Oncorhynchus mykiss*), Plötzen (*Rutilus rutilus*) und Rotfedern (*Scardinius erythrophtalmus*). Fischerei und Naturschutz 2, 22–40.
Schwoerbel, J., Brendelberger, H., 2005. Einführung in die Limnologie. Spektrum Akademischer Verlag, München, p. 340.
Siepker, M.J., Ostrand, K.G., Wahl, D.H., 2006. Effects of angling on feeding by largemouth bass. J. Fish Biol. 69, 783–793.
Stecyk, J.A.W., Farrell, A.P., 2006. Regulation of the cardiorespiratory system of common carp (*Cyprinus carpio*) during severe hypoxia at three seasonal acclimation temperatures. Physiol. Biochem. Zool. 79, 614–627.
Strange, R.J., Cech Jr., J.J., 1992. Reduced swimming performance of striped bass after confinement stress. Trans. Am. Fish. Soc. 121, 206–210.
Suski, C.D., Killen, S.S., Morrissey, M.B., 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 live-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.
Tanck, M.W.T., Booms, G.H.R., Eding, E.H., Wendelaar Bonga, S.E., Komen, J., 2000. Cold shocks: a stressor for common carp. J. Fish Biol. 57, 881–894.
Wang, Y., Heigenhauser, G.J.F., Wood, C.M., 1994. Integrated responses to exhaustive exercise and recovery in rainbow trout white muscle: acid-base, phosphogen,

carbohydrate, lipid, ammonia, fluid volume and electrolyte metabolism. J. Exp. Biol. 195, 227–258.
Weil, L.S., Barry, T.P., Malison, J.A., 2001. Fast growth in rainbow trout is correlated with a rapid decrease in post-stress cortisol concentrations. Aquaculture 193, 373–380.
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.
Wood, C.M., Turner, J.D., Graham, M.S., 1983. Why do fish die after severe exercise? J. Fish Biol. 22, 189–201.
Woodward, C.C., Strange, R.J., 1987. Physiological stress responses in wild and hatchery-reared rainbow trout. Trans. Am. Fish. Soc. 116, 574–579.
Wydoski, R.S., Wedemeyer, G.A., Nelson, N.C., 1976. Physiological response to hooking stress in hatchery and wild rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 105, 601–606.
Zwirnmann, E., Krüger, A., Gelbrecht, J., 1999. Analytik im zentralen Chemielabor des IGB. Berichte des IGB 9, 3–24.