Socially induced stress and behavioural inhibition in response to angling exposure in rainbow trout

Magnus Lovén Wallerius[1], Albin Gräns[2], Barbara Koeck[1,3], David Berger[1], Erik Sandblom[1], Andreas Ekström[1], Robert Arlinghaus[4, 5] and Jörgen I. Johnsson[1]

1. Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden.

2. Department of Animal Environment and Health, Swedish University of Agricultural Sciences, Gothenburg, Sweden.

3. Institute of Biodiversity, Animal Health, and Comparative Medicine, University of Glasgow, Glasgow, UK

4. Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany.

5. Division of Integrative Fisheries Management, Department for Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität, Berlin, Germany.

Abstract

It is well known that fish can learn to avoid angling gear after experiencing a catch-and-release event, *i.e.* after a private hooking experience. However, the possible importance of social information cues and their influence on an individual's vulnerability to angling remains largely unexplored, *i.e.* social experience of a conspecific's capture. We examined the effects of private and social experience of hooking on the stress response of fish and subsequent catch rates. Hatchery reared rainbow trout (*Oncorhynchus mykiss*) were implanted with heart rate loggers and experimentally subjected to private or social experience of hooking. Private and social experience of angling induced an increased heart rate in fish compared to naïve control fish. While private experience of hooking explained most of the reduced vulnerability to capture, we found no clear evidence that social experience of hooking affected angling vulnerability in fish that had never been hooked before. While both private and social experiences of angling constitute significant physiological stressors for rainbow trout, only the private experience reduces an individual's vulnerability to angling and in turn affecting population-level catchability.

Introduction

Recreational fishing is common in all industrial countries (Arlinghaus et al. 2015). In contrast to commercial fisheries, recreational fishing is a leisure activity were only a portion of the catch is kept for nutritional purpose (Cooke & Cowx, 2006; Cooke et al. 2018). Worldwide reports about declining and collapsed fish populations have mainly been attributed to commercial fisheries (Worm et al. 2009). However, increasing attention about recreational fishing and its induced impact on fish population has risen in some countries (Cooke & Cowx 2004; Post et al. 2002; Lewin et al. 2006). To support angler satisfaction and reduce the impact of recreational fishing, fisheries managers have implemented harvest regulations and other management strategies, such as stocking (Arlinghaus et al. 2007; FAO, 2012). One approach to deal with the potential of angling-induced overfishing are size-based harvest regulations that involve mandatory catch-and-release (C&R) of undersized fish, and the promotion of voluntary C&R of harvestable fishes where fish are released back to the water following capture and unhooking (Bartholomew & Bohnsack 2005; Cooke & Schramm, 2007; Policansky, 2002). The concept behind C&R relies on the conservation of fish populations, with the intention to sustain catch rates (Arlinghaus et al. 2007). Achieving these aims demands releasing fish without substantial injuries and other lasting sub-lethal physiological and behavioural impacts. Literature reviews have revealed substantial interspecific and contextual variation in post-release impacts and mortality, including hook-related injuries and physiological/behavioural responses to C&R, demanding species-specific research to evaluate the effects of C&R (Arlinghaus et al. 2007; Cooke & Suski, 2005).

In addition to potential lethal impacts, C&R can produce multiple sub-lethal stress responses, including elevated plasma concentrations of cortisol (Meka & McCormick 2005; Pankhurst & Dedual 1994), increased cardiac activity (*i.e.* heart-rate, cardiac output and stroke volume) (Anderson et al. 1998; Cooke et al. 2001; Cooke et al. 2002), as well as behavioural changes for a certain period following the release (Koeck et al. in press; Klefoth et al. 2011). As a consequence, individual fish can develop hook avoidance behaviour through private experiences of hooking (Askey et al. 2006; Beukema, 1970a, 1970b; Klefoth et al. 2013; Raat, 1985; van Poorten & Post, 2005; Young & Hayes, 2004). In addition, population-level catchability has been found to be affected by angling effort without necessarily all fish being hooked and released (e.g. Koeck et al. in press; Kuparinen et al. 2010; Alós et al. 2015; Wegener et al. 2018). Experimental pond studies with carp (*Cyprinus carpio*) (Beukema, 1970a; Klefoth et al. 2013; Raat, 1985) and pike (*Esox Lucius*) (Beukema, 1970b) have suggested that social learning might play a role in observed decreases of overall catchability. These studies suggested that physiological and behavioural stress responses from previously caught individuals may also carry over to affect non-hooked conspecifics, eliciting a hook avoidance behaviour in these individuals through a social learning mechanism (Laland et al. 2003), thereby decreasing the overall catchability of the targeted fish population. The only study directly testing this hypothesis was conducted in largemouth bass (*Micropterus salmoides*) (Wegener et al. 2018), but it failed to find evidence that social learning reduced catchability in this species. However, as social behaviours and the ability to learn differ considerably in freshwater fishes (Coble et al. 1985), the results on largemouth bass by Wegener et al. (2018) may not be generalizable to other species.

Social learning is defined as long term behavioural changes to a stimuli derived from the interactions with or observations of other individuals, *i.e.* public information use (Mesoudi et al. 2016). Social learning has an obvious adaptive value to private learning in terms of risk avoidance. For example, if an individual can learn to identify a threat by observing the behaviour of experienced individuals without taking the risk itself, it could have an equally good chance of responding adequately when faced with a similar threat (Laland et al. 2003).

Social learning is however not restricted to observation. For example, chemicals cues released from the epidermis of injured fish are known to function as alarm signals (Schreckstoff) that can trigger a response in the receiving fish (Brown & Smith, 1997; Chivers & Smith, 1998). Moreover, by developing associations between alarm chemicals and the aversive response of conspecifics towards an initially neutral predator, an individual may learn to identify the predator and evoke an avoidance response against it, even in the absence of conspecifics or alarm chemicals (Griffin 2004). It is unknown whether such effects occur in hook-and-line fishing, where the threat cues are mainly related to olfactory and visual stimuli, and if the experience of observing conspecifics being hooked and released will affect physiological responses and cause behavioural changes (Meekan et al. 2018).

The aim of the present study was to evaluate the effect of angling experience and its impact on catch rate and heart rate - used as a proxy to measure stress response (Wendelaar Bonga, 1997) - by exposing rainbow trout (*Oncorhynchus mykiss*) in ponds to different levels of angling exposure, followed by catch-and-release angling. Based on the documented learning capacities of fish, as well as the known physiological and behavioural stress responses of previously hooked fish, we tested the following hypotheses: i) social experience of C&R reduces the vulnerability compared to naïve fish and fish only exposed to angling associated disturbance, but not to the same extent as fish with private experience of hooking, and ii) the physiological stress response will reflect the angling experience that fish have been subjected to, *i.e*. the highest stress response is expected in fish with private experience of angling, followed by fish with social experience and be the lowest in naïve fish.

Methods

Experimental design

To evaluate the relative contribution of private vs. social experience of fish to angling, we conducted a triplicated angling experiment in 4 semi-controlled ponds stocked with size matched rainbow trout. The experiment consisted of two steps; first the angling exposure treatments (Fig 1B) followed by a period of angling trials during which catch-rates were quantified and compared across treatments, and served as a vulnerability assessment of fish to the different levels of angling exposure they had been subjected too (Fig 1C). The angling exposure consisted of four treatments (Fig 1B): 1) a private exposure treatment during which fish were caught and released back to the same pond to ensure the private experience of angling; 2) a social exposure treatment where fish experienced only the social stimuli of other conspecifics fighting on the line, 3) a control: were fish had no exposure treatment and remained naïve to angling; and 4) a second control treatment called disturbance treatment with fish exposed to hook-less angling gear to account for the possible effects of the disturbance related to the angling method itself. The experiment was repeated 3 times between 8th September and 9th November 2016. To control for possible pond effects, the treatment order was changed between experimental rounds so that no treatment was repeated within the same pond. Additionally, stress response of fish was assessed by implanting a subset of fish in the last round of the experiment with heart-rate loggers, recording changes in heart rate as a proxy of stress response of fish to angling treatments. The experiments were approved by the Ethical Committee for Animal Research of the University of Gothenburg (Licence 15.2014 and licence 165-2015) and comply with Swedish and European law.

Experimental set-up and fish

The study was conducted in the facilities of the Swedish sport fishing association (Sportfiskarna) at Sjölyckan, Gothenburg, Sweden (57°41'36.1"N 12°2'11.8"E). The experimental system consisted of four ponds (30 × 24 × 2 m; L × W × D, 1440 m^2 each) with a constant inflow from Lake Delsjön (mean temperature ± s.d: round 1: 18.1 ± 1.0 ^{o}C; round 2: 12.0 ± 2.0 ^{o}C; round 3: 7.8 ± 0.9 ^{o}C). Prior to the experiment, the ponds were drained and cleaned from macrophytes and debris, then stocked before each experimental round with sized-matched rainbow trout *(*163 fish per round; mean ± s.d: mass = 391.6 ± 55.1 g; fork length = 31.6 ± 1.5 cm) transported from the Källefall hatchery (58°10'12.3"N 14°4'47.6"E). On arrival, fish were first let to settle for at least an hour in holding tanks (2 × 2 × 0.5 m; L × W × D) supplied with aerated Lake Delsjön water at ambient temperature, then anaesthetized (in round 1 and 3: MS-222 at 150 mg l^{-1} buffered with $NaHCO_3$ at 300 mg l^{-1}; in round 2: benzocaine 400 mg l^{-1}), measured for mass and fork length and tagged with a passive integrated transponder (PIT) (23 × 3.65 mm, 0.6 g, Texas Instruments, Dallas, Texas, USA) to enable individual identification. PIT-tags were inserted into the abdominal cavity trough a small incision and followed by cutaneous application of an antiseptic paste (Vetofish, SELARL Vétérinaire, Martigues, France). Following tagging and surgical implantation, fish were placed in a recovery tank (1 × 1 × 0.5 m; L × W × D) for observation. When each fish had resumed normal swimming and respiratory motion, they were distributed randomly among the four experimental ponds and left to acclimate for 8 days (Fig 1A). No difference in mass was found between the treatments following the random pond distribution (ANOVA: $F = 0.486$, $p > 0.05$ for all comparisons). No food was provided during the experiment, but naturally occurring invertebrates such as Trichoptera were present in the ponds.

Heart rate logger implantation

To measure the stress response in fish during the different angling exposures, a subset of 30 individuals in round 3 - equally distributed between social exposure, private exposure and control treatment - were surgically implanted with bio-loggers (39.5 × 13 mm and 11.8 g, DST milli-HRT, Star-Oddi, Gardabaer, Iceland) capable of measuring time-stamped (accuracy ± 1 min month^{-1}) heart rate and temperature (resolution 0.032 ^{o}C, accuracy ± 0.2 ^{o}C). These fish are from here on referred to as the heart rate logger-fish. For consistency between treatments, since in the disturbance exposure treatment no fish received a bio-logger, a subset of 10 individuals were sham operated, which means that they underwent identical surgical treatment as the heart rate logger-fish, but no bio-loggers were implanted.

The bio-loggers were programmed to derive an average heart rate from 6 second-long measures of electrocardiogram (ECG) sampled at a frequency of 100 Hz. The bio-loggers were programmed to record at two different sampling frequencies; one high frequency period (one measurement per min) that covered the 5 hours around the angling trials between 13:30 and 18:30 (see below for details) and one low frequency period (one measurement per 10 min) that covered the other 19 hours of the day. For validation purposes, all logged heart rate measurements are graded with a data verification quality index (QI) by the software supplied by the manufacturer, ranging from 0-3, whereby QI0=Great, QI1=Good, QI2=Fair and QI3=Poor. To ensure the highest possible accuracy, only measurements graded with QI0 were used in the present study following Brijs et al. (2018) and Brijs et al. (2019).

Before implantation of the bio-loggers, the fish were first individually anaesthetized in MS-222 as described above. When the fish had lost equilibrium and stopped ventilating they were positioned on its side on water-soaked rubber foam on a surgical table. During the surgery, the gills were continuously flushed with aerated 10 °C water containing 75 mg l^{-1}

MS-222 and 150 mg l^{-1} $NaHCO_3$ to maintain anesthesia. The bio-loggers were inserted through a ~30 mm incision along the mid-ventral line approximately 40 mm posterior to the pectoral fins, and positioned longitudinally in the pericardial cavity and anchored to the muscle, following Brijs et al. (2018) and Ekström et al. (2018).

Angling exposure treatments

Following the 8-days acclimation period, fish from each pond were exposed to different angling treatments (Fig 1B). The initial sample size in each treatment was set to 40 except for the social exposure (n=43) (see social exposure treatment section). In each round, all exposure treatments were conducted simultaneously for one hour of angling per day on three consecutive days.

In the private exposure treatment, the aim was to evaluate how the private experience of being caught and released affected the stress response and angling vulnerability. Two experienced anglers, placed on each short side of the pond, used a spinning rod (braided line: resistance 4.5 kg; 1 m fluorocarbon leader, resistance 4.9 kg; and barbless hook (Gamakatzu G-code, Worm 39, Size 3)) baited with a dead shrimp. Anglers chose freely where to cast, how long to keep the bait at one spot and the depth at which the bait was presented. Caught fish were landed as quickly as possible and transferred with a knotless landing net to a water-filled bucket, to be unhooked and identified. During the remainder of the angling event, the caught fish were kept in recovery tanks (1 × 1 × 1 m; L × W × D) with a constant refill of aerated water Immediately after the angling event, all caught fish were transferred back to their corresponding pond, hence a fish could only be caught once in each angling event but potentially up to three times during the three days of treatment. In the event of deep-hooking, fish were euthanized with a sharp blow to the head.

In the social exposure treatment, the aim was to evaluate the effect on vulnerability and stress by exposing the fish to the social stimuli of other conspecifics being hooked and fighting on the line. To ensure that the fish experienced the social stimuli of other individuals being hooked, each daily exposure began with an angler catching one fish in the pond. When the first fish was caught and identified by its PIT-tag number, it was not released back to the same pond, instead it was transferred to a non-experimental pond. This procedure was done to reduce the risk of confounding effects from catching all the vulnerable fish first while leaving less vulnerable fish within the pond (Koeck et al. 2018). During the remainder of the social exposure, rainbow trout not used in the experiment were caught in the non-experimental pond and gently transferred to the treatment pond where they were displayed for approximately 30 seconds, fighting freely in the pond while on the angler's line. After the display, the fish were transferred back to the non-experimental pond and a new fish was caught for display. The number of displayed individuals (including the first catch) was kept equal to the number of individuals caught in the simultaneously conducted private exposure treatment (total captures in round 1; n = 37, round 2; n = 41, round 3; n = 39). The purpose of this procedure was to expose the fish to a similar level of disturbance/opportunity to acquire social information about fishing threat, as experienced directly by individuals in the private exposure treatment, without providing any focal fish with private experience of C&R. The difference in initial sample size between the social exposure and the other angling treatments (43 compared to 40 per replicate) was set to compensate for the daily removal of one individual.

A disturbance treatment was included in the experimental design to account for the possible effects of disturbance related to the angling method itself *i.e.* likely non-threatening disturbance caused by casting and retrieving the tackle and the anglers´ movements around the ponds. The disturbance treatment was performed in the same way as in the private exposure treatment but without using bait or hooks. No angling was conducted in the control treatment.

Vulnerability assessment

48 hours after the last day of angling exposure treatment (Fig 1B), standardized angling was conducted simultaneously in all experimental ponds for one hour during four consecutive days (Fig 1C). Two experienced anglers were randomly allocated to each pond, with one angler positioned on each short side of the pond. Every tenth minute, the anglers changed ponds and position to randomize differences in fishing technique and skills. As in the private exposure treatment, barbless hooks baited with shrimp were used. Caught fish were kept in recovery tanks during the remainder of the angling event and, after identification, released back to their respective ponds. Each individual could thus potentially be caught up to four times. When one round of angling was complete, the ponds were drained and the fish were sampled for mass and length measurements, before the ponds were refilled and stocked with a new batch of fish for the next experimental round following the same procedure. The time of day of the angling exposure was adjusted between rounds to account for seasonal changes in light conditions, so that each angling exposure ended approximately one hour before sunset.

Data handling and statistical analysis

All data subjected to statistical analyses were assessed to ensure that they did not violate the assumptions of the models used. A Cox proportional hazard regression ("coxph" function, "survival" package, R) was modelled to analyse associations between treatment and time-to-event, *i.e.* to what degree the angling exposure treatments affected the chances of an individual being caught over time. The model accounted for only one event per individual, *i.e.* the response variable was the time until first catch. Because of the marked decrease in water temperature over the course of the experiment, temperature (instead of round) was added as a covariate to the survival model. Non-significant interaction between temperature and treatments indicated however that temperature did not affect catch rate in a specific treatment, and the interaction term was thus excluded from the final model (Table 1). Furthermore, not all individuals in the private exposure treatment were caught during the exposure angling (proportion caught fish round 1; 0.8, round 2; 0.825, round 3; 0.75). Since uncaught individuals in the private exposure treatment lacked private experience of C&R, they were discarded from the main analysis.

For quantifying heart rate response to angling, an individual hourly mean heart-rate was calculated and used in further analyses. The effects of angling disturbances on heart-rate following the three periods (*i.e.* acclimation period, angling exposure and vulnerability assessment) was investigated using a linear mixed model. In this model, hourly mean heart rate was used as dependent variable. Angling exposure treatment, period and day were included as fixed factors. Fish ID and hour of day were used as random effects. In this analysis, heart rates recorded between the start of an angling period and the following 24 h (*i.e.* 15:00-15:00) were defined as a day so that the acclimation period included the last three days and angling exposure and vulnerability assessment included three and four separate days, respectively. The heart rate data was analyzed using SPSS Statistics 22 (IBM Corp., Armonk, NY, USA).

Results

Effects of angling exposure on subsequent vulnerability to angling

Across all treatments, the private exposure treatment had the most pronounced effect on subsequent catchability and significantly reduced capture vulnerability by 72.6% relative to fish from the control treatment (Table 1, Fig. 2). The social exposure treatment produced a non-significant decrease in angling vulnerability of 23.4% relative to fish in the control treatment (Table 1, Fig. 2). Fish in the disturbance treatment reduced angling vulnerability by only 8.9% relative to control treatment, which was not significant (Table 1, Fig. 2). Capture vulnerability was generally increased with temperature (Table 1), which did not interfere with exposure treatment (non-significant interaction; see method section). No difference in catch rate was found between the sham, control and private heart rate logger-fish when comparing proportions of individuals caught for the first time ($\chi^2 = 1.14$, df =2, $p > 0.05$), indicating that the implantation procedure and presence of heart-rate logger did not bias the catch rate results.

Heart rate response to angling treatments

No difference in heart rate was found between the private exposure and control treatment during the acclimation period (Table 2, Fig 3A). However, during the two last days of the acclimation period, the heart rates in the social exposure was significantly higher than the control treatment while private exposure and social exposure showed no differences in their heart rates (Table 2, Fig 3A). During the first day of angling exposure, we found a pronounced significant increase in heart rate in the private exposure treatment, while an intermediate significant increase was seen in the social exposure treatment relative to the control treatment (Table 2, Fig 3B). During the second and third day of angling exposure, the peak heart rate response in the private exposure treatment was somewhat reduced relative to the first treatment day such that the private exposure treatment were not significantly different from the social exposure treatment (private vs. social; mean daily difference in heart rate ± S.E, p-value; Day 1: 3.19 ± 0.70, $p < 0.001$; Day 2: 0.07 ± 0.68 $p = 0.91$; Day 3: 0.74 ± 0.68 $p = 0.28$) (Fig 3B). However, both the private and social exposure treatment had a significantly higher heart rate compared to the control treatment during all three days of angling treatment (Table 2, Fig 3B). When analysing the daily effects of angling on heart rate across treatment groups, all three treatments differed significantly during the first day of vulnerability assessment (Social > Private > Control: Table 2, Fig 3C). In the subsequent days, the peak heart rate response during angling was gradually reduced in all treatments, and during the last two days of vulnerability assessment no difference in heart rate was found between the treatments except between private and control treatment during the final day (Table 2, Fig 3C). For cardiogram of all individual fish, see supplementary figure S1.

Discussion

In agreement with previous studies on decreased catch rate and catchability in C&R recreational fisheries (e.g. common carp: Beukema 1970a; Klefoth et al. 2013; rainbow trout: Askey et al. 2006; van Poorten & Post 2005; and brown trout (*Salmo trutta*): Young & Hayes 2004), we found that the private experience of C&R is the main contributor to decreased vulnerability in rainbow trout and that caught individuals demonstrate a more distinct physiological stress response (Anderson et al., 1998), as indicated by elevated heart rate, compared to uncaught individuals. Our results also indicate that social experience and angling disturbance do not significantly contribute to decreased vulnerability in C&R fisheries for rainbow trout. However, our results also point out that the social experience of hooked conspecifics alone suffices to induce an increase in heart rate, providing evidence of a cardiovascular stress response in rainbow trout to social experience of C&R.

The fact that fish that had previously experienced hooking (*i.e.* fish from the private exposure treatment) were caught substantially less frequently than fish indirectly exposed to angling (*i.e.* socially experienced fish) and fish naïve to angling (*i.e.* from the control treatment) suggests that additional mechanisms (e.g. physiological and behavioural) not quantified here are affecting vulnerability. Possible factors that were unique to previously hooked fish that might explain their increased subsequent hook avoidance relative to fish in the social exposure treatment, include repeated visual stimuli of other conspecifics being hooked, combined with hook injury, physical exhaustion and air exposure, which have been found to result in elevated plasma levels of stress indicators, such as cortisol and glucose (Arlinghaus et al. 2009; Cooke et al. 2001; Donaldson et al. 2010; Pullen et al. 2017). Moreover, it is possible that these factors triggered a tertiary stress response in the privately hooked fish (Barton, 2002; Wendelaar Bonga, 1997), leading to behavioral changes following C&R (Halttunen et al. 2010; Schreer et al. 2005; Arlinghaus et al. 2009; Klefoth et al. 2011). In addition, the reduced heart rate displayed during the subsequent days in the private exposure treatment may also indicate that fish habituated to the stressor of C&R angling (Barton et al. 1987). However, the continuous decrease in heart rate in the private exposure treatment might also have been related to the gradual decrease in water temperature (Eliason & Anttila, 2017), as indicated by the continuous decrease in heart rate in the control group.

Our study was conducted with hatchery fish, which represent both a strength and a limitation. First, hatchery fish are a suitable model when studied in semi-natural environments such as the ponds used here because they are likely better adapted to ponds compared to wild conspecifics. The greater degree of domestication of hatchery reared fish and the associated adaptation to stressful situations during handling (Woodward & Strange, 1987) seems to increase the readiness to take baits presented by anglers compared to wild fish (Koeck et al. 2018; Mezzera & Largiadèr, 2001). Indeed, the rainbow trout used in the present study have been artificially selected since the 90s (personal communication with Källefall Hatchery), which has probably favoured bold and stress-resistant phenotypes (Berejikian 1995; Johnsson & Abrahams, 1991; Biro & Post 2008), while decreasing the overall phenotypic variation compared to a wild population (Fleming & Einum, 1997). As learning capacities might differ between individuals within a population, some individuals might rely on social information to a higher degree (Lucon-Xiccato & Bisazza 2017). Thus, the use of hatchery fish, which have been selected for bold phenotypes, could have influenced the importance of social information transfer, which potentially could be more important in wild populations with less bold phenotypes.

There are also other reasons that could have reduced the importance of social information transfer on subsequent vulnerability in the present study. Importantly, in addition to the direct experience of being hooked, fish in the private exposure treatment were surrounded by other fish with previous hook experience, whereas fish in the social exposure treatment only briefly experienced already hooked individuals. Experienced individuals could act as demonstrators (Johnsson & Sundström, 2007; Kelley et al. 2003; Vilhunen et al. 2005), reinforcing the hook avoidance behaviour in other individuals during the final vulnerability assessment. The behavioural influences of social learning could thus be stronger in conditions were hooked fish are present, in contrast to the experimental conditions we induced. However, in the absence of such experimental information, our work on rainbow trout joins a related paper on largemouth bass (Wegener et al. 2018), suggesting that social learning to avoid future capture may not be strongly expressed in hatchery-reared rainbow trout. Whether social learning exists in wild trout constitutes an important question for the future.

In conclusion, the results presented in the current study show that social exposure to caught individuals can transmit sensory information that is received by nearby observers and translated into a stress response. However, such stress responses were not strong enough to cause significant declines in subsequent vulnerability to angling. In contrast, private experience of hooking strongly affected subsequent vulnerability to capture, which can negatively affect angler satisfaction (Arlinghaus et al. 2014; Beardmore et al. 2015) and reduce the ability of managers to assess fish stocks based on catch rate data alone (Arlinghaus et al. 2017). Our study adds a mechanistic insight into the repeated empirical observation that continued C&R angling will lead to a drop in catchability. These declines in catch rates constitutes a challenge to fisheries managers interested in maintaining high catch rates for the benefits of anglers (Camp et al. 2015). Previous studies suggesting effects of social learning on catch rates (e.g, Beukema 1970b, Raat 1985) may indicate either species-specific effects or the need for continuous presence of demonstrators with private experience for social learning to exert an impacts on catch rates.

References

Alós, J., Palmer, M., Trías, P., Díaz-Gil, C., & Arlinghaus, R. (2015). Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. *Canadian Journal of Fish and Aquatic Sciences*, *72*, 217–225.

Anderson, W. G., Booth, R., Beddow, T. A., Mckinley, R. S., Finstad, B., Økland, F., & Scruton, D. (1998). Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon , Salmo salar (L .). *Hydrobiologia*, 371/372, 233–240.

Arlinghaus, R., Beardmore, B., Riepe, C., Meyerhoff, J., & Pagel, T. (2014). Species-specific preferences of German recreational anglers for freshwater fishing experiences, with emphasis on the intrinsic utilities of fish stocking and wild fishes. *Journal of Fish Biology*, *85*(6), 1843–1867. http://doi.org/10.1111/jfb.12546

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. *Reviews in Fisheries Science, 15*, 75–167. http://doi.org/10.1080/10641260601149432

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 .). *Fisheries Research*, *97*, 223–233. http://doi.org/10.1016/j.fishres.2009.02.005

Arlinghaus, R., Tillner, R., & Bork, M. (2015). Explaining participation rates in recreational fishing across industrialised countries. *Fisheries Management and Ecology*, 22, 45–55. http://doi.org/10.1111/fme.12075

Arlinghaus, R., Laskowski, K. L., Alós, J., Klefoth, T., Monk, C. T., Nakayama, S., & Schröder, A. (2017). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries*, (18), 360–373. http://doi.org/10.1111/faf.12176

Askey, P. J., Richards, S. A., Post, J. R., & Parkinson, E.A. (2006). Linking Angling Catch Rates and Fish Learning under Catch-and-Release Regulations. *North American Journal of Fisheries Management, 26*, 1020–1029. http://doi.org/10.1577/M06-035.1

Bartholomew, A., & Bohnsack, J. A. (2005). A Review of Catch-and-Release Angling Mortality with Implications for No-take Reserves. *Reviews in Fish Biology and Fisheries, 15*, 129–154. http://doi.org/10.1007/s11160-005-2175-1

Barton, B. A. (2002). Stress in Fishes: A Diversity of Responses with Particular Reference to Changes in Circulating Corticosteroids. *Integrative and Comparative Biology, 42*(3), 517–525. http://doi.org/10.1093/icb/42.3.517

Barton, B., Schreck, C., & Barton, L. (1987). Effects of chronic Cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Diseases of Aquatic Organisms, 2*, 173–185. http://doi.org/10.3354/dao002173

Beardmore, B., Hunt, L. M., Haider, W., Dorow, M., & Arlinghaus, R. (2015). Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers. *Canadian Journal of Fisheries and Aquatic Sciences, 72*, 500–513. http://doi.org/10.1139/cjfas-2014-0177

Berejikian, B. A. (1995). The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 2476–2482. http://doi.org/10.1139/f95-838

Beukema, J. J. (1970a). Angling Experiments With Carp (Cyprinus Carpio L.). II Decreasing catchablity through one-trial learning. *Netherlands Journal of Zoology*, *20*(1), 81–92.

Beukema, J. J. (1970b). Aquired hook-avoidance in the pike Esox lucius L. fished with artificial and natural baits. *Journal of Fish Biology*, *2*, 155–160.

Biro, P. A., & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences*, *105*, 2919–2922.

Brijs, J., Sandblom, E., Axelsson, M., Sundell, K., Sundh, H., Huyben, D., Broström, R., Kiessling, A., Berg, C., & Gräns, A. (2018). The final countdown: Continuous physiological welfare evaluation of farmed fish during common aquaculture practices before and during harvest. *Aquaculture*, *495*, 903–911. http://doi.org/10.1016/j.aquaculture.2018.06.081

Brijs, J., Sandblom, E., Rosengren, M., Sundell, K., Berg, C., Axelsson, M. & Gräns, A. (2019). Prospects and pitfalls of using heart rate bio-loggers to assess the welfare of rainbow trout (Oncorhynchus mykiss) in aquaculture, *Aquaculture*. 509, 188–197.

doi: 10.1016/j.aquaculture.2019.05.007.

Brown, G. E., & Smith, R. J. F. (1997). Conspecific skin extracts elicit antipredator responses in juvenile rainbow trout (Oncorhynchus mykiss). *Canadian Journal of Zoology*, *75*, 1916–1922.

Camp, E. V., van Poorten, B. T. and Walters, C. J. (2015) ‘Evaluating Short Openings as a Management Tool to Maximize Catch-Related Utility in Catch-and-Release Fisheries’, *North American Journal of Fisheries Management*, 35, pp. 1106–1120. doi: 10.1080/02755947.2015.1083495.

Chivers, D. P., & Smith, R. J. F. (1998). Chemical alarm signalling in aquatic predator-prey systems: A review and prospectus. *Écoscience*, *5*, 338–352. http://doi.org/10.1080/11956860.1998.11682471

Coble, D. W., Farabee, G. B., & Anderson, R. O. (1985). Comparative Learning Ability of Selected Fishes. *Canadian Journal of Fish and Aquatic Sciences*, *42*, 791–796.

Cooke, S. J., & Cowx, I. G. (2004). The Role of Recreational Fishing in Global Fish Crises. *BioScience*, *54*, 857–859. http://doi.org/10.1641/0006-3568(2004)054[0857:TRORFI]2.0.CO;2

Cooke, S. J., & Cowx, I. G. (2006). Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conservation*, *128*, 93–108. http://doi.org/10.1016/j.biocon.2005.09.019

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. *North American Journal of Fisheries Management*, *21*, 333–342. http://doi.org/10.1577/1548-8675(2001)021<0333:TIOTTO>2.0.CO;2

Cooke, S. J., & Schramm, H. L. (2007). Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology*, *14*, 73–79. http://doi.org/10.1111/j.1365-2400.2007.00527.x

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. *American Fisheries Society Symposium*, (30), 121–134.

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? *Biodiversity and Conservation*, *14*, 1195–1209. http://doi.org/10.1007/s10531-004-7845-0

Cooke, S. J., Twardek, W. M., Lennox, R. J., Zolderdo, A. J., Bower, S. D., Gutowsky, L. F. G., Danylchuk, A.J., Arlinghaus, R., & Beard, D. (2018). The nexus of fun and nutrition : Recreational fishing is also about food. *Fish and Fisheries*, *19*, 201–224. http://doi.org/10.1111/faf.12246

Donaldson, M. R., Clark, T. D., Hinch, S. G., Cooke, S. J., Patterson, D. A., Gale, M. K., Frappell, P.B., & Farrel, A. P. (2010). Physiological responses of free-swimming adult coho salmon to simulated predator and Fisheries Encounters. *Physiological and Biochemical Zoology*, *83*, 973–983. http://doi.org/10.1086/656336

Ekström, A., Axelsson, M., Gräns, A., Brijs, J., & Sandblom, E. (2018). Importance of the coronary circulation for cardiac and metabolic performance in rainbow trout (Oncorhynchus mykiss). *Biology Letters*, *14*. http://doi.org/10.1098/rsbl.2018.0063

Eliason, E. J., & Anttila, K. (2017). *Temperature and the Cardiovascular System*. *Fish Physiology* (1st ed., Vol. 36). Elsevier Inc. http://doi.org/10.1016/bs.fp.2017.09.003

FAO, (Food and Agricultural Organisation of the United Nations). (2012). Technical Guidelines for Responsible Fisheries. *Rome: Food and Agriculture Organisation of the United Nations*, 176 pp.

Fleming, I. A., & Einum, S. (1997). Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES*, 54, 1051–1063.

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Learning & Behavior*, *32*(1), 131–140. http://doi.org/10.3758/BF03193188

Halttunen, E., Rikardsen, A. H., Thorstad, E. B., Næsje, T. F., Jensen, J. L. A., & Aas, Ø. (2010). Impact of catch-and-release practices on behavior and mortality of Atlantic salmon (Salmo salar L.) kelts. *Fisheries Research*, *105*, 141–147. http://doi.org/10.1016/j.fishres.2010.03.017

Johnsson, J. I., & Abrahams, M. V. (1991). Interbreeding with Domestic Strain Increases Foraging under Threat of Predation in Juvenile Steelhead Trout (*Oncorhynchus mykiss*): An Experimental Study. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(2), 243–247. http://doi.org/10.1139/f91-033

Johnsson, J. I., & Sundström, F. L. (2007). Social transfer of predation risk information reduces food locating ability in European minnows (Phoxinus phoxinus). *Ethology*, *113*(2), 166–173. http://doi.org/10.1111/j.1439-0310.2006.01296.x

Kelley, J. L., Evans, J. P., Ramnarine, I. W., & Magurran, A. E. (2003). Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Animal Behaviour*, *65*, 655–662. http://doi.org/10.1006/anbe.2003.2076

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. *Knowledge and Management of Aquatic Ecosystems*, (403), 1–18. http://doi.org/10.1051/kmae/2011072

Klefoth, T., Pieterek, T., & Arlinghaus, R. (2013). Impacts of domestication on angling vulnerability of common carp, Cyprinus carpio : the role of learning, foraging behaviour and food preferences. *Fisheries Management and Ecology*, *20*, 174–186. http://doi.org/10.1111/j.1365-2400.2012.00865.x

Koeck, B., Závorka, L., Aldvén, D., Näslund, J., Arlinghaus, R., Thörnqvist, P.-O., Winberg, S., Björnsson, B.T., & Johnsson, J. I. (2018). Angling selects against active and stress-resilient phenotypes in rainbow trout. *Canadian Journal of Fisheries and Aquatic Sciences*, 1–14.

Koeck B., Lovén Wallerius M., Robert Arlinghaus R., Johnsson J.I. (2019). Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. *Canadian Journal of Fisheries and Aquatic Sciences* http://doi.org/10.1139/cjfas-2019-0064

Kuparinen, A., Klefoth, T., & Arlinghaus, R. (2010). Abiotic and fishing-related correlates of angling catch rates in pike (Esox lucius). *Fisheries Research*, *105*, 111–117. http://doi.org/10.1016/j.fishres.2010.03.011

Laland, K. N., Brown, C., & Krause, J. (2003). Learning in fishes: From three-second memory to culture. *Fish and Fisheries*, *4*, 199–202. http://doi.org/10.1046/j.1467-2979.2003.00124.x

Lewin, W.-C., Arlinghaus, R., & Mehner, T. (2006). Documented and Potential Biological Impacts of Recreational Fishing: Insights for Management and Conservation. *Reviews in Fisheries Science*, *14*, 305–367. http://doi.org/10.1080/10641260600886455

Lucon-Xiccato, T., & Bisazza, A. (2017). Individual differences in cognition among teleost fishes. *Behavioural Processes*, *141*, 184–195. http://doi.org/10.1016/j.beproc.2017.01.015

Meekan, M. G., McCormick, M. I., Simpson, S. D., Chivers, D. P., & Ferrari, M. C. O. (2018). Never Off the Hook—How Fishing Subverts Predator-Prey Relationships in Marine Teleosts. *Frontiers in Ecology and Evolution*, *6*. http://doi.org/10.3389/fevo.2018.00157

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. *Fisheries Research*, *72*, 311–322. http://doi.org/10.1016/j.fishres.2004.10.006

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The Evolution of Individual and Cultural Variation in Social Learning. *Trends in Ecology and Evolution*. http://doi.org/10.1016/j.tree.2015.12.012

Mezzera, M., & Largiadèr, C. R. (2001). Evidence for selective angling of introduced trout and their hybrids in a stocked brown trout population. *Journal of Fish Biology*, *59*, 287–301. http://doi.org/10.1006/jfbi.2001.1639

Pankhurst, N.W., Dedual, M., 1994. Effects of capture and recovery on plasma levels of cortisol, lactate and gonadal steroids in a natural population ofrainbow trout. J. Fish Biol. 45, 1013–1025.

Policansky D. (2002) Catch-and-release recreational fishing: a historical perspective. In: T.J. Pitcher & C.E. Holling- worth (eds) Recreational Fisheries: Ecological, Economic and Social Evaluation. Oxford: Blackwell Science, pp. 74– 94.

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*, 6–17. http://doi.org/10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2

Pullen, C. E., Hayes, K., O'Connor, C. M., Arlinghaus, R., Suski, C. D., Midwood, J. D., & Cooke, S. J. (2017). Consequences of oral lure retention on the physiology and behaviour of adult northern pike (Esox lucius L.). *Fisheries Research*, *186*, 601–611. http://doi.org/10.1016/j.fishres.2016.03.026

Raat, A. J. P. (1985). Analysis of angling vulnerability of common carp , Cyprinus carpio L ., in catch-and-release angling in ponds. *Aquaculture and Fisheries Management*, *16*, 171–187.

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. *North American Journal of Fisheries Management*, *25*, 1513–1517. http://doi.org/10.1577/M05-050.1

van Poorten, B. T., & Post, J. R. (2005). Seasonal Fishery Dynamics of a Previously Unexploited Rainbow Trout Population with Contrasts to Established Fisheries. *North American Journal of Fisheries Management*, *25*, 329–345. http://doi.org/10.1577/M03-225.1

Vilhunen, S., Hirvonen, H., & Laakkonen, V.-M. M. (2005). Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (Salvelinus alpinus). *Behavioral Ecology and Sociobiology*, *57*, 275–282. http://doi.org/10.1007/s00265-004-0846-x

Wegener, M. G., Schramm, H. L., Neal, J. W., & Gerard, P. D. (2018). Effect of fishing effort on catch rate and catchability of largemouth bass in small impoundments. *Fisheries Management and Ecology*, *25*, 66–76. http://doi.org/10.1111/fme.12268

Wendelaar Bonga, S. E. (1997). The stress response in fish. *Physiological Reviews*, *77*, 591–625. http://doi.org/stress physiologie comportement cortisol cerveau hypophyse catecholamine osmoregulation branchie

Woodward, C. C., & Strange, R. J. (1987). Physiological Stress Responses in Wild and Hatchery-Reared Rainbow Trout. *Transactions of the American Fisheries Society*, *116*(4), 574–579. http://doi.org/10.1577/1548-8659(1987)116<574

Worm, B., Hilborn, R., Baum, J. K., Branch, T. a, Collie, J. S., Costello, C., … Zeller, D. (2009). Rebuilding global fisheries. *Science*, *325*, 578–85. http://doi.org/10.1126/science.1173146

Young, R. G., & Hayes, J. W. (2004). Angling Pressure and Trout Catchability: Behavioral Observations of Brown Trout in Two New Zealand Backcountry Rivers. *North American Journal of Fisheries Management*, *24*, 1203–1213. http://doi.org/10.1577/M03-177.1

Figure Legend

Figure 1. Schematic figure of experimental setup with the different angling treatments in each pond. Blue = Control; Purple = Disturbance; Red = Private; Green = Social; and Black = demonstrator fish from the non-experimental pond used in the social exposure treatment. A) Acclimation period before angling; B) Angling exposure treatment; and C) Vulnerability assessment when all ponds were fished. Timeline represent the duration in hours for each period as well as the resting time between the angling treatments and vulnerability assessment.

Figure 2. Survival curves based on the Cox proportional hazard regression model, illustrating the remaining proportions of uncaught individuals across days, for the four exposure treatments (Blue = Control; Purple = Disturbance; Red = Private; and Green = Social) during the vulnerability assessment. Day 0 denotes the day before angling, and day 4 denotes the last angling day.

Figure 3. Mean heart rate per treatment following acclimation period, angling exposure and vulnerability assessment. Statistical change in heart rate was analysed from the start of an angling period (symbolized by the angler) until the following angling event (15:00-15:00). A) Acclimation period before angling, B) Heart rate during the angling exposure treatment and C) Heart rate during the vulnerability assessment. (Blue = Control; Red = Private; Green = Social).

Table Legend

Table 1. Cox-proportional hazard regression, estimating the effect of treatment and temperature on the time individuals remained uncaught during the vulnerability assessment. Control treatment is the reference level. The number of events refers to the total number of caught fish.

Table 2. Parameter estimates from the linear mixed model examining the effect of angling treatment, period (*i.e.* acclimation, angling exposure treatment and vulnerability assessment) and the corresponding day on heart rate response. Control treatment was used as reference levels. Fish ID and time was used as random effects.

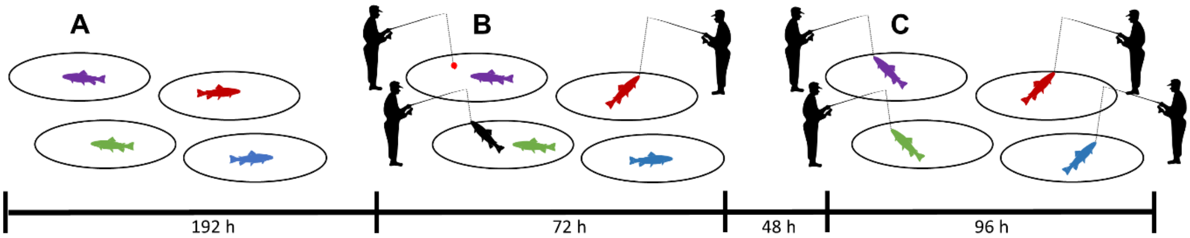
Parameter	*Estimate*	*exp(coef)*	*Se(coef)*	*z-value*	*p-value*
Disturbance	-0.0924	0.9116	0.1422	-0.605	0.515
Social Exp.	-0.2672	0.7654	0.1445	-1.849	0.064
Private Exp.	-1.2968	0.2733	0.1907	-6.799	< **0.001**
Temperature	0.0264	1.0267	0.0125	2.104	< **0.05**

n= 411, number of events= 328. Likelihood ratio test= 68.21 on 4 df, $p < 0.001$

TABLE 1

Period	*Day*	*Parameter*	*Estimate*	*Std. Err*	*Df.*	*t-value*	*p-value*
Acclimation	1	Intercept	67.80	4.202	577.63	16.13	< **0.001**
		Private	0.75	0.562	647.46	1.34	0.179
		Social	0.11	0.599	647.49	0.19	0.848
Acclimation	2	Intercept	65.62	4.610	508.57	14.23	< **0.001**
		Private	0.51	0.620	651.67	0.82	0.408
		Social	1.36	0.656	651.67	2.07	< **0.05**
Acclimation	3	Intercept	59.86	5.929	263.84	10.09	< **0.001**
		Private	1.31	0.808	425.66	1.63	0.104
		Social	1.82	0.857	425.70	2.13	< **0.05**
Exposure	1	Intercept	49.75	4.964	189.18	9.41	< **0.001**
		Private	6.94	0.676	656.95	10.26	< **0.001**
		Social	3.75	0.716	656.95	5.23	< **0.001**
Exposure	2	Intercept	34.19	4.445	13.92	7.69	< **0.001**
		Private	5.49	0.658	647.58	8.35	< **0.001**
		Social	5.42	0.699	647.95	7.75	< **0.001**
Exposure	3	Intercept	51.23	4.880	296.20	10.49	< **0.001**
		Private	4.32	0.661	660.97	6.54	< **0.001**
		Social	3.58	0.701	660.98	5.11	< **0.001**
Vulnerability	1	Intercept	39.77	5.203	58.41	7.64	< **0.001**
		Private	3.12	0.725	663.80	4.30	< **0.001**
		Social	5.08	0.770	663.65	6.60	< **0.001**
Vulnerability	2	Intercept	30.69	4.013	3.71	7.64	< **0.01**
		Private	2.30	0.649	625.28	3.54	< **0.001**
		Social	2.98	0.688	622.61	4.32	< **0.001**
Vulnerability	3	Intercept	38.48	4.792	49.16	8.03	< **0.001**
		Private	0.55	0.674	658.89	0.82	0.408
		Social	0.76	0.715	658.37	1.06	0.287
Vulnerability	4	Intercept	24.92	0.631	234.21	39.47	< **0.001**
		Private	1.36	0.651	619.00	2.10	< **0.05**
		Social	0.43	0.673	619.00	0.650	0.516

TABLE 2



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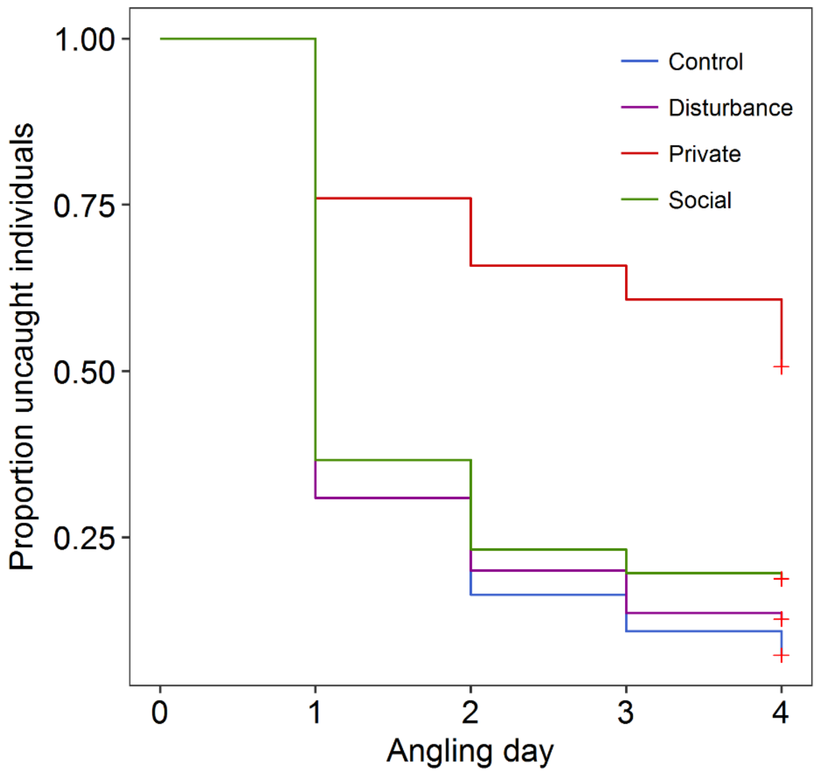
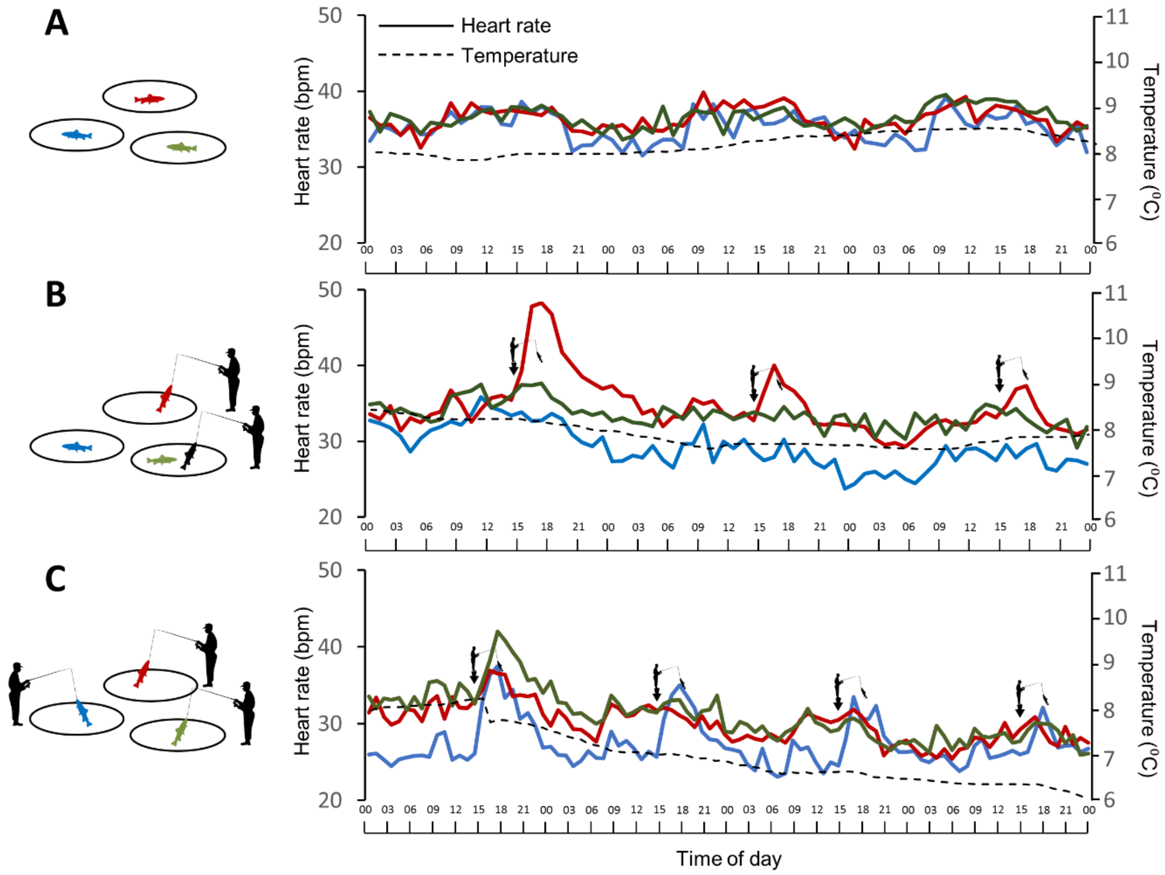
661 FIGURE 1

662



1.00
0.75
0.50
0.25
Proportion uncaught individuals
0
1
2
3
4
Angling day
Control
Disturbance
Private
Social

FIGURE 2



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680 FIGURE 3