

Impact of catch-and-release on behaviour, recovery, and fate in two fish species: a before-after-control-impact study in a shallow lake

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Abstract

Catch-and-release (CR) is widespread in recreational fisheries, but can affect behavior and survival of released fish. We used whole-lake high-resolution acoustic telemetry and a before-after control-impact paired series design to study post-release mortality and movement activity in Eurasian Perch (*Perca fluviatilis*) and Common Carp (*Cyprinus carpio*) in a natural lake. Fish caught with hook-and-line and uncaptured controls were monitored for 6 months after CR. We found no significant hooking mortality in either species after accounting for natural and surgery-based mortality of controls. Sublethally, movement activity declined significantly in perch, with recovery to pre-capture levels taking a mean of 7 days; 36% of significantly impacted perch (4 of 11 captures) had not recovered by the end of the 10-day monitoring period. Carp showed weaker and more variable responses. Under similar conditions as examined here (e.g., shallow capture depth and hooking, moderate temperature), CR is suited to reduce fishing mortality and maintain populations despite heavy fishing pressure, but this comes at the cost of a multi-day, reversible behavioral impairment to the individuals that are caught and released.

Key words: high-resolution acoustic telemetry, catch-and-release, behavioral impairment, hooking mortality, Eurasian Perch (*Perca fluviatilis*), Common Carp (*Cyprinus carpio*)

Introduction

Catch-and-release (CR) is the practice of unhooking fish caught by recreational angling and releasing the fish back into the water alive (Wydoski 1977; Muoneke and Childress 1994; Arlinghaus et al. 2007; Cooke and Schramm 2007; Brownscombe et al. 2017). It is a byproduct of most harvest regulations in recreational angling, such as daily bag limits and size limits and is also practiced voluntarily by many anglers (Arlinghaus et al. 2007; Blyth and Rönnbäck 2022; Birdsong et al. 2025). Globally, it is estimated that around two thirds of the catch by anglers is released back into the water (Cooke and Cowx 2004), with the assumption that fish recover with no long-term consequences for fitness and mortality (Cooke and Schramm 2007). Yet, hooking mortality rates in recreational fishing can range from near zero to 90%, depending on species, degree of injury, depth of capture, environmental conditions and post-release predation risk (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007; Hühn and Arlinghaus 2011;

Maggs et al. 2024). In cases where fish life history is slow (e.g., late maturation, high longevity) and fishing effort is relatively high, hooking mortalities exceeding ~25% can contribute to recruitment overfishing (Coggins et al. 2007; Pine et al. 2008; Johnston et al. 2015). Insights that support minimizing CR impacts can therefore make substantial improvements to the sustainability of fish stocks (Brownscombe et al. 2017; Cooke et al. 2025; Corsi et al. 2025).

The social acceptability of CR angling, and its contribution to lowering fishing mortality at high fishing efforts, depends on high post release survival rates (Coggins et al. 2007; Johnston et al. 2015; Cooke et al. 2025). Surviving a CR event, however, does not mean that a fish is not impacted. A CR event may also induce sublethal impacts through injury, exhaustion and a related stress response that can impair fitness (e.g., lowered growth, reduced reproductive success) (Cooke et al. 2002; Klefoth et al. 2011; Richard et al. 2013). Exposure to CR-related stressors (e.g., exhaustive exercise, air exposure, and injury) induces a stress response from which an individ-

ual fish may not fully recover or only in a delayed fashion (Suski et al. 2006; Klefoth et al. 2008; Arlinghaus et al. 2009; Cooke et al. 2013, 2025; LaRochelle et al. 2026). Irrespective of whether sublethal impacts have population-level impacts or not (Corsi et al. 2025), minimizing them is a moral imperative in recreational fisheries (Cooke et al. 2025). Exposure to CR-related stressors can induce a cascade of stress responses in fish (Arlinghaus et al. 2007; Cooke et al. 2013). The primary stress response (see Wendelaar Bonga 1997, for a review) takes place in the neuro-endocrine system (e.g., increased adrenaline levels), which is followed by a secondary stress response quantifiable in the blood and muscle tissues (e.g., release of glucose, accumulation of lactate, or increased heart rate and blood pressure) (Schreck et al. 1997; Cooke et al. 2002; Arlinghaus et al. 2009). This may in turn elicit a tertiary stress response in the form of whole-organismal change in performance, such as altered behavior (Donaldson et al. 2008), reduced growth (Klefoth et al. 2011) or altered immune function (Chapman et al. 2020). Behavioral responses as an indicator of a tertiary stress response are an integrative measure of an impaired function in response to stressors (Iwama 1998; Schreck et al. 1997) and is thus particularly suited to study the sublethal impacts of CR in fishes in the wild (LaRochelle et al. 2025, 2026).

A range of studies that assessed behavioral metrics as sublethal outcomes of CR in fish have been completed in both laboratory and field settings. These studies regularly have documented that fish are behaviorally impaired for certain periods of time after release (reviewed by Donaldson et al. 2008; LaRochelle et al. 2025). Fish may compensate for these sublethal impacts without any impaired fitness (Cline et al. 2012; Skov et al. 2023), or they may face fitness costs, such as reduced growth (Klefoth et al. 2011) or reduced individual reproductive success (Richard et al. 2013). Fitness costs are most likely when the CR event happens in a challenging environment (e.g., at high density and high competition for food, Klefoth et al. 2011) or in a sensitive period of the life-cycle (e.g., directly prior to spawning, Richard et al. 2013; Papatheodoulou et al. 2022). However, CR studies face a number of challenges that may bias the estimation of CR impacts (Wilde et al. 2003; Pollock and Pine 2007; Donaldson et al. 2008; Eberts and Sommers 2017) and that may prevent generalization of CR impacts across contexts. Most importantly, it is a challenge to design studies with proper controls in the wild that are observed in the same environment at the same point in time as the CR-exposed fish (Pollock and Pine 2007). The lack of unharmed control fish in study designs may systematically overestimate hooking mortalities (Wilde et al. 2003) and sublethal impacts because fish may die naturally or due to causes unrelated to the influences of CR (e.g., due to tagging, Shorgan et al. 2026), e.g., as a result of holding or handling stress (Pollock and Pine 2007). Wilde et al. (2003) raised an unequivocal call to not trust any post-release mortality estimate that was derived in the absence of proper control fish, but studies on CR impacts continue to be published in the absence of controls. As a further issue, some CR studies employ extreme treatments that are non-representative of the conditions in real fisheries (e.g., very long air exposure times, compare the air exposure treatments

in Gingerich et al. 2007 with the data reported from real fisheries in Lamansky and Meyer 2016), or only measure immediate mortality rates or other immediate impacts (e.g., behavioral changes) within a short time period after release (e.g., days). Extreme treatments can bias CR impacts high, while only examining immediate effects may underestimate the total CR impacts by neglecting delayed impacts (e.g., Ramsay et al. 2025) or carry-over effects that happen weeks to months after the exposure to stressors (O'Connor et al. 2010). Studies that are conducted in the field provide the greatest amount of ecological realism but it is a challenge to capture fish randomly, including control fish, and to control for tagging effects that tend to bias CR impacts high if not properly controlled (Donaldson et al. 2008). It is for all these methodological reasons that CR impacts are challenging to study in the wild. We address this challenge in our work, by establishing a before-after-control-impact design with free ranging fishes in a natural lake.

Past studies assessing the behavioral impacts of CR have relied on a range of behavioral metrics and methodological approaches, including visual observations of fish in laboratories or in the wild (e.g., Cooke and Philipp 2004; Arlinghaus et al. 2009), use of biologgers (LaRochelle et al. 2022; Madden et al. 2024) and various telemetry techniques (e.g., radio and acoustic, Klefoth et al. 2011; LaRochelle et al. 2026; reviewed by Donaldson et al. 2008; LaRochelle et al. 2025). A common behavioral metric used in past CR studies with high ecological relevance is movement activity. Only a handful of studies have been completed studying the responses of fishes in terms of free ranging movement activity in the wild (e.g., Gurshin and Szedlmayer 2004; Klefoth et al. 2011; Baktoft et al. 2013; Ferter et al. 2015a; Howel et al. 2024; LaRochelle et al. 2026), and as far as we are aware only two studies have used whole-lake, high-resolution acoustic telemetry to study CR on freshwater fish in a natural lake: Baktoft et al. (2013) in northern pike (*Esox lucius*), though without the inclusion of unharmed control fish, and LaRochelle et al. (2026), who combined acoustic telemetry with pop-off biologgers to quantify post-release behavioural recovery in largemouth bass (*Micropterus nigricans*) and northern pike. These and related (e.g., Klefoth et al. 2008) studies have reported that behavioural recovery in pike may be relatively rapid within 2 days (e.g., Baktoft et al. 2013), while other work has revealed the resumption of normal movement activity may take up to a week in largemouth bass and pike (Klefoth et al. 2008; LaRochelle et al. 2026). In CR studies, alteration of fish swimming distances in response to CR has been reported, most often a reduction in activity or minimum displaced distances for a certain period of time (usually days) (Sundström and Gruber 2002; Gurshin and Szedlmayer 2004; Klefoth et al. 2008; Baktoft et al. 2013; Rapp et al. 2012, 2014; LaRochelle et al. 2026). Other papers have looked at changes of nest guarding activity in species engaging in parental care (Cooke et al. 2000), and have reported abnormal migration behavior in anadromous salmonids (Mäkinen et al. 2000; Thorstad et al. 2003; Halttunen et al. 2010). Generally, stress is assumed to cause a decrease in activity and movement propensity as fish need to manage the physiological load (e.g., clear accumulated lactate and rebuild lost energy stores, Kieffer 2000).

In turn, fish may seek shelter to recover or simply move less to avoid exposure to predators while being in a vulnerable, exhausted state (Siepker et al. 2006; Klefoth et al. 2008; Rapp et al. 2012; Stålhammar et al. 2012). Fish also learn from past capture and release events through private hooking experiences (e.g., Raat 1985; Arlinghaus et al. 2017a, 2017b; Czapla et al. 2023), which might lower the propensity to swim around a system and be exposed to anglers as predators (Lennox et al. 2017; Monk et al. 2021). However, reduced movement in response to CR has not always been reported as some studies also revealed hyperactivity (Cooke et al. 2000; Thorstad et al. 2004; Arlinghaus et al. 2008a; Ferter et al. 2015a; Pullen et al. 2017). Individual variability in stress responsiveness may play an important role in determining response type (Koolhaas et al. 1999; Koeck et al. 2019)—some fish may show no change or even increased activity following CR, while others may show prolonged impairment. However, most CR only examine mean responses, overlooking heterogeneity in how individual fishes deal with CR stressor. Importantly, much of past research in the wild has relied on only coarse positioning (e.g., radio tagging where positional fixes were only done at irregular intervals, e.g., weekly, Klefoth et al. 2008). These coarse tracking studies are not able to resolve CR-induced movement responses and recovery dynamics relative to controls at a fine temporal resolution.

Using high-resolution telemetry over a period of more than a year at a whole-ecosystem scale, the objective of this study was to assess the behavioral and lethal impacts of CR under natural conditions in two freshwater species of high importance to European recreational angling: Eurasian Perch (*Perca fluviatilis*; hereafter, “perch”) (Vainikka et al. 2012; Heermann et al. 2013) and Common Carp (*Cyprinus carpio*; hereafter, “carp”) (Arlinghaus and Mehner 2004; Arlinghaus 2007). Both species are heavily targeted by anglers and experience regular exposure to CR (Birdsong et al. 2025). However, both species have received comparatively limited attention in CR research. There exists no CR study on Eurasian Perch. The impact of CR on Common Carp was studied in both laboratory and wild conditions using coarse-grained radio telemetry (Rapp et al. 2012, 2014). These studies revealed that carp are resilient to CR-related mortality, but showed reduced movement activity (measured as minimum displaced distance per unit time) up to 12 h post release (Rapp et al. 2012, 2014). Yet, due to the coarse temporal and spatial resolution of the telemetry approaches used, these studies were unable to resolve fine-scale recovery trajectories of carp.

We addressed these shortcomings using fine-scale acoustic telemetry (Lennox et al. 2023; LaRochelle et al. 2026), tagging perch and carp in the wild within a natural ecosystem and letting the fish recover for multiple days from the capture and tagging impact. After a long-enough recovery phase a subset of fish were experimentally captured and released with standard rod-and-reel angling techniques, while the remaining tagged fish served as concurrent controls to capture time and tagging impacts unrelated to the capture and release event. The time trajectory of responses to the CR impact was assessed with a novel statistical method relying on a robust before-after-control-impact time series design (Thiault et al. 2017)—a design already followed by LaRochelle et al. (2026)

in a catch-and-release study. We specifically addressed, for both species, whether reductions in relative movement activity occurred directly after a CR event and if so, whether a recovery to pre-capture relative activity occurred and whether these results varied by species. We also robustly addressed the mortality impacts of CR on both species (relative to controls), and whether any CR responses were modulated by environmental parameters including water temperature, dissolved oxygen, and turbidity. Past research has shown that water temperature is a key stressor that may aggravate CR impacts (Gale et al. 2013). Swimming activity in the wild and mortality after CR were chosen as our study metrics because they are useful indicators of a tertiary stress response (Schreck et al. 1997) and are indicative of fitness impacts, respectively. Our work was meant to support improved management of recreational fisheries, through a methodologically robust estimate of the behavioral and mortality effects of CR. Additionally, the BACIPS (Before-After Control-Impact Paired Series) approach developed in this paper could serve as a valuable approach to assess CR behavioral impacts in comparative studies across waterbodies, species or fishing gear types when relying on freely moving individuals of which a sample is caught and released and conspecific serve as proper controls for robust inference (compare LaRochelle et al. 2026).

Methods

We combined whole-lake high-resolution acoustic tracking in the wild (Baktoft et al. 2015) with a BACIPS statistical design (Thiault et al. 2017) using a time series of telemetry-derived daily movement distances to quantify the behavioral impact of CR in perch and carp relative to uncaptured controls. The study was conducted under natural conditions in a shallow natural research lake using common fishing techniques without extreme treatments, thereby achieving a high degree of ecological realism. The impact of, and possible recovery from, CR angling were statistically modelled from high-frequency positional data, by fitting an impact-recovery function on daily movement activity of caught and released fish before and after release, relative to controls. The model (detailed below) was fitted in a Bayesian hierarchical approach, with the population-level fit informing the individual level fits separately for the two study species.

Study site

The study was conducted in Kleiner Döllnsee in Germany, which is a shallow, relatively small (25 ha) and weakly eutrophic lake (total phosphorus at spring overturn $41.3 \mu\text{g L}^{-1}$ in 2014, and $37 \mu\text{g L}^{-1}$ in 2015) located about 80 km north-east of Berlin ($52^{\circ}59'32.1''\text{N}$, $13^{\circ}34'46.5''\text{E}$) (Monk and Arlinghaus 2018). The lake has a maximum depth of 7.8 m and a mean depth of 4.4 m. The lake shoreline is covered by 2–55 m wide reed belts (*Phragmites australis*, *Typha latifolia*) (Klefoth et al. 2008), which provide shelter and spawning habitat to phytophilic fish. Additionally, there is abundant underwater vegetation and one extended shallow zone (Monk and Arlinghaus 2018). The water below ca. 4 m depth is anoxic between May and October (Baktoft et al. 2015). The dimictic lake is a controlled research lake not accessible to the public.

A whole-lake high-resolution acoustic telemetry system based on coded division multiple access (CDMA) technology was deployed at Kleiner Döllnsee in 2009 (for details and system performance assessment, see Baktoft et al. 2015). In brief, twenty hydrophones (Lotek MAP System, WHS 3050; 200 kHz; Lotek Wireless Inc., Newmarket, Ontario, Canada) were positioned approximately 2 m below the water and evenly distributed across the entire lake (for layout see Fig. S1). The hydrophones received and stored acoustic signals from transmitters that were surgically implanted into the fish (see Baktoft et al. 2015, for full details and below for transmitter models). The signals contained information on transmitter ID, temperature, and depth. After manually downloading the data from the hydrophones, latitude and longitude of fish positions were calculated based on difference in signal arrival times at multiple hydrophones using multilateration in the manufacturer-supplied software (ALPS v.2.2, Lotek Wireless Inc.). The data were further cleaned and filtered using a Hidden Markov Model to reduce any impact from positioning error (as described in Baktoft et al. 2015). Whole-lake system performance assessments were completed, as described at length elsewhere (Baktoft et al. 2015). Our array and the associated positioning after filtering had a mean positional accuracy of 3.1 m and a mean positional precision of 1.1 m, estimated using sentinel tags deployed at fixed known positions within the lake (see Baktoft et al. 2015 for details). Positioning performance varied among habitat types and was lowest in dense macrophyte and reed habitats (Baktoft et al. 2015). Overall, the telemetry system provided highly reliable positioning coverage in pelagic and sublittoral habitats, but detections were reduced when fish entered dense reed refuges. The resulting data thus represent the movement behaviours of fishes when residing outside dense macrophytes. The system allowed positioning fish across the entire lake with no opportunity for emigration.

Study species

Common Carp were used as a model for a non-piscivorous freshwater species that is commonly targeted by recreational anglers under CR in Europe (Arlinghaus 2007; Britton and Valle 2026). Carp are benthivorous and large bodied and can reach over 110 cm and over 40 kg in weight. In recreational angling, the species is usually attracted to a fishing site using groundbait (Mehner et al. 2019). Individuals are targeted by specialized carp anglers using a self-hooking rig (Rapp et al. 2008) baited with corn and other plant materials or with purposely made so-called boilies, which can contain fish meal and other animal protein (Arlinghaus and Mehner 2003; Niesar et al. 2004). Captured fish who often are caught at night are regularly kept in retention sacks for up to several hours overnight before release the next morning to facilitate photography (Rapp et al. 2012, 2014). The carp that we studied were stocked into Kleiner Döllnsee from fish held in ponds (see Monk and Arlinghaus 2017). This represents common practice in Germany where the species only rarely naturally recruits.

Perch were used as a model for a piscivorous freshwater species that is heavily targeted in European predator fishing

(Heermann et al. 2013) and where CR is common (Birdsong et al. 2025). Although smaller-bodied relative to carp, the species becomes piscivorous at about 15 cm total length and may reach 60 cm and over 3 kg of weight. Perch is targeted with both natural baits (e.g., worms, maggots, small bait-fish; Vainikka et al. 2012) and artificial lures, the latter being the dominant fishing approach in more specialized perch angling for larger bodied piscivorous individuals (Monk and Arlinghaus 2018). The species naturally recruits in most rivers and lakes across Eurasia (Craig 2008; Ning et al. 2025).

Fish sampling and tagging

All fish in this study were anaesthetized using a 9:1 95% EtOH-clove oil solution added to water at 1 ml L⁻¹ before acoustic telemetry tags were surgically implanted. The tags were implanted into the body cavities through a small incision, following methods described in Monk and Arlinghaus (2017, 2018). Using built-in temperature and pressure sensors, the tags were programmed to send temperature once per minute, and otherwise always send pressure (i.e., depth) sensor data. A passive integrated transponder (PIT) tag (12 mm; Oregon RFID, Portland) was also implanted through the incision to enable easy identification upon recapture. To minimize the influence of tag weight on fish behavior, fish were chosen for tagging if the transmitter to body weight ratio was below 2% (following Jepsen et al. 2015) (Table S1). Fish were measured for total length (TL) and mass (wet weight, WW) during tagging and prior to release.

In mid-June 2014, 91 pond-born, raised and kept carp (total length, TL: 40.6–72.2 cm; wet weight, WW: 945–6934 g) were seined from one holding pond and kept in oxygenated tanks before tagging, transport and release into Kleiner Döllnsee (water temperature at seining: 23.6 °C) (Monk and Arlinghaus 2017). Before transport (approximate transport duration 90 min), all fish were equipped with acoustic transmitters of the model MM-M-TP-16-50 (burst rate: 5 s, dimension: 16 × 85 mm, wet mass: 21 g; Lotek Wireless Inc., Newmarket, Ontario). As we found significant tag loss in carp (an issue commonly observed in this species, Økland et al. 2003; Monk and Arlinghaus 2017), an additional 24 carp of same origin (TL: 43.0–70.7 cm; WW: 1117–5872 g) were implanted with transmitters of the same type, and released into Kleiner Döllnsee, early in September 2014 (water temperature: 18 °C). An additional three carp of the same origin were tagged and released on 13 October 2014, during the experimental angling period, and served exclusively as undisturbed control fish in the BACIPS analysis. None of the carp had been exposed to angling prior to tagging and release. By the beginning of experimental carp angling, the carp sample size in the study lake with active transmitters was $N = 43$ (TL: 550 ± 82 mm; WW: 2991 ± 1348 g). Most carp had experienced an extended post-surgical acclimatization period before the onset of experimental angling, thereby reducing the likelihood that observed behavioural responses reflected acute tagging effects rather than the CR event itself. During experimental carp angling, happening between 12 August and 15 October 2014, water temperature was on average 17.5 ± 1.9 °C (mean $\pm$ SD).

On two sample occasions, in autumn 2014 ($N = 31$, water temperature: $10\text{ }^{\circ}\text{C}$) and post-spawning in spring 2015 ($N = 19$, water temperature: $13.5\text{ }^{\circ}\text{C}$), 50 large piscivorous perch (TL: $374 \pm 20\text{ mm}$, WW: $744 \pm 140\text{ g}$) were sampled with multimesh gill nets from Kleiner Döllnsee and a neighboring ecologically similar lake Großer Vätersee ($53^{\circ}00'16''\text{N}$, $13^{\circ}33'09''\text{E}$). Gill nets were set for short durations of up to 60 min to minimize stress and allow the fish to be recovered alive from the nets (Monk and Arlinghaus 2018). Upon capture, the fish were put in a live-well and equipped with transmitters within 30 min after capture. Perch were equipped with telemetry tags of the model MM-M-11-28-TP (transmission rate: 27.5 s, wet mass: 6.5 g; Lotek Wireless Inc., Newmarket, Ontario). Six of the 31 perch released in autumn 2014 were sampled from Großer Vätersee to increase sample size. The perch population in this study had never been exposed to targeted angling before the onset of this and a related study (Monk and Arlinghaus 2018). By the beginning of experimental perch angling, sample size was $N = 36$, as 14 perch (28%) either suffered tag loss, tag failure or naturally died; the most likely reason was tag failure as seen from recaptures of perch where the transmitter prematurely died. During perch angling, between 7 September and 19 October 2015, the average water temperature was $12.9 \pm 2.5\text{ }^{\circ}\text{C}$ (mean $\pm$ SD); for additional details, see Monk and Arlinghaus (2018). Experimental perch angling commenced after an acclimatization period of at least 4 months (spring 2015 cohort) and approximately 11 months (autumn 2014 cohort) following transmitter implantation.

Experimental angling

The tagging and release of the fish into Kleiner Döllnsee was followed by an acclimatization period that for the vast majority of fish lasted several weeks to months, after which the fish were exposed to experimental angling following the details described in Monk and Arlinghaus (2017) for carp and Monk and Arlinghaus (2018) for perch, and further described below. Because experimentally angled fish were evaluated relative to concurrent control fish observed during the same period, seasonal environmental variation (e.g., temperature) was shared between treatment and control groups within the BACIPS comparison. Upon capture, species, WW, TL, capture time, angler ID, and hooking location were recorded for all captured fish. Anomalies and injuries were noted as well.

Carp angling was conducted between 12 August and 15 October 2014, about two months after the majority of the tagged carp were introduced to the study lake. Experimental anglers, all experienced anglers from the research team and close networks, were provided with standardized carp fishing gear: standard bolt rigs common in carp angling (Rapp et al. 2008) and 2–3 rods per angler (BeastMaster BX 12 2 3/8 16 T/C, Shimano, Osaka, Japan) each with a BaitRunner X-Aero 8000AR reel (Shimano, Osaka, Japan), a size 6 G-carp super-hook (Gamakatsu USA, Tacoma, USA) attached to a bolt rig with a hair rig to facilitate shallow self-hooking (see Rapp et al. 2008) and an 85 g fixed lead weight to achieve ground fishing as is typical for carp (Monk and Arlinghaus 2017). The bait on each rod and the corresponding hair rig was either

2–3 pieces of boiled corn or 14 mm diameter boilies (fish-meal or birdseed mix; 1–2 pieces; M&M Baits Neuenkirchen-Vörden, Germany) (Monk and Arlinghaus 2017). Fishing sites were pre-baited with corn and boilies at spots along the shoreline of Kleiner Döllnsee as part of another experiment (Monk and Arlinghaus 2017; Mehner et al. 2019). Four of these were used as angling sites which were fished for a total of 2142 rod hours ($85.7\text{ rod hours ha}^{-1}$), both during the day (1299 rod hours) and at night (843 rod hours) (details in Monk and Arlinghaus 2017). Captured carp were held overnight in carp sacks and released the next morning, as is common in CR angling for carp (Rapp et al. 2012, 2014). Thus, the impact of CR for carp involved both the capture and the retention overnight.

Between 7 September and 19 October 2015, about 1 year after initial tagging, 104 experimental anglers participated in a single day of perch angling as part of a separate experiment (Monk and Arlinghaus 2018). Each angler was given a small electric battery powered boat and standardized fishing gear (Favorite 210 cm VRN-702 M rod (Favorite Co., Kiev, Ukraine), Shimano Exage 2500FD reel (Shimano Germany Fishing GmbH, Krefeld, Germany), Power-Pro, 0.13 mm braided yellow-colored line (Shimano Germany Fishing GmbH, Krefeld, Germany), and Trilene 0.32 mm fluorocarbon leader (Berkley Fishing, Spirit Lake, Iowa, USA) (Monk and Arlinghaus 2018). Anglers could fish freely in space, but could only choose between two artificial lures, a copper color Mepps spinner, size 3.0 (Mepps SNC, Contes, France), and an 8.5 cm soft plastic shad with an Arkansas shiner design (“Shaker”, Lunker City, Connecticut, USA) rigged with a 7 g jighead (Monk and Arlinghaus 2018). Angling was done by up to six anglers per day, from around 10:00 until sundown around 19:00 (local German time, CET/CEST), interrupted by a lunch break around 13:00, for a total of 710 rod hours ($28.4\text{ rod hours ha}^{-1}$) (Monk and Arlinghaus 2018). The anglers were instructed to alert a researcher via a supplied walkie talkie when catching a perch with a TL above 28 cm. Because all tagged perch in this study were larger than 33 cm TL, this ensured that all captures of tagged perch were assessed by researchers. After capture, the perch were held in a live-well for a short period (at most 15 min) until the researcher arrived and recorded the data. Afterwards the fish was released back into the lake. Thus, the perch experienced the capture and a brief holding period in a live well, as is common in recreational angling for perch from boats, especially in tournaments.

Hooking mortality assessment

The telemetry system was operated from 12 June 2014 to 31 March 2016, allowing an assessment of natural or hooking mortality for up to 6 months after the first CR event. To assess mortality, we visualized the positional data on a daily level as described in Monk and Arlinghaus (2017, 2018). Days on which the recorded activity of an individual fish was low, potentially indicating mortality (or tag loss) were flagged (Villegas-Ríos et al. 2020). Mortality dates were then determined by visually analyzing whether the pattern of positions on that day and subsequent days suggested that they were

produced by a live fish rather than a dead fish that no longer moved (Fig. S2). In the study lake, stationary transmitters produce triangle or line shaped patterns in close proximity due to positioning inaccuracies (Baktoft et al. 2015), which can be easily identified. Such patterns were interpreted as mortality as shown in Fig. S2. A degree of uncertainty remained in ascribing mortality this way, as a stationary transmitter may be the result of tag loss. But we considered this to be a systematic error that affected both the CR fish and the uncaptured control fish.

Calculation of daily minimally displaced distances as behavioral metric

We focused on changes in telemetry-derived movement activity shown by the experimental fish in response to CR compared to controls. The filtered positional data consisted of latitude and longitude coordinates representing fish positions at given time points, which were used to calculate minimally displaced distances across consecutive 24 h intervals for each fish following eq. 1. For estimation, the calculated distance between two detections in metres (d) was below a threshold of 3 m, the distance between those detections was set to zero because such small positional changes could not be reliably distinguished from horizontal positioning error of the telemetry system (mean positional accuracy: 3.1 m; Baktoft et al. 2015). All other distances were summed for each fish and for each day (eq. 1), to serve as an estimate of minimally displaced daily distance, alternatively called daily movement activity. Positional estimates themselves were retained for subsequent calculations, such that only sub-threshold step distances were excluded from the cumulative daily displacement estimates. This filtering approach resulted in conservative estimates of fish movement and therefore reflects minimally displaced distances rather than true daily swimming paths.

$$(1) \quad d = \sqrt{(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2}$$

where x and y represent UTM Easting and Northing coordinates (m) at times t and $t - 1$, respectively.

We acknowledge that acoustic telemetry does not directly measure swimming behaviour or fine-scale locomotion. Instead, our metric represents telemetry-derived minimally displaced distances between consecutive positional estimates and therefore provides a proxy for movement-based activity. Throughout the manuscript, the term “movement activity” is used as shorthand for telemetry-derived minimally displaced distances, i.e., displacement-based movement estimates derived from acoustic positioning data rather than direct observations of swimming behaviour.

Statistical analysis

The behavioral impacts of CR were assessed by combining a modified Progressive-Change BACIPS approach to identify impact and recovery trajectories, a cluster analysis to group similar CR response trajectories, and generalized linear models (GLMs) to explore environmental correlates of the CR response. Mortality following CR was assessed following Wilde

et al. (2003) using a mortality difference approach by comparing mortality estimates and their associated 95% confidence intervals between caught-and-released treatment fish and concurrent control fish, thereby accounting for natural and tagging-related background mortality. Corrected aggregated angling mortality was considered nonsignificant when confidence intervals encompassed zero, with no further formal statistical testing performed (as per Wilde et al. 2003). Potential correlates of mortality were further explored using generalized linear models (GLMs) including fish total length (TL), capture status (Captured (y/n)), and number of captures (CatchNr) as predictors. Candidate models were compared using Akaike Information Criterion (AIC), with the model showing the lowest AIC considered the best-supported model. Because mortality events were rare, these analyses should be interpreted cautiously. All analyses were conducted in the statistical environment R (version 3.5.2) (R Core Team 2018) unless specified otherwise.

In classic Before-After Control-Impact (BACI) designs, linear models are typically applied to estimate mean differences between impact and control groups before and after an intervention, thereby testing for lasting changes (so-called step-changes) (Stewart-Oaten and Bence 2001). Crucially, this approach does not allow investigation of progressive changes as only two time points (before and after) are assessed (Kerr et al. 2019). Thiault et al. (2017) proposed a progressive-change BACIPS approach for environmental impact assessment in BACI designs. This approach allows detecting delayed impacts and progressive changes (e.g., recovery) caused by an intervention in a time series of data (in our case telemetry-derived minimally displaced distances of individual fishes). The analysis is based on paired time series of impact and control subjects, from which a time series of differences between the two groups is derived (Thiault et al. 2017, for an application to catch-and-release, see also LaRoche et al. 2026). To these time series, we fitted a customized impact-recovery function specifically developed to describe the impact of, and recovery from, CR angling across a wide parameter range encompassing different impact directions, magnitudes, and durations. For each fish, daily minimally displaced distances were calculated for 5 days before and up to 10 days after the CR event. Ten days were chosen because previous work has shown that recovery of movement activity generally occurs within the first week after release (e.g., Klefoth et al. 2008). The relative pre-capture movement level was represented by parameter $k1$:

$$(2) \quad \Delta_{t=-4, \dots, 0} = k1$$

where Δ represents the difference in daily minimally displaced distance during any 24 h interval t between an impacted fish and the mean of all other individuals not previously captured and released for each species, the controls, measured in metres.

The impact-recovery function was used to model changes in Δ following capture and release:

$$(3) \quad \Delta_{t=1} = k1 + r * k1 \left(1 - \frac{k1}{k2} \right) - \frac{\alpha}{(1 + \beta * t)} * k1$$

$$(4) \quad \Delta_{t=2, \dots, 10} = \Delta_{t-1} + r * \Delta_{t-1} \left(1 - \frac{\Delta_{t-1}}{k2} \right)^\alpha - \frac{1}{(1 + \beta * t)} * \Delta_{t-1}$$

The function consisted of an impact component (eq. 3), representing the acute disturbance caused by CR, and a recovery component (eq. 4), describing the return toward a stabilized post-impact movement level. The impact component proportionally increased or decreased the relative movement estimates (Δ) based on parameter α . This initial impact could decay over successive 24 h intervals according to parameter β . The recovery component was based on a logistic growth function, where parameter $k2$ represented the predicted average Δ value toward which the fish recovered under full recovery, and parameter r represented the recovery rate. Parameters r and $k2$ are conceptually related to the r and k parameters in the classic logistic growth function (Verhulst 1838). The impact and recovery components were modelled simultaneously because acute post-release disturbance and recovery processes may overlap temporally within the 10-day observation window. During the first 24 h interval after CR, $k1$ was used as the starting value to derive the predicted change in Δ (eq. 3). For subsequent 24 h intervals, $k1$ was replaced by the predicted Δ value from the previous interval Δ_{t-1} (eq. 4).

Model fitting and choice of priors

Δ_{Before} represents the observed mean difference in daily minimally displaced distance between a focal fish and concurrent controls during the five days preceding the CR event, whereas Δ_{After} represents the corresponding post-capture difference during the ten days following CR. The model was fitted to the data using a Bayesian hierarchical framework. Weakly informative priors initially resulted in unstable parameter exploration and biologically unrealistic trajectories for some parameter combinations (e.g., high values of r and low values of α , can result in chaotic behavior or the model trending towards infinity). We therefore implemented increasingly informative priors to constrain estimation to biologically plausible parameter space and improve convergence stability. Initial priors were chosen on the population level for r , α , and β , and individual priors were drawn from uniform distributions around these values (see Table S2). Initial estimates for $k1$ and $k2$ were fitted at the individual level, $k1$ estimates were chosen from a normal distribution around Δ_{Before} and those for $k2$ from a uniform distribution within the range of Δ_{Before} . The model was implemented in JAGS (Plummer 2003) through the R2jags package (Su and Yajima 2012), using five Markov chains, each running for 100 000 iterations with a thinning rate of 10, after an initial burn-in period of 10 000 iterations. Model convergence was assessed using Gelman–Rubin diagnostics (Gelman and Rubin 1992) and visual inspection of trace plots. Most population-level parameters showed satisfactory convergence, whereas convergence for $k2$ was weaker in cases where recovery was not observed within the 10-day observation window, reflecting limited identifiability of fully recovered activity levels under incomplete recovery trajectories. Model fit was evaluated by

comparing posterior predictive trajectories against observed Δ time series.

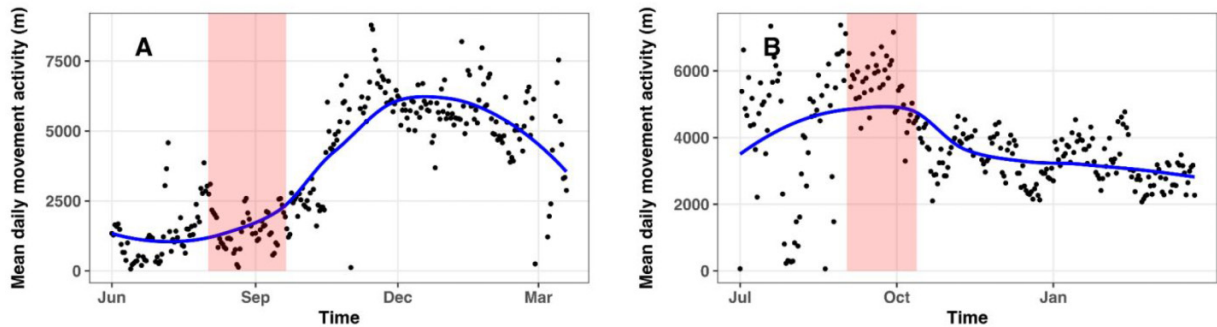
Impact assessment

Changes in activity were classified as significant if relative pre-capture activity (Δ_{Before}) was outside the 95% credible intervals (CrI) for Δ_{After} . If an initial impact of the CR event, i.e., a significant change of Δ at $t = 1$, was recovered so that the 95% CrI again included Δ_{Before} within 10 post-release observation days, the response was interpreted as “impact and recovery”. The mean difference (MD) between Δ_{Before} and the average prediction of Δ_{After} as well as the single largest difference (LD) between Δ_{Before} and any 24 h interval in the predicted daily activity estimate of Δ_{After} , were used as descriptive summary metrics to compare the severity and temporal dynamics of CR responses across individuals. Because both metrics depend on the observation window and the degree of recovery achieved within the 10-day post-release period, they should be interpreted as comparative descriptors rather than mechanistic model parameters. A combination of high LD and low MD values indicates steep decline followed by quick recovery, whereas high LD and high MD indicates sustained reductions in movement activity that did not return to pre-capture levels within the 10-day monitoring period.

Grouping of impact types

For each species, the posterior distribution medians of the impact model parameters r , α , β , and $k2$, as well as the MD and LD estimates of each CR event were used in a cluster analysis to identify and group individuals showing a similar response. Variables were standardized to a mean of zero and an SD of one. Using the standardized parameter values, a random forest proximity matrix was constructed using the R package randomForest (Breiman et al. 2018) and subsequently converted into a distance matrix. A hierarchical cluster analysis using Ward’s minimum variance agglomeration method (“ward.D2” in the R function “hclust” from the base stats package (R Core Team 2018) was then applied to identify groups of fish showing similar CR response trajectories. The number of clusters was determined by visual inspection of the dendrogram combined with biological interpretability of the resulting response groups. Although MD and LD are derived from the fitted impact-recovery trajectories, exploratory correlation analyses indicated that they were not redundant with the fitted model parameters (Fig. S3), supporting their retention as complementary descriptors of CR response dynamics in the clustering analysis. If a fish died within 5 days upon capture it was excluded from the cluster analysis. Mean predicted trajectories per cluster were derived by averaging the individual impact parameter values within any cluster. Clusters were then comparatively ranked using their corresponding LD and MD estimates and assigned relative impact severity levels (i.e., low, medium, high impact). Low impact severity was assigned in cases of non-significant changes in predicted Δ , medium impact severity in cases of significant changes followed by recovery to Δ_{Before} and high

Fig. 1. Mean daily movement activity estimates in meters per day for Common Carp (*Cyprinus carpio*; A) and Eurasian Perch (*Perca fluviatilis*; B). Experimental angling phases are marked in red, the blue lines (LOESS smoother) were fit to the mean daily activity estimates of all tagged fish of the species (CR fish and uncaptured controls combined; black points).



impact severity in cases without recovery within the observation window.

Environmental correlates of catch-and-release responses

Water parameters were measured at 15 min intervals from an in-lake water quality sensor (YSI 6600, YSI Inc., Yellow Springs, USA), positioned two meters deep in the pelagic zone, in the epilimnion of Kleiner Döllnsee. GLMs were applied to evaluate the effects of fish total length (TL), mean daily water temperature, mean daily dissolved oxygen (DO), and mean daily turbidity on predicted changes in relative movement activity. To this end, MD and LD were used as response variables in separate GLMs with identical predictor structures. Statistical significance was evaluated at $\alpha = 0.05$.

Results

Descriptive information

We analyzed a total of 30.1 million carp positions over the period of 13 July 2014 to 30 April 2015. Over these 292 observation days, the carp population exhibited a mean daily movement activity of 3.97 ± 2.87 (mean $\pm$ SD) km per day ($n = 69$). Over 49 days of experimental carp angling, the mean daily movement activity of carp was 1.56 ± 1.43 km per day (Fig. 1a). The carp population showed an unexpected increase in daily movement activity over time from summer to winter (Fig. 1a).

We analyzed a total of 11.8 million perch positions between 7 July 2015 and 31 March 2016. Over 268 consecutive observation days, the mean movement activity estimate of the perch population was 3.92 ± 2.38 km per day and 5.59 ± 2.51 km per day ($n = 43$) over 40 days of experimental perch angling (Fig. 1b). In contrast to the carp, the perch showed a declining movement activity from summer to winter (Fig. 1b).

Out of 43 tagged carp, nine fish were captured and released during the experimental angling phase. As two individuals were captured twice, there were a total of 11 CR events, and a control group of 34 uncaptured carp. The first carp capture took place on 19 August 2014, and the last on 8 October 2014. Immediate hooking mortality was zero, and all fish were re-

Table 1. Candidate mortality models of carp and perch.

ID	Model structure	AIC (Carp)	AIC (Perch)
1	Null Model	44.9	22.8
2	Captured (y/n)	41.5	24.6
3	CatchNr	41.9	24.5
4	Captured (y/n) + Total Length	42.3	27.3
5	Total length	44.9	25.4

Note: Candidate model set for Generalized Linear Models predicting mortality using both impact and control group fish per species. CatchNr = Number of captures, zero for control group. Best performing models in bold. AIC = Akaike information criterion.

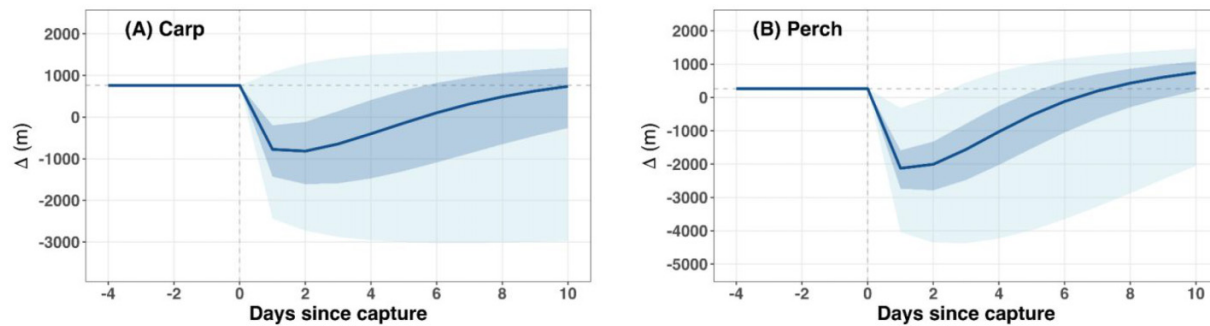
leased alive after spending one night in a carp sack. The body size of captured carp was 598 ± 98 mm (mean $\pm$ SD). The mean DO during carp captures was 10.6 ± 1.5 mg/L, and water temperatures were 17.8 ± 1.6 °C (mean $\pm$ SD).

Out of 36 tagged perch, 14 were caught during experimental angling. As four individuals were caught twice and one individual three times, there were a total of 20 perch CR events. The control group consisted of 22 uncaptured perch individuals. The first perch capture took place on 8 September 2015, and the last on 19 October 2015. Immediate hooking mortality was zero, and all fish were released. The body size of captured perch was 379 ± 18 mm (mean $\pm$ SD). The mean DO during perch captures was 11.6 ± 0.9 mg/L and water temperature was 13.3 ± 2.8 °C (mean $\pm$ SD).

Hooking mortality

Between the beginning of experimental angling and 6 months after the last angling day, $n = 8$ carp died. Out of these, $n = 4$ carp had experienced CR, while the other $n = 4$ were concurrent control fish. Raw mortality of caught-and-released carp exceeded control mortality (44.4% vs. 11.8%); however, the corrected mortality estimate following a mortality difference model was not significantly different from zero because the 95% confidence interval encompassed zero (95% CI [-2.2, 67.6]). Exploratory model comparison of the determinants of mortality suggested that models including capture status and number of recaptures received greater support than the null model based on AIC values (Table 1), although inference is limited by the low number of mortality events.

Fig. 2. Population level model predictions of (A) carp and (B) perch Δ (difference in mean displaced distance between CR fish and concurrent control fish, in m per day). CrI of the posterior distributions are shown as lightblue ribbons (95% CrI), mediumblue ribbons (50% CrI), and darkblue lines (median prediction). The horizontal dashed line denotes the observed mean Δ pre-capture, and the vertical dashed line marks the moment of capture.



Within 6 months after the last perch angling day, $n = 4$ perch died. Out of these, $n = 2$ perch had experienced CR, while the other $n = 2$ were concurrent control fish. Raw mortality of caught-and-released perch exceeded control mortality (14.3% vs. 9.1%); however, the corrected mortality estimate was not significantly different from zero because the 95% confidence interval encompassed zero (95% CI [-17.1, 27.6]). The null model received the strongest support among the candidate mortality models for perch (Table 1).

Behavioral impact of catch-and-release

In carp, the 95% CrI of individual model fits to fish that were caught and released encompassed a significant increase in predicted levels of relative movement activity in $n = 1$ case (9% of carp captures), no change in $n = 1$ case (9%), minor decreases in $n = 5$ cases (45%), and more pronounced decreases in $n = 4$ (36%) cases (Fig. S4). In two of the CR events evoking decreases in relative activity, the 95% CrI encompassed a recovery to pre-capture level within 7 and 10 days, respectively. Both cases were first captures, the other seven cases did not recover within 10 days post-capture (Fig. S4). On the population level, while the median prediction (Fig. 2, darkblue line) suggested a decline in activity and recovery within 10 days, a statistically conclusive impact of CR on carp activity was not detected, as the 95% CrI encompassed pre-capture activity levels at any time (Fig. 2a). Captured carp were on average more active relative to controls with a mean pre-capture Δ of 761.1 ± 995.1 m per day. Mean MD following capture was -1159.4 ± 1023.2 m per day, whereas the mean LD was -1378.1 ± 952.8 m per day.

The 95% CrI of individual model fits showed significant decreases in relative activity following $n = 11$ (55%) perch captures (Fig. S5). No individual significantly increased their relative activity after CR. For $n = 9$ captures (45%), the 95% CrI showed no significant change in relative activity post CR (Fig. S5). In seven (64%) of the cases with significant impact, a recovery to pre-capture levels (Δ_{Before}) followed within 6 ± 2 days (Fig. S5). The four remaining cases with significant impact (36%) did not achieve recovery within the ten-day observation window. On the population level, the 95% CrI did not overlap zero and indicated a significant decrease in rela-

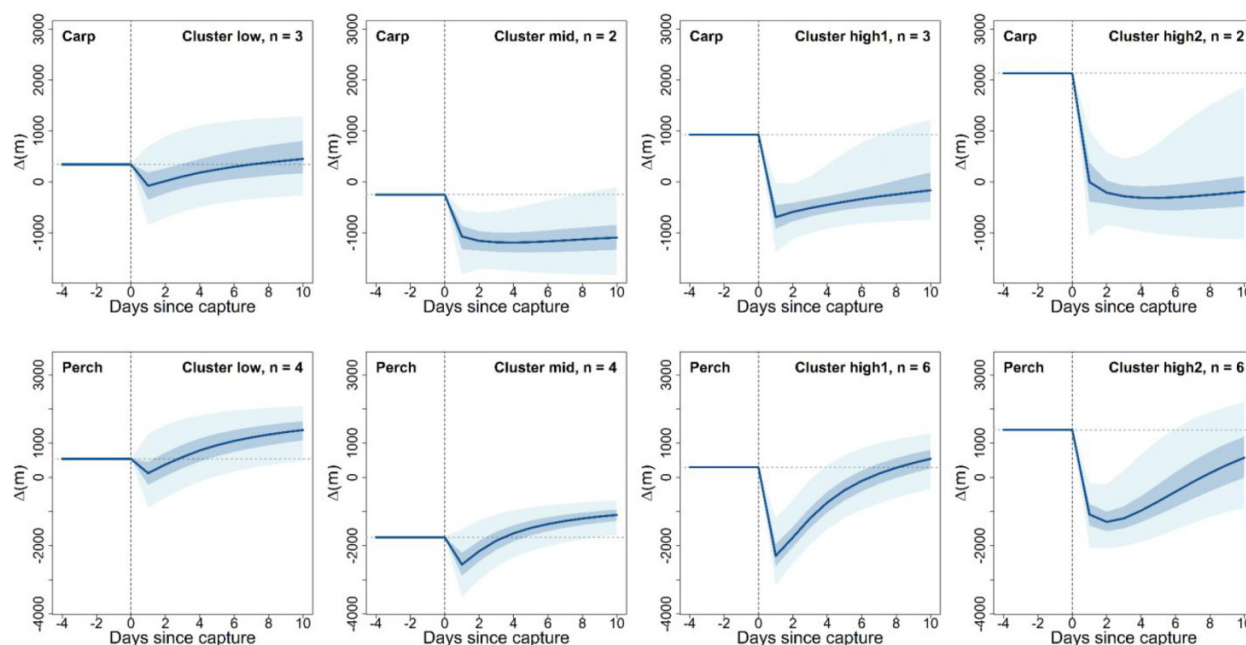
tive activity in perch post CR and a recovery within two days when judged by the upper limit of the 95% CrI (blue line) and 7 days when judging the mean prediction (black line) (Fig. 2b). As in the case of carp, CR perch were, on average, more active than controls, with a pre-capture Δ of on average 280.5 ± 1755.8 m per day. The mean MD following capture was -1081.6 ± 1251.2 m per day, and the mean LD was -1904.6 ± 1362.8 m per day.

The hierarchical cluster analysis visually identified four clusters of CR response trajectories in both perch and carp (Figs. 3 and 4). Ranking clusters by LD and MD indicated a gradient of increasing impact severity and delayed recovery from the low impact cluster, to mid impact cluster, to the high1, and high2 impact clusters with a asymptotic and sigmoidal recovery curves respectively, particularly in carp (Figs. 3 and 4).

Four distinct CR response trajectory types were found in both species, a relatively unimpacted “low” impact cluster (27% in carp and 20% in perch), a slightly more impacted “mid” impact cluster (18% in carp and 20% in perch), characterized by swift recovery times and below average pre-capture movement activity, and two groups showing much greater reductions in activity which differed in recovery time, the “high1” impact cluster (27% in carp and 30% in perch) and the “high2” impact cluster (18% in carp and 30% in perch).

In carp, in the low impact cluster ($n = 3$), the 95% CrI indicated no change in relative movement activity in response to CR (Fig. 3). The 95% CrI of the mid impact cluster ($n = 2$) showed a significant decline and a subsequent recovery (LD: -1004.2 ± 57.6 m per day, MD: -964.4 ± 32.4 m per day) within 7 days. The 95% CrI in the high1 impact cluster ($n = 3$) showed a steeper decrease in activity (LD: -1618.5 ± 500.7 m per day, MD: -1366.4 ± 368.7 m per day), followed by recovery to pre-capture activity levels again within 7 days. In the final cluster high2 ($n = 2$), comprised of highly active carp (Δ_{Before} : 2132.8 ± 1039.0 m per day), the 95% CrI showed an even steeper, significant decrease (LD: -2496.5 ± 163.4 m per day, MD: -2395.7 ± 205.2 m per day) followed by a trend towards recovery, which however did not reach Δ_{Before} within the 10 observation days post-release. Of all carp capture and released events assessed, 70% responded by significant reduc-

Fig. 3. Posterior distributions of impact and recovery trajectories of relative carp (upper row) and perch (lower row) movement activity before and after CR, in meters per day, by response cluster. Sorted by impact severity from left to right: low, medium, high1, high2, with credible intervals (CrI) (95% CrI: lightblue ribbons, 50% CrI: mediumblue ribbons, median prediction: darkblue line). The horizontal dashed line denotes the observed mean Δ (difference in mean daily movement activity between each C&R fish and the mean of concurrent control fish) and the vertical dashed line marks the moment of capture.



tions of relative movement activity and 20% of captured carp did not recover within 10 days, according to the 95% CrI (Fig. S4).

In perch, investigation of the 95% CrI for relative movement activity in the low impact cluster ($n = 4$) suggested no response to CR (Fig. 3). The mid impact cluster ($n = 4$) comprised of comparatively inactive perch ($\Delta_{\text{Before}}: -1755 \pm 302.8$), the 95% CrI similarly indicated neither increase nor decrease in relative movement activity, whereas the mean prediction indicated a slight decrease followed by recovery within five days (LD: 772.9 ± 413.1 per day, MD: 29.1 ± 461.7 per day). In the high1 impact cluster ($n = 6$), comprised of slightly more active perch ($\Delta_{\text{Before}}: 323.7 \pm 2198.2$), the 95% CrI indicated a clear decline in relative activity, and recovery to pre-capture activity levels within around five days, and the mean prediction showed a recovery within ten days (LD: -2733.9 ± 1038 per day, MD: -1210.2 ± 641.8 per day). In the high2 impact cluster ($n = 6$, $\Delta_{\text{Before}}: 1420 \pm 1202$) the 95% CrI indicated a steep decline in relative activity and a trend towards recovery within around 7 days. The mean prediction (LD: -2839 ± 975.3 m per day, MD: -2459.5 ± 937.1 per day) also showed a trend towards recovery, though not within 10 days post-release. On average the sharpest decline in relative movement activity was found in the high1 impact cluster, whereas the longest average time until recovery was seen in the impact cluster high2 (Fig. 3).

Results of GLMs relating MD and LD in relative movement activity following CR in carp to environmental conditions and fish total length did not identify statistically significant predictors of movement impairment severity (Table 2), although

warmer water temperatures during CR capture and release showed non-significant trends toward steeper and longer lasting reductions in relative movement activity than in cooler water temperature. In perch, the GLMs relating MD and LD in relative movement activity following CR to environmental conditions and fish total length identified several environmental correlates of movement impairment severity (Table 3). High turbidity during capture events was associated with steeper and longer-lasting declines in relative movement activity. Higher DO and temperature values were associated with steeper declines in activity (LD), while associations with longer-lasting reductions in activity (MD) were weaker and not statistically significant. Larger perch also tended to show more pronounced declines in relative movement activity, although these relationships were not statistically significant (Table 3).

Discussion

Using a Before-After Control-Impact Paired Series design, based on high-resolution behavioral measurements from two species in the wild, we detected support for sublethal impacts from CR lasting in the order of days. Specifically, at the population level we found (1) that CR reduced relative movement activity in perch, and also carp, though less pronounced, (2) that behavioral changes recovered to pre-capture levels within a mean of 7 days, (3) that CR behavioral impacts varied within species (representing impact types) and among species (with greater impacts in perch compared to carp), and (4) that the behavioral responses were moderated by water tempera-

Fig. 4. Boxplots showing the distributions of mean difference (MD) and largest difference (LD) in relative movement activity following capture per impact clusters for carp (A and B) and perch (C and D). The central line of each boxplot represents the median, box boundaries the interquartile range (IQR; 25th and 75th percentiles), whiskers extend to $1.5 \times$ the IQR from the box edges, and points represent outliers.

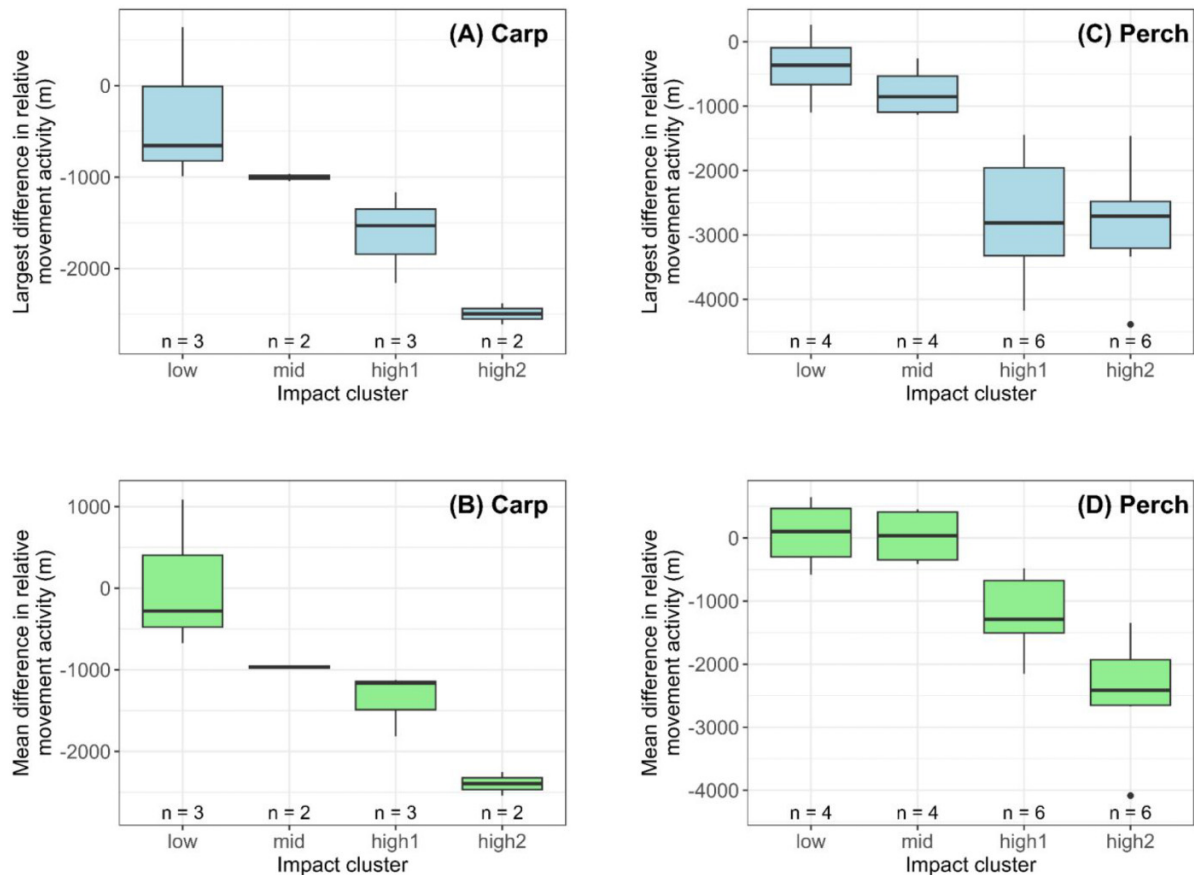


Table 2. Results of generalized linear model predicting largest difference (LD) and mean difference (MD) in relative movement activity following carp captures ($N = 11$).

Carp	LD			MD		
	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Intercept	- 1159.4	270.9	0.004	- 1378.1	266.3	0.001
TL	- 215.2	288.5	0.480	- 170.6	283.6	0.566
Temperature	- 605.6	356.2	0.133	- 582.3	350.2	0.140
DO	- 105.4	360.6	0.778	- 3.9	354.5	0.992

Note: TL = fish total length; DO = dissolved oxygen content.

Table 3. Results of generalized linear model predicting largest difference (LD) and mean difference (MD) in relative movement activity following perch captures ($N = 20$).

Perch	LD			MD		
	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Intercept	- 1904.6	260.3	2.54e-06	- 1081.6	247.6	0.001
TL	- 562.3	292.3	0.0736	- 442.4	278.1	0.133
Temperature	- 956.2	407.2	0.0330	- 794.1	387.4	0.058
DO	- 733.7	315.1	0.0343	- 620.5	299.8	0.057
Turbidity	- 1060.2	373.1	0.0124	- 961.6	355.0	0.0162

Note: TL = fish total length; DO = dissolved oxygen content.

ture, dissolved oxygen, and turbidity (in perch only). However, we did not find any lethal impacts of CR under our study conditions, although the evidence was not conclusive for carp due to small sample size. The impact of CR on long-term carp mortality should be investigated further with larger sample sizes.

In both perch and carp, no fish died immediately following the CR event. The techniques we used (bolt rig for carp angling, artificial lures for perch) facilitate shallow hooking (Arlinghaus et al. 2008b; Rapp et al. 2008) and therefore minimize injury through deep hooking, which is known to be a key factor for hooking mortality in fish (Munoeke and Childress 1994; Hühn and Arlinghaus 2011). Moreover, the study lake was shallow and all capture events happened at water depth below 4 m due to the anoxic hypolimnion, which limits impacts of barotrauma in percids (Knight et al. 2018). Previous studies are consistent with our findings. For example, Rapp et al. (2012, 2014) also reported zero hooking mortality in caught and released wild carp in Canada and Ghazal et al. (2025) revealed that domesticated stocked carp generally show a high stress resiliency to stressors. Although our work suggests limited to no hooking mortality impacts due to CR in a shallow lake over the course of half of a year, hooking mortality might be different in other situations. Especially physioclists such as perch will face more issues when hooked and released from deeper water due to barotrauma impacts that can damage internal organs and lead to high post release mortality (Keniry et al. 1996; Knight et al. 2018; Lyon et al. 2022; Madden et al. 2024), in particular without quick recompression (Fertner et al. 2015b).

Based on the mean relative movement activity differences among CR and uncaptured control fish on the population level, we found a non-significant trend for reduced activity of carp after CR and recovery within ten days after capture. For perch, significant reductions in activity were found following CR, which lasted a mean of 7 days before recovery, but variation was high, with 36% of significantly impacted perch (4 of 11 captures) not having recovered within the 10-day observation window. Especially for perch but also for selected individuals of carp, the results revealed prolonged changes in behavior that exceeded previous research reports in the same species, but were comparable with a recent study in largemouth bass and pike who also used fine-scale telemetry and a BACIPS design to examine recovery from CR (mean recovery of 5–6 days, LaRochelle et al. 2026). Specifically for carp, Rapp et al. (2012, 2014) revealed that caught, retained (in carp sacks, as in our study) and released carp showed inactivity the first few hours post release and recovery of normal patterns after 12 h. However, Rapp et al. (2012, 2014) used coarse positioning with radio telemetry and were thus unable to resolve fine-scale recovery trajectories. Our high-resolution study statistically agreed with Rapp et al. (2012, 2014) in revealing limited behavioral impact of CR in carp. However, when disaggregating beyond the population level to the level of individuals, sustained reductions in activity lasting multiple days, and exceeding ten days in some cases were reported for selected subgroups of carp. These results suggest that behavioral tracking at high-resolution may be necessary for robust assessment of the impact of CR on fish in the wild (Donaldson

et al. 2008; LaRochelle et al. 2025), in particular when investigating individual effects, beyond population averages. Overall, our results were in broad agreement with a range of previous studies that CR leads to reduced swimming activity in both marine and freshwater fishes (e.g., Sundström and Gruber 2002; Gurshin and Szedlmayer 2004; Klefoth et al. 2008; Baktoft et al. 2013; Rapp et al. 2012, 2014; LaRochelle et al. 2026).

The behavioral impairment of angling we found lasted a mean of 7 days in perch before recovering to pre-capture activity levels. There are only two high-resolution tracking studies that investigated the same question in other freshwater predators. Baktoft et al. (2013) found behavioral recovery of northern pike within 48 h in cool water (5–16 °C). However, under warmer summer conditions (20–28.5 °C), LaRochelle et al. (2026) found that northern pike required 145 h (about 6 days) to behaviourally recover from CR and largemouth needed on average 129 h (about 5 days), closely matching the mean seven-day recovery we found for perch. Together, these findings suggest that a) behavioural recovery may take surprisingly long after CR and b) specific for pike water temperature may be a key moderator of behavioural recovery duration, with warm summer conditions extending recovery well beyond the 48 h observed in cooler water, at least in the cold-water adapted northern pike (Schlautmann et al. 2026). The unexpectedly long recovery period in perch in our work may, in part, be related to the holding of the fish for 30 min in a live-well prior to release, as this is known to elevate physiological stress in percids (Suski et al. 2005). However, live-well holding is not uncommon in real perch recreational fisheries, particularly for large perch, especially when preparing for photography of trophies. Best practices of CR suggest to avoid any type of holding of fish and engage in quick releases, to minimize the stress response of the individuals (Brownscombe et al. 2017).

A behavioral recovery period with an estimated mean of seven days (at minimum two days based on the 95% CrI, with one third of our perch not having recovered by day 10) found for perch strongly exceeds the expectation of recovery of basal physiological functions in the blood and in the muscle, which typically return to pre-capture levels within 4–6 h in shallow hooked freshwater fishes (Gustaveson et al. 1991; Suski et al. 2006; Arlinghaus et al. 2009). Therefore, the more sustained decrease in swimming activity, specifically in perch, found in our work cannot be explained with physiological recovery (e.g., rebuilding of metabolic load, clearing of lactate after exhaustive exercise, Kieffer 2000) alone. In line with arguments in Klefoth et al. (2008) and LaRochelle et al. (2026) we speculate that in addition to a physiological cost, the experience of a stressful CR and associated injuries via the hooking wound can lead to an anti-predation response, which fish may show through reduced activity and increased use of refuges. Specifically, in predatory species such as perch, the hook wound may damage important tissues that reduce their ability for suction feeding (Thompson et al. 2018, but see Hlina et al. 2021) and which might lower the tendency to move. In addition, the reduced activity may be explained via a cognitive mechanism triggered via the experience of CR (LaRochelle et al. 2026). There is evidence that caught and

released fish learn from past hooking experiences and subsequently reduce their foraging rates (Siepker et al. 2006; Ferter and Rochow 2010; Stålhammar et al. 2012; Klefoth et al. 2013; Czaplá et al. 2023; Lucas et al. 2023, but see Camargo-Dos-Santos et al. 2021 for a different finding) and reactivity to fishing lures (e.g., Raat 1985; Askey et al. 2006; Louison et al. 2019; Czaplá et al. 2023; Roser et al. 2025). Although wounds may heal, negative experiences may be forgotten over time and fish might simply get used to the new situation, the private memory of a harmful CR event, especially when it also involves being retained overnight (which further increases the stress response, Rapp et al. 2012, 2014), may still be remembered for a long period of time and affect subsequent behavior (as evidenced in a memory of hooking of 7 months in carp, Czaplá et al. 2023). Perch are social foragers (Eklöv 1992) and so are carp (Monk et al. 2023). We therefore interpret the reduced activity in response to CR as a way to limit predation risk by natural and human predators. Depending on local prey density, the short-term reduced swimming and associated foraging may have negative impacts on growth (as found in northern pike in the same study lake, Klefoth et al. 2011) and subsequent reproductive output (Richard et al. 2013). If a local fishery is fished intensively over multiple days, weeks and months, the behavioral response may also be one explanation for the strongly reduced catch rates observed under total catch and release policies at continued fishing effort in several species of fish (Askey et al. 2006; Wegener et al. 2018; Koeck et al. 2020).

Across both species, we found more intrinsically active individuals were more severely impacted in terms of reduced movement activity, indicating the importance of intrinsic differences in individual traits or state in moderating the response to CR. We assume these intrinsic differences are in part related to personality differences (Mittelbach et al. 2014; Conrad et al. 2011) or systematic differences in stress coping styles (Koolhaas et al. 1999; Koeck et al. 2019; Laskowski et al. 2016). The large role of individual differences in CR responses we found in perch and carp is worth highlighting, which can blur population-level significance. For example, on the population level, we did not detect a significant reduction in the swimming activity in carp, while the cluster analyses indicated that certain individuals were heavily behaviorally impacted, recovering only after ca. 6 days (clusters “mid” and “high1,” based on the 95% CrI) and some individuals not recovering at all within the ten days observation period (cluster “high2”). While individual variability in a range of traits is common in fishes (Conrad et al. 2011) and high variability in terms of how individual fish respond to CR stressors has been reported in the literature (Eberts et al. 2018), the CR literature has largely focused on the mean population response. Our work shows that a more disaggregated perspective focusing on groups of individuals sharing behavioral responses can provide more nuanced insights.

An obvious follow up question is what drives whether an individual belongs to one of these four clusters. We speculate individual differences in stress coping style are a strong candidate. Previous work has shown that fish that vary in stress responsiveness also vary in their probability of being captured with lures (Louison et al. 2017; Koeck et al. 2019),

which can carry over to affect recovery dynamics as suggested by the more general coping style and stress responsiveness literature (Koolhaas et al. 1999; Øverli et al. 2005). Moreover, individuals can differ in state and condition, which will affect the energy stores they have to deal with after CR and the ability and speed to recover from energy depletion and general stress (Kieffer et al. 1995; Suski et al. 2004; Keiling and Suski 2019). A better physiological condition allows a fish to allocate more resources towards activity (Enberg et al. 2012), while food deprivation, either before or due to the capture and release event, will lower activity and an individual’s willingness to inspect lures (Keiling and Suski 2019). We did not measure individual traits other than body length, and we are therefore unable to track down why the different groups of fish behaved so differently in response to CR. Unraveling what makes an individual responsive or not to CR stressors and how individuals vary in ability to cope with CR stress is an important avenue for future research.

The behavioral impact of CR was modified by both intrinsic, but also external factors. For perch, environmental factors (temperature, dissolved oxygen, and turbidity) influenced the severity of the behavioral impact, whereas environmental factors did not affect the response of carp to CR. Especially the role of temperature is well known in CR studies, where warmer temperature usually increases the degree of stress (Tomasso et al. 1996; Bartholomew and Bohnsack 2005; Gale et al. 2013; Alfonso et al. 2021). Similarly, fish will be able to cope with exhaustive exercise less when oxygen levels are low (Lee and Bergerse 1996; Kieffer 2000; Shultz et al. 2011; Keretz et al. 2018), and the risk of predation upon release as well as foraging rate is moderated by the turbidity of the water in visually oriented predators such as perch (Skov et al. 2007; Jacobsen et al. 2014). In contrast to carp, almost all focal environmental variables had an influence on the sublethal behavioral effects of CR on perch. The impact of body size of perch on post-release activity may be related to higher baseline activity in larger individuals (Jacobsen et al. 2002), or increased antipredator behavior in response to stressors in small-sized individuals (Westerberg et al. 2004). Higher temperature likely increases the stress response (Gale et al. 2013) and in turn the needs for behavioral adjustment. It is also reasonable that turbidity impacted perch because perch rely on vision for foraging (Diehl 1988, but see Jacobsen et al. 2014) and because perch might be less able to sense and avoid predators in more turbid water. Normally, in situations without behavioral impairment, turbidity increases activity and space use in predatory freshwater fish because turbidity may act as a prey refuge and to increase encounter rates with prey (Vøllestad et al. 1986). However, we found increasing turbidity enhanced the reduction in swimming in response to CR, perhaps because the weakened perch preferred to not take the risk to move around as predators of perch may have higher attack successes as visibility drops (Pitcher and Turner 1986). The positive correlation between higher DO during capture and severity of behavioral impacts was a bit surprising. Perhaps this relationship was due to higher swimming activity of fish under optimal conditions, i.e., larger reductions are statistically possible during highly active periods.

The strengths of our study relates to examination of CR impacts under natural conditions in the wild, based on a sample of acoustically tagged fish, which were allowed to recover from tagging impacts for several weeks to months and from which a subset was captured and released and the uncaptured fish served as a control. A further strength may be the application of a novel time-series BACI approach and its introduction to CR studies. However, several limitations are worth noting. The most important limitation relates to the small sample size due to the difficulty in achieving high recaptures rates, specifically in carp despite immense sampling effort of more than 2000 experimental rod hours. Carp are known to be relatively hard to capture and to show rapid hook avoidance behavior (Raaf 1985; Czapla et al. 2023). However, the small sample size for carp prevented us from reaching robust, statistically supported conclusions regarding the CR impacts in this species. Another key limitation relates to the differential vulnerability of fish to angling gear (Arlinghaus et al. 2017a), which may have resulted in a systematic bias in the fish that ultimately were caught and released, thus forming the treatment group. Swimming distance has previously been found unrelated to vulnerability to capture in both perch (Monk and Arlinghaus 2018) and carp (Monk and Arlinghaus 2017), but we detected that the fish that were caught and released exhibited greater swimming activity compared to controls, similar to what is known in pike (Monk et al. 2021). Other traits might systematically differ among those fish vulnerable to angling gear and the unsampled controls, including aggression, boldness and exploration in perch (Härkönen et al. 2016; Monk and Arlinghaus 2018) and variation in boldness and foraging rate in carp (Klefoth et al. 2017; Monk and Arlinghaus 2017). A more robust study might perhaps be to limit the tagging to fish vulnerable to angling gear, thereby producing a more homogenous treatment and control group, similar to LaRochelle et al. (2026) who did not report substantial movement-related differences among the fish initially tagged that were recaptured and those serving as uncaptured (but tagged) controls. Finally, our study relied on telemetry data collected from the wild. Especially when fishes moved into refuges, data gaps occurred, which very likely influenced swimming distance calculations. As both CR and control fish were subject to similar detection limitations, this effect is partially controlled by the BACIPS comparison; however, to the extent that impaired fish preferentially sought refuges post-release, activity may be underestimated, resulting in conservative impact estimates.

Based on this research and for the conditions prevailing in our study system (shallow capture depth, moderate water temperature) and for the gear we used (which causes shallow hooking) our study shows zero or very low hooking mortality for perch and carp. Thus, our study supports the proposition that CR is of no major mortality concern for perch and carp (in line with previous papers, Rapp et al. 2012). Thus, based on our work CR can be recommended for managing intensively exploited perch and carp stocks without causing managerial concern when taking a population conservation perspective (Corsi et al. 2025). For example, given the low mortality rates, we do not foresee any major issues with the effectiveness of harvest regulations (e.g., bag limits or minimum length limits

which lead to mandatory CR) even when fishing effort is high. However, our work also shows delayed behavioural recovery in perch, perhaps caused by the short live-well handling period, implying that it is in the interest of anglers to engage in best-practices during CR to minimize harm to fishes through rapid live releases (Brownscombe et al. 2017, see also Cooke et al. 2025). So to sort out further uncertainties we recommend further field studies that examine the lethal and sub-lethal impacts of CR on perch when captured from deeper water, from a broader temperature range, and after multiple CR events throughout the fishing season.

Our work underscores the high potential of well-planned biotelemetry to help understanding the behavioral impacts and fate of caught and released fish in the wild. In particular small lakes where biotelemetry can cover an entire system and where the likelihood of losing trace of tagged fishes that are captured and released (compared to controls that are not) is low, seem to be excellent research arenas for applied telemetry-based research on CR impacts (LaRochelle et al. 2026). For the future we recommend designs where a large sample of rod-and-reel sampled fish are captured in the wild and equipped with transmitters to then be returned to recover from the initial tagging and handling event. After a recovery period of several weeks or month, strategically recapturing and releasing a subsample of these fish and assigning treatments of interest to them (e.g., capture in different temperature periods or different depths) would provide a highly robust BACI design with uncaptured temporal controls that would circumvent many of the methodological issues identified previously for CR studies (Wilde et al. 2003; Pollock and Pine 2007). It is encouraging to see that during the write-up of the present paper another article from Canada appeared that exactly followed this approach (LaRochelle et al. 2026). Our study is a related case showing the feasibility of such controlled telemetry-related studies in the wild, where the aim is to generate robust science for use in fisheries management under realistic ecological conditions.

To conclude, our tracking study suggests that both Common Carp and Perch are resilient to hooking mortality when they are captured in shallow water and deep hooking can be avoided. Carp are also behaviorally resilient, while CR leads to a sustained reduction in swimming activity in Eurasian Perch, which can last multiple days and from which the fish eventually recover. The behavioral response to CR as tertiary stress response showed strong individual differences and may have ecological (e.g., altered predator-prey relationships, reduced fitness, Klefoth et al. 2011) and social consequences (e.g., altered catchability for recreational anglers, Arlinghaus et al. 2017a, 2017b). We did not assess fitness impacts resulting from CR, which is an important topic of future research in carp and perch.

Acknowledgements

The original study that generated the data analyzed in this work was financially supported by the project B-Types (SAW-2013-IGB-2) to RA from the Leibniz Community. The invasive animal procedures were approved by the Landesamt für Umwelt, Gesundheit und Verbraucherschutz of Brandenburg

Germany under the project “Fangbarkeit, project No. 2347-21-2014.” We thank T. Damerau for help with operating the perch experiment. In this context, we thank the 104 anglers who volunteered to fish for science for 1 day and the many individuals from tackle shops, fishing clubs, and internet forums who helped to advertise the study and recruit participants. B. Chéret, J. Alós, and J. Briege assisted with carp angling. We thank A. Türck, J. Hallermann, D. Hühn, J. Weinrautner and J. Nickl for their extremely supportive assistance in the field work as well as A. Mühlbradt for his leadership in operating the telemetry system and positioning the telemetry data, and H. Baktoft for constant support. Reviewers and editors provided excellent feedback that strongly improved this paper.

Article information

History dates

Received: 26 October 2025

Accepted: 7 August 2026

Accepted manuscript online: 27 August 2026

Version of record online: 9 October 2026

Notes

This paper is part of a collection entitled “**Fish telemetry to address management and conservation**,” reflecting presentations from the 7th International Conference on Fish Telemetry held in Traverse City, MI, USA, in June 2025.

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Data availability

Data and code supporting the findings of this study are available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.80gb5mm5q>. The deposit includes raw telemetry data, catch records, model outputs, and the full R analysis pipeline, released under a CC0 waiver (data) and MIT License (code).

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Competing interests

The authors declare there are no competing interests.

Funding information

The study was financed by the Leibniz-Community within the Pact for Innovation and Research.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2025-0348>.

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