



Estimating and mitigating post-release mortality of European eel by combining citizen science with a catch-and-release angling experiment

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ABSTRACT

Several anguillid eel species have experienced severe population declines over the past decades, particularly the European eel (*Anguilla anguilla*), which is listed as critically endangered by the International Union for Conservation of Nature. To reduce fishing mortality, many European countries have introduced strict recreational eel fishing regulations increasing regulatory catch-and-release (C&R) practice. Despite high release rates, only limited information exists on the potential consequences of C&R on eels. A field experiment was conducted with pre-tagged eels in a semi-natural environment to investigate lethal and sublethal impacts of C&R. The experiment was combined with a citizen science study evaluating the effects of different hooks on catch rates, fish size, and hooking location to develop best practice guidelines. Short-term mortality (≤ 72 h) ranged from 0.0–18.2%, and adjusted long-term mortality (> 72 h) from 0.0–46.2% depending on treatments, resulting in adjusted total mortality rates between 8.4% and 64.4% at the end of the study period (≥ 43 d). The only significant predictor of mortality was the occurrence of bleeding from hooking injuries. Deep hooking was common, and only few deep-hooked eels for which the fishing line was cut and the hook left in place shed the hook after release. However, no significant effect of C&R on eel condition was found. The citizen science study showed that anglers can significantly decrease the catch of small eels, and thus release rates, by using large J-hooks. Furthermore, large J-hooks or circle hooks reduced the likelihood of deep hooking compared to small J-hooks. Post-release mortality of eels caught in recreational fisheries needs to be considered in future stock assessments and management plans to ensure conservation of the European eel. This study also highlights the strength of combining citizen science with experimental studies to develop best practice guidelines promoting fish conservation.

1. Introduction

Globally, several catadromous, anguillid eel populations including the American (*Anguilla rostrata*), Japanese (*Anguilla japonica*) and European eel (*Anguilla anguilla*) have experienced severe declines to less than 10% of their population levels compared to the 1970s, in recent decades (reviewed in [Jacoby et al., 2015](#); [Tzeng, 2016](#)). This is particularly true for the European eel (hereinafter referred to as ‘eel’), a socio-economically important target species for both commercial and recreational fishers (e.g., [Dekker, 2003](#); [Dekker and Beaulaton, 2016](#);

[Dorow et al., 2010](#); [Moriarty and Dekker, 1997](#); [Ringuet et al., 2002](#)), which has been listed as critically endangered by the International Union for Conservation of Nature ([Jacoby and Gollock, 2014](#)) and in Annex II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora to control its trade ([CITES, 2014](#)). Multiple potential threats, including fishing pressure, climate change, spread of parasites and diseases, increased predation, pollution, and waterbody obstructions have been identified (reviewed in [Bevacqua et al., 2015](#); [Dekker, 2008](#); [FAO and ICES, 2007](#); [Feunteun, 2002](#)). Due to the critical stock situation, a council regulation of the European

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Union (EU) came into force in 2007 obliging all EU member states to provide national eel conservation management plans by 2009. These management plans aim to ensure escapement of at least 40% of the adult eels from river and coastal catchments into the sea, where they can spawn, relative to the estimated escapement without anthropogenic impacts (EC, 2007). Various management measures such as restocking, habitat improvements, and commercial and recreational fishing regulations have been introduced by EU member states to meet the 40% escapement target. Some countries (e.g., United Kingdom, the Netherlands, and Sweden) have prohibited all recreational harvest of eel to reduce recreational fishing mortality (Ferber et al., 2013; ICES, 2013, 2016a,b) while others introduced seasonal closures, bag limits or higher minimum landing sizes in the recreational fishery (ICES, 2013, 2016a,b).

Several studies have indicated that recreational eel harvest is substantial compared to the commercial fishery in some regions (Baisez and Laffaille, 2008; Dorow and Arlinghaus, 2011; ICES, 2016a,b; van der Hammen et al., 2015). A recent comparison of recreational and commercial eel landings from six European countries (Denmark, Italy, Lithuania, Norway, Poland, and the Netherlands) revealed that recreational landings represented at least 7–32% of the total landings in these countries (ICES, 2016a). Yet, for many European countries, recreational eel catch data are still missing or incomplete, and the proportion of the recreational catches might be even higher in some countries. Even though few studies quantifying release rates in European recreational eel fisheries are available, there are indications for substantial release rates in many countries, mainly as a result of recreational harvest regulations, i.e., bag limits, minimum landing sizes, and protection of the eel (Ferber et al., 2013; ICES, 2016a,b). For example, a nation-wide recreational fishery survey from the Netherlands showed a release proportion of 72%, corresponding to 890,000 released eels in 2010 (van der Hammen et al., 2015).

The underlying assumption of catch-and-release (C&R) is that the released fish survive (Arlinghaus et al., 2007). However, C&R can have both lethal and sublethal impacts on the fish, which may render recreational fishing regulations and conservation strategies, resulting in C&R, less effective (Arlinghaus et al., 2007; Coggins et al., 2007; Lewin et al., 2006) and may have negative consequences on the population level (Hessenauer et al., 2018; Kerns et al., 2012). Considering the precarious eel stock situation, and the significant releases in the recreational fishery, there is an urgent need to investigate lethal and sublethal consequences of C&R on eels to improve management and conservation (ICES, 2016a). To the best of our knowledge, there is only one study dealing with the post-release fate of eels caught with rod-and-line (Weltersbach et al., 2016). It focused on hook shedding and post-release fate of deep-hooked eels for which the fishing line was cut and the hook left in place (hereinafter referred to as deep-hooked, line-cut eels) monitored under unnatural holding conditions for 23 weeks. However, this study did not provide absolute post-release mortality estimates that may be used for stock assessment purposes (Weltersbach et al., 2016).

Beside the need for post-release mortality estimates, it is also important to develop and communicate best practice guidelines to minimize post-release mortality and sublethal effects of C&R on eels (Weltersbach et al., 2016). Such best practice guidelines should be evidence-based, and many studies exist where best practice guidelines have been developed for other species based on C&R experiments in the field or in the laboratory (reviewed in Brownscombe et al., 2017). However, there is a risk that best practice guidelines derived from experimental work do not represent real fishing practices, which may result in ineffective guidelines and low acceptance by the recreational fishing community (Brownscombe et al., 2017).

Citizen science provides an opportunity to involve members of the public in academic research programmes, and has gained increasing attention as a cost-effective tool for the collection of scientific data (e.g., Conrad and Hilchey, 2011; Roy et al., 2012; Silvertown, 2009; Thiel

et al., 2014; Tulloch et al., 2013). Even though citizen science has become an important data source in recreational fisheries research (e.g., Fairclough et al., 2014; Granek et al., 2008; Papenfuss et al., 2015; Venturelli et al., 2016; Williams et al., 2015), only few studies focusing on C&R fishing and post-release mortality have incorporated citizen science in the past (but see e.g., Danylchuk et al., 2011; McClellan Press et al., 2016; Weltersbach and Strehlow, 2013). Nevertheless, the development of best practice guidelines can benefit from the inclusion of data collected by anglers on a voluntary basis leading to improvements in fisheries management and conservation (Cooke et al., 2017a; Granek et al., 2008).

To estimate post-release mortality and to develop best practice guidelines reducing negative impacts of C&R on eel, a C&R angling experiment combined with a citizen science study was performed. The C&R angling experiment was conducted with pre-tagged fish under semi-natural conditions to (i) estimate post-release mortality rates, (ii) identify factors affecting mortality, and (iii) investigate sublethal effects of C&R on physical condition of eels. The citizen science study involving voluntary eel anglers was conducted to evaluate (iv) catch rates, (v) length-frequency distributions, (vi) hooking locations, and (vii) angler attitude towards three different hooks (a J-hook model in two sizes and a circle hook). The results of both studies were used to develop species-specific best practice guidelines to increase post-release survival, mitigate the catch of undersized fish, and thus reduce recreational fishing mortality.

2. Material and methods

2.1. C&R angling experiment

2.1.1. Study site, tagging, and stocking

The C&R angling experiment was carried out in a freshwater pond system in Mecklenburg-Western Pomerania, Germany between May and September 2015. Three adjacent, drainable ponds (two angling ponds and one holding pond) with similar dimensions (rectangular; length \times width \times depth: 41 m \times 9 m \times 1.5 m) and muddy substrate were used. Each pond was supplied with flow-through freshwater (5000 L \times h⁻¹) from a nearby river to ensure adequate water quality. The in- and outlets of the ponds were covered with nets (7 mm mesh size) to prevent eel escapement. Water inflow, water source, and light conditions were the same for all three ponds to ensure similar environmental conditions. To prevent predation by avian predators such as herons (*Ardea cinerea*) and cormorants (*Phalacrocorax carbo*), warning tape was fixed 1 m above the water surface at regular intervals (1.5 m) to act as a deterrent. The ponds contained some natural littoral and submerged vegetation (*Carex* spp. and *Myriophyllum* spp.) and were equipped with hiding places (ceramic pipes: 10 cm \varnothing \times 100 cm length). Natural populations of invertebrates (e.g., Chironomidae and Lymnaeidae) and three-spined sticklebacks (*Gasterosteus aculeatus*) were available for the eels to feed on.

A total of 306 wild eels (yellow eel stage according to Durif et al., 2005) were caught using fyke nets by a local commercial fisher in several lakes of the Mecklenburg Lake Plateau in May and June 2015. These eels were transported to the study site in an aerated 1000-L tank in three batches. Upon arrival, all eels were anaesthetized using aqueous solution of 2-Phenoxyethanol (1.5 mL \times L⁻¹), length measured (total length [TL] to the nearest cm), weighed (total weight to the nearest g), and individually tagged with passive integrated transponder tags (PIT tag; ID 162-8-PM, EURO I.D., Weilerswist, Germany; dimensions: 2.12 mm \varnothing \times 9 mm length) inserted into the posterior abdominal cavity through a surgical incision (2 mm length). This tagging procedure has been proven to provide fast healing and high survival rates (Baras and Jeandrain, 1998; Weltersbach et al., 2016). After a 1 h recovery period in a container filled with fresh pond water, eels were distributed equally to two angling ponds, resulting in 153 eels in each pond by 11th of June 2015. TLs of the stocked eels ranged from 36 cm

to 63 cm (mean TL \pm SD = 52.7 \pm 4.6 cm) and total weight between 64 g and 364 g (mean total weight \pm SD = 227.0 \pm 55.9 g). The mean TLs and total weights of the stocked eels did not differ significantly between the two angling ponds (Student's *t*-test: *t*_{length} = 1.06; *t*_{weight} = 1.01; both *p* > 0.05). Depending on the date of stocking, eels were held for 19–50 d in the ponds prior to the start of the C&R angling experiment allowing for recovery and acclimatisation.

2.1.2. Experimental angling and catch of control fish

The experimental eel angling was conducted from the shorelines of the two angling ponds during 16 angling sessions between June 30th and July 22nd 2015. Eel angling took place at dusk and night, reflecting common eel angling practice, and the mainly nocturnal behaviour of eels (Riley et al., 2011; Tesch, 2003; Walker et al., 2014). To simulate realistic eel angling practices, five anglers fished with common eel angling equipment (medium casting rods, medium sized spinning reels and 6–8 kg breaking strain fishing line) and fishing methods (bait fishing with a fishing float [bobber] or a sinker at the bottom).

A large (size #1) and a small (size #6) version of a common offset baitholder style single hook model (Gamakatsu®, Japan, model LS-3113R) attached to 50 cm monofilament leader line (Balzer®, Germany, Platinum Royal, 0.30 mm \varnothing and 9.1 kg breaking strain) were used (Fig. 1). This hook model and the two hook sizes were selected as they represent hooks commonly used by eel anglers in Germany (M. S. Weltersbach, pers. comm., July 2017). The hooks were baited with 1–3 live earthworms (*Eisenia hortensis* or *Lumbricus terrestris*) depending on hook size.

Simultaneously, two bottom-set fyke nets (5 mm mesh size; one in each angling pond) were used to catch control fish to account for potential mortality caused by handling, holding, and natural mortality (Pollock and Pine, 2007). The fyke nets were checked at the start of each angling session, and all captured control fish underwent the same treatment (handling and holding) as the angled fish.

2.1.3. Data collection, handling, and holding

The following data were recorded: date and time of capture, pond ID, PIT tag number, total weight (to the nearest g) and water temperature ($^{\circ}$ C) for each eel (control and treatment group). Additionally, angler ID, hook size, hooking location, hooking injury (presence or absence of bleeding), and unhooking procedure (successful or failed attempts to remove the hook, or if the fishing line was cut and the hook left in place) were recorded for each angled eel. Anatomical hooking locations were categorized into two classes defined as shallow hooking (hooked in the lips, jaws or oral cavity) and deep hooking (hooked in the gills or in the gastrointestinal tract). A hook removal attempt was

conducted by hand or with pliers for all shallow-hooked eels. In addition, for each hook size (small and large), 11 deep-hooked eels were randomly selected during the C&R angling experiment and hook removal was attempted with a dehooking device (hook disgorging). The fishing line was cut as close as possible to the mouth when the hook removal attempt failed. Line cutting was also conducted for the remaining deep-hooked eels, but without any attempt to remove the hook. This experimental design resulted in six angling treatments (for both hook sizes: (i) shallow-hooked; (ii) deep-hooked – line-cut; (iii) deep-hooked – hook removal attempted), and an additional control treatment. The presence or absence of bleeding was determined by observing the eel in a white 10-L bucket filled with 10 cm of fresh pond water at the end of the handling procedure. Eels were categorized as bleeding when blood was visible in the exhaled water. Water temperature was measured every 30 min in each pond (angling and holding ponds) by an automated data logger (ONSET®, USA, model: HOBO Pendant UA-001-64) installed in 1 m depth. Water temperatures ranged between 15.3–23.8 $^{\circ}$ C, and mean water temperatures (mean \pm SD; angling pond 1 = 20.1 \pm 1.8 $^{\circ}$ C; angling pond 2 = 19.9 \pm 2.3 $^{\circ}$ C; holding pond = 19.9 \pm 2.3 $^{\circ}$ C) did not differ significantly (Welch's ANOVA; *F* = 1.72; *p* > 0.05) between the three ponds during the angling period.

Afterwards, all eels (control and angled fish pooled) were randomly placed into rectangular keep nets (length \times width \times height: 4 m \times 0.5 m \times 0.4 m) consisting of black, knotless netting (1.5 mm mesh size) located in the holding pond to monitor short-term (\leq 72 h) mortality. This holding period in keep nets was included in the experimental design to obtain exact short-term mortality rates, as it is known for other species that most post-release mortality occurs within 72 h of capture (reviewed in Muoneke and Childress, 1994). For each eel, the ID of the keep net into which it was released was recorded. Maximum stocking density was 10 eels for each keep net, and the occurrence of dead fish was checked by visual inspection of the lifted keep nets (air exposure < 1 min) every 24 h. The additional stress due to this handling was assumed to be negligible as eels are known to be eurythermal and tolerant towards hypoxia (reviewed in Wilson, 2013). Eels were classified as dead when they showed common death signs such as no response to physical stimuli, no body movements and rigor mortis. Dead fish were removed, identified by their tag number, weighed, and frozen for later dissection. Keep nets were visually inspected for ejected hooks before reuse.

All surviving eels were released into the holding pond to monitor long-term mortality and sublethal effects after the 72 h holding period. Eels were held for 43–65 d after release (depending on the date of capture) in the holding pond, and the pond was daily inspected for mortalities. Visible dead fish were removed with a dip net, identified by their tag number, weighed and frozen for later dissection. Water temperature (in 1 m depth) was measured using the automated data logger and dissolved oxygen was measured daily with a hand-held probe (Xylem Analytics®, USA, model: WTW TA 197-Oxi) in 1 m depth during the holding period. Water temperature ranged between 13.4–23.5 $^{\circ}$ C (mean \pm SD = 18.4 \pm 1.9 $^{\circ}$ C) and dissolved oxygen between 6.8–14.3 mg \times L⁻¹ (mean \pm SD = 12.2 \pm 1.2 mg \times L⁻¹) during the holding period.

At the end of the holding period, the water level of the holding pond was lowered and the pond was electrofished several times until no more eels were captured. Afterwards the pond was completely drained, and the bottom was searched for remaining dead or alive eels. All eels that survived until the end of the experiment were euthanized (aqueous solution with 5 mL \times L⁻¹ 2-Phenoxyethanol), and together with the dead individuals identified by their tag number, weighed (to the nearest g), and frozen. Subsequently, a comprehensive dissection was conducted with all recovered eels to determine potential cause of death, hooking injury, occurrence of hook shedding (only deep-hooked, line-cut fish), and physical condition.

All appropriate permissions were obtained for the C&R angling

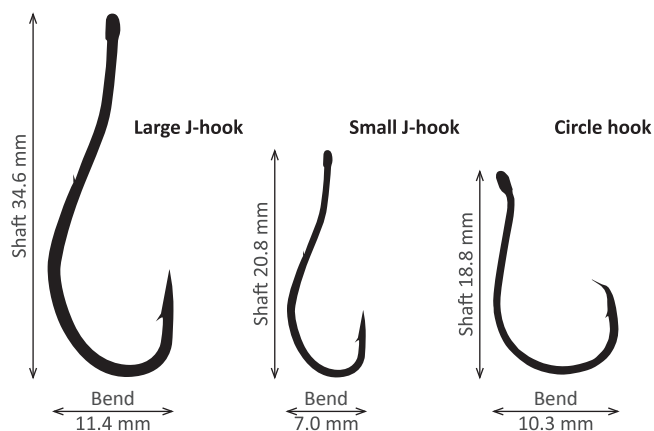


Fig. 1. Schematic drawings and dimensions (shaft length and bend width) of the two J-hooks (Gamakatsu®, Japan, model LS-3113R, size #1 and #6) used in both the C&R angling experiment and the eel angler study, and the circle hook (Gamakatsu®, Japan, model Octopus Circle, size #6) used only in the eel angler study.

experiment, and the experimental protocol was approved by the animal ethics committee of the State Office for Agriculture, Food Safety and Fisheries of Mecklenburg–Western Pomerania, Germany (reference: 7221.3-1-071/13).

2.2. Eel angler study

As the C&R angling experiment was performed under semi-natural conditions, a citizen science eel angler study was conducted to provide representative data on the effects of three hooks (a small and a large J-hook and a circle hook; Fig. 1) on catch-per-unit-effort (CPUE), harvest-per-unit-effort (HPUE), size selectivity (i.e., mean TL) and hooking location under realistic angling conditions. A total of 183 voluntary eel anglers from Lower Saxony, Germany were recruited via the Angling Association of Lower Saxony (Anglerverband Niedersachsen e.V.) and their associated angling clubs between June and August 2015. All anglers received a package including 25 small (size #6), 25 large (size #1) J-hooks (Gamakatsu®, Japan, model LS-3113R), and 10 circle hooks (Gamakatsu®, Japan, model Octopus Circle, size #6) together with 150 m of the same leader line used in the C&R angling experiment (Fig. 1). The circle hook was added in the eel angler study as several studies on other species have shown that circle hooks have the potential to decrease the likelihood of deep hooking due to their design compared to conventional J-hooks resulting in reduced post-release mortality (reviewed in Cooke et al., 2012; Cooke and Suski, 2004). However, the performance of circle hooks is species- and fishery-specific (Cooke et al., 2012; Cooke and Suski, 2004), and their use is not very widespread among German eel anglers (M. S. Weltersbach, pers. comm., July 2017). Therefore, the eel angler study was also used to investigate the utility of circle hooks and their acceptance in the German recreational eel fishery.

The fishing tackle was sent together with a cover letter explaining the objectives of the study and a diary including instructions on how to collect the required information. The anglers were asked to fish with all three hooks simultaneously (three rods), and to record the date, name of the water body, fishing time (h) per hook and eel catches (including zero catches) for each eel angling trip until the end of October 2015 (i.e., the end of the eel fishing season). TL (cm), hook used, hooking location (shallow- or deep-hooked as defined before), and unhooking procedure (unhooked or line-cut) were recorded for all eels caught. To evaluate the performance of each hook type/size, anglers were asked to answer a six-point Likert scale (from 1 = very good to 6 = insufficient) based on their personal experience during each fishing trip. At the end of the study period, all anglers were reminded up to two times via telephone or e-mail to return their catch diaries. Additionally, return reminders were distributed via newsletters and the website of the Angling Association of Lower Saxony.

2.3. Data analysis

All statistical analyses and calculations were conducted using the software R version 3.2.5 (R Core Team, 2016). Significance was set at $\alpha < 0.05$ for all statistical hypothesis testing.

2.3.1. C&R angling experiment

Mean TLs and total weights of the stocked eels in the two angling ponds at the start of the C&R angling experiment were compared using Student's *t*-test. Student's *t*-test was also used to compare mean TLs of eels caught on small and large hooks, and Welch's *t*-test to compare the mean TLs of angled (data of all angled fish pooled) and control fish. A logistic regression model with a binomial probability distribution and a logit link function was used to describe the relationship between the presence/absence of bleeding and hook size (small and large), hooking location (shallow and deep hooking), unhooking treatment (unhooked, line-cut, and unsuccessful attempt to unhook), and all corresponding interaction terms. Model selection was based on backward elimination

using the second order Akaike information criterion (AICc) for small sample sizes (Anderson and Burnham, 2002) calculated with the R package "AICcmodavg" (Mazerolle, 2016). Likelihood ratio tests were performed to compare the full, null and reduced model, and the Wald test was used for significance testing of the estimated model coefficients.

Confidence intervals (95%) for short-term mortality rates were calculated using the Clopper-Pearson exact method (R package "binom", Dorai-Raj, 2014). A Bayesian generalized linear mixed model (GLMM) with a logit link function and a binomial probability distribution was used to describe the relationship between short-term mortality (≤ 72 h), TL, water temperature at capture, hooking location, hook size, presence or absence of bleeding and unhooking treatment, and their corresponding interaction terms (using the R package "blme", Dorie, 2015). Angler ID, holding keep net ID and pond ID were added as random effects. The Bayesian approach (with a Gaussian prior imposed to the fixed effects) was chosen as complete separation occurred in one predictor variable (unhooking treatment) leading to the non-existence of a finite maximum likelihood regression parameter for unhooking treatment in the GLMM (Albert and Anderson, 1984; Dorie, 2015). Model selection, significance testing for model comparisons, and the estimated model coefficients were conducted as described for the GLM.

The observed mortality rates (recovered dead eels from the pond) and the proportion of non-recovered eels (i.e., not found after the pond had been drained) were combined for each treatment to calculate adjusted long-term (> 72 h) mortality rates under the assumption that the likelihood of not being recovered was similar for all eels at the end of the experiment. A two-tailed Fisher's exact test was performed to verify this assumption. The adjusted long-term mortality rates ($M_{Adj.}$) were calculated using a modified version of the methods proposed by Wilde (2002) to account for non-recovery:

$$M_{Adj.} = \frac{(nM_A + nR_A)}{n_A} - \frac{(nM_C + nR_C)}{n_C}, \quad (1)$$

where nM_A is the number of angled fish that died and were recovered, nR_A the number of angled fish that were not recovered, n_A the total number of fish angled and released, nM_C the number of control fish that died and were recovered, nR_C the number of control fish that were not recovered, and n_C the total number of control fish captured and released in the pond. The corresponding 95% confidence intervals were calculated following the equations proposed by Wilde (2002) for C&R experiments containing a control group. Total adjusted mortality rates were calculated by summing the short-term mortality rate and the adjusted long-term mortality rate for each treatment. The corresponding 95% confidence intervals were calculated using the Clopper-Pearson exact method (R package "binom", Dorai-Raj, 2014).

Hook shedding rates were calculated for all deep-hooked, line-cut eels that were recovered (dead or alive) in a condition allowing assessment of the hook fate (i.e., excluding dead eels that showed progressed decomposition). A two-tailed Fisher's exact test was used to investigate the independence of hook shedding rates after up to 68 d from hook size.

Total weight change per day was calculated for all eels that survived and were recovered at the end of the long-term holding period to evaluate sublethal effects of C&R expressed in the physical condition of eels. Mean absolute total weight changes per day were compared between control fish ($n = 26$), shallow-hooked fish ($n = 14$; data from both hook sizes pooled), deep-hooked fish caught on small hooks ($n = 24$) and deep-hooked fish caught on large hooks ($n = 20$) using ANOVA.

2.3.2. Eel angler study

Mean CPUEs (number of eels caught per hour fished with a certain hook model [$n \times \text{hook}^{-1} \times \text{h}^{-1}$]) and mean HPUEs (number of eels harvested per hour fished with a certain hook model [$n \times \text{hook}^{-1} \times \text{h}^{-1}$]) of the three hook types/sizes were compared using Welch's ANOVA (heteroscedasticity) and ANOVA, respectively. In

case of significance, Games-Howell post-hoc test (Welch's ANOVA) or Tukey's HSD post-hoc test (ANOVA) were used. Pearson's chi-squared test (χ^2) was used to determine whether release rates were similar between hook types/sizes. Subsequently, post-hoc pairwise chi-squared tests with Holm's sequential Bonferroni correction were conducted for multiple pairwise comparisons (Holm, 1979). For comparison of mean TLs of the eels caught on the three hook types/sizes, an ANOVA and a subsequent Tukey's HSD post-hoc test were conducted. A logistic regression model with a binomial probability distribution and a logit link function was fitted to the data to describe the relationship between deep hooking rates and the three hook types/sizes. Model comparison was accomplished by using a likelihood ratio test (LRT), and Wald tests were performed for significance testing of the estimated model coefficients.

For the analysis of the angler evaluation of the three hooks during eel fishing, only data from trips where all three hooks were fished and evaluated simultaneously ($n = 173$) was included. A non-parametric Kruskal-Wallis test was applied to compare the probability distributions of the Likert scale scores for the three hooks, and Dunn's test with Holm's sequential Bonferroni correction was conducted for follow-up multiple pairwise comparisons (R package "PMCMR", Pohlert, 2014).

3. Results

3.1. C&R angling experiment

3.1.1. Capture characteristics

In total, 110 eels were angled and 38 control eels were captured with fyke nets during the C&R angling experiment (Table 1). TLs of the angled eels ranged from 44 cm to 62 cm, and mean TLs did not differ significantly between eels caught on small (mean TL \pm SD = 52.4 \pm 4.0 cm) and large (mean TL \pm SD = 52.7 \pm 4.2 cm) hooks (Student's t -test: $t = 0.43$; $p > 0.05$). There was also no significant difference (Welch's t -test: $t = -0.05$; $p > 0.05$) in mean TLs between angled (mean TL \pm SD = 52.6 \pm 4.1 cm) and control fish (mean TL \pm SD = 52.5 \pm 5.5 cm).

Hook removal from deep-hooked eels with a dehooking device failed in seven out of 11 eels (63.6%) caught on small hooks, and in 10 out of 11 eels (90.9%) caught on large hooks. Bleeding occurred in 21.4–81.8% of angled eels depending on hook size, hooking location and unhooking treatment (Table 1). A logistic regression analysis revealed that a model only including the factor unhooking treatment and excluding hook size, hooking location, and all corresponding interaction terms was the most parsimonious model (AICc_{full model} = 143.9; AICc_{reduced model} = 143.7), and that this model explained the presence/absence of bleeding significantly better than a null model including only the intercept ($\chi^2 = 14.4$; $p < 0.001$; AICc_{null model} = 153.9). The likelihood of bleeding was 2.8-fold (95% CI = 1.0–7.9) higher for unhooked eels ($z = 2.0$; $p < 0.05$) and 6.3-fold (95% CI = 2.3–19.5) higher for eels with an unsuccessful hook removal attempt ($z = 3.4$; $p < 0.001$) compared to line-cut eels, indicating additional injuries caused by hook removal attempts, particularly of deep-hooked eels.

Table 1

Capture characteristics of the C&R angling experiment showing number of fish (n), mean total length (TL in cm) \pm standard deviation (SD), mean total weight (g) \pm SD, mean water temperature (temp. in °C) \pm SD at the time of capture, and proportion (%) of bleeding fish. The angling data is grouped by hook size (small and large J-hook), hooking location (shallow and deep hooking) and for deep-hooked fish further by treatment (hook removal attempt or line-cut).

	n	Mean TL [cm] \pm SD	Mean weight [g] \pm SD	Mean temp. [°C] \pm SD	Bleeding [%]
Control	38	52.5 \pm 5.5	214.6 \pm 61.8	19.9 \pm 1.8	n/a
Small J-hook, shallow	14	52.6 \pm 3.2	209.6 \pm 39.6	20.1 \pm 1.7	42.9
Small J-hook, deep, line-cut	28	52.5 \pm 4.7	219.6 \pm 61.9	20.6 \pm 1.1	21.4
Small J-hook, deep, removal attempt	11	51.7 \pm 3.3	224.7 \pm 49.0	19.1 \pm 1.5	81.8
Large J-hook, shallow	10	54.0 \pm 4.0	239.3 \pm 61.6	20.1 \pm 1.4	60.0
Large J-hook, deep, line-cut	36	52.6 \pm 4.5	219.5 \pm 46.9	19.9 \pm 1.5	41.7
Large J-hook, deep, removal attempt	11	52.0 \pm 3.7	216.0 \pm 52.8	19.4 \pm 1.6	81.8

3.1.2. Post-release mortality and mortality factors

Short-term post-release mortality of angled eels ranged between 0.0% and 18.2% for the various treatments after the 72 h holding period in keep nets, whereas none of the control fish died (Table 2). Only one out of the 14 short-term mortalities (7.1%) occurred within the first 24 h of the keep net holding period. The GLMM revealed that a model including the presence or absence of bleeding and the unhooking treatment as fixed effects and pond ID, angler ID and keep net ID as random effects provided the best fit to the short-term mortality data (AICc_{full model} = 93.6; AICc_{reduced model} = 87.7). This model explained the data significantly better than the null model including only the intercept and the random effects ($\chi^2 = 11.2$; $p < 0.05$; AICc_{null model} = 92.2). Short-term (≤ 72 h) mortality was significantly higher for bleeding eels compared to non-bleeding eels ($z = 2.2$; $p < 0.05$), whereas the unhooking treatment did not significantly predict short-term mortality. The components of variance from the random effects were low (all < 0.001), suggesting that short-term mortality rates did not systematically vary across anglers, ponds and keep nets.

Between 8.3% and 44.4% of the eels were not recovered at the end of the C&R angling experiment (Table 2). Non-recovery was independent of the treatments, indicating that there was no significant difference in the likelihood of recovery for all groups (Fisher's exact test; $p > 0.05$). Adjusted long-term (≥ 43 d) mortality rates ranged from 0.0–46.2% for angled, eels and adjusted total mortality rates (combining adjusted short- and long-term mortality) ranged between 8.4% and 64.4% depending on hook size, hooking location and unhooking treatment (Table 2).

Four dead and recovered eels were already heavily decomposed preventing a dissection. The dissection of all recovered, dead, deep-hooked eels showed that the hook had penetrated the oesophagus or the stomach/cecum in 79% (15 out of 19) of the eels causing ruptures and holes of various size likely leading to internal haemorrhaging and the intrusion of digestive fluids into the coelomic cavity. In some dead, deep-hooked eels, the hook had punctured further into muscular tissue or vital organs such as the liver, heart and gills. One shallow-hooked, dead eel with retained hook was hooked in the upper oral cavity and the hook penetrated into the cranial cavity leading to haemorrhaging in the brain.

3.1.3. Hook shedding and sublethal effects

The dissection of all recovered, deep-hooked, line-cut eels revealed that the hook shedding rate was 22.2% (six out of 27 eels) for eels caught on small hooks and 6.3% (two out of 32 eels) for eels caught on large hooks, resulting in an overall hook shedding rate of 13.6% (eight out of 59 eels) after a mean holding period of 50 d. Hook shedding rates were independent of the hook size (Fisher's exact test; $p > 0.05$). Two small hooks that were shed during the 72 h holding period were found in the keep nets. Twenty-five percent of the retained hooks showed no signs of corrosion, while 75% showed slight signs of corrosion such as damaged coatings and blunted hook and barb tips. All retained hooks were located in the oesophagus, stomach or cecum and no hook was found in the intestine. In one of the recovered dead eels, a second

Table 2

Summary of the C&R angling experiment showing number of fish (*n*), number of fish that died and short-term mortality (%) with 95% confidence intervals (CI) for the short-term holding period (≤ 72 h) in keep nets, and number of fish (*n*), number of dead (recovered) fish (*n*), number of non-recovered fish (*n*), proportion (%) of dead (recovered) and non-recovered fish and adjusted long-term (> 72 h) mortality (%) with 95% confidence intervals (CI) for the long-term holding period (up to 65 d) in the pond, and adjusted total mortality (%) with 95% confidence intervals (CI). The angling data is grouped by hook size (small and large J-hook), hooking location (shallow and deep hooking) and for deep-hooked fish further by treatment (hook removal attempt or line-cut).

	Short-term mortality (≤ 72 h)			Long-term mortality (> 72 h)				Adj. total mortality (CI) [%]	
	<i>n</i>	Dead [<i>n</i>]	Mortality ≤ 72 h (CI) [%]	<i>n</i>	Dead [<i>n</i>]	Not recovered [<i>n</i>]	Dead and not recovered [%]		Adj. mortality > 72 h (CI) [%]
Control	38	0	0.0 (0.0–9.3)	38	5	7	31.6	n/a	n/a
Small J-hook, shallow	14	1	7.1 (0.2–33.9)	13	1	4	38.5	6.9 (0.0–38.2)	14.0 (1.7–42.5)
Small J-hook, deep, line-cut	28	4	14.3 (4.0–32.7)	24	5	2	29.2	0.0 (0.0–23.9)	14.3 (4.0–32.7)
Small J-hook, deep, removal attempt	11	1	9.1 (0.2–41.3)	10	1	2	30.0	0.0 (0.0–33.5)	9.1 (0.2–41.3)
Large J-hook, shallow	10	0	0.0 (0.0–30.8)	10	1	3	40.0	8.4 (0.0–43.7)	8.4 (0.1–42.5)
Large J-hook, deep, line-cut	36	6	16.7 (6.4–32.8)	30	3	9	40.0	8.4 (0.0–31.7)	25.1 (12.2–42.3)
Large J-hook, deep, removal attempt	11	2	18.2 (2.3–51.8)	9	3	4	77.8	46.2 (13.7–78.7)	64.4 (31.4–89.5)

fishing hook not originating from the experiment with median signs of corrosion was found in the cecum. The dissection of all recovered survivors with retained hooks (*n* = 35) showed that 71% of the eels had no visible (18 out of 35) or already healed hooking injuries (seven out of 35). In a few eels, cicatricial tissues were found in the oesophagus and stomach indicating progressed healing of larger holes and ruptures. The hook was lying freely in the stomach or cecum in 74% of the deep-hooked eels, whereas in 26% of the eels the hook had punctured the gastric wall. Nine out of 14 eels (64%) that had survived and where the hook was manually removed showed no (six out of 14) or already healed (three out of 14) hooking lesions. None of the survivors that had shed the hook (*n* = 8) had any macroscopic hooking injuries.

Most of the eels that had survived and were recovered lost weight during the long-term holding period in the pond with the exception of two eels from the control group with a slight increase in total weight. Mean absolute total weight change per day was -0.36 (SD = ± 0.40) $g \times d^{-1}$ for control fish, -0.39 (SD = ± 0.24) $g \times d^{-1}$ for shallow-hooked fish (data from both hook sizes pooled), and -0.56 (SD = ± 0.26) $g \times d^{-1}$ and -0.54 (SD = ± 0.25) $g \times d^{-1}$ for deep-hooked fish caught on small and large hooks, respectively. Although the weight reduction of all angled groups was generally higher than of the control group, there was no significant difference in the mean absolute weight change per day between the four groups (ANOVA: *F* = 2.5; *p* > 0.05).

3.2. Eel angler study

Seventy out of 183 eel anglers (38%) sent back their catch diaries at the end of the study. Three out of these 70 anglers did not go fishing for eel during the study period. The remaining 67 anglers conducted 389 eel angling trips (89% in rivers/channels and 11% in lakes/ponds) with a total fishing effort of 4,550 hook \times h and caught 523 eels. The overall mean CPUE was 0.12 (SD = ± 0.30) eels per hook \times h, and the overall mean HPUE was 0.06 (SD = ± 0.16) eels per hook \times h (Table 3). The mean CPUEs were significantly different between the three hooks (Welch’s ANOVA: *F* = 5.1; *p* < 0.01), and the post-hoc test showed

that mean CPUEs were significantly lower when large J-hooks (*t* = 3.1; *p* < 0.01) and circle hooks (*t* = 2.7; *p* < 0.05) were used compared to small J-hooks, whereas no significant difference was found between large J-hooks and circle hooks (*t* = 0.3; *p* > 0.05). The mean HPUEs did not differ significantly between hook types and sizes (ANOVA: *F* = 1.3; *p* > 0.05). Overall, 47.5% of the eels caught during the eel angler study were released (Table 3). Release rates were significantly different between the three hooks ($\chi^2 = 54.9$; *p* < 0.001). Post-hoc pairwise comparisons showed that release rates were significantly higher when small J-hooks (61.2%; $\chi^2 = 52.9$; *p* < 0.001) or circle hooks (50.4%; $\chi^2 = 21.9$; *p* < 0.001) were used compared to large J-hooks (22.8%), while no significant difference in release rates was found between small J-hooks and circle hooks ($\chi^2 = 3.6$; *p* > 0.05).

TLs of eels ranged from 15 cm to 91 cm, and the mean TLs were significantly different between the hooks (ANOVA: *F* = 23.1; *p* < 0.001; Fig. 2). Eels caught on large J-hooks had a significantly higher mean TL (mean TL \pm SD = 52.1 ± 14.0 cm) compared to fish caught on small J-hooks (mean TL \pm SD = 42.4 ± 13.3 cm) and circle hooks (mean TL \pm SD = 44.8 ± 15.1 cm; Tukey’s HSD post-hoc tests; both *p* < 0.001). In contrast, the mean TLs of eels caught on small J-hooks and circle hooks did not differ significantly (*p* > 0.05).

Deep-hooking occurred in 46.5% of the eels (Table 3), and the likelihood of deep hooking was significantly influenced by the hook type and size ($\chi^2 = 21.5$; *p* < 0.001). The likelihood of deep hooking was 2.6 times higher for small J-hooks than for large J-hooks (*z* = 4.3; *p* < 0.001), while no significant difference was found between circle hooks and large J-hooks (*z* = 1.2; *p* > 0.05). Line cutting instead of hook removal was conducted for 74.0% and 59.1% of the deep-hooked and released eels that were caught on small J-hooks and circle hooks, respectively, and the line was cut for 53.8% of the deep-hooked and released eels caught on large J-hooks.

The evaluation of the fishing performance of the three different hooks revealed that anglers were similarly satisfied with the hooks (all median Likert scale score of 3). However, there was a significant difference in the distributions of scores for the three hook types (Kruskal-Wallis test: *H* = 10.00; *p* < 0.01). The probability of observing worse

Table 3

Summary of the eel angler study showing angling effort (hook \times h), number of captured eels (*n*), mean catch-per-unit-effort (CPUE: $n_{\text{catch}} \times \text{hook}^{-1} \times \text{h}^{-1}$), mean harvest-per-unit-effort (HPUE: $n_{\text{harvest}} \times \text{hook}^{-1} \times \text{h}^{-1}$), both \pm standard deviation (SD), release rate (%), and proportion (%) of deep-hooked eels by hook types and sizes.

Hook	Effort (hook \times h)	<i>n</i>	Mean CPUE ($n \times \text{hook}^{-1} \times \text{h}^{-1}$) \pm SD	Mean HPUE ($n \times \text{hook}^{-1} \times \text{h}^{-1}$) \pm SD	Release rate (%)	Deep-hooked (%)
Small J-hook	1,535	242	0.17 \pm 0.36	0.07 \pm 0.17	61.2	57.1
Large J-hook	1,611	150	0.10 \pm 0.26	0.07 \pm 0.17	22.8	34.2
Circle hook	1,404	131	0.10 \pm 0.28	0.05 \pm 0.15	50.4	41.2

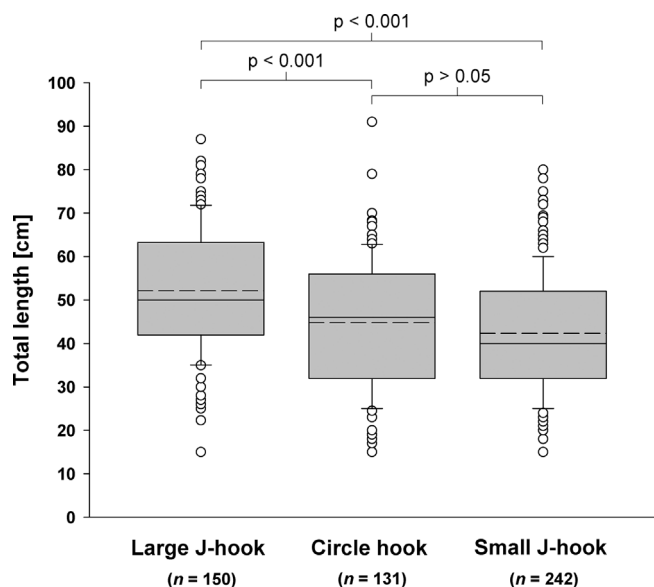


Fig. 2. Comparison of TLs (cm) of eels caught with large and small J-hooks and circle hooks during the eel angler study representing realistic angling conditions (dashed lines indicate means and solid lines medians in the boxes). The p-values indicate the results of the corresponding pairwise comparisons (Tukey's HSD post-hoc tests) of the mean TLs after global ANOVA.

Likert scale scores when using circle hooks was significantly higher compared to small J-hooks (Dunn's test: $p < 0.01$), whereas no significant differences were found between the small and large J-hook and the large J-hook and circle hook (Dunn's test; both $p > 0.05$).

4. Discussion

This study provides the first comprehensive investigation of lethal and sublethal effects of C&R on eels. The C&R angling experiment revealed that eels experience post-release mortality, which needs to be taken into account to quantify recreational removals in future stock assessments. Mortality rates varied depending on hook size, hooking location, and unhooking treatment, and were mainly influenced by the incidence of bleeding caused by hooking injuries. Some eels may also suffer sublethal consequences (e.g., fitness reduction) after C&R, which needs to be further evaluated to identify if this has consequences on the population level. The citizen science study showed that anglers can reduce deep hooking and catch of small eels by appropriate hook choice, thereby mitigating negative effects of C&R and promoting the eel's conservation.

4.1. C&R angling experiment

4.1.1. Post-release mortality and mortality factors

A comprehensive literature review revealed that there is only one study available providing information on the post-release fate of eels caught in recreational fisheries (Weltersbach et al., 2016). However, that study focused on hook shedding mechanisms and rates in deep-hooked, line-cut eels held in a tank for up to 23 weeks using radiography and did not include a control group to account for potential lethal or sublethal effects of frequent handling (anaesthesia and radiography) and holding conditions (Weltersbach et al., 2016). Thus, only limited comparisons with the deep-hooked, line-cut fish from the present study are possible.

Short-term mortality (≤ 72 h) was 0.0% for deep-hooked, line-cut eels caught on small J-hooks (size #6; $n = 17$) and 13.3% for eels caught on large J-hooks (size #2; $n = 15$) in the study by Weltersbach et al. (2016) compared to 14.3% and 16.7% in the present study (Table 2), indicating that short-term mortality rates in both studies

were of similar magnitude. The observed differences may be attributed to small sample sizes in both studies and is reflected in the confidence intervals of the present study. In this study, the incidence of bleeding was the only significant predictor of short-term mortality. Hooking injuries and associated bleeding have been identified as dominating factors increasing post-release mortality of many fish species (reviewed in e.g., Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011; Muoneke and Childress, 1994). Although unhooking treatment and hooking location failed to be significant predictors of short-term mortality in the GLMM, both are associated with the occurrence of bleeding. Successful hook removal and hook removal attempts significantly increased the incidence of bleeding by inducing more severe hooking injuries, particularly in deep-hooked eels, compared to deep-hooked eels for which the line was cut and the hook left in place. Overall, hook removal success was low (22.7%) for deep-hooked eels caught during the C&R angling experiment which is in line with observations made by Tesch (2003) and Weltersbach et al. (2016), who concluded that hook removal from deep-hooked eels is more challenging compared to other fish due to their anatomy, behaviour and the low light conditions during night fishing. Thus, line cutting rather than hook removal should be preferred in deep-hooked eels to minimize mortality.

Total adjusted mortality rates (combining short- and long-term mortality) after ≥ 43 d holding ranged from 8.4–64.4% depending on hook size, hooking location and unhooking treatment (Table 2). The higher adjusted total mortality rates observed for deep-hooked eels caught on large hooks with and without hook removal attempt (Table 2) may indicate that larger hooks cause more physical damage when swallowed by eels compared to small hooks, in particular, when hook removal is attempted.

4.1.2. Hook shedding and sublethal effects

The hook shedding rate was 22.2% for deep-hooked, line-cut eels caught on small J-hooks and 6.3% for fish caught on large J-hooks after an average 50-d holding period in the pond. Weltersbach et al. (2016) found similar hook shedding rates (35.3% for eels caught on small J-hooks (size #6) and 0.0% for eels caught on large J-hooks (size #2)) after 54 d of holding in a tank indicating that deep-hooked, line-cut eels have only limited capabilities to shed hooks compared to other species (reviewed in Hall et al., 2009). This is further supported by the fact that an old hook not originating from the experiment was found in one eel during dissection. Hook shedding rates did not significantly differ between eels caught on small and large hooks. In contrast, Weltersbach et al. (2016) found significantly higher hook shedding rates for eels caught on small hooks compared to large hooks. This may be explained by differences in the size distribution of eels used in both studies, with on average larger eels being used in the present study. Hook shedding in eel has been found to be influenced by total fish length (Weltersbach et al., 2016), and the size-related effects influencing hook shedding may be less pronounced in larger eels. Hook retention is, however, also influenced by other factors, such as environmental conditions, hook design and materials, and may differ between fisheries (McGrath et al., 2011; Robert et al., 2012; Tsuboi et al., 2006). In addition, the question arises whether hook retention may have further lethal and sublethal effects beyond the time frame covered in both studies, in particular, during maturing, gonadal development and spawning migration, and therefore on the population level (Hall et al., 2009). Accordingly, further studies should investigate fisheries-specific hook retention rates and potential adverse effects of long-term hook retention on eels by using mark-recapture or biotelemetry studies.

Another aim of the study was to evaluate the effects of C&R on eel condition. However, most eels, including control fish, lost weight during the experiment indicating that habitat conditions and food supply may not have been optimal in the holding pond hampering the interpretation of the results. Even though there was no significant difference in mean weight loss between the treatments, mean weight loss

was smaller for control fish than for angled fish, in particular deep-hooked fish, which may indicate potential negative effects of C&R on eel condition and growth. Explanations for the higher weight loss in angled eels may be hooking injuries observed during dissection and inflammations of the digestive system caused by embedded hooks aggravating food consumption, digestion and assimilation (Broadhurst et al., 2007; Weltersbach et al., 2016). Therefore, further research is needed to investigate effects of C&R on growth in the eel's natural habitat and should be complemented by physiological studies (e.g., using blood sampling) to evaluate potential physiological disturbances arising from C&R affecting fish welfare (Cooke et al., 2013).

4.1.3. Study limitations of the C&R angling experiment

Investigating lethal and sublethal impacts of C&R can be challenging as the fish are often impacted by factors other than the actual C&R event. For example, artificial holding conditions in tanks or cages, tagging, and extra handling during the experiment can exacerbate lethal and sublethal impacts (Donaldson et al., 2008; Pollock and Pine, 2007; Rogers et al., 2014). When tagging is necessary to identify individuals, tagging with a recovery period of several days or weeks prior to the C&R experiment has been shown to be beneficial to separate tagging effects from actual C&R effects (Baktoft et al., 2013; Ferter et al., 2015; Klefoth et al., 2008). In the present study, eels were tagged and released ≥ 19 d prior to the start of the C&R angling experiment to minimize potential lethal and sublethal impacts due to handling, tagging, and translocation of the eels from their natural environment into the ponds. Even though it is not likely that the tagging procedure caused significant lethal and sublethal impacts beyond this recovery period (Baras and Jeandrain, 1998; Weltersbach et al., 2016), it cannot be ruled out that the translocation caused sublethal, long-term behavioural and physiological effects that may be reflected e.g., by the observed overall body weight reduction across all treatments potentially influencing individual fish fitness.

This study used a combination of a short-term holding period (≤ 72 h) in captivity (keep nets) and a long-term holding period (43–65 d) in a semi-natural pond environment. This approach allowed a more detailed investigation of the potential short-term impacts of C&R under controlled conditions while reducing the risk of confounding effects influencing post-release mortality, behaviour and fish condition due to containment in the long term. Nonetheless, when interpreting the results, one should account for the potential lethal and sublethal impacts caused by handling and short-term containment (Donaldson et al., 2008; Pollock and Pine, 2007; Rogers et al., 2014). However, eels where held at low stocking densities in the keep nets and the non-occurrence of short-term mortality in the control group indicated a low potential for any additional holding- and handling-related short-term mortality. In contrast, some mortality occurred in the control group during the long-term holding period in the pond, which was accounted for in the calculations of the adjusted long-term mortality rates. Most likely this mortality was induced by natural causes (e.g., predation, parasites, and diseases), but cumulative impacts of different stressors (capture, translocation, handling, environmental conditions) may also have contributed.

Recovery of dead and living eels from the holding pond proved to be challenging despite repeated electrofishing and draining of the pond at the end of the experiment. Multiple potential reasons may have caused the non-recovery including non-discovery of eels hidden in vegetation or mud at the end of the experiment, natural predation by birds and mammals, escape from the pond, poaching, and decomposition of dead eels. However, the inclusion of a control group in the experimental design allowed accounting for non-recovery in the calculation of long-term mortality rates and the investigation of C&R-related effects on fish condition. The ultimate fate of the not recovered eels remained unknown, therefore, a precautionary approach was chosen to calculate long-term mortality rates assuming that missing eels across all treatments (including control fish) died. As the non-recovery rates were not

significantly different between treatments and the control group, this approach seemed to be reasonable. However, due to some variation in non-recovery rates and the unknown fate of the missing fish, no further statistical analysis of the long-term mortality data was conducted and caution should be exercised when interpreting the observed hook shedding rates and changes in fish condition. Furthermore, it cannot be ruled out that some additional delayed mortality could have occurred beyond the time period covered in the present study, e.g., as a result of impaired feeding abilities or pathological consequences, in particular in deep-hooked eels with retained hooks (Weltersbach et al., 2016). Therefore, further studies are required to assess long-term mortality (i.e., at a temporal scale of months to years) of C&R on eels.

Water temperatures (15.3–23.8 °C) and dissolved oxygen levels (6.5–14.4 mg \times L⁻¹) during the C&R angling experiment represented typical conditions in freshwater ecosystems in western Europe in summer, which is the main eel angling season. Furthermore, as eels are known to have broad temperature and oxygen tolerances (reviewed in Wilson, 2013), the effect of abiotic factors on lethal and sublethal impacts of C&R on eel may be less pronounced compared to other species (reviewed in e.g., Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011; Muoneke and Childress, 1994; Raby et al., 2014). However, further research is required to investigate the effects of different environments (e.g., marine and brackish ecosystems) and abiotic and biotic factors on lethal and sublethal effects of C&R in eel.

Even though angling practice in the C&R angling experiment was kept as realistic and representative as possible (e.g., the experiment was conducted during the main eel angling season using common angling tackle), differences in individual and regional eel angling practices in relation to angler behaviour, angling methods, hook types and sizes, bait types and fish handling techniques may affect post-release mortality rates and factors influencing mortality (reviewed in e.g., Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011; Muoneke and Childress, 1994), but also hook shedding rates and sublethal effects (Weltersbach et al., 2016). However, in the present study, mortality rates have been calculated only for different treatments and no mortality rate on a stock level should be derived directly from these estimates without taking into account regional differences in eel angling practice. This could be achieved by collecting country-specific data on eel angling practices, e.g., by using representative national recreational fisheries surveys asking questions regarding hook type and size used, and proportion of deep-hooked or bleeding fish in the recreational eel fishery. This information can then be used to extrapolate the experimental post-release mortality rates to provide country-specific post-release mortality rates for use in stock assessments (Capizzano et al., 2016; Lewin et al., 2018).

4.2. Eel angler study

A citizen science diary study with voluntary eel anglers was conducted to investigate the effects of different hooks on catch rates, fish sizes, and hooking locations in the recreational eel fishery. One advantage of this approach was that the anglers collected the data themselves under realistic angling conditions increasing the significance of the results compared to experimental work in the field or in the laboratory. The study involved 67 anglers with various eel angling skills, covered a relatively large geographical area, and achieved a high temporal resolution during the study period.

The eel angler study showed that fish size significantly increased with increasing hook size, which is in line with several other studies that found a strong positive correlation between hook size and fish size (e.g., Alós et al., 2008a,b; Cerdà et al., 2010; Cooke et al., 2005; Grixti et al., 2007; Piovano et al., 2010). The effect of hook size on fish size was also reflected by differences in catch rates. The mean CPUE was significantly higher when using small hooks compared to large and circle hooks, but this difference was mainly driven by a higher catch rate of small eels that were released, reflected in a non-significant

difference of HPUEs for the three hooks. Hook size selectivity is strongly correlated to the size and shape of the fish mouth, which is related to the fish's body length, as the maximum prey size of a fish, and therefore also the maximum bait or hook size, is limited by the dimensions of the fish's mouth (Erzini et al., 1997; Karpouzi and Stergiou, 2003). In terms of hook size selectivity, the most important hook property limiting the capability of an eel to ingest a hook is the bend width as in most cases the hook is swallowed in a longitudinal direction (Weltersbach et al., 2016). Therefore, eel anglers may significantly influence the proportion of undersized fish that must be released, by the choice of hook size (bend width).

The probability of deep hooking was significantly reduced for eels caught on large J-hooks and circle hooks compared to small J-hooks. The lower incidence of deep hooking when using large J-hooks was most likely caused by similar size selectivity effects as the capability to ingest or deeply swallow a hook is physically restricted by the dimensions of the fish's mouth and oesophagus (Alós et al., 2008b; Erzini et al., 1997; Grixti et al., 2007; Karpouzi and Stergiou, 2003). Similar size selectivity effects may have occurred when fishing with the circle hook (bend width: 10.3 mm; Fig. 1) compared to the small J-hook (bend width: 7.0 mm; Fig. 1; Cooke et al., 2005). However, several studies showed that the likelihood of deep-hooking is reduced when using circle hooks compared to conventional J-hooks due to the special shape of the circle hooks promoting shallow hooking of the fish (reviewed in Cooke et al., 2012; Cooke and Suski, 2004). Therefore, the use of large J-hooks or circle hooks to reduce deep-hooking rates is likely to be also beneficial in the recreational eel fishery.

The eel angler study showed that overall the line was cut in 68.5% of the deep-hooked eels that were released. A line cutting rate of about 45% for deep-hooked released eels has been observed during a nationwide recreational fishing survey in the Netherlands (M. de Graaf, unpublished data, May 2017), indicating that line cutting is a common practice among eel anglers. Therefore, despite the need for further studies quantifying eel release rates in different countries, there is also a need to study the prevalence of line cutting of deep-hooked eels in different regions to account for differences in line cutting practices and the potential associated impacts on post-release mortality.

The evaluation of the anglers' satisfaction regarding the fishing performance of the three hooks revealed that circle hooks received significantly less approval compared to small and large J-hooks. Several anglers who rated circle hooks as "bad" reported that they had problems to bait the circle hook due to its special shape and that they missed more bites compared to J-hooks. The latter might be explained by the fact that circle hooks are not widely used in the German recreational fishery resulting in a lack of experience in the correct application (M. S. Weltersbach, pers. comm., July 2017). After a bite, circle hooks should be set by tightening the line with gentle but steady pressure instead of striking. A wrong hook setting technique might even increase the likelihood of severe hooking injuries (Cooke and Suski, 2004). Therefore, there is a need for angler education and outreach programmes to obtain the potential conservation benefits offered by circle hooks and increase angler acceptance when promoting the use of circle hooks (Cooke et al., 2012).

4.2.1. Study limitations of the eel angler study

Even though the recruitment of study participants was voluntary and based on a self-selection process, the response rate was relatively low (38%) at the end of the study that results in a high potential for non-response bias (Duda and Nobile, 2010; Jones and Pollock, 2013; Pollock et al., 1994). Possible reasons for this relatively low participation rate could be that some anglers initially indicated their willingness to participate to receive the free fishing tackle package, some may have decided not to fill in the diary because it caused too much effort, or some did not go eel angling during the study period. Further bias might be introduced by the non-representative recruitment process as most likely more avid and conservation oriented anglers participated in the

study (Duda and Nobile, 2010). Taking the potential non-response and self-selection bias into account, the observed absolute CPUEs and HPUEs, release, deep hooking and line cutting rates cannot be assumed as being representative for the entire recreational eel fishery. Furthermore, the study covered only the federal state of Lower Saxony in north-west Germany and eel angling practices in other regions or countries may differ. However, the aim of the eel angler study was to compare catch rates, fish size, and hooking location between different predetermined hooks under realistic angling conditions rather than to collect representative information on the recreational eel fishery.

4.3. Implications for anglers and fisheries management

By combining a C&R angling experiment with a citizen science study, the present study provides evidence-based best practice guidelines for anglers and managers taking into account realistic eel angling practices. To mitigate post-release mortality, eel anglers are encouraged to use large J-hooks or circle hooks instead of smaller J-hooks to minimize the catch of small eels and the likelihood of deep-hooking. For example, by choosing a hook with a bend width > 11 mm, anglers can ensure that $\geq 50\%$ of the captured eels are above a minimum landing size of 50 cm. Consequently, hook size recommendations that are adapted to country-specific minimum landing sizes may act as useful management tools to minimize the catch of undersized eels and thereby reduce recreational fishing mortality (Cerdà et al., 2010). Furthermore, anglers may decrease the catch of small eels by using appropriate baits, e.g., bait fish, because stomach content analyses revealed that larger eels preferentially prey on macrozoobenthos and fish (reviewed in Tesch, 2003). Line cutting instead of trying to remove the hook is preferable for deep-hooked eels as hook removal is challenging and may cause severe internal injuries, bleeding and more handling stress particularly when using large hooks. However, as swallowed hooks are often retained inside the eels, deep-hooking should be avoided in the first place. Eel anglers should therefore concentrate on bite detection, especially under low light conditions, and may facilitate bite detection by fishing with tight fishing lines and the use of proper bite detectors enabling the angler to set the hook as fast as possible after a bite to prevent deep hooking (Cooke et al., 2017b; Grixti et al., 2007; Schill, 1996). In general, anglers should minimize the catch of eels in countries where eel harvest is prohibited or when targeting other species by adjusting their angling practice as this study showed that some eels may suffer lethal or sublethal consequences after C&R.

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