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Hook shedding and post-release fate of deep-hooked European eel

Marc Simon Weltersbach [a,*], Keno Ferter [b,c], Florian Sambraus [d], Harry V. Strehlow [a]

[a] *Thünen Institute of Baltic Sea Fisheries (TI-OF), Alter Hafen Süd 2, 18069 Rostock, Germany*
[b] *University of Bergen, Department of Biology, P.O. Box 7803, N-5020 Bergen, Norway*
[c] *Institute of Marine Research, Fisheries Dynamics, P.O. Box 1870, N-5817 Bergen, Norway*
[d] *Institute of Marine Research, Matre Research Station, Reproduction and Development Biology, N-5984 Matredal, Norway*

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A B S T R A C T

The European eel (*Anguilla anguilla*) is a commercially and recreationally important fishery target species. In the last decades, the eel has experienced dramatic stock declines and has been listed as critically endangered. To reduce fishing mortality, several European countries have closed the fishery or introduced stricter management measures which increase the likelihood of catch-and-release in the recreational fishery. This study investigated hook shedding mechanisms of deep-hooked, line-cut eels via radiography, and quantified hook shedding rates, post-release mortality and sub-lethal effects in captivity. Eels were caught with four different hook treatments, monitored in a tank for 23 weeks, and radiographed 0, 1, 3, 10, 24, 54, 115 and 163 days after capture. After 163 days, total hook shedding rate was significantly higher for smaller hooks (41.2%) compared to larger hooks (0.0%), and increased with fish length. Post-release mortality rates ranged between 27.3% and 50.0% after 23 weeks (not adjusted for handling and holding) and did not differ significantly between hook treatments. The majority of dead eels showed gastric perforations caused by the hooks leading to internal haemorrhaging and the intrusion of digestive fluids into the body cavity inducing lethal degradation and inflammation of vital organs. Anglers are encouraged to minimise bycatch of eel in countries where eel harvest is prohibited. Anglers targeting eel should use selective and appropriate fishing gears, baits and tactics (e.g. very large hooks, immediate hook setting after a bite) to reduce deep hooking and the catch of undersized eels, ultimately promoting the eel's conservation.

1. Introduction

The catadromous European eel (*Anguilla anguilla* L.) is a socio-economically and culturally important commercial and recreational fisheries resource throughout Europe (Bernotas et al., 2016; Dekker and Beaulaton, 2016; Moriarty and Dekker, 1997; Pawson et al., 2007; Ringuet et al., 2002; van der Hammen et al., 2015). However, since the late 1970s, the European eel population has experienced dramatic declines and is currently considered to be outside safe biological limits (Aalto et al., 2016; Dekker, 2003, 2008; Dekker and Beaulaton, 2016; FAO and ICES, 2007). As a result, the European eel 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 (CITES, 2014) to control its trade. Amongst others, climate change, overfishing, pollution, habitat loss as well as an introduced parasite (i.e. *Anguillicoloides crassus*) and diseases are suggested as possible causes (reviewed in Bevacqua et al., 2015; Dekker, 2008; FAO and ICES, 2007; Feunteun, 2002). Since 2007, a Council regulation of the European Union (EU) obligates all European Member States to provide eel management plans for each river basin ensuring at least 40% escapement of the original biomass of mature eels to the sea (relative to undisturbed life conditions [CEC, 2007]).

For many European anglers, eel is still an important target species, and several European studies have shown that recreational eel harvest can exceed commercial eel harvest on a regional scale (Dorow and Arlinghaus, 2011; ICES, 2016; van der Hammen et al., 2015). To reduce fishing mortality, some countries (e.g. United Kingdom, the Netherlands, Sweden and Norway) have prohibited harvest of eel (Ferter et al., 2013; ICES, 2016). Other countries have introduced stricter bag limits or higher minimum size limits (ICES, 2016). Stricter recreational harvest regulations increase the likelihood of regulatory catch-and-release (C&R) which means catching a fish using hook and line, and releasing it alive to the waters where it was caught under the general assumption that it will survive (Arlinghaus et al., 2007). C&R is a widely spread practice and has gained broad acceptance worldwide as fisheries management tool and conservation strategy (reviewed in

* Corresponding author.
E-mail addresses: Simon.Weltersbach@thuenen.de (M.S. Weltersbach), Keno.Ferter@imr.no (K. Ferter), Florian.Sambraus@imr.no (F. Sambraus), Harry.Strehlow@thuenen.de (H.V. Strehlow).

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Arlinghaus et al., 2007; Cooke and Schramm, 2007). A study from the Netherlands revealed high release rates up to 72% for eel resulting in 887,000 released eels in the Netherlands alone (van der Hammen et al., 2015), and there is also evidence for high eel release proportions in other European countries (ICES, 2016).

Amongst others, anatomical hooking location, specifically deep hooking, has been identified as dominating factor having lethal and sub-lethal effects for a variety of fish species post release (reviewed in Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Cooke and Wilde, 2007; Hühn and Arlinghaus, 2011; Muoneke and Childress, 1994). Deep hooking is defined as the hook penetrating the oesophagus, stomach, gills, or other vital tissues or organs beyond the mouth cavity (Fobert et al., 2009), and is associated with severe injuries and haemorrhaging. Eel anglers are often faced with deep-hooked fish due to the commonly used fishing method (passive bottom fishing with conventional J-style hooks and small live baits at night) and the foraging behaviour of eels (rapid swallowing of the bait) resulting in a difficult bite detection (Tesch, 2003; MSW, pers. obs.). The question arises what anglers should do when they catch a deep-hooked eel that has to be released (e.g. due to management regulations such as minimum landing sizes). They can either attempt to remove the hook with fingers, pliers or other hook removal devices, or cut the fishing line and leave the hook in place (Fobert et al., 2009). Hook removal from deep-hooked eels is very challenging because of the eel's slim, snake-like body shape, the pronounced mucous layer and the extreme agility (all hindering hook localization and removal), and may lead to severe injuries of the eel (Tesch, 2003; MSW, pers. obs.). Several studies have shown that post-release survival is higher when ingested hooks are left in the fish compared to cases where the hook was removed (e.g. Butcher et al., 2007; Fobert et al., 2009; Grixti et al., 2010; Mason and Hunt, 1967; Tsuboi et al., 2006; Warner, 1979). Moreover, it has been demonstrated that many species are able to shed the embedded hook after cutting the line in the short- to long-term, and that hook degradation occurs due to corrosion processes (reviewed in Hall et al., 2009). Nevertheless, post-release survival and hook shedding rates after cutting the line are highly variable both within and between species, and depend on a variety of factors such as hook style and material, environmental conditions and the functional morphology of the digestive system (Broadhurst et al., 2007; DuBois and Pleski, 2007; Hall et al., 2009; McGrath et al., 2009). Even if survival is high, fish may still suffer sub-lethal effects such as hindered feeding, impaired growth and fitness, behavioural changes (e.g. Aalbers et al., 2004; Hall et al., 2009) or long-term pathological consequences (Borucinska et al., 2002) due to hook retention.

According to some anecdotal information from anglers, eels also seem to be able to shed retained hooks (MSW, pers. comm.). However, to the best of our knowledge, no literature describing either hook shedding, post-release mortality or sub-lethal effects of deep hooking in eels or other Anguilliformes exists (ICES, 2016). Considering the precarious situation of the European eel stock, there is an urgent need for such studies to provide fisheries manager and anglers with better information on the effects of C&R on eel, and with ways to enhance post-release survival and fish welfare to promote the conservation of the European eel. Therefore, this study aimed to (i) describe hook shedding mechanisms including hook corrosion, (ii) quantify hook shedding rates, and (iii) investigate post-release fate (both sub-lethal effects and mortality) in deep-hooked eels.

2. Material and methods

2.1. Study site and fish capture

The experiment was carried out at the Matre Research Station of the Institute of Marine Research (IMR) in Matre, Norway between May and October 2014. Thirty-two eels were caught using rod and line in lake Hillandsvatnet (60°34.495′N, 5°12.565′E), province Hordaland, southwest Norway from the shoreline at night between the 20th and 22nd of May 2014. Surface water temperatures ranged between 9.8 and 15.0 °C during this period. Fishing methods (angling with a fishing float [bobber] or a sinker at the bottom) and tackle (hook, line and bait) representing common eel angling practice were used to simulate representative angling conditions (Tesch, 2003). Either large (size #2, 10.0 mm gap width) or small (size #6, 6.8 mm gap width) common offset baitholder style single hooks (Gamakatsu®, Japan, model LS-3113R) were used which consisted of red-lacquer coated carbon steel and had a barb at the hook point and a baitholder barb on the shank (Fig. 1). This hook model was selected as it represents a hook shape commonly used by European eel anglers (MSW, pers. obs.).

Both hook sizes were used in original configuration (with hook and baitholder barbs present; henceforth called: "barbed") and with the barbs pinched down with handheld pliers (henceforth called: "barbless") resulting in four versions of the same hook model. This treatment was chosen to test if the presence or absence of barbs affect hook shedding rates in deep-hooked eels as the use of barbless hooks would be an easy to apply management measure, but only few studies with contrary findings exist (DuBois and Pleski, 2007; Robert et al., 2012; Stein et al., 2012).

All hooks were attached to a 7.0 kg monofilament leader line, and baited with 1–2 live earthworms (*Eisenia hortensis*). During a bite, each eel was given sufficient time to swallow the bait (1–5 min) to increase the likelihood of deep hooking. After setting the hook, eels were landed immediately and, when deep-hooked (defined as fish hooked beyond the mouth cavity), the line was cut as close as possible to the mouth. Afterwards, each eel was placed individually in a numbered, lockable 10-L bucket filled with fresh lake water. Condition of the fish, occurrence of immediate hook shedding as well as oxygen and water temperature in the buckets were regularly monitored. Holding water was periodically exchanged to ensure an adequate water quality (dissolved oxygen ≥ 8.0 mg/L, temperature difference to the lakes' surface water temperature ≤ 2.0 °C). Total holding times in the buckets ranged from 3.5 to 9.5 h. Time of capture, hook size and type (barbed or barbless) were recorded for each eel.

2.2. Data collection and holding

At the end of each fishing session, the eels were transported to the Matre Research Station (~50 min transportation time). Upon arrival, all eels were anaesthetized using aqueous solution of 2-Phenoxyethanol (1.5 mL/L), length measured (total length [TL] to the nearest cm), weighed, and individually tagged with passive integrated transponder tags (PIT tag; ID 162–8-PM, EURO I.D., Weilerswist, Germany; dimensions: 2.12 mm Ø × 9 mm length) inserted into the posterior abdominal

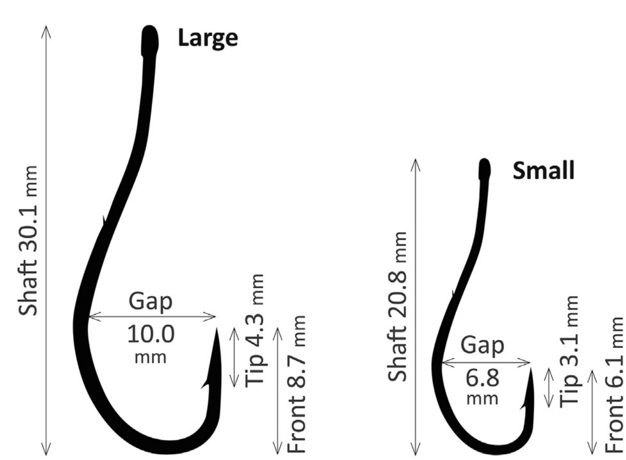

Fig. 1. Schematic drawings and dimensions of the two hooks (large: size #2 and small: size #6) used in the study. Both hook sizes were used in a barbed (as shown in the figure) and a barbless version (barbs pinched down) resulting in a total of four different treatments.

cavity through a surgical incision (1 mm length). The water temperature of the anaesthesia bath was adjusted to the water temperature of the holding buckets to minimise thermal stress. No further adjustment of water quality was conducted as eels are eurytherm and tolerant towards hypoxia and pH disturbances (reviewed in Wilson, 2013). Subsequently, each eel was radiographed (Porta 100 HF, Eickemeyer Medizintechnik für Tierärzte KG, Tuttlingen, Germany) at a distance of 70 cm (40 kV and 10 mAs) onto a 18 × 24 cm rigid cassette, containing an image plate (Dürr Medical, Bietigheim-Bissingen, Germany). The image plate was scanned (CR 35 VET, Dürr Medical Bietigheim-Bissingen, Germany) and the digital image was filtered (bone II) to obtain sharper images before they were saved as high resolution TIFF files (Vet-Exam Plus Software, version 4.14.0.). The TIFF files were further processed (i.e. contrast adjustment, cutting and positioning) using Adobe InDesign and Photoshop CS5. Radiography under anaesthesia was repeated to detect hook shedding and changes of hook position for all surviving eels 1, 3, 10, 24, 54, 115 and 163 days after capture. To minimise handling and disturbance in the holding tank, radiography was conducted for all eels on the same day from radiography day 10 onwards (i.e. the radiography data refer to the 21st of May [median catch date] from day 10). These radiography intervals were chosen to increase the likelihood of observing the hook shedding mechanism as several studies showed that hook shedding in fish most likely occurs within a relatively short time period after release (Broadhurst et al., 2007; Bugley and Shepherd, 1991; Diggles and Ernst, 1997; Fobert et al., 2009; Stein et al., 2012).

Between radiography sessions, eels were held in a tank (L × W × H: 1.1 m × 1.1 m × 0.65 m) with a lowered water level (0.3 m) to prevent escapement. The tank was supplied with flow-through freshwater (90 L/h) from a nearby river to hold dissolved oxygen at ambient levels (≥85% saturation, equal to ≥8.1 mg/L dissolved oxygen) and equipped with hiding places. Holding water temperature ranged from 9.1 to 17.7 °C (mean = 13.0 °C, SD = ±1.8 °C) and followed natural seasonal fluctuations. Eels were held under a natural light regime but light intensity was decreased by a dark cover to reduce holding stress. As eels have been shown to develop agonistic behaviour in captivity (Knights, 1987; Peters et al., 1980) which can be minimised by high holding densities (Peters et al., 1980; Seymour, 1984) all eels were kept in one tank to reduce social stress. Condition of the eels, occurrence of mortality and hook shedding as well as holding water parameters were checked daily. Eels were regularly fed with midge larvae (Chironomidae) and earthworms, and the tank was cleaned periodically. The feeding frequency and food quantity were adjusted to the eels' food intake based on the amount of food left in the tank after 24 h.

Eels that died or shed the hook were length measured, weighed and identified by their PIT tag. A comprehensive necropsy was performed to determine potential causes of death, state of hooking injury, physical condition, occurrence of wound infections and location of the hook (if applicable). All eels that survived until the end of the experiment were euthanized (aqueous solution with 5 mL/L 2-Phenoxyethanol), weighed and a similar examination and necropsy was performed. After necropsy, all ingested hooks were removed and, along with previously shed hooks, visually inspected and radiographed to evaluate hook corrosion.

2.3. Data analysis

The unpaired, two-tailed Student's t-test was used to compare the mean TLs of the eels caught on large and small hooks (no separation in barbed and barbless hooks). The distance between the end of the hook eye and the snout of the eel was measured on each X-ray picture to evaluate hook movements in the eel. A hook was classified as “mobile” when the sum of the absolute distances moved was ≥10 mm based on all X-ray pictures of an individual eel, or when the hook was shed. The 10 mm threshold was chosen to minimise the risk that a hook was classified as “mobile” due to biased distance measurements caused by differences in the perspectives between consecutive X-ray pictures. Subsequently, a two-tailed Fisher's exact test was used to investigate the independence of the hook version on hook movement. In addition, the difference in distance between the hook position from the first and from the last X-ray picture was calculated for all eels that retained hooks classified as “mobile” to evaluate overall changes in the hook position.

Hook corrosion was analysed for all hooks and hook residues that remained in the eels (n = 12) during the whole study period. A hook corrosion score (ordinal scale) with four categories (0 = no corrosion; 1 = slight corrosion, 2 = medium corrosion; 3 = heavy corrosion) was developed. After radiology, each hook was visually classified into one of the four categories. Due to the small sample size, the data was divided into barbed (n = 8) and barbless (n = 4) hooks and not further by hook size. A non-parametric, unpaired, two-tailed Mann–Whitney-U-test was used to test for significant differences in the corrosion rate between barbed and barbless hooks.

A priori data exploration revealed that quasi-complete separation occurred in the hook shedding data. This situation often occurs in small data sets when a dichotomous or categorical outcome (here: hook shed or not shed) can be nearly perfectly predicted by a linear combination of predictors (in this case caused by the variable “hook type”) leading to the non-existence of finite maximum likelihood regression parameter estimates in logistic regression models (Albert and Anderson, 1984; Heinze and Schemper, 2002). To cope with this problem, the variable “hook type” was aggregated from four categories (large, barbed; large, barbless; small, barbed and small, barbless) to two categories (large and small hooks) resulting in a new binary variable called “hook size”. This approach seemed reasonable as differences of hook shedding rates between barbed and barbless hooks were small (small hooks) or non-existent (large hooks; Table 1). However, a two-tailed Fisher's exact test was used to investigate the independence of the presence or absence of barbs (data from all barbless and barbed hooks pooled independently from hook size) on hook shedding. Afterwards, Firth's bias reduced logistic regression approach implemented in the “logistf” package in the software R was applied which has been proven to be a good solution when dealing with separation (Firth, 1993; Heinze and Schemper, 2002; Heinze, 2006). A Firth's bias reduced logistic regression model with a logit link function was fitted to the data using penalized maximum likelihood estimation to describe the relationship between total hook shedding rates within 163 d (binary response variable) and hook size (categorical variable), TL (continuous variable) and the corresponding interaction term. Model selection was based on backward elimination using the second order (corrected) Akaike information criterion (AIC_c) for small sample sizes (Anderson and Burnham, 2002). The comparison between the full (saturated) model and the optimal (reduced) model as well as significance testing of the estimated model coefficients were accomplished using penalized likelihood ratio tests.

A two-tailed Fisher's exact test was used to investigate the independence of the four hook treatments on post-release mortality after 23 weeks.

Table 1
Summary of eels caught with four different hook versions showing number of fish (n), mean total length (TL in cm) ± standard deviation (SD), proportion (%) of hooks classified as “mobile” in the eels (total distance moved ≥10 mm), proportion (%) of eels that shed the hook during the study, and post-release mortality (%) after 23 weeks.

Hook size and type	n	Mean TL (cm) ± SD	Hooks “mobile” (%)	Hooks shed (%)	Mortality (%)
Large, barbed	10	40.9 ± 5.5	60.0	0.0	50.0
Large, barbless	5	42.6 ± 5.4	60.0	0.0	40.0
Small, barbed	11	39.2 ± 4.5	81.8	45.5	27.3
Small, barbless	6	39.7 ± 6.4	66.7	33.3	50.0

All statistical analyses and calculations were conducted using the software R version 3.2.2 (R Core Team, 2015), and for all statistical hypotheses testing, significance was evaluated at $\alpha \leq 0.05$.

3. Results

In total, 32 deep-hooked eels were captured (n = 5 on the 20th, n = 15 on the 21st, and n = 12 on the 22nd of May 2014) and included in the study (Table 1). Total length of the eels ranged from 31–50 cm with a slightly, but insignificant, higher mean total length (Student's t-test: $t = 1.15$; $p > 0.05$) for eels caught on large hooks (mean = 41.5 cm, SD = ±5.3 cm) compared to small hooks (mean = 39.4 cm, SD = ±5.0 cm).

3.1. Hook shedding mechanism

The visual analysis of the X-ray pictures taken ≤9.5 h after capture revealed that the hooks were located in the pharynx in 9.7% (3 out of 31) of the eels, in the oesophagus in 16.1% (5 out of 31), in the anterior (cardiac) stomach in 29.0% (9 out of 31), and in the posterior (pyloric) stomach and cecum in 45.1% (14 out of 31) of the eels (one eel was excluded from the analysis as it shed the hook before the first X-ray picture was taken). The hook shedding mechanism was not directly observed, however, one eel shed the hook within 2 h of capture suggesting that the hook was most likely regurgitated. Furthermore, no hooks were detected in the lower intestine or near the anus during any radiography session (Fig. 2) or during dissection. Most hook shedding occurred during the first 24 days of holding (71.4% of all shed hooks, 5 out of 7) but two eels shed the hook later between day 24 and 115 (Fig. 3).

Hook movement rates ranged from 60.0% to 81.8% (overall mean = 68.8%, 22 out of 32) depending on the hook type (Table 1; Fig. 2, eels a and c). Nevertheless, the difference in hook movement rates between the four hook treatments was not significant (Fisher's exact test; $p > 0.05$). The difference between the hook position on the first X-ray picture and on the last X-ray picture was negative in 86.7% (13 out of 15) of the eels that retained hooks classified as "mobile", resulting in a backward movement of the hook in the direction of the posterior stomach and the cecum (e.g. Fig. 2, eel c).

Hook corrosion rates were relatively low as only one hook that broke into two pieces during the study period was categorized as heavily corroded, and was partly shed (Fig. 2, eel b). In general, hook corrosion occurred predominantly in the regions of the points as well as of the barbs (barbed hooks) and where the barbs had been pinched down (barbless hooks [Fig. 4]). There was no significant difference between the median hook corrosion rate of barbless (median corrosion score = 1.5, both hook sizes pooled) and barbed hooks (median corrosion score = 1.0, both hook sizes pooled) after 23 weeks (Mann–Whitney-U-test; $W = 21$; $p > 0.05$).

3.2. Hook shedding rates

The hook shedding rate was 45.5% (5 out of 11 eels) for eels caught on small, barbed hooks and 33.3% (2 out of 6 eels) for eels caught on small, barbless hooks, resulting in an overall hook shedding rate of 41.2% (7 out of 17) for small hooks. In contrast, none of the eels (0 out of 15) caught on either the large, barbed or barbless hooks shed the hook during the study period (Table 1, Fig. 3). Firth's bias reduced logistic regression revealed that a model including hook size and total length without the corresponding interaction term provided the best fit to the hook shedding data ($AIC_{c\text{ full model}} = -4.8$; $AIC_{c\text{ reduced model}} = -8.2$), and that this model explained the data significantly better than a null model including only the intercept (penalized likelihood-ratio test: $\chi^2 = 13.1$; $p < 0.01$). The model confirmed that the hook shedding

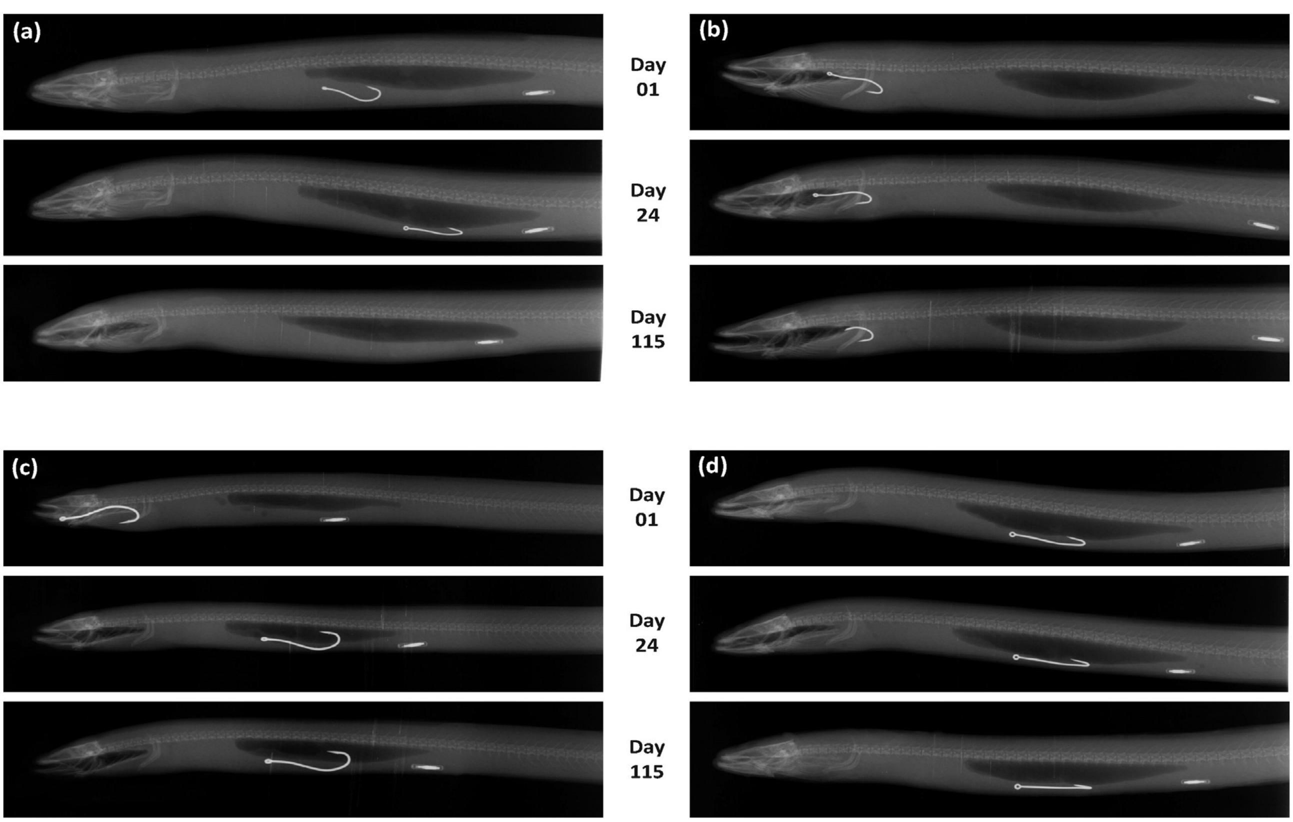

Fig. 2. Lateral radiographs of four deep-hooked eels 1, 24 and 115 d after capture. The white rectangular object is the inserted PIT tag. Eel (a) is an example for an eel that shed the small hook. Eel (b) shows a small hook that broke due to corrosion. Eels (c) and (d) did not shed the hooks (both large hooks) during the study period, but in contrast to eel (d) the hook in eel (c) was "mobile".

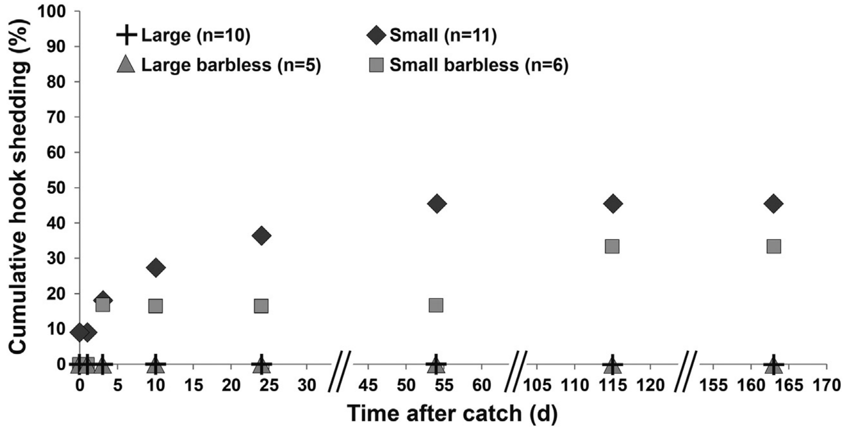

Fig. 3. Cumulative hook shedding rates (%) of 32 deep-hooked eels for the four hook versions in relation to time after catch (days). Please note that the time after catch is relative to the median catch date (21st of May) from day 10. The x-axis is interrupted three times for better illustration, and the data points of both large hook versions are superimposed on the x-axis.

rate was significantly higher for eels caught on small hooks compared to large hooks (penalized likelihood-ratio test: $\chi^2 = 11.4$; $p < 0.001$), and increased significantly with increasing total fish length (penalized likelihood-ratio test: $\chi^2 = 5.2$; $p < 0.05$). Hook shedding rates were independent of the presence or absence of barbs (no separation between hook sizes; Fisher's exact test; $p > 0.05$).

3.3. Post-release fate

Only one out of the 32 deep hooked eels (3.1%) died within the first day of capture, but mortality after 23 weeks ranged between 27.3% and 50.0% (Table 1). Most deaths of eels caught on large hooks occurred within 10 days of capture (85.7%, 6 out of 7), whereas all eels caught on small hooks that died (6 out of 17) did so later during the holding period (between days 11 and 113 after capture). The two-tailed Fisher's exact test showed that mortality rates of deep-hooked eels after 23 weeks were independent of the hook versions ($p > 0.05$).

The necropsy of all dead eels showed that ~77% (10 out of 13) of the hooks penetrated the stomach or oesophagus wall leading to holes and ruptures of various size in the gastric wall (Fig. 5, eels b and c). In some eels, the hooks penetrated trough the gastric wall into muscular tissue (e.g. abdominal wall [Fig. 5, eel b]) and in one eel the hook punctured the kidney. The gastric perforation caused internal haemorrhaging and led to the intrusion of digestive fluids as well as chyme into the coelomic cavity, which led to the accumulation of bloody ascites in the body cavity inducing the degradation and inflammation of vital organs and tissues (e.g. liver and digestive system).

The dissection of all survivors with retained hooks showed that 50% (6 out of 12) of the hooks had penetrated the stomach or oesophagus wall. However, penetration holes were considerably smaller compared to eels that died. In one of these eels, the hook tip was encapsulated with fibrous material. In another eel, the cut fishing line had perforated the oesophagus wall twice and was tangled in the guts. In addition, one eel had developed an inflamed and pervasive hole in the abdominal wall, where the hook had penetrated through the stomach into the abdominal wall. In the surrounding area of this hole, parts of the liver and stomach were adhered to the peritoneum with connective tissue. Four eels out of the 12 eels (33.3%) that had survived with retained hooks showed signs of slight to moderate gastritis or esophagitis (Fig. 5, eel a).

All eels that had survived and shed the hook (n = 7), did not have any significant macroscopic hooking lesions except for one eel which had a very small hole in the stomach wall.

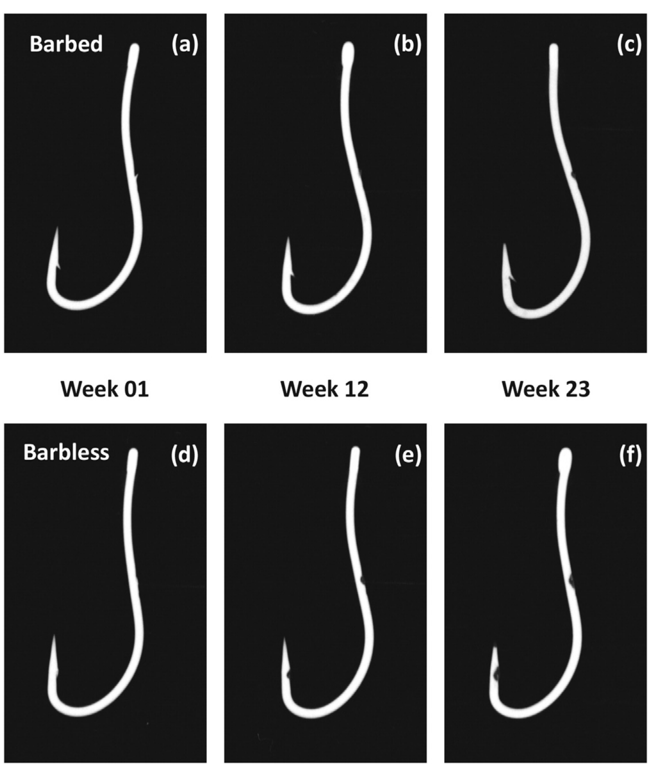

Fig. 4. Two examples of lateral radiographs of barbed and barbless versions of the small hook model used in the study 1, 12 and 23 weeks after ingestion by eels. Dark notches indicate areas were corrosion has started. Pictures (a) and (d) show no corrosion (corrosion scores = 0), pictures (b), (c) and (e) show slight corrosion (corrosion scores = 1), and picture (f) shows medium corrosion (corrosion score = 2).

4. Discussion

4.1. Hook shedding mechanism

The specific hook shedding mechanism was not observed and remained unclear even though the eels were radiographed periodically. Other studies also failed to investigate the actual hook shedding mechanism indicating that it is most likely a rapid process which is difficult to observe (e.g. Aalbers et al., 2004; Broadhurst et al., 2007; Hulbert and Engstrom-Heg, 1980; Schill, 1996; Schisler and Bergersen, 1996). However, given the small dimension of the eel's anus, the fact that one eel shed the hook within a few hours of capture and that no hooks were found in the intestine neither during radiology nor during dissection, it is most likely that the hooks were shed orally.

Most hook shedding (~71%) occurred within 24 days of capture but some delayed shedding was also observed (Fig. 3). This result is consistent with other studies showing high hook shedding rates in a relatively short time period (<4 weeks) after release (Broadhurst et al., 2007;

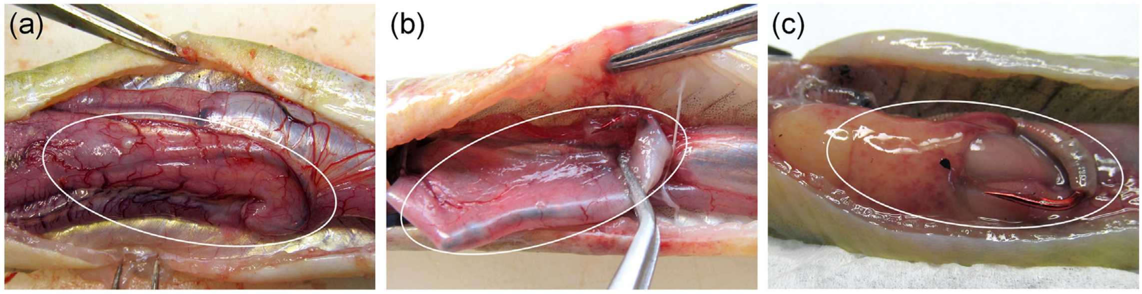

Fig. 5. Examples of hooking locations in the stomachs of three deep-hooked eels that retained the hooks. The hook in eel (a) did not penetrate the stomach but the stomach shows signs of gastritis. The hook in eel (b) penetrated slightly through the stomach wall into the abdominal wall. Eel (c) shows a large penetration hole in the stomach and the hook (with bait residues) is pushed into the body cavity. The locations of the hooks are encircled with white rings.

Bugley and Shepherd, 1991; Diggles and Ernst, 1997; Fobert et al., 2009; Stein et al., 2012). The low rates of delayed hook shedding may be explained by the observed overall backward movement of the retained hooks into the posterior stomach and the cecum. In view of the eel's stomach morphology, with the pylorus located in the anterior stomach, the shedding of hooks which passed the anterior part of the stomach could have been aggravated (Tesch, 2003), although some hooks were also shed from this region (e.g. Fig. 2, eel a). Broadhurst et al. (2007) also found that most hooks ingested by yellowfin breams (*Acanthopagrus australis*) were re-orientated in positions less suitable to allow hook shedding through the digestive tract after four weeks of holding. Nonetheless, in contrast to the present study, no significant longitudinal displacement of the hooks was observed. In conclusion, similar to hook shedding rates, hook shedding speed appears to be species-specific as well probably dependent on hook type and material and environmental conditions.

Several studies have shown that hook shedding is significantly promoted by hook corrosion (e.g. Aalbers et al., 2004; Hall et al., 2009; McGrath et al., 2011a, 2014). However, hook corrosion rates are highly influenced by the hook material (i.e. wire material, diameter, and coating), the environmental conditions (i.e. salinity), and the position of the hook in the digestive system (Aalbers et al., 2004; Hall et al., 2009; McGrath et al., 2011a, 2011b, 2014). Even though hook corrosion was not quantitatively measured in this study, hook corrosion rates appeared to be relatively low (Fig. 4) compared to studies conducted in marine and brackish waters (Broadhurst et al., 2007; McGrath et al., 2011a, 2011b), and could not be considered as important mechanism of hook shedding in the present study. This can probably be attributed to the freshwater holding conditions and the hook material (i.e. the anticorrosive red lacquer coating; (Aalbers et al., 2004; McGrath et al., 2011b). Nevertheless, a longer time perspective (>23 weeks), or different hook designs, materials and coatings (McGrath et al., 2011b) may have led to some additional hook shedding. Therefore, the use of other technical measures or modifications regarding the fishing hook, e.g. use of less corrosion-resistant hook materials, narrower wire diameters or the incorporation of predetermined breaking points, could help to increase hook shedding rates due to increased corrosion when dealing with deep-hooked eels (McGrath et al., 2011b). Though, the utility and angler acceptance of such measures which may lead to new management regulations needs to be evaluated before implementation (Dorow et al., 2009).

4.2. Hook shedding rates

The overall hook shedding rate was 22% (7 out of 32 eels) after 23 weeks of holding and falls within the lower range of 0–77% (mean: 42%) for other line-cut, deep-hooked fish (11 different marine and freshwater species) observed ≥4 weeks (reviewed in Hall et al., 2009; complemented by McGrath et al., 2011a). One possible explanation for the relative low hook shedding rates observed in this study could be the eel's natural diet and functional morphology of the digestive system. Many of the fish with high hook shedding rates feed on hard-bodied prey (e.g. on hard-shelled molluscs) and have a pharyngeal jaw apparatus capable to process hard materials (Hall et al., 2009; Helfman et al., 2009). Eels mainly feed on small molluscs, crustaceans and fish, and their buccal morphology does not allow processing very hard food components (Tesch, 2003). Therefore, eels are incapable to crush the hook before swallowing it.

The hook shedding rate was significantly higher for eels caught on small hooks compared to large hooks. This result differs from two other studies that did not find any significant effect of hook size on hook retention in bluegills (*Lepomis macrchirus* [Robert et al., 2012]) and bonefish (*Albula vulpes* [Stein et al., 2012]). In addition, the likelihood of hook shedding increased significantly with increasing total fish length. McGrath et al. (2011a) also found a positive relationship between total fish length and hook shedding rate for yellowfin bream (*Acanthopagrus australis*). One possible explanation for the observed effects of both factors is the relative high hook-to-gut size ratio compared to other species caused by the serpentinous physique of the eel. McGrath et al. (2009, 2011a) argued that fish need to rotate the hook in the digestive system to facilitate hook shedding. This rotation process is easier for smaller hooks as well as for hooks with short shaft and front lengths and for larger fish (McGrath et al., 2009, 2011a). Considering the eel's morphology, the range of total length (31–50 cm) of the eels used in this study and the dimensions of the large hooks (Fig. 1), it seems likely that the large hooks were too large to be rotated and shed. Bearing this in mind, one could argue that the use of smaller hooks is preferable to increase hook shedding rates of deep-hooked, line-cut eels. However, the use of small hooks/baits will most likely increase the likelihood of catching and deep hooking undersized eels as smaller hooks/baits are swallowed more easily (e.g. Alós et al., 2008b; Grixti et al., 2007). Thus, very large hooks (i.e. larger than the large hook model used in this study) may be a better choice as they could minimise deep hooking and the catch of undersized eels in the first place (Alós et al., 2008b; Grixti et al., 2007; Piovano et al., 2010). The effect of the presence or absence of barbs on hook shedding in deep-hooked fish differs between studies, as two studies by DuBois and Pleski (2007) and Robert et al. (2012) found no effect which is in line with the present study, while a study by Stein et al. (2012) showed an accelerated hook shedding process for fish caught on barbless hooks.

Even though temperature and light regime as well as water parameters followed natural fluctuations, hook shedding rates might have been biased due to the holding conditions. For example, holding as well as social stress and associated disturbed behaviour, significant handling due to frequent anaesthesia and radiology may have affected hook shedding. In addition, the absence of specific food (e.g. harder food items such as crustaceans), reduced feeding, and the lack of specific bottom structures and substrate found in the eel's natural environment may have influenced hook shedding (Tsuboi et al., 2006). The present hook shedding rates should therefore be validated under more natural conditions (e.g. via mark-recapture studies). Furthermore, only one hook model (offset baitholder style single hook) was used, as this hook represents a hook shape which is popular among eel anglers (MSW, pers. obs.). As hook shape can influence hook shedding rates significantly (Robert et al., 2012), the present hook shedding rates may not be directly applicable to other hook models used in the recreational eel fishery or fisheries where eels are a common bycatch. However, due to local regulations (i.e. the protection of eels in Norway) the sample size was kept to a minimum and did not allow for the testing of additional factors in the present study. In this context, further studies are needed to assess the effects of different hook styles/shapes (e.g. octopus, single egg or Aberdeen style) on hook shedding in eel.

4.3. Post-release fate

Post-release mortality rates after 23 weeks of holding ranged between 27% and 50% depending on the hook version (Table 1), and fall within the range of 15–67% for other line-cut deep-hooked fish monitored ≥4 weeks (reviewed in Hall et al., 2009; complemented by DeBoom et al., 2010; McGrath et al., 2011a, 2014). Many studies show that the majority of post-release mortality occurs within a few days after release for a variety of species (reviewed in Muoneke and Childress, 1994). In some cases, this also applies to deep-hooked fish with retained hooks (e.g. Aalbers et al., 2004; Broadhurst et al., 2007; McGrath et al., 2014; Schill, 1996). However, our results demonstrate that substantial delayed mortality may occur in deep-hooked, line-cut eels, e.g. caused by long-term lethal effects of internal hooking injuries or bacterial infections (Fig. 5, eel b). Other studies also found significant delayed post-release mortality in line-cut fish (e.g. DuBois and Pleski, 2007; Hall et al., 2009; Mason and Hunt, 1967) suggesting that monitoring periods need to be extended when investigating post-release survival of fish with retained hooks compared to studies dealing with shallow-hooked fish only or studies involving hook removal for deep-hooked fish.

In the present study, hook version (i.e. hook size and presence or absence of barbs) did not significantly affect mortality rates of deep-hooked eels. Robert et al. (2012) found a positive correlation between hook size and post-release mortality of deep-hooked bluegills (*Lepomis macrchirus*) but no difference between barbed and barbless hooks. Nevertheless, the monitoring time was short (10 d) and the hooks were manually embedded (Robert et al., 2012) which aggravates comparison with the present study. DuBois and Pleski (2007) neither found any difference in mortality rates between barbed and barbless hooks for deep-hooked brook trout (*Salvelinus fontinalis*). Therefore, the potential positive effect of the use of barbless hooks on post-release survival of deep-hooked fish compared to barbed hooks (reviewed in Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Cooke and Wilde, 2007; Hühn and Arlinghaus, 2011; Muoneke and Childress, 1994) may only play a role when anglers remove or attempt to remove a hook due to shortened handling and air exposure times and less severe hooking injuries, but not when the line is cut (Aalbers et al., 2004; Robert et al., 2012).

Even though speculative, considering the relatively high proportion of surviving eels with retained hooks that showed internal injuries and inflammations after the 23 weeks holding period, it is most likely that some additional delayed mortality would have occurred later on. In addition, the ingested hooks and their decomposition products may cause sub-lethal long-term consequences negatively influencing the individual fitness of the eels such as impaired feeding ability and growth reduction, disturbance of behaviour and gonadal development, immunosuppression leading to a higher vulnerability to diseases and parasites, and pathological consequences (e.g. the observed gastritis and oesophagitis in some eels [Fig. 5, eel a]; Borucinska et al., 2002; Broadhurst et al., 2007; DuBois and Pleski, 2007; Hall et al., 2009; Margenau, 2007; McGrath et al., 2011a, 2014; Robert et al., 2012).

Particular caution should be exercised when assessing the observed mortality rates as no control group was included in this study. A control group was not included to minimise the number of eels used in this study considering the protection of eels in Norway. As the aim was to compare mortality rates between treatments but not to estimate absolute mortality rates given the significant handling and unnatural holding conditions, omission of a control group may be justified (Pollock and Pine, 2007). Therefore, mortality rates are likely to be biased (e.g. due to intensive handling, radiographing, tagging and holding in captivity) as known from containment-based post-release mortality studies and should only be compared between hook versions (Pollock and Pine, 2007). Future studies should, therefore, investigate post-release mortality of eels and sub-lethal effects of the C&R process in their natural environment by using mark-recapture or biotelemetry studies (Donaldson et al., 2008; Pollock and Pine, 2007). These studies need to be carefully designed to best represent common eel angling practice (i.e. representing common eel angling methods and tackle) and should cover various ecosystems and parameters allowing the provision of reliable post-release mortality estimates which are urgently needed for stock assessment (ICES, 2016). In this context, it would also be important to assess if line cutting of deep-hooked eels also results in reduced post-release mortality compared to hook removal as it has been shown for several other species (e.g. Butcher et al., 2007; Fobert et al., 2009; Grixti et al., 2010; Mason and Hunt, 1967; Tsuboi et al., 2006; Warner, 1979). Sub-lethal consequences of C&R and hook retention in eel should be investigated by using physiological indicators e.g. cortisol and glucose levels from blood samples (Broadhurst et al., 2007; Cooke et al., 2013; Fobert et al., 2009; Wilson, 2013). Growth reduction due to impaired feeding caused by hook retention should be investigated under more natural conditions. In the present study, a mean weight loss of 16.7% was observed for eels that survived with retained hooks, but considering the lack of a control group and the substantial handling in this study, it remains unclear if the weight loss was due to the retained hooks or the experimental conditions.

In addition, future research should focus on what anglers can do *a priori* to minimise the catch of undersized eels or the occurrence of deep hooking as this would be the most effective strategy to reduce post-release mortality. Circle hooks may be an appropriate tool to minimise deep hooking and associated mortality but catch efficiency is species- and fishery-specific and needs to be tested to achieve angler acceptance (Cooke and Suski, 2004; Cooke et al., 2012). Furthermore, the effects of hook and bait type commonly used by eel anglers on fish size selectivity should be investigated to provide information on how terminal gear modifications and bait choice can limit deep hooking and the catch of undersized eels.

4.4. Conclusion and implications

The present findings provide first information on hook shedding and post-release fate of deep-hooked eels for anglers and fisheries managers, and may help to develop best practice guidelines to reduce post-release mortality rates in the recreational eel fishery contributing to the conservation of the European eel. Furthermore, the study provides first insights on the effects of C&R for other closely related species such as the endangered American or Japanese eel (*Anguilla rostrata* and *Anguilla japonica*) and new information on hook shedding in fish in general. Considering the precarious stock status of the European eel, there is an urgent need to minimise post-release mortality in the recreational eel fishery to promote stock recovery.

In general, the present findings suggest that deep-hooked eels have only limited capabilities to shed hooks after the line has been cut. The hook shedding rates were variable and mainly influenced by the size of the hook and total fish length, suggesting that a substantial amount of recreationally released eels may not be able to shed the hook, leading to sub-lethal and lethal effects. The best way to prevent such negative effects is to minimise the catch of undersized or unwanted fish, and to minimise hooking injures (i.e. deep hooking and bleeding) by using selective and appropriate fishing methods, terminal gear types and baits from the outset (e.g. Alós et al., 2008a, 2008b; Cerdà et al., 2010;

Grixti et al., 2007). Eel anglers may decrease the catch of undersized eels by using only very large hooks which are more difficult to ingest (Alós et al., 2008b; Grixti et al., 2007; Piovano et al., 2010). However, considering the observed adverse effect of larger hooks on hook shedding and taking into account that also small eels are capable to ingest relatively large hooks the positive effect of using larger hooks only becomes visible for hooks with a gap width ≥ 11 mm (MSW, unpublished data). As the proportion of fish prey in the eel's diet increases significantly with increasing fish size, the use of larger bait fish instead of invertebrates (e.g. earthworms) as bait appears to be a potential option to reduce the catch of undersized eels (reviewed in Tesch, 2003). Furthermore, eel anglers should be encouraged to fish with tight lines to facilitate bite detection and to set the hook as fast as possible after the fish has taken the bait to minimise deep hooking (Grixti et al., 2007; Schill, 1996). In addition, proper leader material should be used to mitigate line breaking and escapement of eels with retained hooks (Tesch, 2003). Finally, considering the relatively low hook shedding rates and high mortality, anglers are encouraged to adjust their angling practices to minimise bycatch of eel when eel harvest is prohibited.

5. Ethics statement

The experiment was carried out in accordance with the Norwegian regulation on animal experimentation (Forskrift om forsøk med dyr), and the experimental protocol was approved by the Norwegian animal research authority (Forsøksdyrutvalget; ID 6229). As eel is a protected species in Norway, a certificate of exemption to fish eel in Hillandsvatnet was provided by the Norwegian Environment Agency.

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