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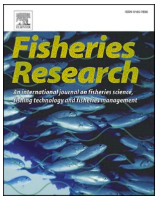

Post-release effects of catch and release angling for sea trout: Mortality, growth and wound healing

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ABSTRACT

Sea trout (anadromous brown trout, *Salmo trutta* L.) is a popular recreational angling target species in the Baltic Sea region and beyond. Across countries, a substantial part of angled sea trout is released after capture either due to management regulations or due to voluntary decisions by the anglers. However, information about post-release impacts of catch and release (C&R) on survival and growth in saline waters is largely missing. We used a flow-through seawater raceway (4–10 °C) to investigate impacts on survival and growth of angled and released sea trout (< 40 cm) up to 29 days post release. Bleeding was common among angled sea trout, but differed between angling treatments, i.e., lure fishing with treble hook (size 4), lure fishing with single hook (size 1/0) and fly fishing with single hook (size 12). However, no mortality and no significant differences in growth were found after a 26–29 days monitoring period among a control group and the three treatment groups, but a small subset (6%) of the angled fish caught on lure had unhealed/infected hooking wounds at the end of the experiment. The results infer that adverse effects of C&R on coastal sea trout due to high post-release mortality or reduced growth can be limited and may not pose a significant problem for sea trout stocks. Nevertheless, further studies are required to corroborate these results under more natural field conditions and at higher water temperatures. In addition, further studies on long-term sublethal impacts of C&R on sea trout are needed.

1. Introduction

Recreational fishing is a common outdoor activity around the world with implications for the environment, societies and economies (Hyder et al., 2018, 2018; Lewin et al., 2019; Arlinghaus et al., 2021). Although recreational fishers can use various fishing methods (e.g., gill netting, Veneranta et al., 2018), rod-and-reel fishing, commonly known as angling, is generally the most popular method (Arlinghaus et al., 2007). Releasing parts of the catch is becoming more and more common in freshwater and marine recreational fisheries (e.g., Arlinghaus and Mehner, 2003; Ferter et al., 2013) and is often referred to as catch and release (C&R). Its practice may be prompted by the angler's own free will (i.e., voluntary C&R) or by mandatory regulations such as minimum landing sizes, bag limits, seasonal closures or species protection (i.e., regulatory C&R) (Arlinghaus et al., 2007).

Both in freshwater (e.g., Hühn and Arlinghaus, 2011) and in the marine environment (e.g., Ferter et al., 2013), C&R is used as a management tool to reduce fishing mortality while maintaining angling opportunities. The fundamental premise of C&R is that it implies no or little effect on the released fish (Arlinghaus et al., 2007). For several species and fisheries, high survival and good welfare can be achieved by following best practice guidelines (Brownscombe et al., 2017; Ferter et al., 2020). However, C&R can also have lethal and sublethal effects, which can reduce the efficiency of C&R management measures. For example, if angling effort is high and C&R is a common practice, the cumulative post-release mortality and thus the total fishing mortality of a certain fish stock can be high even if post-release mortality is medium to low (Post et al., 2003; Walters and Martell, 2004; Bartholomew and Bohnsack, 2005; Coggins et al., 2007; Kerns et al., 2012). In extreme cases, this may render common fish conservation measures (e.g.,

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minimum or maximum landing sizes) ineffective, and may thus lead to overfishing of the stock, which can limit fishing opportunities in the long term (Nelson, 2002; Coggins et al., 2007; Kerns et al., 2012; Hessenauer et al., 2018). Furthermore, if certain individuals in the stock are more susceptible to C&R impacts, there may be changes in the size and age structure and genetic diversity of the stock and even changes on ecosystem level (Cooke and Cowx, 2006; Lewin et al., 2019; Hessenauer et al., 2018).

According to literature reviews (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011), the anatomical hooking location and related hooking injuries/bleedings are important factors affecting post-release mortality in rod-and-reel fishing, i.e., deep-hooked fish or fish hooked in the gills suffer from higher mortality than fish hooked in the outer parts of the mouth (e.g., Weltersbach and Strehlow, 2013; Lewin et al., 2018). In addition, post-release mortality is species- and fishery-specific and influenced by various abiotic and biotic factors, including water temperature, air exposure, capture depth, fish condition, and predation risk (Wood et al., 1983; Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011).

Sea trout (anadromous brown trout, *Salmo trutta* L.) is a popular target species for anglers in the Baltic Sea region (Ferter et al., 2013) and recreational catches of sea trout exceed the commercial catches in several countries (ICES, 2021a). Nevertheless, Baltic sea trout stocks are under pressure in several regions due to high fishing mortality, poor habitat quality in some rivers, high level of predation and low recruitment (Jepsen et al., 2019; ICES, 2021b). The Baltic recreational sea trout fishery is regulated by several measures such as minimum landing sizes (e.g., DK, 40–45 cm depending on region, DE, 40–45 cm depending on region, SE, 50 cm), sometimes in combination with bag limits, seasonal and area closures, and even full protection of wild sea trout as in the Finnish Baltic waters where all wild fish have to be released. In addition, anglers often release legal-sized sea trout voluntarily (ICES, 2021a; Skov et al., 2022; Blyth and Rönnbäck, 2022). Therefore, sea trout angling practice often implies a substantial amount of C&R and release rates of 70–80% in Denmark, 52% in Germany and 86% in Sweden have been reported for the Baltic recreational sea trout fishery (Ferter et al., 2013; Weltersbach et al., 2021; Skov et al., 2022; Blicharska and Rönnbäck, 2018).

There are several studies on the effects of C&R on brown trout in freshwater (e.g., Anderson and Nehring, 1984; Taylor and White, 1992; Boyd et al., 2010; Carline et al., 2021), but so far very few explore post-release impacts on angled sea trout in marine environments. A recent study explored the condition of released sea trout at the coast of Gotland, Sweden (salinities 6–8 ppt) by a combination of reflex impairment tests, blood glucose and lactate sampling and assessments of hooking injury (Blyth and Bower, 2022). The study suggests that post-release mortality rates are generally low and that the stress response to the angling event is generally limited. The authors back this up by reports of recapture events of previously released and tagged sea trout, but at the same time acknowledge that their study lacks thorough information about delayed post-release mortality (Blyth and Bower, 2022). Considering the high contribution of recreational angling to the total catches, high release rates as well as the poor status of some Baltic sea trout stocks, there is an urgent need to study the post-release mortality of sea trout caught and released by recreational anglers in the Baltic Sea.

This study aims to explore post-release impacts on growth and survival of angled sea trout. Therefore, we conducted a mesocosm C&R angling experiment with standardized experimental spin (lure) and fly fishing to explore post-release mortality, growth and hooking wound healing of sea trout up to four weeks after the C&R event in a seawater raceway system. Specifically, the study aimed to (i) evaluate patterns of hooking locations and bleeding of sea trout, caught on lures with single or treble hooks or with flies equipped with single hooks, (ii) assess post-release mortality, growth and hooking wound healing of caught and released sea trout, and (iii) identify key factors influencing post-release mortality, growth and wound healing.

2. Methods

To explore post-release mortality and growth of sea trout under saline conditions, an angling experiment was conducted at DTU Aqua facilities in Hirtshals, Denmark, using a modified raceway with a total water volume of approx. 310 m^3 (Fig. 1). The raceway had an inlet that received water pumped directly from the North Sea. Salinity was adjusted by supplementing ground fed freshwater. The inside of the raceway was lined with heavy duty PVC to prevent leakage. Prior to the experiment, the raceway was covered with heavy nets (mesh size 75 mm, 0–50 cm above the water surface) mounted on poles to prevent avian predation. The pond was also equipped with floating plastic mats providing shelter for the fish (Fig. 1). To increase the water flow in the raceway system and to minimize water use, part of the water from the end of the raceway was pumped back to the inlet and reused. Prior to fish stocking, the salinity in the raceway was adjusted to around 21–25 ppt by balancing the flow of recirculated water, saltwater and ground fed freshwater. Subsequently, salinity could be increased or decreased by increasing/decreasing the share of saltwater. Furthermore, water flow could be adjusted by simultaneously increasing flow of freshwater and saltwater, as well as the amount of recirculated raceway water, to, e.g., maintain oxygen levels or water temperature.

The experimental fish were juvenile brown trout reared in a freshwater aquaculture facility. These were offspring of wild sea trout electrofished in River Kolding (close to the aquaculture facilities) in November/December 2019. On 4th March 2021, approximately 550 fish were transported in aerated tanks from the fish farm to the facilities at DTU Aqua. Here, the fish were transferred to holding tanks and subsequently individually measured (fork length in mm), weighed (g) and tagged with a Passive Integrated Transponder (PIT) tag to enable individual identification. PIT tagging followed well-established procedures, i.e., fish were anesthetized (Benzocain, 50 mg/L, Sigma Chemical Co., St Louis, USA) and a 23 mm PIT tag (HDX, Oregon RFID, Portland, USA) was inserted into the body cavity through a 2–3 mm ventral incision. A few of the sea trout were euthanized due to damages or otherwise poor condition. Hence, a total of 524 brown trout were tagged (fork length: average 309 mm, range: 235–374 mm; weight: average 375 g, range:

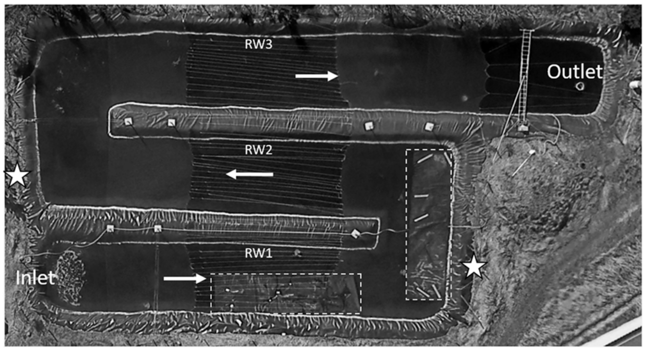

Fig. 1. Aerial photo of the experimental seawater raceway as it appeared during the C&R experiment. White arrows indicate water flow direction. The system consisted of three connected raceways (RW) with solid bottom and sloped sides covered by heavy duty PVC foil. RW 1 and 2 were each 26 × 4.5 m and RW 3 was 36 × 4.5 m, all with an average depth of 0.80 m. The water inlet (left part of RW 1) included three water streams, supplying prefiltered seawater (33 ppt), freshwater and recirculated RW water pumped from the outlet of RW 3 (right side), respectively. The raceway was covered by 75 mm net tied with thin rope (mid part in all three sections) and two rectangular floating plastic covers (2.5 *9 m) were placed in RW 1 and 2 to provide shelter (indicated by broken lines). The angling locations of the experimental anglers are indicated by the white stars. Drone footage by K.J.D.J. Gregersen.

162–649 g). One fish died during handling and tagging. After recovery from tagging (15–30 min), the fish were transferred to a 2.5 m^3 freshwater outdoor acclimation tank (Ø 3 m, 1.1 m depth), where salinity was slowly increased to 20 ppt over the following days until 10th March 2021. Water temperature in the acclimation tank was 5–6 °C. Three fish died during the acclimation period.

On 10th March 2021, the remaining 520 brown trout (hereafter called sea trout) were released into the raceway system where they were fed and monitored daily until the experiment was terminated on 3rd May 2021. Sea trout were classified as dead when they showed common death signs such as no operculum and body movements, flaring of the gills, and rigor mortis.

2.1. *Abiotic conditions and feeding*

Salinity (handheld refractometer, Akudim, Esbjerg, DK), water visibility (Secchi depth), pH, water temperature and dissolved oxygen (HQ40D portable multi meter; Hach, Brønshøj, DK) were measured once every day (always at daylight) and the raceway system was inspected daily for mortalities or unusual behavior of the fish.

Water flow through the pond varied between 1.4 and 8.0 m^3 per hour during the study period. To decrease retention time and dilute the water, the water flow was increased in mid-April to combat an emerging algae bloom that occurred during a period with increasing water temperatures. Oxygen saturation, as measured during daytime, varied between 96.3% and 210.2% (average = 130.0%, SD = 29.4%; Supplementary Fig. S1A). A marked increase in dissolved oxygen was observed in mid-April concurrent with the transient algae bloom mentioned above, which reflects increased levels of photosynthesis. Increased algae growth was also reflected by increased turbidity and reduced Secchi depth in the raceway, which decreased down to 30 cm at the peak. Before that, the Secchi depths were stable around 80 cm, similar to the depth of the raceway which was uniform in time (i.e., no fluctuations in water levels during the study period) and space (i.e., water depth was the same throughout the raceway).

During the study period, water temperature varied between 3.4 and 10.6 °C (average = 7.3 °C, SD = 1.89 °C) (Supplementary Fig. S1B), whereas pH varied between 7.2 and 9.5 (average = 8.7, SD = 0.44), with a peak at the time when the algae bloom peaked in mid-April (Supplementary Fig. S1C). Salinity varied between 21 and 30 ppt (average = 24.3 ppt, SD = 2.2 ppt) (Supplementary Fig. S1D). In combination with increased waterflow, salinity was also increased in mid-April to combat the algae bloom, which succeeded, i.e., oxygen levels and pH normalized in the last part of the study period, and Secchi depths stabilized between 50 and 60 cm.

After transfer to the raceway, fish were rapidly accustomed to feed on pellets in open water. Fish were fed with between 100 and 1400 g commercial-grade trout feed (4.5. mm EFICO Enviro 920 Advance, Biomar, Brande, DK) per day, depending on water temperature, observed feeding behavior and apparent appetite. The fish frequently hid under the plastic cover when approached, indicating an active behavior. Likewise, during feeding they were generally very active. However, in mid-April during the algae bloom, the appetite of the fish ceased, but after a few days when the algae bloom was reduced, appetite reached previous levels.

2.2. *Capture of control fish and experimental angling*

After an acclimation period of 27 days in the raceway, fish were exposed to experimental angling over two days (6th and 7th April 2021). On 6th April, before angling was initiated, a batch of fish ($n = 75$) was collected by seining in a random section of the raceway system. This group was to serve as controls, i.e., fish exposed to handling like the C&R fish, but without the hooking and fight. Fish trapped in the seine net were captured individually by a landing net (the same as used in the angling experiment afterwards) and transferred to a measuring station (10 m distance) next to the raceway. Here they were measured, weighed, had their PIT tag scanned and finally released back into the raceway system. The duration the fish spent out of the water (air exposure time) was recorded for each control fish.

After sampling and processing the control fish, we conducted the angling experiment to evaluate how C&R with different hook types (treble vs. single hook) and different fishing styles (spin (lure) vs. fly fishing) affected post-release mortality and growth. All angling was conducted by three anglers who were alternating fishing at two angling locations. We aimed to catch and release approximately 75 fish with lures mounted with single hooks (Owner®, Japan, model S-61, size 1/0), 75 fish with lures mounted with treble hooks (S.F.G., Denmark, size 4), and 75 fish with single-hook flies (Mustad, Norway, streamer, size 12), representing commonly used lure/hook combinations (Skov et al., 2022; Supplementary Fig. S2). All hooks were barbed. In the first part of the experiment, where spin fishing was used as fishing method, two anglers were fishing at each end of the raceway (Fig. 2) using almost identical fishing gear (Table 1). Medium casting rods and medium-sized spinning reels with monofilament fishing line (0.24 mm Ø, 5.5 kg breaking strain, Trilene line, Berkeley®, USA) were used for spin fishing. The only difference was the use of hook type, i.e., the two anglers always used the same lure but alternated between the use of single and treble hooks, to aim for equal number of fishes caught with each type. Fly fishing was done using a 8 feet, # 7 flyrod with floating line and a 6lbs monofilament leader of 9 feet length.

After catching sufficient numbers of fish with spin fishing gear, it was originally planned to catch 75 fish with fly fishing equipment. However, due to an increasing number of multiple recaptures which reduced, and eventually jeopardized, the size of the control group, we chose to only catch 25 fish on fly (Table 1). By that time, the size of the control group was reduced to 52 fish, as 23 of the 75 control fish had subsequently been angled and some of these more than once (Table 1).

When an angler hooked a fish, the angler immediately shouted out and the fight time was recorded. At the same time, the second angler stopped angling to ensure that only one fish was processed at a time. When the fish was reeled in, the fish was landed with a rubberized knotless landing net. As soon as the fish was out of the water, the angler shouted out, the fight time stopped and the air exposure time was recorded. Hereafter, the angler transported the fish in the landing net to a measuring station where close-up photos of the hook and hooking location were taken. The hooking locations were defined into six groups similar to Skov et al. (2022) (Fig. 2), and tissue injuries from hooking and any abnormalities were noted. Afterwards, the fish was dehooked (using pliers when needed), scanned for the PIT-ID, weighed (g) and returned to the raceway system. At that point the recording of air exposure was stopped. If the hook came off the fish in the landing net during transportation from the angling spot to the measuring station, hooking location was estimated by inspecting for marks, wounds and/or occurrence of bleeding. The level of bleeding was classified as none, slight or heavy bleeding.

2.3. *Study termination*

On 3–5th May 2021, the study was terminated and the raceway was drained. All fish were caught in a seine net and euthanized in a lethal dose of Benzocain (200 mg/L). Afterwards, they were identified, measured, weighed and visually inspected. Injuries were categorized between fully healed/no signs of hooking to infected, unhealed open hooking wounds. A photo was taken of each fish's mouth to document potential hooking injuries. Based on the notes taken and the photos, each fish was subsequently assigned a healing score from 1 to 4, with 1 representing no signs of injury and 4 representing severe disfiguration and/or scar tissue (Fig. 3).

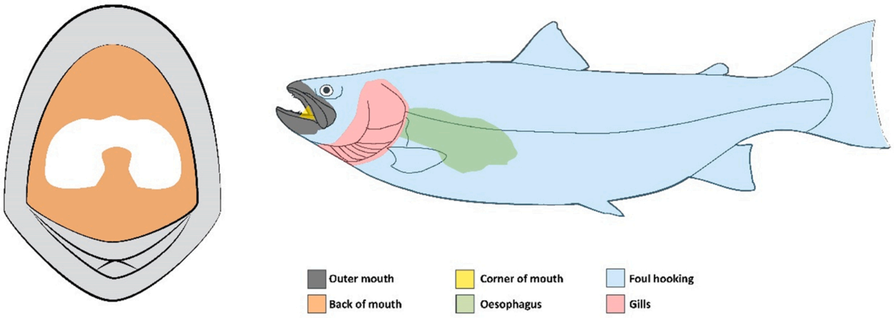

Fig. 2. Schematic figure of the various hooking locations assigned in the study. The left picture illustrates an open mouth viewed from the front.

Table 1
Timeline of the experimental angling in the raceway system. On 6th April 2021, the experimental anglers fished exclusively with "Boss" lures (Westin ®, Denmark, weight 16 g) equipped with either single or treble hooks. On 7th April 2021, the anglers used "Boss" lures and "Cyclops" lures (Mepps®, USA, 5 g) both equipped with either single or treble hooks and fly fishing gear (see also Fig. S2). Numbers in parenthesis indicate the number of fish within the group that had already been handled (control fish) or caught before (multiple captures).

Date	Time slot	End gear	Hook type	#fish
06–04–2021	14.00–17.00	Westin Boss 16 g	Treble	22 (10)
06–04–2021	14.00–17.00	Westin Boss 16 g	Single	20 (5)
07–04–2021	08.00–10.00	Westin Boss 16 g	Treble	13 (2)
07–04–2021	08.00–10.00	Westin Boss 16 g	Single	11 (3)
07–04–2021	10.00–14.00	Mepps Cyclops 5 g	Treble	39 (11)
07–04–2021	10.00–14.00	Mepps Cyclops 5 g	Single	45 (10)
07–04–2021	14.30–16.00	Fly	Single	25 (7)

2.4. *Animal welfare and permits*

This study was carried out in accordance with the European regulation on animal experimentation and the experimental protocol was approved by the Danish animal research authority (permission 2020–15–0201–00729).

2.5. *Data analyses*

Sea trout that experienced multiple capture events (Table 1), i.e., control fish that were subsequently angled or angled fish that were caught twice, were excluded from the statistical analyses. Due to the violation of the assumptions for parametric tests, Kruskal Wallis (KW) and subsequent Dunn's post-hoc tests with Bonferroni-Holm adjustment were used for comparisons of continuous data. Fisher's exact tests followed by Fisher's exact post-hoc tests were applied for comparisons of frequency data.

An ordinal regression model with a cumulative link (proportional odds model) function was applied to investigate which experimental factors influenced the level of bleeding. Ordinal regression was chosen because the dependent variable "bleeding" has "ordered" multiple categories including no, slight and heavy bleeding, respectively. The predictor variables were "total weight" (measured after capture), "fight time", "angling treatment" (fly with single hook, lure with single hook, lure with treble hook), "hooking location" (shallow hooking, deep hooking, foul hooking), "angler" (angler 1, 2, 3), and "angling day" (angling day 1 and 2). For the variable "hooking location", the previously defined hooking locations were grouped into the three categories "shallow hooking" (corner mouth/outer mouth), "deep hooking" (back of mouth/gills/esophagus), and "foul hooking" (outside in body area).

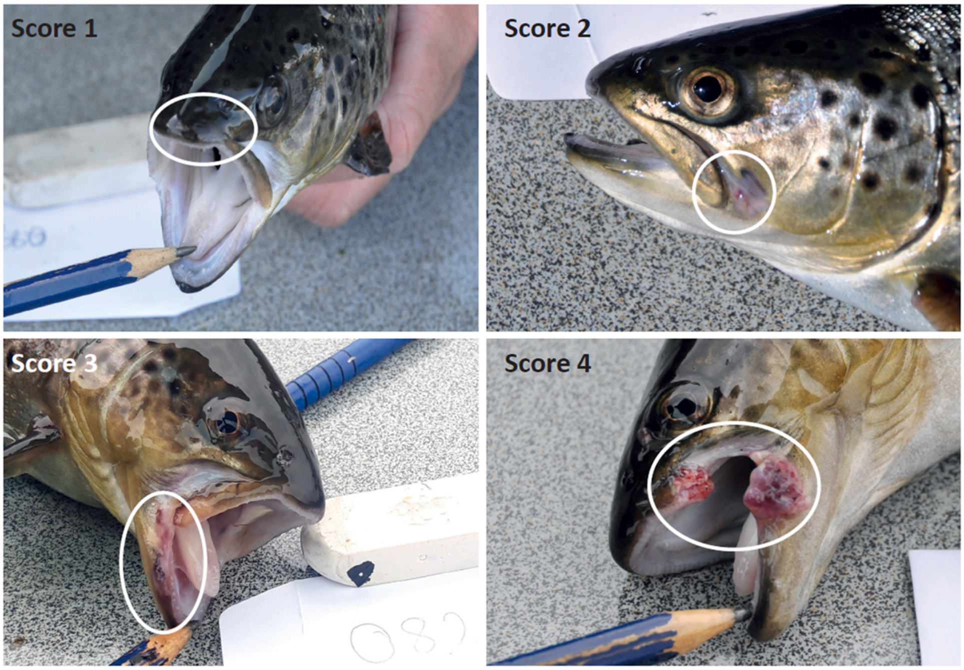

Fig. 3. Examples of different categories of wound healing and their respective healing scores. The white circles indicate the position of the hook and the subsequent location of the hooking wound.

In case of multiple hooking locations (the hook penetrated more than one of the defined hooking locations), the primary hooking location was used for classification except for multiple hooking events where the hook penetrated the gills/esophagus. In this case, the hooking location was always classified as "deep hooking". The variable "air exposure time" was not included in the initial model because it was correlated with the variable "hooking location". The full model was:

$$\text{Bleeding} \sim \text{total weight} + \text{fight time} + \text{angling treatment} + \text{hooking location} + \text{angler} + \text{angling day} \tag{1}$$

For non-significant variables, it was tested whether their removal would increase the model fit. This was not the case, therefore all variables remained in the model. Model comparisons were conducted using the AIC, McFadden's, Cox and Snell's, and Nagelkerkes pseudo-r^2, and the classification performance (correct classification rate, CCR). The superiority of the model containing the predictor variables over a model containing only the intercept was assessed by likelihood ratio tests. The ordinal regression assumption of proportional odds was assessed with the Brant test (Brant, 1990).

Specific growth rates (SGRs) were calculated according to Ricker (1975) and Crane et al. (2020) using the following formulas:

$$g = \frac{Ln(w_1) - Ln(w_2)}{\Delta t} \tag{2}$$

and

$$SGR = 100(e^g - 1) \tag{3}$$

w_1 is the weight of the individual fish at t_1 (either start of the experiment or start of the experimental angling) and w_2 is the weight at t_2 (end of the experiment). Accordingly, Δt is the difference between t_1 and t_2. Therefore, we calculated two different SGRs using the same formula. The overall SGR was calculated using the initial weight of the fish at the start of the experiment, i.e., at the day of tagging and stocking and the weight of the fish at the end of the experiment. This specific growth rate could be calculated for all fish including the non-treatment fish. A second SGR was calculated based on the weight of the fish at the day of their capture (either experimental angling or control group) and at the end of the experiment to evaluate effects of the actual treatments on growth.

The influence of the independent variables "total weight" (measured at the beginning of the experimental angling), "fight time", "angling treatment" (fly with single hook, lure with single hook, lure with treble hook), "bleeding" (no, slight, heavy bleeding), "air exposure time", "angler" (angler 1, 2, 3), "healing score" (1–4) and "angling day" (angling day 1 and 2) on the SGRs of angled sea trout was examined using a generalized linear model based on a Gaussian distribution and with log link function. "Bleeding" entered the model as ordinal variable coded 0 for no bleeding, 1 for slight, and 2 for heavy bleeding. A constant of 1 was added to the specific growth rate to avoid negative values which impacted model performance. The variable "hooking location" did not enter the model because a previously conducted Chi^2 test indicated a strong correlation of hooking location and bleeding ($Chi^2 = 33.1$, $p < 0.0001$, Cramer's $V = 0.4$). Model comparisons were conducted using the AIC and Cox and Snell's pseudo-r^2. The model fit was assessed by residual diagnostics plots, accompanied by tests for the residual distribution (Kolmogorov-Smirnov (KS) test), dispersion, outliers, and zero inflation (Hartig, 2021).

The full model was:

$$SGR + 1 \sim \text{total weight} + \text{fight time} + \text{angling treatment} + \text{bleeding} + \text{air exposure time} + \text{angler} + \text{healing score} + \text{angling day} \tag{4}$$

Some fish ($n = 37$) showed negative SGRs at the end of the experiment. Spearman's correlations and Mann–Whitney U tests were applied to test whether fork length and total weight at the beginning of the experiment influenced the overall SGRs. In addition, a KW test was applied to test for a relationship between treatment and negative SGRs.

2.6. Software tools used

All statistical analyses were conducted in R version 4.0.5 (R Core Team, 2021). The additional R package "VGAM" (Yee, 2021) was used for calculating the ordinal logistic regression model and the package "binom" (Dorai-Raj, 2014) for calculating the 95% Clopper Pearson binomial confidence intervals for the post-release mortality estimates. The package "DHARMa" (Hartig, 2021) was used to assess the model fit of the generalized linear model, and the package "brant" (Schlegel and Steenbergen, 2020) was used to conduct the Brant test.

3. Results

3.1. Capture characteristics

Out of the 127 angled sea trout that were included in the analyses (excluding fish caught multiple times and control fish), 51 and 58 fish were captured with spinning lures equipped with treble and single hooks, respectively. In addition, 18 sea trout were caught on fly equipped with single hooks (Table 2). Fork length and total weight of the angled sea trout ranged from 27.4 to 37.2 cm and 274–755 g, respectively, and of the control fish from 27.5 to 39.9 cm and 279–535 g, respectively. Both parameters did not differ significantly between sea trout caught on lures with single and treble hooks, caught on fly and the control group (Table 2).

The fight times ranged from four to 65 s and were significantly different between the three angling treatments (Table 2). Post-hoc comparisons revealed that fight times between sea trout caught on spinning lures equipped with single and treble hooks did not differ whereas fight times for sea trout caught on fly were significantly longer compared to fish caught on lures with single and treble hooks, respectively (Supplementary Table S1). Overall, air exposure times ranged from 21.9 to 201.4 s and were significantly higher for angled sea trout compared to the control fish (Table 1; Supplementary Table S1). Among the angled sea trout, air exposure times were significantly longer for sea trout caught on lures with treble hooks compared to sea trout caught on fly. In contrast, no significant differences were found between fish caught on lures with single and treble hooks and between fly-caught fish and fish caught on lures with single hook (Supplementary Table S1).

3.2. Hooking location and bleeding

Most angled sea trout were hooked in the mouth region and no fish was hooked in the esophagus (Table 3). The frequencies of anatomical hooking locations did not differ between the three angling treatments ($Chi^2 = 16.1$, $p = 0.1$). When the hooking locations were grouped into the three categories "shallow hooking" (corner mouth/outer mouth), "deep hooking" (back of mouth/gills/oesophagus), and "foul hooking" (outside the mouth), a Chi^2 test did not indicate an association between angling treatment and hooking location ($Chi^2 = 3.76$, $p = 0.4$). Depending on angling treatment, multiple hooking locations (the hook penetrated more than one of the defined hooking locations) occurred in 5.6% (fly with single hook), 11.8% (lure with treble hook), and 12.1% (lure with single hook) of the angled sea trout. The most common hooking location combinations were body/outer mouth ($n = 4$), back of mouth/gills ($n = 3$), outer mouth/gills ($n = 2$), and corner of mouth/body ($n = 2$). Two-thirds of the sea trout that were caught on lure with treble hook were only hooked with one hook tip, 24.4% with two hook tips and 6.7% with all three hook tips.

Hooking location significantly influenced air exposure times (KW test, $Chi^2 = 7.0$, $p = 0.03$). Post-hoc comparisons revealed that air exposure times were significantly longer for deep-hooked compared to shallow-hooked fish, while no significant difference was found between deep- and foul-hooked fish and shallow- and foul-hooked fish,

Table 2
Summary table showing i) number of sea trout (n), mean ± standard deviation of fork length (mm) and total weight (g) separated by treatment group at the start of the experiment (tagging and stocking), ii) mean ± standard deviation of total weight (g), air exposure, and fight time (s) separated by treatment group during the experimental angling, iii) mean ± standard deviation of fork length (mm), total weight (g), and specific growth rates (SGRs) as well as the corresponding results of the statistical comparisons and the mortality rates with 95% Clopper Pearson binomial confidence interval (Dorai-Raj, 2014) separated by treatment group at the end of the experiment. In addition, overall specific growth rates calculated from the start to the end of the experiment separated by treatment group as well as the corresponding results of the statistical test are presented.

Treatment	None ($n = 312$)	Control ($n = 52$)	Lure with treble hook ($n = 51$)	Lure with single hook ($n = 58$)	Fly with single hook ($n = 18$)	Statistical test
Start of experiment (tagging and stocking)						
Fork length (mm)	308.7 ± 17.8	308.3 ± 16.0	312.3 ± 18.9	310.1 ± 18.5	302.8 ± 11.0	KW test, $Chi^2 = 4.6$, $p = 0.3$
Total weight (g)	374.0 ± 67.5	374.2 ± 65.6	381.3 ± 76.6	377.1 ± 73.2	349.6 ± 34.9	KW test, $Chi^2 = 2.8$, $p = 0.6$
Experimental angling						
Total weight (g)	-	427.4 ± 90.4	423.2 ± 81.6	427.5 ± 90.1	383.8 ± 47.0	KW test, $Chi^2 = 4.2$, $p = 0.3$
Fight time (s)	-	-	16.0^{1} ± 6.3	15.9^{2} ± 4.8	27.9^{1,2} ± 11.7	KW test, $Chi^2 = 25.1$, $p < 0.0001$
Air exposure (s)	-	34.4^{1,2,3} ± 7.6	73.1^{1} ± 17.5	72.4^{2} ± 25.5	59.3^{3} ± 13	KW test, $Chi^2 = 109.4$, $p < 0.0001$
End of experiment						
Fork length (mm)	325.6 ± 19.4	326.8 ± 18.2	326.4 ± 19.9	331.1 ± 17.6	321.8 ± 17.3	KW test, $Chi^2 = 5.9$, $p = 0.2$
Total weight (g)	454.3 ± 90.7	452.2 ± 90.6	447.5 ± 85.7	442.5 ± 95.5	410.4 ± 50.9	KW test, $Chi^2 = 5.4$, $p = 0.3$
SGR	-	0.2 ± 0.2	0.2 ± 0.3	0.1 ± 0.2	0.3 ± 0.2	KW test, $Chi^2 = 5.2$, $p = 0.2$
Mortality (CI) [%]	-	0.0 (0.0–6.8)	0.0 (0.0–7.0)	0.0 (0.0–6.2)	0.0 (0.0–18.5)	-
Overall SGR	0.31 ± 0.20 ($n = 305$)	0.30 ± 0.20	0.26 ± 0.17	0.25 ± 0.17	0.26 ± 0.20	KW test, $Chi^2 = 8.5$, $p = 0.08$

The same superscript numbers indicate significant differences between the corresponding treatments according to Dunn's post-hoc tests with Bonferroni-Holm adjustment.

Table 3
Incidences of anatomical hooking locations in percentage and numbers (in brackets) separated by angling treatment.

Treatment	Corner mouth (%)	Back of mouth (%)	Outer mouth (%)	Gills (%)	Esophagus (%)	Body (foul hooking) (%)	Multiple locations (%)
Fly with single hook	55.6 (10)	0.0 (0)	33.3 (6)	0.0 (0)	0.0 (0)	5.6 (1)	5.6 (1)
Lure with single hook	17.2 (10)	5.2 (3)	48.3 (28)	5.2 (3)	0.0 (0)	12.1 (7)	12.1 (7)
Lure with treble hook	21.6 (11)	2.0 (1)	49.0 (25)	0.0 (0)	0.0 (0)	15.7 (8)	11.8 (6)

respectively (Fig. 4).

The occurrence and intensity of bleeding differed between the angling treatments (Table 4). Non-bleeding sea trout were most commonly caught on fly with single hook whereas slight and heavy bleeding occurred most frequently if fish were caught on lure with single hook. When looking at the hooking locations, non-bleeding fish were most frequently foul-hooked in the body or hooked in the back of mouth, whereas slight bleeding was mostly observed in fish that were hooked in the corner of the mouth or the outer mouth region. Heavy bleeding occurred mostly if the fish were hooked in the gills (Table 4).

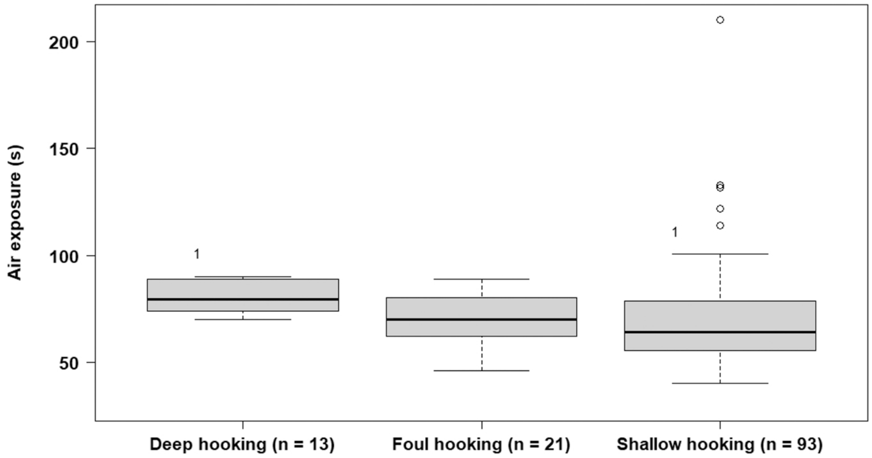

Fig. 4. Box plot showing the air exposure times (in seconds) of angled sea trout in relation to the anatomical hooking location. The same superscript numbers indicate significant differences in air exposure times between the hooking locations based on Dunn's post-hoc tests with Bonferroni-Holm adjustment.

Table 4
Incidences (% and *n* in brackets) and intensity (no, slight, or heavy) of bleeding of sea trout by angling treatment and hooking location. FLY: Fly with single hook SI: Lure with single hook, TR: Lure with treble hook.

Treatment	No bleeding (%)	Slight bleeding (%)	Heavy bleeding (%)
FLY	83.3 (15)	11.1 (2)	6.6 (1)
SI	50 (29)	29.3 (17)	20.7 (12)
TR	60.7 (31)	25.5 (13)	13.8 (7)
Hooking location			
Corner mouth (%)	61.3 (19)	35.5 (11)	3.2 (1)
Outer mouth (%)	61 (36)	27.1 (16)	11.9 (7)
Back of mouth (%)	75 (3)	0 (0)	25 (1)
Gills (%)	33.3 (1)	0 (0)	66.7 (2)
Body (%)	68.8 (11)	18.8 (3)	12.4 (2)
Multiple locations (%)	35.7 (5)	14.3 (2)	50 (7)

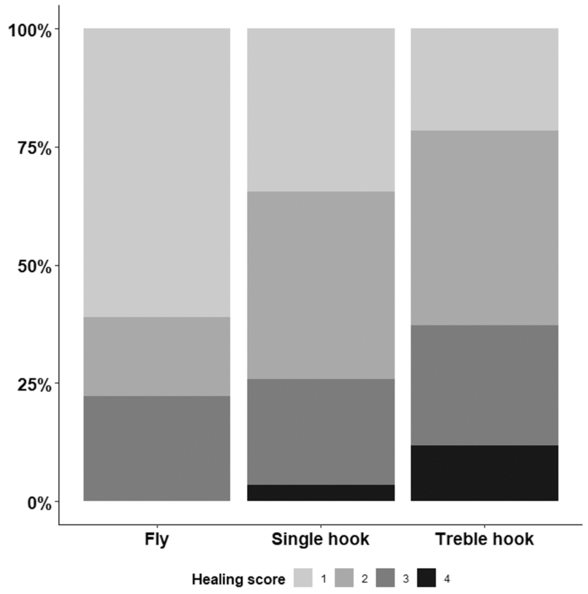

Fig. 5. Relative occurrence of healing scores separated by the angling treatments (fly fishing with single hook, lure fishing with single hook, and lure fishing treble hook, respectively). 1 = no signs of injury and 4 = severe disfiguration and/or scar tissue.

The full regression model including the independent variables “total weight”, “fight time”, “angling treatment”, “hooking location”, “angler” and “angling day” provided the best fit to the bleeding data and explained the data significantly better than the null model including only the intercept (Table 5). However, “total weight”, “fight time”, “angler” and “angling day” had no significant effect on the occurrence/ intensity of bleeding. The hooking location significantly influenced the occurrence/intensity of bleeding with the odds of heavy bleeding versus no or slight bleeding being significantly higher for deep-hooked sea trout compared to shallow hooked fish (Table 4).

3.3. *Post-release behavior and physical condition*

Two of the 127 angled fish (one with heavy bleeding and one with long air exposure) struggled up to an hour to regain equilibrium before displaying normal swimming behaviour. All other fish swam away vigorously after release.

During the period between angling and termination of the study, all fish seemed to display normal behaviour and were feeding in a similar manner as before. Only during the period with an emerging algae bloom in April, the fish lost appetite for a few days.

When inspecting for hooking wounds and healing at the end of the holding period, 33% of the fish did not show any signs of damage related to hooking. However, wound healing was significantly associated with angling treatment (Pearson’s Chi-squared test, $Chi^2 = 13.1$, df = 6, $p = 0.04$; Fig. 5). According to the post-hoc comparisons, the wound healing score differed significantly only between fish caught with fly and those caught with lure with treble hook ($p_{adj.} = 0.047$). Fish caught on fly had a median healing score of 1 on the 1–4 scale of wound healing whereas fish hooked with lures with single and treble hooks had a median score of 1.9 and 2.0, respectively. There was a significant association between wound healing and the level of bleeding (Pearson’s Chi-squared test, $Chi^2 = 16.5$, df = 6, $p = 0.01$; Fig. 6). The post-hoc tests revealed significant differences only between fish with high level of bleeding and those that showed no bleeding ($p_{\mathrm{adj.}} = 0.02$). In eight cases, hooking events in the eye-region were observed. These seem to have healed well and no incidence of unhealed eye injury or blindness was observed at the end of the experiment.

3.4. *Post-release mortality and growth rates*

Beside one sea trout that died immediately after release (a control fish that was subsequently angled and therefore excluded from the analyses), there were no mortalities in control or angled and released fish during the 26–29 d post release period (Table 2). In general, mean fish total weight and mean fork length increased over the course of the

Table 5
Summary of the ordinal regression model describing the relationship between the occurrence/intensity of bleeding (no, slight, and heavy bleeding) of angled sea trout and the total weight at capture, fight time, angling treatment (lure with single hook, lure with treble hook, fly with single hook), hooking location, angler and angling day.

	Estimate	S.E.	z	Exp.coeff	*p*
(Intercept):1	-2.79	2.07	-1.35	-	0.18
(Intercept):2	-4.41	2.09	-2.11	-	0.04
Total weight	0.002	0.002	0.74	1.00	0.46
Fight time	-0.03	0.04	-0.75	0.97	0.46
Lure single hook	1.29	0.81	1.59	3.64	0.11
Lure treble hook	0.86	0.83	1.03	2.36	0.30
Deep hooking	2.59	0.66	3.90	13.29	0.0001
Foul hooking	-0.50	0.56	-0.90	0.60	0.37
Angler 1	0.90	1.50	0.60	2.45	0.55
Angler 2	0.77	1.50	0.51	2.15	0.61
Angling day 2	0.42	0.50	0.83	1.52	0.41
Model fit					
Res. Deviance	200.355	239 d.f.	Log-likelihood	-105.177	239 d.f.
Full model vs. constant only model	Df. Dev.= −26.3	$p = 0.002$			
AIC	232.36				
r^2 McFadden	0. 11	Cox/Snell	0.19	Nagelkerke	0.22
Correct classification rate	0.62				

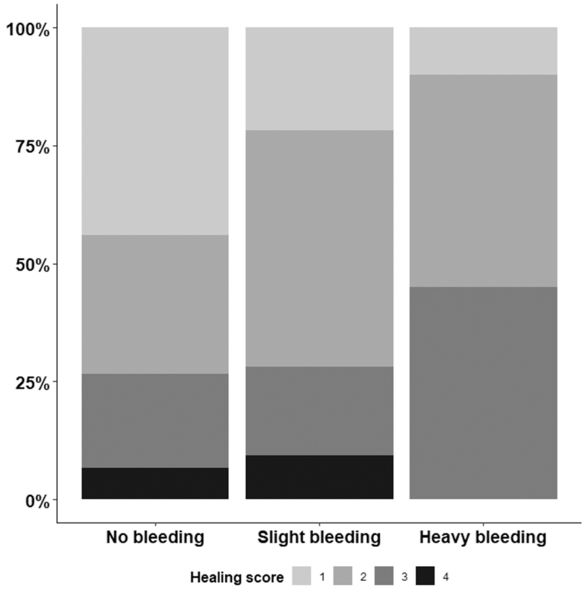

Fig. 6. Relative incidences of the healing score separated by the occurrence/intensity of bleeding. 1 = no signs of injury and 4 = severe disfiguration and/or scar tissue.

experiment for all treatment and non-treatment fish (Tables 2 and 6).

SGRs for the treble hook, single hook, fly and the control treatment ranged from − 0.54 to 0.89, − 0.28 to 0.60, − 0.23 to 0.56 and − 0.38 to 0.69, respectively (Table 2). The SGRs did not differ between the treatments and the control group over the 26–29 d post-release period (Table 2; Fig. 7). Nevertheless, some fish ($n = 37$) showed negative growth rates. However, a KW test indicated that there was no relationship between treatment and negative SGRs ($Chi^2 = 1.5$, $p = 0.7$). There was also no correlation between fish with negative SGRs and fork length and total weight at the beginning of the experiment (Spearman's correlation, fork length: $rho = 0.12$, $p = 0.5$; total weight: $rho = 0.04$, $p = 0.8$). Accordingly, fish with negative SGRs at the end of the experiment did not differ from those with positive growth rates either in weight or length at the beginning of the experiment (Mann Whitney U tests: fork length: z: 0.26, $p = 0.8$, total weight: z: 0.25, $p = 0.8$).

Table 6

Summary of the generalized linear model describing the relationship between the specific growth rate (SGR) of angled sea trout and the angling treatment (lure with single hook, lure with treble hook, fly with single hook), bleeding (no, slight, heavy bleeding), total weight at capture, air exposure time, fight time, angler, angling day, and healing score.

	Estimate	2.5%	97.5%	Std. Error	t value	*p*
(Intercept)	0.28	0.19	-0.09	0.64	1.48	0.14
Lure single hook	-0.11	0.06	-0.24	0.02	-1.70	0.09
Lure treble hook	-0.02	0.06	-0.14	0.11	-0.30	0.77
Slight bleeding	0.00	0.04	-0.08	0.09	0.10	0.92
Heavy bleeding	0.04	0.06	-0.08	0.15	0.65	0.52
Total weight	-0.0003	0.0003	-0.001	0.0003	-1.04	0.30
Air exposure time	-0.0003	0.001	-0.003	0.002	-0.25	0.80
Fight time	-0.0003	0.003	-0.01	0.005	-0.11	0.91
Angler 1	0.20	0.13	-0.04	0.46	1.55	0.12
Angler 2	0.17	0.13	-0.07	0.44	1.32	0.19
Angling day 2	-0.06	0.05	-0.15	0.04	-1.17	0.24
Healing score	-0.03	0.02	-0.07	0.01	-1.35	0.18
Model fit						
Null deviance	6.65	124 d.f.	Residual. dev.	6.04	113	d.f.
AIC	2.08					
Cox/Snell pseudo r^2	0.09					

The SGRs were neither influenced by the hooking location (KW test, $Chi^2 = 2.5$, $p = 0.5$) nor the occurrence of bleeding (KW test, $Chi^2 = 1.0$, $p = 0.8$). The SGRs (mean and 95% CI) were similar for angled sea trout with healing scores 1–3 (healing score 1: 0.22 (0.14 to 0.30), healing score 2: 0.15 (0.09 to 0.21), healing score 3: 0.28 (0.19 to 0.37)) and lower for fish with healing score 4: 0.023 (−0.12 to 0.16), Fig. 8). However, the difference was not significant (Kruskal-Wallis test, $Chi^2 = 7.75$, df = 3, $p = 0.054$). The generalized linear model revealed the non-significant effects of the variables "angling treatment", "bleeding" and "healing score" as well as "total weight at capture", "air exposure", "fight time", "angler" and "angling day" on the specific growth rates of the angled sea trout (Table 6).

4. Discussion

Previous studies of post-release effects on angled brown trout and other trout species have indicated that deep hooking and bleeding increase the risk of post-release mortality (e.g., Manson and Hunt, 1967; Taylor and White, 1992; Schill, 1996; DuBois and Kuklinski, 2004; High and Meyer, 2014). However, these studies have all been carried out in freshwater and no studies have, to our best knowledge, specifically evaluated delayed post-release mortality and growth patterns of sea trout caught and released in saltwater, where fish physiology and the (pathogenic) environment is different. Hence, this study aimed at mimicking the salinity (20–25 ppt) and water temperature that sea trout experience in most places along the Danish Baltic Sea coast during spring and autumn which is the prime season for sea trout angling in that region (Skov et al., 2022). C&R is very common in sea trout angling in Denmark and especially with regards to sea trout below the mandatory minimum landing size. It has been shown that these smaller sea trout bleed more than larger sea trout, at least for some angling methods, and may therefore experience elevated post-release mortality rates compared to larger fish (Skov et al., 2022). Hence, this study focused on sea trout below or close to the mandatory minimum landing size of 40 cm in Denmark. Furthermore, the choice of fishing methods and hook types used in the angling experiment included fly fishing (with single hook) and spin fishing (with treble and single hook), which are common angling methods and hook choices among sea trout anglers in the region (Skov et al., 2022; Blyth and Bower, 2022).

4.1. *Air exposure and fight time*

The different fishing methods used in the C&R experiment introduced a variation in fight time, i.e., the mean fight time was longer for fly-caught sea trout than for sea trout caught with lures. The experimental angling protocol inferred to reel in the fish as fast as possible after hooking, but apparently the fly fishing gear did not allow for the same retrieval speed as the spin fishing equipment. Our decision about fast retrieval speed in the experimental protocol was reflected by the fight times which, depending on angling method, were short and averaged between 16 and 28 s. This was markedly lower than fight times observed among sea trout anglers on the Swedish coast of Gotland, a comparable fishery in the Baltic region, which averaged 92 s (+/- 67 s) (Blyth and Bower, 2022). This discrepancy was likely influenced by several factors. First, the study from Gotland included sea trout between 34 and 87 cm (average 52 cm) and showed that fight time increases with fish length. In the present study, sea trout were smaller and shorter fight times could therefore be expected. Second, the raceway dimensions did not allow long casts (and subsequently longer fight times) which is common under natural conditions. Third, Pedersen et al. (2008) showed that wild brown trout have a significantly higher swimming performance than hatchery brown trout which also may partly explain the

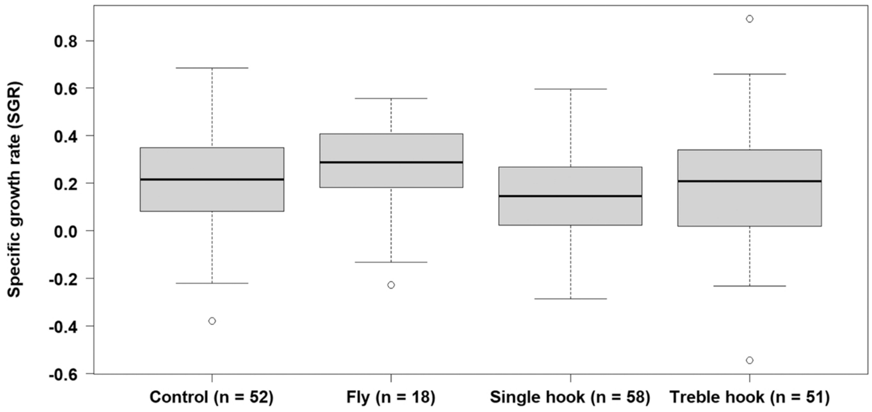

Fig. 7. Box plot showing the specific growth rates (SGRs) of sea trout separated by treatment group.

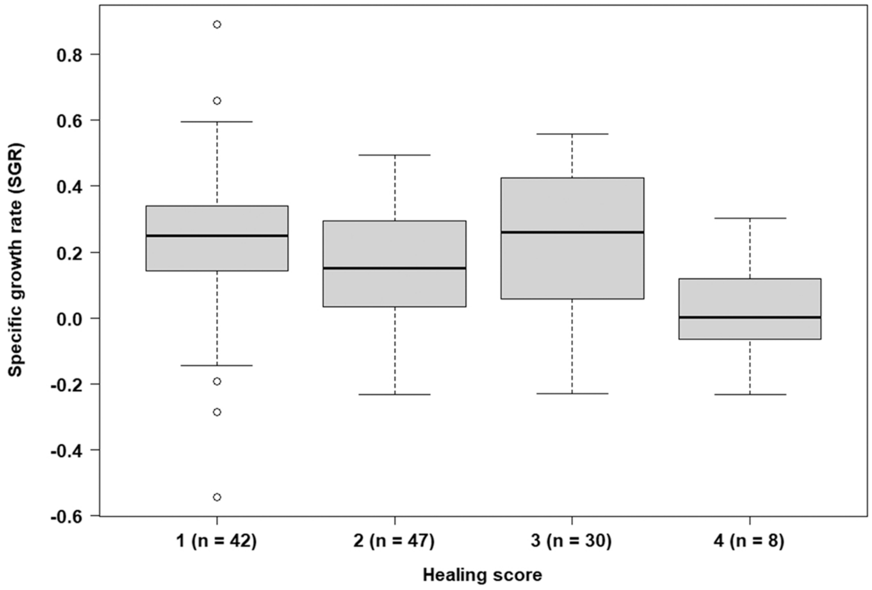

Fig. 8. Box plot showing the specific growth rates (SGRs) of sea trout over a 26–29 d post release period separated by the healing score.

differences in fight time between our and the Gotland study.

Depending on the anglers dehooking technique and skills, air exposure times during a C&R event in coastal sea trout angling varied between 0 and 155 s with an average of 20 s (Blyth and Bower, 2022). Similar air exposure durations have been reported in freshwater by Lamansky and Meyer, (2016). Anglers exposed various trout species including brown trout to air on average 26.1 s (range: 0–160 s) and only 4% of the anglers held fish out of the water continuously for > 60 s (Lamansky and Meyer, 2016). Hence, the air exposure duration in the present angling experiment was likely well above what most sea trout experience on-site at the coast during a C&R event. In the C&R angling experiment, hooking location clearly influenced air exposure time with deep-hooked fish having longer air exposure than shallow-hooked fish, likely a result of dehooking time for deep-hooked fish which is in line with other studies (Diggles and Ernst, 1997; Lewin et al., 2018; Blyth and Bower, 2022). We also found that air exposure for sea trout caught on lure with treble hooks was longer than for fly-fished sea trout, which is consistent with studies showing that handling time and hence air exposure is shorter for fish caught with flies (e.g., Lamansky and Meyer, 2016; but see Meka, 2004). Further, the fact that one third of the sea trout caught on treble hooks were hooked by more than one hook tip supports that the use of treble hooks prolongs hook removal and handling times and therefore also air exposure times, if the hook is not removed under water (Davie and Kopf, 2006; Blyth and Bower, 2022). Interestingly, we found no difference in air exposure times between single hooks and treble hooks when mounted on lures, which suggests that also hook size and angling method play a role for dehooking durations as the single hook on the lure was larger than the single hook used in fly fishing. Finally, long handling times were also observed for some shallow hooked fish, especially in cases where treble hooks got entangled in the landing net which has been observed in other studies as well (e.g., Davie and Kopf, 2006; Lamansky and Meyer, 2016).

4.2. Hooking location and bleeding

Most sea trout were hooked in the outer parts of the mouth with only 10% being classified as deep-hooked fish (i.e., hooked in the back of the mouth, gills or esophagus). This is in accordance with results from Blyth and Bower (2022) and Skov et al. (2022). The latter used a citizen science approach to show that among ~ 1500 sea trout reported by a subset of 14 anglers, deep hooking in the gills and the esophagus occurred in 1% of the cases and hooking in the back of the mouth in 7% of the cases. This relative low frequency of deep hooking may be species-specific (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011), but probably also reflects that the angling methods used in the present study, and in Skov et al. (2022), can be categorized as active type of angling, e.g., moving bait/lure, in contrast to passive angling where the bait is at a fixed position at the time of the strike. Passive angling often gives the fish time to swallow the bait and consequently results in a higher frequency of deep-hooked fish which has been shown for other trout species (e.g., Persons and Hirsch, 1994; Schisler and Bergersen, 1996; Sullivan et al., 2012).

When grouped into the three hooking location groups ("shallow hooking", "deep hooking" and "foul hooking"), angling treatments did not influence hooking location. Hence, the present study could not confirm the results from Skov et al. (2022) and Blyth and Bower (2022) who found that hooking locations varied between fly fishing and spin fishing. However, this could likely be an artefact of a relative low sample size of fly-fished sea trout in the present study.

It has been shown that hooking location and fishing method play a role for the amount of bleeding during capture of coastal sea trout (Skov et al., 2022; Blyth and Bower, 2022). Similar to their results, the present study found that heavy bleeding was most frequent when the fish was hooked in the gills and in the back of the mouth, and the share of non-bleeders was highest for fish caught on fly.

Specifically, for sea trout caught on lures, the present study suggests that the risk of bleeding may be higher when single hooks are used. In contrast, other studies have shown that fish hooked deeply with treble hooks may have increased post-release mortality compared to fish hooked deep with single hooks (e.g., Nuhfer and Alexander, 1992; Ayvazian et al., 2002), and that treble hooks generally are more likely to be embedded in sensitive areas (e.g., foul hooked, gullet, gills, and/or eyes) compared to single hooks (e.g., Trahan et al., 2021). On the other hand, several other studies have indicated that single hooks can cause more damage than treble hooks and meta-analysis studies have not been able to make clear conclusions whether treble hooks or single hooks are likely to cause higher post-release mortality (Taylor and White, 1992; Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011). We speculate if differences in absolute hook dimensions between single and treble hooks (e.g., gap width and wire diameter) may explain the contradictory results when comparing effects of single vs treble hooks on hooking injuries and bleeding. In the present study, gap width of the single hook was larger (17 mm) than of the treble hook (6 mm) which may has influenced levels of bleeding. However, when including a larger size span and sample size than in the present study, Skov et al. (2022) found no effect of hook size on bleeding patterns in coastal sea trout angling, which is in line with other studies on salmonids (e.g., Taylor and White, 1992; Pauley and Thomas, 1993).

Multiple hooking with treble hooks could also impair the fish's breathing abilities, e.g., when one hook tip is located in the upper and one in the lower jaw preventing the fish to open the mouth properly (hereafter referred to as "stapling"). In particular, this could be relevant for larger fish with longer fight times. In the present study, "stapling" occurred in 15% of the sea trout caught on treble hook but effects on post-release mortality were not observed. Nevertheless, future studies should investigate potential sublethal physiological and behavioral effects of "stapling".

Across a larger size span of angled sea trout, Skov et al. (2022) observed heavy bleeding in 2% and bleeding in around 25% of the sea trout catches reported by citizen scientists. This was similar to Blyth and Bower (2022) who observed bleeding in 22% and heavy bleeding in 5.5% of angled sea trout at the coast of Gotland. In the present experiment, the frequencies of bleeding and heavy bleeding seemed higher and varied, depending on fishing method, between 17% and 50% and between 7% and 21%, respectively. Several factors probably play a role for this discrepancy. First, Skov et al. (2022) and Blyth and Bower (2022) reported catches of many sizes of sea trout, whereas this experiment included only smaller sea trout and, as discussed above, the frequency of bleeding can be higher for smaller sea trout. Second, the dominant fishing method in both studies was fly fishing, implying that bleeding was less frequent compared to spin fishing. In fact, when exploring average bleeding frequencies in the study from Skov et al. (2022) separately for spin-fished (32%) and fly-fished (17%) sea trout, these appear somewhat similar to the bleeding patterns for spin-fished (45%) and fly-fished (16%) sea trout found in the present experiment.

4.3. Post-release mortality, growth and healing of hooking wounds

Despite observations of substantial bleeding from some of the gill-hooked fish and the overall long air exposure durations, no post-release mortality occurred among the control and treatment fish during the 26–29 d holding period. The only mortality that occurred was a single fish that was removed from the analyses due to being subject to multiple capture treatments, i.e., one former control fish that was subsequently angled. This fish was caught on lure with treble hook and was bleeding heavily from a gill hooking and died just a few hours after release.

The absence of mortality among the treatment fish was in contrast to several other studies which found elevated post-release mortality rates related to hooking locations and/or levels of bleeding in brown trout and other salmonids (e.g., Manson and Hunt, 1967; Taylor and White, 1992; Schill, 1996; DuBois and Kuklinski, 2004; Lindsay et al., 2004; High and Meyer, 2014; Carline et al., 2021). Common for these studies was that they were conducted in freshwater where hooking injuries, bleeding patterns and/or wound healing may be different than under saline conditions. However, post-release mortality has also been reported for other salmonids in marine waters (e.g., Gjernes et al., 1993). Consequently, more studies are recommended to further elucidate if post-release survival of sea trout and other salmonids is higher in marine waters and if so, the mechanisms behind this. Blyth and Bower (2022) used reflex impairments as indicators of potential post-release stress among sea trout and found that C&R at water temperatures > 10 °C in combination with long air exposure times (>10 s) is suboptimal. We cannot corroborate these results, as angling in the present study took place at lower water temperatures, but we still find it noteworthy from this study that when practicing C&R at water temperatures around 5 °C, air exposure times apparently can be several magnitudes higher than 10 s without implying post-release mortality and growth impairments. Nevertheless, the present study is consistent with the general conclusion of Blyth and Bower (2022) that properly conducted C&R can have minimal negative impacts on the majority of sea trout caught in saltwater, which is also consistent with findings in freshwater (Carline et al., 2021).

Several studies observed growth reductions after the release of angled fishes (Aalbers et al., 2004; Pope and Wilde, 2004; Pope et al., 2007). In the present study, we compared growth among a control group and angled fish 26–29 days after the C&R event and evaluated growth among fish that were bleeding and not bleeding at the time of release. Despite a period with suboptimal abiotic conditions in the raceway system and associated restricted feeding, the experimental fish grew during the study period. This also included the fish that were angled, and we found no significant effect of angling method, hooking location or bleeding on growth patterns, i.e., even fish with heavy bleeding seemed to recover from this well enough to keep up a comparable growth rate. This aligns with other post-release growth evaluations of salmonids (e.g., Pope and Wilde, 2004) and supports that adverse effects of C&R overall can be relative short-lasting. However, we acknowledge that the sample size was smaller than we had aimed for, which may have reduced the statistical power of our analyses. Future studies should evaluate other potential sublethal effects of C&R on sea trout, e.g., predation risk, reduction of reproductive success, behavioral effects, and vulnerability to diseases or parasites.

When exploring the wound healing upon study termination, we found clear differences in the status of wound healing. For most of the inspected fish, there were no signs of injury (healing score 1) or only small signs of hook wound injury (healing score 2). A small part (6%) of the fish had wounds that were poorly healed and even infected (healing score 4). Interestingly, although not statistically significant, this group also showed signs of reduced growth compared to the other wound healing groups, which may suggest that mortality or long-term sublethal effects that impact overall fitness may have occurred if the study period had been longer. When further exploring the healing characteristics, we found that the share of fish with no signs of injury (healing score 1) decreased with bleeding intensity, and that the proportion of sea trout with badly healed/infected hooking wounds differed between angling methods and was clearly highest among fish caught with lures, i.e., not present among the group of sea trout caught with fly fishing gear. The latter could relate to the smaller hook size used in fly fishing and could suggest that in terms of avoiding long-term infected hooking wounds, the use of smaller single hooks and maybe barbless hooks could be favourable (Brownscombe et al., 2017). Similar, Blyth and Bower, (2022) recommended the use of smaller single hooks rather than larger treble hooks as this can reduce hooking injury. However, we acknowledge that the sample size of fly-fished sea trout in the present study was lower than for fish caught on lures, and that poor wound healing was only found in a small subset of fish, i.e., eight of the 127 fish. Both factors reduce the strength of the conclusions about hook size effects from the present study, and we therefore suggest additional studies to explore the role of hook size further.

4.4. Potential study limitations

Many studies have shown that lethal and sublethal impacts of C&R depend on environmental conditions such as water temperature, dissolved oxygen, capture depth and predation risk (Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007). In the raceway, we aimed to create an environment for the fish that could mimic natural conditions. Nevertheless, we had to find compromises, e.g., with regards to food type and availability (artificial), predation risk (not present) and fish density (unnaturally high). Also, the rapid increase of the water temperature in the raceway in mid-April associated with an algae bloom was likely an unnatural condition for the fish. However, this particular event may act conservative to our results, as it probably added additional stress to the study fish for some time. The wound healing process and the observed wound infections might also have been influenced by the holding conditions, e.g., due to lower water quality and higher pathogen load compared to the wild.

We also acknowledge that the majority of the sea trout in this study were not fully smoltified, i.e., silverish with loose scales, as it is the case among most natural living coastal sea trout. We have no knowledge about the role of the fishes' physiological state on vulnerability to C&R, but a higher degree of scale loss can be expected among wild sea trout which may impair fish health. However, Black and Tredwell (1967) did not find a significant effect of the partial loss of scales and mucus on mortality in rainbow trout (*Oncorhynchus mykiss*) but this might be species-specific. Furthermore, sea trout used in this study were hatchery-born and reared in an aquaculture facility. These fish may differ from wild fish in morphology, physiology, genetic composition, behavior and stress response (Brown and Day, 2002), and wild fish may be more susceptible to handling stress than aquaculture-reared fish (Salonius and Iwama, 1993). Further studies should elucidate if the results from the present study would be similar for wild and smoltified sea trout.

Varying metabolism between individual fish (Metcalfe et al., 2016) could also have influenced our results. For example, if hungry fish with high metabolism rates and faster growth were more prone to be angled in our experiment, then our study design might have failed to detect this. It cannot be ruled out that in undisturbed conditions the angled fish might have had a higher growth rate than the control group, while being angled their growth could be reduced and therefore no longer higher (but similar) to the non-angled group with lower metabolism.

In the C&R angling experiment, we aimed to establish a sample size of 75 fish in each of the treatment groups. This did not go as planned and we had to deal with smaller sample sizes. We clearly recognize that especially the sample size of the flyfishing group was small and all conclusions that involve this group should be done with special care.

Our experimental protocol implied that fight time should be as short as possible and the experimental angling was conducted at low water temperatures. It is possible that other combinations of these variables, e.g., long fight times in combination with long air exposure times in warmer water and air temperatures could have resulted in stronger adverse post-release effects. For example, studies have shown that extended fight times followed by long air exposures increase post-release mortality (Ferguson and Tufts, 1992; Joubert et al., 2020). Blyth and Bower (2022) found that increased fight time duration affected reflex action mortality predictors (RAMP) and lactate levels at water temperatures above 10 °C but not at lower water temperatures although glucose levels were affected by fight time at both temperature spans. However, in the present study, the water temperature during the angling experiment and in the holding period afterward corresponded to water temperatures in spring and autumn, when most angling for sea trout takes place in the Baltic Sea (e.g., Skov et al., 2022), which, in combination with the long air exposures in the present study, suggests some generalizability of the present results.

5. Conclusion

Recreational sea trout fisheries in Denmark, a potential indicator of Baltic recreational sea trout fisheries, imply widespread C&R not least of smaller fish below the minimum landing size. Our experiment confirmed previous studies that bleeding is frequent in sea trout angling (and related to hooking location and fishing method), but also that post-release mortality is very low. Moreover, the growth of angled sea trout was not significantly affected by C&R. However, a small subset (6%) of the angled fish had unhealed/infected hooking wounds at study termination and showed a tendency of reduced growth. These fish were all caught on lures. However, the small sample size of fish with infected hooking wounds and the relative low sample size of sea trout caught by fly fishing hamper clear recommendations of the impact of fly fishing vs lure fishing, and further studies on the difference between these two methods and different hook sizes are warranted. Further studies are also recommended that should explore if the current patterns of post-release mortality and growth would differ if abiotic conditions were different (e.g., higher water temperatures or lower salinities), if the post-release observation periods were longer, if the maturation/physiological state of the fish were different and if the interactions between fight time, air exposure duration and water temperature were changed. Furthermore, follow-up studies are needed that include mark-recapture or biotelemetry studies in the field to corroborate the results from our mesocosm C&R angling experiment (Pollock and Pine, 2007).

CRediT authorship contribution statement

Christian Skov: Conceptualization, Planning, Field work, Data curation, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Keno Ferter:** Conceptualization, Planning, Writing – original draft, Writing – review & editing. **Niels Jepsen:** Planning, Field work, Data analysis, Writing – review & editing. **Lars-Flemming Pedersen:** Planning, Field work, Writing – review & editing. **Casper Gundelund:** Writing – review & editing. **Wolf-Christian Lewin:** Data analysis, Writing – review & editing. **Marc Simon Weltersbach:** Conceptualization, Planning, Data analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106637.

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