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After the spawn and on the hook: Sea trout *Salmo trutta* biophysical responses to different components of catch and release in a coastal fishery

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Abstract

This study investigated the biophysical responses of sea run brown trout *Salmo trutta* to catch-and-release in the coastal fishery around Gotland, Sweden. It used information recorded on individual angled *S. trutta* ($n = 162$), including fight time, handling time, total air exposure time, injury, bleeding, fish length, body condition, spawning status, water temperature, hook location and difficulty of hook removal. Reflex action mortality predictors (equilibrium, operculum beats, tail grab response, body flex response and vestibular-ocular response), tests of blood glucose and lactate, and observation of hooking injury were used to measure the relative impact of the angling event on the fish's physical state and stress experienced. The results of this study suggest low rates of post-release mortality and generally limited stress responses to angling events, and relatively high post-release survival supported by the recapture of many tagged *S. trutta*. However, a number of scenarios were identified in which stress responses are likely to be compounded and where anglers should take additional action to reduce sublethal physiological disturbances and the risk of delayed mortality. Particular care should be taken to limit cumulative total air exposure to <10 s, and to reduce handling time and risk of additional injury in angling events with extended fight times, when water temperatures >10°C, or where *S. trutta* show evidence of being physically compromised by injury or having recently spawned. The results also indicate the importance of using appropriately sized single hooks rather than larger treble hooks to reduce hooking injury and handling time during unhooking.

KEYWORDS

angler behaviour, angling, catch-and-release, fish impairment, recreational fisheries, stakeholder collaboration

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Supporting Information S1 Figures of the predicted versus actual responses for the linear regression models presented in Table 3

1 | INTRODUCTION

Recreational fishing, often referred to as ‘angling’ when a rod and reel are used, is an important and popular human–environment interaction, practiced by at least 220 million people globally, that provides substantial social and economic benefits (Arlinghaus *et al*., 2020; World Bank, 2012). Many of the fish that are caught in recreational fisheries are returned to the water presumably unharmed in a practice known as catch-and-release (C&R), which is performed voluntarily or to comply with fishing regulations (Arlinghaus *et al*., 2007). In Sweden and other European countries where fishing has a traditionally consumptive focus, the use of this management tool is relatively new and growing in popularity (Ferter *et al*., 2013; Stensland *et al*., 2013). Voluntary C&R is assumed or intended to allow anglers to have reduced biological impacts on target fish populations, while still enjoying many or most of the benefits associated with recreational fishing (Arlinghaus *et al*., 2007). Involuntary C&R is intended to protect or reduce the impacts of angling on vulnerable fish populations or sections thereof, often exemplified by rules that state anglers cannot keep particular species of fish, a particular sex of fish, or fish under a minimum size limit or outside a size window (Policansky, 2002). However, C&R remains controversial and is opposed by some groups who believe that released fish are unlikely to survive after the angling event (Aas *et al*., 2007; Arlinghaus, 2007; Arlinghaus *et al*., 2020).

Salmonid fishes are an important target of recreational fishers around the world, and the effects of C&R on salmonids has been the focus of extensive research in lake and lotic environments, particularly anadromous species making spawning migrations (Havn *et al*., 2015; Joubert *et al*., 2020; Kerr *et al*., 2017; Lennox *et al*., 2015). In contrast, relatively few studies on C&R have looked at the biophysical responses of anadromous salmonids caught in coastal waters (Whitlock *et al*., 2016). Native to European freshwater and coastal ecosystems, the anadromous strain of brown trout known as sea trout *Salmo trutta* L. 1758 is an important element of recreational fisheries in several countries (Blicharska & Rönnbäck, 2018; Butler *et al*., 2009; Gundelund *et al*., 2020; Liu *et al*., 2019; Stensland *et al*., 2017). *S. trutta* attract thousands of anglers a year to fish in coastal areas, such as the Swedish island of Gotland, and in these fisheries C&R rates are particularly high (86%) (Blicharska & Rönnbäck, 2018). This is a relatively new tool for some stakeholders in this fishery and the country as a whole, and as a result best practices for releasing *S. trutta* are not necessarily widely known or engaged in by all anglers (Blyth & Rönnbäck, 2022; Hanindyawan Handoko, 2018).

While there are many factors that can be considered universally important for post-release survival, there are species- and fishery-specific components that are more or less important on a case-by-case basis (Brownscombe *et al*., 2017). These components vary greatly and can include environmental factors (*e.g*., water temperature, capture depth), the biology of the individual or species of fish (*e.g*., spawning status, physical condition), the angling gear used (*e.g*., hook size, hook type), and the fishing and handling techniques (*e.g*., fight time, amount of air exposure, hook removal technique) (Arlinghaus *et al*., 2007; Brownscombe *et al*., 2017; Cooke & Suski, 2005). Understanding the importance of each of these factors is especially relevant when establishing fishery-specific best practices for how and when to apply C&R, and when, in turn, communicating these best practices to anglers (Danylchuk *et al*., 2018). This can be investigated in wild fish in real angling situations through the measurement of blood samples and reflex impairment tests as proxies for angling-related stress, mortality and other sublethal effects (nonlethal injuries, changes to the physiology or behaviour of the fish) (Brownscombe *et al*., 2017; Cooke & Sneddon, 2007; Davis, 2010). These methods also allow assessment of species in fisheries where prolonged observation after release is not practical or possible.

The objective of this study is to identify which angler-related (angling, handling and air exposure times), fish-related (size, body condition and spawning status), or environmental (water and air temperature) factors have the greatest impact on stress levels [as measured by reflex action mortality predictors (RAMP) response, blood glucose and blood lactate levels] and angling-related injuries experienced by *S. trutta* caught in the coastal fishery of Gotland. We expected that reflex impairment and stress levels would be higher in fish with poor physical condition, increase at high water temperatures and increase with angling, handling and air exposure time.

2 | MATERIALS AND METHODS

2.1 | Study site

Sampling for this study took place in May 2019 and between March and September 2020 in coastal waters around the island of Gotland, Sweden. Gotland is located in the central Baltic Sea and has a coastline of approximately 800 km (Figure 1). Tidal action is minimal in the Baltic Sea, but sea levels do change over longer time periods and were noted to vary between −29 and +50 cm during the study period (SMHI, 2021). Surface water temperatures measured at the time of capture ranged from 2 to 19°C during the study period. Salinity commonly varies between 0.6% and 0.8% in the region (SMHI, 2021).

Regulations for coastal *S. trutta* angling around Gotland are limited to a minimum size limit (50 cm) and seasonal fishing closures around the mouths of spawning streams. No license is required for angling in coastal waters in Sweden. There is no limit to the number of *S. trutta* over 50 cm that an angler can retain and there are no restrictions on the type of angling gear that may be used (*e.g*., size of hooks, number of hooks, using barbless hooks). The number of *S. trutta* anglers fishing on Gotland annually has been estimated in the range of 2500–3700 individuals (Blicharska & Rönnbäck, 2018).

2.2 | Capture and sampling

The sampling protocols followed in this study conform to national ethical standards for animal experiments, approved under decision Dnr 2529–2019 issued by the Linköping regional animal experiment ethics committee for the Swedish Board of Agriculture.

Sea run brown trout were captured by anglers fishing with hook and line casting from shore or while wading in the sea. There were also two sea trout captured in a landing net by the researcher without

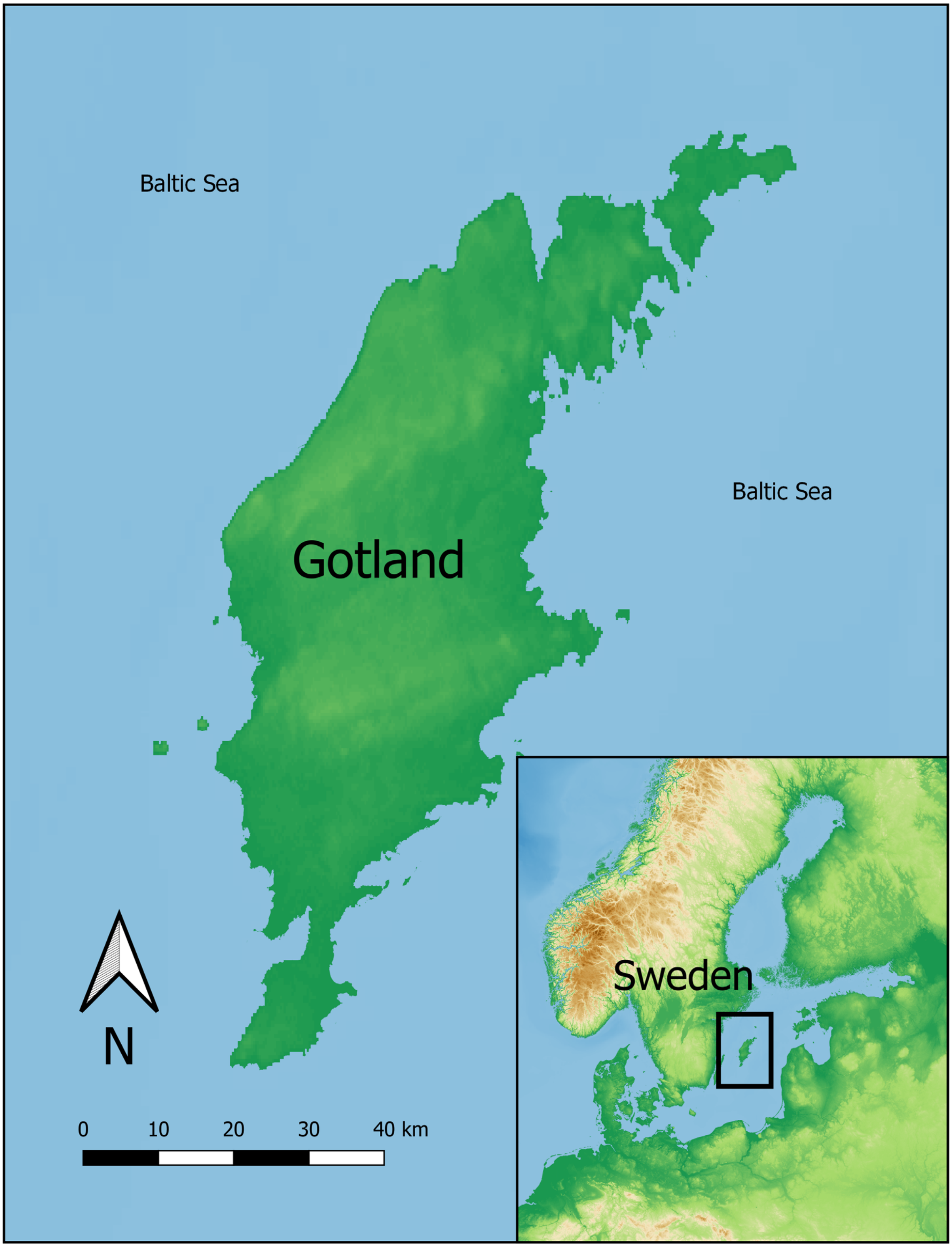

FIGURE 1 Location of Gotland in the Baltic Sea and relative to the Swedish mainland

angling. Individual anglers used either fly or spin fishing gear with their choice of fly or lure based on standard patterns that are currently in common use in this fishery. Flies were tied on single barbed hooks in sizes 8 to 1. Spin lures predominantly had one fixed barbed treble hook in size 4 or size 2, although a number of fish were also landed on lures with single hooks and line-through lures. Seven and eight weight fly rods and medium action spinning rods were used. Angling was performed by experienced local anglers, local fishing guides and the supervised clients of local fishing guides, with the researcher present at all catches. This combination meant that all anglers handling fish in this study were considered to have intermediate or expert skill, which reduced the risk of accidental injury to the sampled fish, but also influenced the results towards being representative of a best-case scenario for handling during C&R (Meka, 2004).

Fight time (measured in seconds) was recorded as the elapsed time between hooking and landing in an appropriately sized, rubberized landing net. Initial handling time was recorded as the duration of time between landing of the fish and its transfer to the researcher for testing. During this handling time the anglers and guides were encouraged to handle the fish as they would under normal angling conditions to establish baselines for normal handling and air exposure times in this fishery. Air exposure was recorded as a cumulative value (in seconds) (Cook *et al*., 2015). To ensure proper animal care and avoid unnecessary mortality, air exposure was avoided when sampling at high water temperatures reducing the number of compounding influences on stress measurements from fish caught in these conditions and the chances of angling-related mortality, as high water temperatures have already been shown to negatively impact post-release survival of salmonids in a number of studies (Gale *et al*., 2013; Meka & McCormick, 2005; Twardek *et al*., 2018). At lower water temperatures longer than normal air exposure events were also simulated by holding fish out of the water in the landing net, or with wet hands and proper body support, to obtain a wider range of sampling times in cases where both angling and handling times were short and additional injuries were not immediately visible. Hooking location and difficulty of hook removal were both recorded as ordinal values from 0 to 5 (Table 1).

Upon transfer to the researcher, the fish were tested for reflex impairment in a landing net that was large enough to allow free movement of the fish (Westin W3 CR Landing Net XL, 70 cm wide × 85 cm long × 80 cm deep), while keeping the gills of the fish in the water for all testing. The tail grab response was tested by the researcher gripping the caudal peduncle of the fully submerged fish and classified as unimpaired if a swim-burst response occurred within 5 s. The body flex response was tested by the researcher gently gripping the submerged fish around the middle of its body, and classified as unimpaired if the fish flexed the lateral musculature that would curve the body into a C shape within 5 s. Vertical orientation was tested by placing the submerged trout upside-down, and classified as unimpaired if the fish could right itself within 5 s. The vesitibulo-ocular reflex (VOR) was classified as unimpaired if the eyes of the trout tracked or followed the horizon when its body was rotated side to side along its central axis. Operculum beats were classified as unimpaired if they were observed to continue in unison and at a regular rhythm throughout the testing of the other reflexes. Reflex measurements were validated on an initial sample of 21 trout for which times were measured to the nearest second for the tail grab, body flex and vertical orientation reflexes, while operculum beats were observed over a longer period. This validation confirmed that the testing protocol was suitable for sea run brown trout. Individual reflexes were categorized as impaired and assigned a score of 0 or unimpaired and assigned a score of 1. Tail grab, body flex and vertical orientation were all recorded as unimpaired if the reflex occurred within 5 s.

During the reflex testing process, the fish were observed for new or old injuries, any bleeding (recorded as 'none', 'some' or 'lots'), clipped adipose fins or evidence of having recently spawned. Spawning status was assessed by body colour, body condition, lesions or scarring on the fins, and residual kypes or hooked mouths on male trout. Kelts or trout that have recently spawned are often more brown, bronze or yellow than the 'silver' trout that have not done so. They also tend to be thinner and less heavily muscled, having invested heavily in the reproductive process, and have scarring on their fins or noses from contact with stones in the spawning streams. A clipped adipose fin is an indication that the trout was raised in a hatchery and released elsewhere around the Baltic before migrating to Gotland, as no hatcheries for *S. trutta* operate on the island (Sportfiskarna, 2020).

At approximately 2 min after transfer to the researcher, and following the initial reflex test and visual assessment, a blood sample was taken from the caudal vasculature of the fish using a lithium heparin-coated syringe (4 ml Vacutainer) (Lawrence *et al*., 2020). The timing of the blood sample at 2 min after what would have been the time of release was intended to capture the slightly delayed change in blood glucose and lactate, but without unnecessarily extending the handling and testing time for the fish (Lawrence *et al*., 2020). Fork length (L_F) was measured to the nearest centimetre with the fish remaining in the water. Body condition was estimated on an ordinal scale from 0 to 4 (Table 2). A numbered T-bar anchor FLOY TAG was

TABLE 1 Scoring system for hooking location

	Score	Description
Hooking location	0	Unknown, when the hook came out before being observed and without leaving a readily visible mark
	1	Lip or corner of the mouth, the normal or ideal hooking location
	2	In the mouth, but not deep, or in and piercing through the chin
	3	Deep, in the tongue or contacting the gills
	4	Stapling, where two or more hooks of a treble hook are embedded and holding the mouth partially or completely shut
	5	Foul, hooked outside the mouth area
Difficulty of hook removal	0	Falling out on its own
	1	Simple pull, not needing to hold onto the fish
	2	Some work required, needing to hold the fish
	3	Challenging, multiple attempts needed, but no major injury from removal
	4	Challenging, multiple attempts needed, and lasting injury caused by hook removal
	5	Fish unlikely to survive unhooking

TABLE 2 Scoring of *Salmo trutta* body condition

	Score	Description
Body condition	0	Emaciated
	1	Skinny (back and belly running parallel), lacking muscle tone
	2	Normal or average body, firm muscles
	3	Noticeably thick, and well-muscled or fat
	4	Obese

inserted next to the dorsal fin to mark the trout in case of future recapture (FLOY TAG Inc., Seattle, WA, USA). Blood lactate and glucose were analysed in the field (Accutrend Plus, Roche Diagnostics, Mannheim, Germany).

Photos were taken of noticeable injuries and scars to aid in documentation of recovery rates in recaptured fish. A second reflex test was performed immediately before release to evaluate the influence of increased handling time and the testing process on the physical status of the trout.

2.3 | Data analysis

Several general linear regression models were constructed to determine the effects of fight time, handling time, air exposure, hook location, hook removal difficulty, injury, bleeding, fork length, body condition, spawning status and water temperature on each of the three dependent variables blood lactate, blood glucose and reflex impairment (McLean *et al*., 2020; Meka & McCormick, 2005). Before stepwise model selection, Spearman rank correlation was used to check for strong relationships between the independent variables, and all the modelled variables were confirmed to have generally linear responses to one another. In cases where significant correlation was identified between variables, such as between length and angling time, both variables were assessed as to whether or not they would have independent impacts on release outcomes. In addition, characteristics of the various independent variables were used to create subsets of the data to further isolate and identify the impacts of each variable, provided there were at least 30 fish fitting the characteristics of the subset to meet assumptions of normalcy. For the regression analysis RAMP scores were transformed to a score of 1.0 for unimpaired fish, 0.5 for slightly impaired fish where only one reflex was absent and 0.0 for moderately to heavily impaired fish to correct for the imbalanced distribution of scores.

A full model (with all 11 independent variables) and a null model (dependent variable ~1) were defined, then both forward and backward stepwise selection of terms were used to establish 2048 candidate models per dependent variable. The candidate models were compared using Akaike information criterion (AIC) to define a final model with the lowest AIC score as the one that best describes the data. The parameters of this final model were assessed at significance of $P = 0.05$. An analysis of variance was performed for the individual terms in the final model, and the model assumptions were checked through plotting of the residuals and plotting the relationship between predicted and actual response values. This process was performed for the total group of 162 fish, as well as approximately 50 different subsets based on exploratory categorization within the independent variables, resulting in the definition of 376 final models for comparison through the multimodel inference approach. These final models were then evaluated to identify patterns and thresholds where the relationships between dependent and independent variables would result in different stress responses from the fish.

Spearman rank correlations were used as a nonparametric test to investigate hooking-related results and identify relationships between hook type, hooking location, difficulty of hook removal, injury, bleeding and physical characteristics of the fish.

All statistical analyses were conducted using RStudio (v. 1.1.442) and R (v. 4.0.2) (R Core Development Team, 2020; RStudio Team, 2020). R code for conducting multiple regression analyses and checking model fit were adapted from the R Companion to the Handbook of Biological Statistics (Mangiafico, 2015).

3 | RESULTS

A total of 162 trout ranging from 34 to 87 cm L_F (51.85 ± 9.70 cm), from which blood samples were obtained and analysed, were captured at water temperatures ranging from 2 to 19°C (8.90 ± 3.85°C). Of these fish, 95.06% ($n = 154$) were wild and 21.60% ($n = 35$) displayed evidence of having spawned during the previous season. The mean fight time was 91.79 ± 67.36 s (range 0–425 s) and was not significantly different between spin and fly anglers ($P > 0.05$). The mean handling time before testing was 212.61 ± 108.26 s (range 47–764 s) and the mean total air exposure before testing was 19.68 ± 24.66 s (range 0–155 s). The mean blood lactate was 3.12 ± 1.31 mg/dl (range 0.79–10.20 mg/dl) and the mean blood glucose was 59.19 mmol/l (range 24–140 mmol/l). Fight time was positively correlated with fish length ($r_s = 0.56$, $P < 0.001$) and body condition ($r_s = 0.20$, $P = 0.011$).

Initial reflex tests showed 48.15% ($n = 78$) of the trout with no reflex impairment, 35.19% ($n = 57$) with minor reflex impairment where only a single reflex was impaired, 14.82% ($n = 24$) showed moderate reflex impairment where two reflexes were impaired and 1.85% ($n = 3$) showed impairment of all five tested reflexes. During initial reflex testing the tail grab response was impaired in 31.48% ($n = 51$) of the trout, the body flex response was impaired in 24.69% ($n = 40$), vertical orientation was impaired in 14.20% ($n = 23$), operculum beats were impaired in 1.85% ($n = 3$) and VOR was impaired in 1.85% ($n = 3$). Final reflex tests before release showed 57.41% ($n = 93$) of the trout with no reflex impairment, 32.72% ($n = 53$) with single reflex impairment, 7.41% ($n = 12$) with two reflexes impaired, 1.23% ($n = 2$) with three reflexes impaired and 1.23% ($n = 2$) with total reflex impairment. The observed mortality rate was 1.23% ($n = 2$) and in both cases total reflex impairment occurred during final reflex testing. During final reflex testing, the tail grab response was impaired in 28.40% ($n = 46$) of the trout, the body flex response was

TABLE 3 Multiple regression outputs for *Salmo trutta* blood lactate, blood glucose and RAMP scores

Group	Dependent variable	Independent variable	Estimate	Std. error	*t* value	Pr(>|*t*|)	
Overall ($n = 162$)	Lactate (adj $R^2 = 0.22$)	(Intercept)	1.35	0.34	3.93	0.00	***
		Fight time	0.01	0.00	5.60	0.00	***
		Handling time	0.00	0.00	3.38	0.00	***
		Water temperature	0.05	0.02	2.05	0.04	*
	Glucose (adj $R^2 = 0.02$)	(Intercept)	48.89	5.12	9.56	<2e-16	***
		Body condition	3.73	2.39	1.56	0.12	
		Fight time	0.03	0.02	1.45	0.15	
	RAMP (adj $R^2 = 0.10$)	(Intercept)	−0.16	0.16	−1.01	0.31	
		Bleeding	0.13	0.05	2.58	0.01	*
		Length	0.01	0.00	2.14	0.03	*
		Injury	0.08	0.04	2.02	0.05	*
		Water temperature	0.01	0.01	1.51	0.13	
Unspawned ($n = 127$)	Lactate (adj $R^2 = 0.15$)	(Intercept)	2.31	0.30	7.83	0.00	***
		Fight time	0.01	0.00	4.07	0.00	***
		Handling time	0.00	0.00	2.58	0.01	*
		Hook removal	−0.16	0.09	−1.83	0.07	
	Glucose (adj $R^2 = 0.01$)	(Intercept)	56.67	2.52	22.44	<2e-16	***
		Fight time	0.03	0.02	1.45	0.15	
	RAMP (adj $R^2 = 0.09$)	(Intercept)	−0.05	0.16	−0.32	0.75	
		Bleeding	0.17	0.05	3.13	0.00	**
		Length	0.01	0.00	2.10	0.04	*
Recently spawned ($n = 35$)	Lactate (adj $R^2 = 0.59$)	(Intercept)	−1.00	0.71	−1.42	0.17	
		Fight time	0.01	0.00	5.49	0.00	***
		Water temperature	0.17	0.05	3.68	0.00	***
		Hook location	0.47	0.23	2.07	0.05	*
		Handling time	0.00	0.00	2.01	0.05	
	Glucose (adj $R^2 = 0.32$)	(Intercept)	−16.09	23.30	−0.69	0.50	
		Body condition	10.14	3.84	2.64	0.01	*
		Handling time	0.06	0.02	2.63	0.01	*
		Air exposure	−0.24	0.09	−2.54	0.02	*
		Length	0.79	0.36	2.21	0.04	*
		Hook location	8.07	4.12	1.96	0.06	
		Hook removal	−3.75	2.13	−1.76	0.09	
	RAMP (adj $R^2 = 0.04$)	(Intercept)	0.20	0.16	1.26	0.22	
		Injury	0.20	0.13	1.54	0.13	
Fork length <50 cm ($n = 65$)	Lactate (adj $R^2 = 0.08$)	(Intercept)	2.33	0.38	6.12	0.00	***
		Handling time	0.00	0.00	2.26	0.03	*
		Fight time	0.01	0.00	2.02	0.05	*
		Hook removal	−0.20	0.11	−1.82	0.07	
	Glucose (adj $R^2 = 0.02$)	(Intercept)	59.79	2.59	23.10	<2e-16	***
		Bleeding	−5.56	3.94	−1.41	0.16	
	RAMP (adj $R^2 = 0.07$)	(Intercept)	−0.52	0.41	−1.25	0.21	
		Length	0.02	0.01	1.84	0.07	
		Injury	0.09	0.05	1.73	0.09	
Fork length ≥50 cm ($n = 97$)	Lactate (adj $R^2 = 0.28$)	(Intercept)	0.71	0.52	1.38	0.17	
		Fight time	0.01	0.00	5.42	0.00	***

(Continues)

TABLE 3 (Continued)

Group	Dependent variable	Independent variable	Estimate	Std. error	*t* value	Pr(>|*t*|)	
		Handling time	0.00	0.00	2.56	0.01	
		Water temperature	0.08	0.03	2.50	0.01	*
	Glucose (adj $R^2 = 0.02$)	(Intercept)	55.84	2.75	20.32	<2e-16	***
		Fight time	0.04	0.02	1.76	0.08	
	RAMP (adj $R^2 = 0.14$)	(Intercept)	−0.36	0.36	−0.99	0.33	
		Bleeding	0.22	0.07	3.30	0.00	**
		Water temp	0.02	0.01	2.28	0.03	*
		Length	0.01	0.01	1.40	0.16	
Water temperature <10°C ($n = 118$)	Lactate (adj $R^2 = 0.24$)	(Intercept)	1.69	0.26	6.42	0.00	***
		Fight time	0.01	0.00	4.34	0.00	***
		Handling time	0.00	0.00	3.73	0.00	***
	Glucose (adj $R^2 = 0.06$)	(Intercept)	74.55	5.77	12.92	0.00	***
		Water temperature	−2.27	0.79	−2.86	0.01	**
	RAMP (adj $R^2 = 0.08$)	(Intercept)	0.23	0.04	5.34	0.00	***
		Bleeding	0.17	0.06	2.72	0.01	**
		Injury	0.07	0.04	1.63	0.11	
Water temperature ≥10°C ($n = 44$)	Lactate (adj $R^2 = 0.27$)	(Intercept)	3.26	0.77	4.21	0.00	***
		Fight time	0.01	0.00	4.26	0.00	***
		Body condition	−0.66	0.41	−1.62	0.11	
	Glucose (adj $R^2 = 0.38$)	(Intercept)	56.48	12.94	4.36	0.00	***
		Fight time	0.10	0.04	2.50	0.02	*
		Body condition	12.33	4.95	2.49	0.02	*
		Length	−0.62	0.23	−2.74	0.01	**
		Bleeding	−8.66	3.27	−2.65	0.01	*
		Injury	7.95	3.53	2.25	0.03	*
	RAMP (adj $R^2 = 0.28$)	(Intercept)	−0.59	0.30	−1.94	0.06	
		Length	0.01	0.01	2.28	0.03	*
		Air exposure	0.01	0.00	2.68	0.01	*
		Fight time	0.00	0.00	2.38	0.02	*
Fight time ≤90 s ($n = 95$)	Lactate (adj $R^2 = 0.11$)	(Intercept)	2.25	0.21	10.86	0.00	***
		Handling time	0.00	0.00	3.40	0.00	***
		Spawned	−0.32	0.22	−1.41	0.16	
	Glucose (adj $R^2 = 0.06$)	(Intercept)	61.89	6.57	9.43	0.00	***
		Fight time	0.19	0.09	2.21	0.03	*
		Water temperature	−1.01	0.54	−1.85	0.07	
		Hook location	−2.73	1.94	−1.40	0.16	
	RAMP (adj $R^2 = 0.12$)	(Intercept)	0.00	0.09	0.05	0.96	
		Injury	0.15	0.05	3.16	0.00	**
		Fight time	0.00	0.00	2.12	0.04	*
Fight time >90 s ($n = 67$)	Lactate (adj $R^2 = 0.20$)	(Intercept)	0.80	0.70	1.14	0.26	
		Fight time	0.01	0.00	3.88	0.00	***
		Water temperature	0.08	0.04	2.04	0.05	*
		Air exposure	0.01	0.01	1.75	0.08	
	Glucose (adj $R^2 = 0.26$)	(Intercept)	33.84	11.94	2.83	0.01	**
		Water temperature	1.09	0.37	2.93	0.00	**
		Fight time	0.07	0.03	2.69	0.01	**

TABLE 3 (Continued)

Group	Dependent variable	Independent variable	Estimate	Std. error	t value	Pr(>|t|)	
		Body condition	8.80	3.11	2.83	0.01	
		Handling time	0.06	0.02	3.09	0.00	**
		Length	−0.44	0.20	−2.15	0.04	*
		Air exposure	−0.18	0.09	−2.08	0.04	*
	RAMP (adj $R^2 = 0.15$)	(Intercept)	0.15	0.10	1.43	0.16	
		Bleeding	0.20	0.07	2.87	0.01	**
		Water temperature	0.02	0.01	2.47	0.02	*

impaired in 17.28% ($n = 28$), vertical orientation was impaired in 9.26% ($n = 15$), operculum beats were impaired in 1.23% ($n = 2$) and VOR was impaired in 1.23% ($n = 2$). Between initial and final reflex test reductions in impairment were recorded for 31.48% ($n = 51$) of the trout, stable levels of impairment were recorded for 50.00% ($n = 81$) and increased impairment was recorded for 18.52% ($n = 30$).

There were no injuries recorded for 41.36% ($n = 67$) of the tested trout. Minor injuries, such as healed scars (from spawning or previous angling events), small visible punctures or very slight tearing from hooking were present on 46.30% ($n = 75$) of the trout. Moderate injury, such as more extensive scarring or sores from spawning, slight tearing from hooking or damage around the eye was present on 9.26% ($n = 15$) of the trout. Severe injuries, such as puncture wounds from predators and serious lacerations, were present on 3.09% ($n = 5$). No angling-induced bleeding was recorded from 78.40% ($n = 127$) of the trout, some bleeding was recorded from 16.05% ($n = 26$) and lots of bleeding was recorded from 5.56% ($n = 9$). Having spawned in the previous season was correlated significantly with the presence of some level of injury ($r_s = 0.31$, $P < 0.001$) as well as reduced body condition ($r_s = -0.26$, $P < 0.001$).

3.1 | Regression analysis

Fight time was a significant explanatory variable for blood lactate levels overall and in most groups of fish, but was less significant for trout under 50 cm ($t = 5.60$, $P < 0.001$; $t = 2.02$, $P = 0.048$, respectively) and was not a significant explanatory variable for trout where fight time was ≤90 s (Table 3). For fish with longer fight times (>90 s) the relative impacts of other explanatory variables increased, with significant impacts on blood glucose from air exposure, water temperature, length, body condition and fight time ($t = -2.08$, $P = 0.042$; $t = 2.93$, $P = 0.048$; $t = -2.15$, $P = 0.036$; $t = 2.83$, $P = 0.006$; $t = 2.69$, $P = 0.009$, respectively). With fight time >90 s impacts of water temperature and bleeding on RAMP scores also increased ($t = 2.47$, $P = 0.016$; $t = 2.87$, $P = 0.006$, respectively).

Higher water temperatures (≥10°C) increased the influences of bleeding, injury, body condition, fish length and fight time on blood glucose levels ($t = -2.65$, $P = 0.012$; $t = 2.25$, $P = 0.030$; $t = 2.49$, $P = 0.017$; $t = -2.74$, $P = 0.009$; $t = 2.50$, $P = 0.017$, respectively), as well as the influence of air exposure, length and fight time on RAMP scores (Table 3) ($t = 2.68$, $P = 0.011$; $t = 2.28$, $P = 0.028$; $t = 2.38$, $P = 0.022$, respectively). Larger trout (L_F ≥ 50 cm) showed greater influences of water temperature on blood lactate and RAMP score ($t = 2.50$, $P = 0.014$; $t = 2.28$, $P = 0.025$, respectively) than smaller trout (L_F < 50 cm). Trout that showed evidence of having recently spawned had increased influences of handling time, air exposure, length and body condition on blood glucose levels when compared to unspawned fish ($t = 2.63$, $P = 0.014$; $t = -2.54$, $P = 0.017$; $t = 2.21$, $P = 0.036$; $t = 2.64$, $P = 0.013$, respectively).

3.2 | Hooking results

Of the 162 fish tested, 51.85% ($n = 84$) were caught using fly fishing gear with single hooks, 4.94% ($n = 8$) were caught with spinning gear using single hooks and 41.98% ($n = 68$) were caught with spinning gear using treble hooks. Two additional *S. trutta* were captured in landing nets without angling (Table 4). The number of hooks on the lure showed significant positive correlation with hooking location ($r_s = 0.21$, $P = 0.009$). Hooking location and hook removal difficulty were significantly correlated with each other ($r_s = 0.52$, $P < 0.001$) (Table 5). Hooking location and difficulty of hook removal were not significantly correlated with fish length or body condition ($P > 0.05$), but in cases of stapling by treble hooks it was often more challenging to remove the hook from smaller fish. Bleeding showed significant positive correlation with hook location ($r_s = 0.19$, $P = 0.016$) and difficulty of hook removal ($r_s = 0.21$, $P = 0.007$). Occasionally, the large hooks that were favoured by the anglers participating in this study fully pierced the chin or upper jaw of the fish. The exact number of cases where this occurred is not clear, as this damage was not always visible when the researcher received the fish, and as a result quantitative data were not recorded on this phenomenon.

3.3 | Reports of tagged fish

A total of 157 *S. trutta* were tagged during this experiment. As of the end of April 2021, 11 had been recaptured and identified by tag number, and an additional three were recaptured with tags that were unreadable or with tag numbers that were not recorded before the fish was released a second time, making a recapture rate of 8.92%.

TABLE 4 Number of *Salmo trutta* caught by fly angling with single hooks, spin angling with single hooks and spin angling with treble hooks organized by hook location and hook removal difficulty

		Fly		Spin							
		Single hook		Single hook		Treble hook		Spin total		Grand total	
Hook location	Hook removal difficulty	#	%	#	%	#	%	#	%	#	%
Unknown	Total	3	3.6%			2	2.9%	2	2.6%	5	3.1%
	0	3	100.0%			2	100.0%	2	100.0%	5	100.0%
Lip or corner	Total	61	72.6%	6	75.0%	42	61.8%	48	63.2%	109	68.1%
	0	5	8.2%			11	26.2%	11	22.9%	16	14.7%
	1	27	44.3%	3	50.0%	9	21.4%	12	25.0%	39	35.8%
	2	23	37.7%	1	16.7%	13	31.0%	14	29.2%	37	33.9%
	3	6	9.8%	2	33.3%	8	19.0%	10	20.8%	16	14.7%
	4					1	2.4%	1	2.1%	1	0.9%
In-not deep/through chin	Total	15	17.9%	2	25.0%	5	7.4%	7	9.2%	22	13.8%
	0			1	50.0%			1	14.3%	1	4.5%
	1	5	33.3%							5	22.7%
	2	1	6.7%	1	50.0%	1	20.0%	2	28.6%	3	13.6%
	3	6	40.0%			1	20.0%	1	14.3%	7	31.8%
	4	3	20.0%			3	60.0%	3	42.9%	6	27.3%
Deep/Tongue/Gill contact	Total	4	4.8%			10	14.7%	10	13.2%	14	8.8%
	2					4	40.0%	4	40.0%	4	28.6%
	3	4	100.0%			4	40.0%	4	40.0%	8	57.1%
	4					2	20.0%	2	20.0%	2	14.3%
Stapled	Total					7	10.3%	7	9.2%	7	4.4%
	1					1	14.3%	1	14.3%	1	14.3%
	3					2	28.6%	2	28.6%	2	28.6%
	4					3	42.9%	3	42.9%	3	42.9%
	5					1	14.3%	1	14.3%	1	14.3%
Foul	Total	1	1.2%			2	2.9%	2	2.6%	3	1.9%
	0					1	50.0%	1	50.0%	1	33.3%
	1	1	100.0%							1	33.3%
	4					1	50.0%	1	50.0%	1	33.3%
Grand total		84	52.5%	8	5.0%	68	42.5%	76	47.5%	160	100.0%

Note: Hook removal difficulty classifications: 0, falling out on its own; 1, simple pull, not needing to hold onto the fish; 2, some work required, needing to hold the fish; 3, challenging, multiple attempts needed, but no major injury from removal; 4, challenging, multiple attempts needed and lasting injury caused by hook removal; 5, fish unlikely to survive unhooking.

The furthest distance travelled between captures was at least 250 km between Gotland and Estonia over a period of 6 months. The shortest distances were fish recaptured on or near their initial capture site. The shortest elapsed time between captures was 2 days with >15 km travelled. One trout was recaptured in a fish trap in one of the spawning streams on Gotland approximately 80 km from where it was tagged, and then captured again by anglers after an additional 4 months and in the general location of the initial tagging. Only two *S. trutta* were reported as captured by net fishers around Gotland and a net fisher in Estonia reported one.

Of the 11 fish identified by tag number four trout showed no reflex impairment, six showed minor reflex impairment where only a single reflex was impaired and one showed moderate reflex impairment where two reflexes were impaired. In the reflex tests performed after sampling, two of the recaptured trout demonstrated impairment of three reflexes. One of the recaptured fish had an initial hook removal score of 4 (challenging, multiple attempts needed and lasting injury caused by hook removal), four had scores of 3 (challenging, multiple attempts needed, but no major injury from removal) and the other six had scores of 1 or 2. No injuries were recorded at the time of initial capture for four of these recaptured fish, while the other seven were recorded as having minor injuries. Minor bleeding was recorded during the initial capture for only one of these fish.

TABLE 5 Difficulty of hook removal by gear type and number of hooks on lure

	Fly		Spin							
	Single hook		Single hook		Treble hook		Spin total		Grand total	
Hook removal difficulty	#	%	#	%	#	%	#	%	#	%
0	8	9.5%	1	12.5%	14	20.6%	15	19.7%	23	14.4%
1	33	39.3%	3	37.5%	10	14.7%	13	17.1%	46	28.8%
2	24	28.6%	2	25.0%	18	26.5%	20	26.3%	44	27.5%
3	16	19.0%	2	25.0%	15	22.1%	17	22.4%	33	20.6%
4	3	3.6%			10	14.7%	10	13.2%	13	8.1%
5					1	1.5%	1	1.3%	1	0.6%
Total	84	52.5%	8	5.0%	68	42.5%	76	47.5%	160	100.0%

4 | DISCUSSION

Our study revealed that properly performed C&R is likely to have a minimal negative impact on the majority of *S. trutta* caught in the coastal fishery around Gotland, suggesting very low levels of mortality, supported by the number of recaptured *S. trutta* that were reported. In addition, this study indicates that there are a number of circumstances where stress influences for *S. trutta* are compounded, including angling events with higher water temperatures, longer fight times or where a pre-existing injury or recent spawning physically compromises the fish. In these situations, anglers should keep air exposure, handling and fight times to a minimum. Moreover, the use of single rather than treble hooks decreases hooking-related injuries and reduces the amount of handling required to unhook fish. The recapture rate of 8.92% in this study can be compared to a 4% recapture rate for Atlantic salmon *Salmo salar* L. 1758 in a similar study that was paired with radio tagging of fish, which only showed a potential 3% mortality post release, suggesting a higher rate of survival for properly handled *S. trutta* (Thorstad *et al.*, 2003). It is possible that unobserved delayed mortality did occur in this study, as fish were not held after testing to observe mortality rates. However, several of the recaptured *S. trutta* were initially captured and tested under varying combinations of factors that call for additional care on the part of anglers, further supporting the conclusion of *S. trutta* resilience in response to C&R in this fishery.

Increased blood lactate levels were generally associated with fight time, which is consistent with results from other studies of salmonids (Meka & McCormick, 2005; Twardek *et al.*, 2018). Notably longer fight times were also an explanatory variable for higher blood glucose and impaired reflexes of *S. trutta* caught and tested when water temperature was ≥10°C. There was no significant difference in fight time between fly and spin anglers in this study. Anglers sometimes needing to wait for the researcher or others to assist with netting the *S. trutta* can partially explain this. However, it is more likely due to the increased casting distance possible with spin fishing gear and the number of *S. trutta* hooked further from spin anglers offsetting the speed at which it is possible to land angled fish. The use of appropriately sized and rubberized fishing nets to land fish in the study, rather than landing fish by tail grab, is factor that has been shown to reduce fight times in a study of C&R in steelhead *Oncorhynchus mykiss* (Walbaum 1792) angling (Twardek *et al.*, 2018). This net choice for landing *S. trutta* can allow for less air exposure, reduced handling stress for the fish, lower levels of elevated glucose, less fin fraying, scale and mucus loss, as well as the net operating as a recovery bag prior to release (Brownscombe *et al.*, 2013; Liu *et al.*, 2014; Lizée *et al.*, 2018; Twardek *et al.*, 2018).

The small sample size at higher water temperatures (≥14°C, $n = 23$) made it difficult to fully investigate the compounding effects of other factors on stress responses of *S. trutta* caught under such conditions, as air exposure and other influences were limited in an attempt to isolate the impact of water temperature and to reduce the risk of post-release mortality occurring as part of this study. Where post-release mortality of *S. salar* caught in rivers during their spawning migrations has been measured in relation to water temperature, observations have shown marked increases in mortality in cases where the water temperature was over 18°C (Havn *et al.*, 2015). Sub-lethal effects on the behaviour of salmonids have also been recorded at lower water temperatures, with greater post-release downstream movements of *S. salar* occurring when caught and released at 13.0–14.5°C than at 10.0–12.5°C (Thorstad *et al.*, 2003). The increase in the number of independent variables identified as influencing blood glucose and RAMP scores at ≥10°C suggest that these trends would continue compounding stress responses at higher water temperatures. This is consistent with results in several studies of salmonids and other species (Baisez *et al.*, 2011; Keretz *et al.*, 2018; Stålhammar *et al.*, 2014; Van Leeuwen *et al.*, 2020). However, *S. trutta* caught and tested at temperatures ≥14°C were caught in areas with intense wave action that would subsequently have relatively high levels of dissolved oxygen, and which might offset some of the negative impacts of higher water temperature. In addition, the higher water temperature sampling occurred at times of the year when the fish were in prime physical condition and not facing stress related to winter temperatures or spawning, which was evident in the absence of lower body condition scores or having recently spawned.

Many studies of anadromous salmonids and C&R have been performed on fish during their spawning migrations into freshwater, with angling events occurring before reproduction (Havn *et al*., 2015; Lennox *et al*., 2015; Robinson *et al*., 2015; Thorstad *et al*., 2007; Twardek *et al*., 2019; Whitney *et al*., 2019). However, to our knowledge, the impact of angling events on post-spawn fish has not been studied extensively in *S. trutta* or other salmonids. Post-spawn *S. trutta* are often released as their poorer body condition makes them less attractive for consumption, but also as it is expected that an individual that has spawned once will do so again (Blyth & Rönnbäck, 2022). This is supported by evidence of *S. trutta* returning to spawning streams to reproduce several times over the course of their life on Gotland (Gydemo *et al*., 1980; Landergren & Vallin, 1998). Such fish also tend to be longer and more visually distinct due to colouring and males having kypes, which are factors that could increase anglers' motivation to photograph these catches. In this study, post-spawn *S. trutta* were shown to be more sensitive to water temperature, handling time, air exposure, hook location, body condition and length than fish that had not recently spawned. On the other hand, due to generally having poorer body condition than unspawned individuals, these fish tended not to fight as hard, leading to a shorter fight time, which may offset some of the angling-related stress. In this study both fish length and body condition were correlated with longer fight times, which is consistent with other studies (Meka & McCormick, 2005; Thorstad *et al*., 2003). These are both factors that contribute to anglers' desire to take photos of their catch and potentially subject the fish to longer air exposure, more handling and subsequently more stress (Blyth & Rönnbäck, 2022; Lamansky & Meyer, 2016; Roth *et al*., 2018).

Air exposure after extended fight times has been shown to increase mortality in *O. mykiss* and has been demonstrated to be a component of delayed mortality in bull trout *Salvelinus confluentus* (Suckley 1859) (Ferguson & Tufts, 1992; Joubert *et al*., 2020). It has also been shown to increase sublethal behavioural impacts in *S. salar*, measured as downstream movement after release (Thorstad *et al*., 2003). Conversely, a study by Lennox *et al*. (2015) showed similar downstream movement between a control group and *S. salar* experiencing C&R, where air exposure is not mentioned during the C&R events. For the *S. trutta* sampled in this study, the stable values between the initial and final reflex tests for 50.00% of the fish, and the improving reflex scores for an additional 31.48%, suggests that the lack of air exposure during testing may have offset additional stress resulting from this process. This could imply that maintaining little or no air exposure for angled *S. trutta* may have an even greater post-release impact than is suggested by the regression analysis in this study. A suggested air exposure threshold of 10 s or less has been identified as an important means of reducing post-release mortality and sublethal impacts for angled *O. mykiss* in a river fishery during their spawning migration (Twardek *et al*., 2018). Air exposure times for recaptured *S. trutta* in this study were often over this 10 s threshold and the results suggest that it is not the most significant determining factor for the success of C&R in this fishery. However, the 10 s or less threshold would be beneficial in reducing the compounding influences of stress factors on angled *S. trutta* and therefore would be a logical recommendation to follow for this fishery (Cook *et al*., 2015).

Photographing the catch has been shown to increase air exposure in studies of multiple species and fish sizes (Lamansky & Meyer, 2016; Roth *et al*., 2018). One of these studies showed that average air exposure for smaller fish was only 22.5 s, while for larger fish the average total exposure time was 36.0 s (Lamansky & Meyer, 2016). These findings are consistent with observations in the Gotland *S. trutta* fishery during this study and in an earlier survey of *S. trutta* anglers, where smaller fish are often released without being photographed, although they may be exposed to the air during unhooking and the relative challenge of catching *S. trutta* on Gotland may lead some anglers to commemorate the event with photographs regardless of fish size (Blyth & Rönnbäck, 2022). However, even for larger individuals air exposure in the Gotland fishery could be kept relatively low, as anglers are usually in the water with the fish and have the opportunity to keep the fish in the water for unhooking in most circumstances. This is emphasised by the fact that in this study the reflex testing, blood sampling, tagging, length measurements and inspection of the fish for injury could all be performed without exposing the gills of the fish to the air.

A study comparing use of single hooks with both spin and fly-fishing gear showed similar injury rates for trout caught by both gear types, and that differences in hooking injury are more significantly related to whether hooks are barbed or not (Meka, 2004). This supports the conclusion that the difference in hook location and difficulty of removal in this study is related more to the difference in the number of hooks (treble versus single) than to the overall fishing technique. This is in line with a study comparing brook trout *Salvelinus fontinalis* (Mitchill 1814) caught with actively retrieved lures using treble hooks to lures using single hooks that has demonstrated treble hooks being associated with increased rates of deep hooking, bleeding and delayed mortality in *S. fontinalis* (Kerr *et al*., 2017; Nuhfer & Alexander, 1992). Hooking in sensitive locations has been shown to cause higher rates of bleeding in angled salmonids and to be a more of an issue for smaller fish than for larger (Meka, 2004). Although this study does not have the data to support rates of delayed mortality, treble hooks did relate to higher rates of deep hooking, more difficult hook removal and extended handling times, which would negatively influence the success of the release. Further investigation regarding the levels of hooking injury and difficulty of hook removal relative to the hook size for both single and treble hooks would be beneficial for informing gear recommendations in this fishery.

The results of this study indicate several clear drivers of angling-related stress responses for *S. trutta*, but also a high degree of intraspecific variation in which factors appear to be driving reflex impairment and changes to blood chemistry. Some of this variation can be attributed to the lack of control over what was happening to the fish prior to the angling event, and physical challenges around the process of sampling and testing in the field. The use of stepwise multiple regression allowed for the comparison of categorical, ordinal and interval measurement variables with some flexibility in sensitivity to deviations from assumptions of homoscedasticity and perfect normal distribution. This choice of analysis was intended to allow the inclusion of as many variables into the model selection process as was reasonably possible. However, the results generated with this method should only be interpreted as the suggestion of patterns in the drivers of stress responses, each of which warrants further investigation under more controlled situations that would allow for more rigorous hypothesis testing to determine more detailed thresholds for C&R-related drivers of stress in *S. trutta*.

The current regulations in the coastal *S. trutta* fishery show a relatively limited formal focus on improving C&R outcomes for *S. trutta*. However, studies have shown that anglers will improve their behaviour and adopt practices that improve the health of released fish if given appropriate guidance, and that anglers will be more likely to release fish if they think that they know how to handle them properly (Mannheim *et al*., 2018; Stensland *et al*., 2013). In this context, flexible systems of interpersonal sanctioning and the institutionalizing of best practices for C&R have demonstrated the potential to reduce unintended mortality and sublethal impacts on released fish (Chapman *et al*., 2018; Danylchuk *et al*., 2018; Guckian *et al*., 2018). Trends in fishing-related social media in Sweden suggest that this practice is underway in the country, but at this stage standards do not appear to be coordinated between organizations or tailored to the needs of specific fisheries (Hanindyawan Handoko, 2018). Regional projects, such as Retrout, focus on the development and sustainable management of coastal fishing tourism around the Baltic Sea with a focus on *S. trutta* (Nigell, 2020). Within the Retrout project, an ethical code for sustainable interaction with fishery resources has been established for fishing tourism businesses, such as fishing guides (Interreg, 2021). Informing such an ethical code with species-specific best practices for C&R would give an important toolkit to key players and role models in the recreational fishing industry and community. Future work examining the relationships between the sizes of fish caught by anglers, which fish are released and why, and the sizes of *S. trutta* returning to spawning streams would help to clarify and quantify the impacts of current C&R practices and the benefits to fish stocks and anglers that could result from any actions that lead to improved outcomes for released fish.

5 | CONCLUSION

The results of this study indicate that C&R can be used successfully as a management tool in the *S. trutta* fishery around Gotland, with high rates of survival for released fish. The utility of this tool can be enhanced if anglers take particular care to limit cumulative total air exposure to <10 s (including when unhooking, during any photographing of the catch or any other air exposure), reduce handling time and avoid any actions that increase risk of additional injury, such as bringing the fish onto land. These actions are particularly important in angling events with long fight times, water temperatures >10°C or where *S. trutta* show evidence of being physically compromised by injury or having recently spawned. The results also indicate the importance of using appropriately sized single hooks, rather than larger treble hooks, to reduce hooking injury and handling time during unhooking. Further research regarding hook size, and in particular hook gape, would be beneficial before making more detailed recommendations on the ideal gear choice for anglers in this fishery.

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CONFLICTS OF INTEREST

Authors declare no competing interests.

CONTRIBUTIONS

S.A.B. collected, processed and analysed the data, and led the writing of the manuscript. S.D.B. conceptualized and supervised the study, and contributed to data analysis and to writing various drafts of the manuscript.

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REFERENCES

Aas, Ø., Thailing, C. E., & Ditton, R. B. (2007). Controversy over catch-and-release recreational fishing in Europe. In T. J. Pitcher, & C. Hollingworth (Eds.), *Recreational fisheries: ecological, economic and social evaluation* (pp. 95–106). Oxford: Blackwell Publishing Ltd. https://doi.org/10.1002/9780470995402.ch7.

Arlinghaus, R. (2007). Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp, *Cyprinus carpio*, angling in Germany. *Fisheries Management and Ecology*, *14*(2), 161–171. https://doi.org/10.1111/j.1365-2400.2007.00537.x.

Arlinghaus, R., Aas, Ø., Alós, J., Arismendi, I., Bower, S., Carle, S., … Yang, Z.-J. (2020). Global participation in and public attitudes toward recreational fishing: International perspectives and developments. *Reviews in Fisheries Science & Aquaculture*, *1-38*, 58–95. https://doi.org/10.1080/23308249.2020.1782340.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., … Thorstad, E. B. (2007). Understanding the complexity of catch-and-release in recreational fishing: An integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, *15*(1–2), 75–167. https://doi.org/10.1080/10641260601149432.

Baisez, A., Bach, J. M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M., & Laffaille, P. (2011). Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research*, *15*(3), 265–270. https://www.int-res.com/abstracts/esr/v15/n3/p265-270/.

Blicharska, M., & Rönnbäck, P. (2018). Recreational fishing for sea trout—Resource for whom and to what value? *Fisheries Research*, *204*, 380–389. https://doi.org/10.1016/j.fishres.2018.03.004.

Blyth, S., & Rönnbäck, P. (2022). To eat or not to eat, coastal sea trout anglers' motivations and perceptions of best practices for catch and release. *Fisheries Research*.

Brownscombe, J. W., Danylchuk, A. J., Chapman, J. M., Gutowsky, L. F. G., & Cooke, S. J. (2017). Best practices for catch-and-release recreational fisheries – angling tools and tactics. *Fisheries Research*, *3*, 693–705. https://doi.org/10.1016/j.fishres.2016.04.018.

Brownscombe, J. W., Thiem, J. D., Hatry, C., Cull, F., Haak, C. R., Danylchuk, A. J., & Cooke, S. J. (2013). Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula* spp.) following exposure to angling-related stressors. *Journal of Experimental Marine Biology and Ecology*, *440*, 207–215. https://doi.org/10.1016/j.jembe.2012.12.004.

Butler, J. R. A., Radford, A., Riddington, G., & Laughton, R. (2009). Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, *96*(2–3), 259–266. https://doi.org/10.1016/j.fishres.2008.12.006.

Chapman, D. A., Gagne, T. O., Ovitz, K. L., Griffin, L. P., Danylchuk, A. J., & Markowitz, E. M. (2018). Modeling intentions to sanction among anglers in a catch-and-release recreational fishery for golden dorado (*Salminus brasiliensis*) in Salta, Argentina. *Human Dimensions of Wildlife*, *1-8*, 391–398. https://doi.org/10.1080/10871209.2018.1429034.

Cook, K. V., Lennox, R. J., Hinch, S. G., & Cooke, S. J. (2015). Fish out of water: How much air is too much? *Fisheries*, *40*(9), 452–461. https://doi.org/10.1080/03632415.2015.1074570.

Cooke, S. J., & Sneddon, L. U. (2007). Animal welfare perspectives on recreational angling. *Applied Animal Behaviour Science*, *104*(3), 176–198. https://doi.org/10.1016/j.applanim.2006.09.002.

Cooke, S. J., & Suski, C. D. (2005, May 01). Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation*, *14*(5), 1195–1209. https://doi.org/10.1007/s10531-004-7845-0.

Danylchuk, A. J., Danylchuk, S. C., Kosiarski, A., Cooke, S. J., & Huskey, B. (2018). Keepemwet Fishing—An emerging social brand for disseminating best practices for catch-and-release in recreational fisheries. *Fisheries Research*, *205*, 52–56. https://doi.org/10.1016/j.fishres.2018.04.005.

Davis, M. W. (2010). Fish stress and mortality can be predicted using reflex impairment. *Fish and Fisheries*, *11*(1), 1–11. https://doi.org/10.1111/j.1467-2979.2009.00331.x.

Ferguson, R. A., & Tufts, B. L. (1992). Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): Implications for "Catch and Release" fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(6), 1157–1162. https://doi.org/10.1139/f92-129.

Ferter, K., Weltersbach, M. S., Strehlow, H. V., Volstad, J. H., Alos, J., Arlinghaus, R., … Veiga, P. (2013). Unexpectedly high catch-and-release rates in European marine recreational fisheries: implications for science and management. *ICES Journal of Marine Science*, *70*(7), 1319–1329. https://doi.org/10.1093/icesjms/fst104.

Gale, M. K., Hinch, S. G., & Donaldson, M. R. (2013). The role of temperature in the capture and release of fish. *Fish and Fisheries*, *14*(1), 1–33. https://doi.org/10.1111/j.1467-2979.2011.00441.x.

Guckian, M. L., Danylchuk, A. J., Cooke, S. J., & Markowitz, E. M. (2018). Peer pressure on the riverbank: Assessing catch-and-release anglers' willingness to sanction others' (bad) behavior. *Journal of Environmental Management*, *219*, 252–259. https://doi.org/10.1016/j.jenvman.2018.04.117.

Gundelund, C., Arlinghaus, R., Baktoft, H., Hyder, K., Venturelli, P., & Skov, C. (2020). Insights into the users of a citizen science platform for collecting recreational fisheries data. *Fisheries Research*, *229*, 105597. https://doi.org/10.1016/j.fishres.2020.105597.

Gydemo, R., Nyman, L., & Westin, L. (1980). Gotlandska sjöar och vattendrag—enfiskeribiologisk inventering. *Information fran Sotvattenslaboratoriet* (in Swedish with English abstract), p. 21.

Hanindyawan Handoko, J. R. (2018). *Presence and quality of catch and release information and guidelines on fishing tourism operators' websites in Sweden (Dissertation) Uppsala University*. Sweden: Uppsala. https://www.diva-portal.org/smash/record.jsf?pid=diva2%3A1219986&dswid=-2082.

Havn, T. B., Uglem, I., Solem, Ø., Cooke, S. J., Whoriskey, F. G., & Thorstad, E. B. (2015). The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon *Salmo salar* during spawning migration. *Journal of Fish Biology*, *87*(2), 342–359. https://doi.org/10.1111/jfb.12722.

Interreg. (2021). *Baltic sea fishing ethical code*. Interreg programme Baltic Sea Region. Retrieved January 5, 2022 from https://balticseafishing.com/ethical-code/

Joubert, B. A., Sullivan, M. G., Kissinger, B. C., & Meinke, A. T. (2020). Can smartphones kill trout? Mortality of memorable-sized bull trout (Salvelinus confluentus) after photo-releases. *Fisheries Research*, *223*, 105458. https://doi.org/10.1016/j.fishres.2019.105458.

Keretz, K. R., Dinken, C. P., Allen, P. J., Colvin, M. E., & Schramm, H. L. (2018). The effect of water temperature, angling time, and dissolved oxygen on the survival of Largemouth Bass subjected to simulated angling and tournament handling procedures. *North American Journal of Fisheries Management*, 38, 606–622. https://doi.org/10.1002/nafm.10058.

Kerr, S. M., Ward, T. D., Lennox, R. J., Brownscombe, J. W., Chapman, J. M., Gutowsky, L. F. G., … Cooke, S. J. (2017). Influence of hook type and live bait on the hooking performance of inline spinners in the context of catch-and-release brook trout *Salvelinus fontinalis* fishing in lakes. *Fisheries Research*, *186*, 642–647. https://doi.org/10.1016/j.fishres.2016.10.001.

Lamansky, J. A., & Meyer, K. A. (2016). Air exposure time of trout released by anglers during catch and release. *North American Journal of Fisheries Management*, *36*(5), 1018–1023. https://doi.org/10.1080/02755947.2016.1184200.

Landergren, P., & Vallin, L. (1998). Spawning of sea trout, *Salmo trutta* L., in brackish waters—lost effort or successful strategy? *Fisheries Research*, *35*(3), 229–236. https://doi.org/10.1016/S0165-7836(98)00073-3.

Lawrence, M. J., Raby, G. D., Teffer, A. K., Jeffries, K. M., Danylchuk, A. J., Eliason, E. J., … Cooke, S. J. (2020). Best practices for non-lethal blood sampling of fish via the caudal vasculature. *Journal of Fish Biology*, *97*(1), 4–15. https://doi.org/10.1111/jfb.14339.

Lennox, R. J., Uglem, I., Cooke, S. J., Næsje, T. F., Whoriskey, F. G., Havn, T. B., … Thorstad, E. B. (2015). Does catch-and-release angling alter the behavior and fate of adult Atlantic salmon during upriver migration? *Transactions of the American Fisheries Society*, *144*(2), 400–409. https://doi.org/10.1080/00028487.2014.1001041.

Liu, S., Gao, G., Palti, Y., Cleveland, B. M., Weber, G. M., & Rexroad, C. E., III. (2014). RNA-seq analysis of early hepatic response to handling and confinement stress in rainbow trout. *PLoS One*, *9*(2), e88492. https://doi.org/10.1371/journal.pone.0088492.

Liu, Y., Bailey, J. L., & Davidsen, J. G. (2019). Social-cultural ecosystem services of sea trout recreational fishing in Norway. *Frontiers in Marine Science*, *6*(178), 1–13. https://doi.org/10.3389/fmars.2019.00178.

Lizée, T. W., Lennox, R. J., Ward, T. D., Brownscombe, J. W., Chapman, J. M., Danylchuk, A. J., … Cooke, S. J. (2018). Influence of landing net mesh type on handling time and tissue damage of angled brook trout. *North American Journal of Fisheries Management*, *38*(1), 76–83. https://doi.org/10.1002/nafm.10033.

Mangiafico, S. S. (2015). Multiple Regression. *An R Companion for the Handbook of Biological Statistics, version 1.3.2*. Rutgers Cooperative Extension. https://rcompanion.org/rcompanion/e_05.html pdfversion: rcompanion.org/documents/RCompanionBioStatistics.pdf

Mannheim, S. L., Childs, A.-R., Butler, E. C., Winkler, A. C., Parkinson, M. C., Farthing, M. W., … Potts, W. M. (2018). Working with, not against recreational anglers: Evaluating a pro-environmental behavioural strategy for improving catch-and-release behaviour. *Fisheries Research*, *206*, 44–56. https://doi.org/10.1016/j.fishres.2018.04.016.

McLean, M. F., Litvak, M. K., Stoddard, E. M., Cooke, S. J., Patterson, D. A., Hinch, S. G., … Crossin, G. T. (2020). Linking environmental factors with reflex action mortality predictors, physiological stress, and post-release movement behaviour to evaluate the response of white sturgeon (*Acipenser transmontanus* Richardson, 1836) to catch-and-release angling. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *240*, 110618. https://doi.org/10.1016/j.cbpa.2019.110618.

Meka, J. M. (2004). The influence of hook type, angler experience, and fish size on injury rates and the duration of capture in an alaskan catch-and-release rainbow trout fishery. *North American Journal of Fisheries Management*, *24*(4), 1309–1321. https://doi.org/10.1577/M03-108.1.

Meka, J. M., & McCormick, S. D. (2005). Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fisheries Research*, *72*(2–3), 311–322. https://doi.org/10.1016/j.fishres.2004.10.006.

Nigell, K. (2020). Retrout—arbete över gränserna värnar vår fisk och fisketurism. *Landsbygd i centrum*, *3*, 12–14.

Nuhfer, A. J., & Alexander, G. R. (1992). Hooking mortality of trophy-sized wild brook trout caught on artificial lures. *North American Journal of Fisheries Management*, *12*(3), 634–644. https://doi.org/10.1577/1548-8675(1992)012<0634:HMOTSW>2.3.CO;2.

Policansky, D. (2002). Catch-and-release recreational fishing: a historical perspective. In T. J. Pitcher & C. Hollingworth (Eds.), *Recreational fisheries: ecological, economic and social evaluation* (pp. 74–94). Oxford: John Wiley & Sons.

R Core Development Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Robinson, K. A., Hinch, S. G., Raby, G. D., Donaldson, M. R., Robichaud, D., Patterson, D. A., & Cooke, S. J. (2015). Influence of postcapture ventilation assistance on migration success of adult sockeye salmon following capture and release. *Transactions of the American Fisheries Society*, *144*(4), 693–704. https://doi.org/10.1080/00028487.2015.1031282.

Roth, C. J., Schill, D. J., & Quist, M. C. (2018). Fight and air exposure times of caught and released salmonids from the South Fork Snake River. *Fisheries Research*, *201*, 38–43. https://doi.org/10.1016/j.fishres.2018.01.007.

RStudio Team. (2020). *RStudio: Integrated Development Environment for R*. RStudio, PBC. http://www.rstudio.com/

SMHI. (2021). *Havsvattenstånd, RH 2000: Vlisby* https://www.smhi.se/data/oceanografi/ladda-ner-oceanografiska-observationer/#param=sealevelrh2000,stations=all,stationid=2080

Sportfiskarna. (2020). *Den gotländska öringen*. Sportfiskarna. Retrieved April 19, 2021 from https://www.fiskelandgotland.se/den-gotlandska-havsoringen/

Stensland, S., Aas, Ø., & Mehmetoglu, M. (2013). The influence of norms and consequences on voluntary catch and release angling behavior. *Human Dimensions of Wildlife*, *18*(5), 373–385. https://doi.org/10.1080/10871209.2013.811617.

Stensland, S., Agnarsson, S., Helgason, T., Jóhannesson, G. Þ., Larsen, F., & Aas, Ø. (2017). A survey of resident anglers fishing for salmon, trout and char in Iceland. *MINA fagrapport*, *43*, 172.

Stålhammar, M., Fränstam, T., Lindström, J., Höjesjö, J., Arlinghaus, R., & Nilsson, P. A. (2014). Effects of lure type, fish size and water temperature on hooking location and bleeding in northern pike (*Esox lucius*) angled in the Baltic Sea. *Fisheries Research*, *157*, 164–169. https://doi.org/10.1016/j.fishres.2014.04.002.

Thorstad, E. B., Næsje, T. F., Fiske, P., & Finstad, B. (2003). Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research*, *60*(2), 293–307.

Thorstad, E. B., Næsje, T. F., & Leinan, I. (2007). Long-term effects of catch-and-release angling on ascending Atlantic salmon during different stages of spawning migration. *Fisheries Research*, *85*(3), 316–320. https://doi.org/10.1016/j.fishres.2007.02.010.

Twardek, W. M., Elmer, L. K., Beere, M. C., Cooke, S. J., & Danylchuk, A. J. (2019). Consequences of fishery gear type and handling practices on capture and release of wild steelhead on the Bulkley river. *North American Journal of Fisheries Management*, *39*(2), 254–269. https://doi.org/10.1002/nafm.10267.

Twardek, W. M., Gagne, T. O., Elmer, L. K., Cooke, S. J., Beere, M. C., & Danylchuk, A. J. (2018). Consequences of catch-and-release angling on the physiology, behaviour and survival of wild steelhead *Oncorhynchus mykiss* in the Bulkley River British Columbia. *Fisheries Research*, *206*, 235–246. https://doi.org/10.1016/j.fishres.2018.05.019.

Van Leeuwen, T., Dempson, B., Burke, C., Kelly, N., Robertson, M., Lennox, R., … Bates, A. (2020). Mortality of Atlantic salmon after catch and release angling: assessment of a recreational Atlantic salmon fishery in a changing climate. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(9), 1518–1528. https://doi.org/10.1139/cjfas-2019-0400.

Whitlock, R. E., Kopra, J., Pakarinen, T., Jutila, E., Leach, A. W., Levontin, P., … Romakkaniemi, A. (2016). Mark-recapture estimation of mortality and migration rates for sea trout (*Salmo trutta*) in the northern Baltic sea. *ICES Journal of Marine Science*, *fsw152*, 286–300. https://doi.org/10.1093/icesjms/fsw152.

Whitney, D. W., Meyer, K. A., McCormick, J. L., & Bowersox, B. J. (2019). Effects of fishery-related fight time and air exposure on prespawn survival and reproductive success of adult hatchery steelhead. *North American Journal of Fisheries Management*, 39, 372–378. https://doi.org/10.1002/nafm.10275.

World Bank (2012). In K. Kelleher, L. Westlund, E. Hoshino, D. Mills, R. Willmann, G. de Graaf, & R. Brummett (Eds.). Report No. 66469-GLB *Hidden harvest: The global contribution of capture fisheries*. Washington, DC: International Bank for Reconstruction and Development.

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