Fisheries Research 243 (2021) 106068

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Examining the effects of authentic C&R on the reproductive potential of Northern pike

Henrik Flink [a], Oscar Nordahl [a], Marcus Hall [a], Anton Rarysson [a], Kristofer Bergström [a], Per Larsson [a], Erik Petersson [b], Juha Merilä [c,d], Petter Tibblin [a,c,*]

[a] Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Department of Biology and Environmental Science, Faculty of Health and Life Sciences, Linnaeus University, SE-39231 Kalmar, Sweden
[b] Swedish University of Agricultural Science, Department of Aquatic Resources, Institute of Freshwater Research, Drottningholm, Sweden
[c] Ecological Genetics Research Unit, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
[d] Research Division of Ecology and Biodiversity, Faculty of Science, University of Hong Kong, Hong Kong Special Administrative Region

ARTICLE INFO

Handled by Dr. Steven X. Cadrin

Keywords:
Angling
Migration
Recreational fishing
Reproduction
Stress

ABSTRACT

The practice within recreational fisheries to release captured fish back to the wild, known as catch-and-release (C&R), is an increasingly important strategy to protect fish stocks from overexploitation. However, C&R is a stressor and since animal reproduction is particularly sensitive to stress there is reason to suspect that such a practice induces sublethal fitness consequences. Here, we investigated whether and how C&R fishing influenced the reproductive potential in an anadromous population of Northern pike (*Esox lucius*). First, female pike were exposed to authentic C&R using rod-and-reel fishing in a coastal foraging habitat prior to the spawning period. Next, we observed the migration to the freshwater spawning habitat and compared both the timing of arrival and maturity stage between C&R-treated and control individuals. Finally, to evaluate effects on the quality and viability of eggs we stripped captured control and recaptured C&R-treated females, measured egg dry mass to assess nutrient content, conducted artificial fertilisations and incubated eggs in a controlled laboratory experiment. We found no evidence of C&R causing alterations in either arrival time, maturity stage, or the quality and viability of fertilised eggs. In combination, our results suggest that long-term effects of C&R-induced stress on key reproductive traits of pike, if any, are minor.

1. Introduction

The release of captured individuals within recreational fisheries, a practice known as catch-and-release (hereafter C&R), is becoming increasingly popular to ensure sustainable use of fish populations and to preserve the quality of fisheries (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005). For C&R to be a sustainable alternative to the traditional recreational fishing (catch-and-kill), it requires sufficient survival and successful reproduction of released fish. Many studies show that mortality rates following C&R are generally low (Arlinghaus et al., 2007; Cooke and Suski, 2005; Ferter et al., 2013). However, the consequences of C&R on reproductive potential have rarely been investigated.

A typical C&R event will impose multiple stressors on fish including hooking-related tissue damage, exercise during landing and exposure to adverse air temperatures, oxygen deficiency and gravity during handling. These will trigger a full stress-response, similar to exhaustive exercise, leading to energetic, ionic and hormonal changes (such as elevated cortisol, lactate and glucose levels) (Arlinghaus et al., 2007). Research in stress physiology recognise that animal reproduction is particularly sensitive to stress, an overabundance of cortisol can due to its anti-developmental, anti-growth and immunosuppressive traits have negative long-term effects in fish and their progeny (Campbell et al., 1992; Espmark et al., 2008; Giesing et al., 2011; Schreck et al., 2001). For the period of gonadal development, stressed fish may have to alter the allocation of energy between reproduction, maintenance or somatic growth which can result in delayed ovulation, reduced gamete quality, lowered progeny survival or, in worst case, complete spawning failure

* Corresponding author at: Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Department of Biology and Environmental Science, Faculty of Health and Life Sciences, Linnaeus University, SE-39231 Kalmar, Sweden.
E-mail address: petter.tibblin@lnu.se (P. Tibblin).

https://doi.org/10.1016/j.fishres.2021.106068
Received 1 March 2021; Received in revised form 2 July 2021; Accepted 6 July 2021
Available online 13 July 2021

due to inhibited vitellogenesis or egg atresia (Campbell et al., 1992; Roff, 1982; Schreck et al., 2001; Sopinka et al., 2016). However, whether C&R-induced stress produce such severe effects in wild fish is largely unexplored despite its clear implications for management and sustainable use of fish stocks.

To date, most studies investigating C&R consequences on the recruitment of wild fish have focused on parental care in black bass (*Micropterus* spp.) rather than direct influences of C&R on gonadal development and reproduction. When nest-guarding black bass males is temporarily removed from their nest by C&R it results in nest abandonment, brood predation and thereby reduced reproductive output (*e. g.* Suski et al., 2003; Steinhart et al., 2004; Stein and Philipp, 2015). Remaining studies have, with few exceptions, addressed the effects of C&R on recruitment by studying movement behaviour in salmonids, subjected to C&R during the stressful and energetically taxing spawning migration rather than during the foraging season. These studies have shown ambiguous results revealing either indirect evidence suggesting impaired reproductive output due to alterations in movement behaviour (Thorstad et al., 2007; Richard et al., 2014; Havn et al., 2015; Lennox et al., 2015, 2016, 2017; Twardek et al., 2019; but see Jensen et al., 2010; Smukall et al., 2019 for examples of no effects) or changes in migratory timing (Thorstad et al., 2007; Havn et al., 2015; but see Smukall et al., 2019 for examples of no effects). While there is a small number of studies that have estimated C&R effects on reproductive success more directly, results are disparate suggesting either none (Roth et al., 2019; Smukall et al., 2019) or size dependent negative effects on reproductive outcome with larger individuals being more susceptible than smaller ones (Richard et al., 2013).

Here, we explore C&R effects on key reproductive traits in Northern pike (*Esox lucius*, hereafter referred to as pike), an important target species in recreational C&R fisheries in the northern hemisphere as well as an ecological and socioeconomical key species (Eklöf et al., 2020; Larsson et al., 2015). In contrast to most salmonids, which at time of spawning migration have completed their reproductive investment (King et al., 2003), female pike vitellogenesis and oocyte development continuous up till spawning (Medford and Mackay, 1978). This has consequences for the putative effects of C&R on reproduction since stress-induced impairments are expected to compromise the development of oocytes during vitellogenesis by energy deficiencies and transfer of stress hormones (Schreck et al., 2001). Further, we chose to assess effects of authentic C&R in natural settings, rather than simulating C&R events in controlled environments. While simulation of C&R is a common method and has some benefits, it might obscure potential consequences relevant for the actual implementation of C&R in management. To the best of our knowledge, this is the first non-salmonid study to consider long-term sublethal effects of authentic C&R in natural settings on migratory timing and reproductive potential. Our approach was to subject female pikes to authentic C&R using rod-and-reel fishing in the coastal foraging habitat, prior to the spawning period. After this, we observed the migratory timing to the defined spawning habitat (wetland) using passive integrated transponder tags (PIT) and compared both timing of arrival and maturity stage between C&R-treated and naïve (control) individuals. Finally, to evaluate effects of C&R on the quality and viability of eggs we stripped gametes from C&R-treated and control females recaptured in the spawning habitat using fyke-nets. We assessed the nutrient content in eggs by measuring dry mass and evaluated egg viability by conducting artificial fertilisations and subsequent incubation of eggs in a controlled laboratory experiment.

2. Material and methods

2.1. Study species

Pike is a large-bodied, iteroparous and long-lived species, important as a top predator in freshwater lakes and brackish waters (Donadi et al., 2017; Eklöf et al., 2020). Anadromous pike in the Baltic Sea migrate to spawn in freshwater streams and wetlands between February to May, forming subpopulations geographically separated during early life stages (Nilsson et al., 2014; Tibblin et al., 2015). Since the 1990s many Baltic Sea coastal pike populations have declined, essentially due to recruitment problems, and this has resulted in regulations of recreational fisheries such as fishery closure during spawning season, bag-limit and size window with mandatory C&R (Ljunggren et al., 2010; Nilsson et al., 2019, 2004). The species serve as an established model organism in ecology and evolution (Forsman et al., 2015) and its homing behaviour support studies of reproductive potential in wild fish by enabling recapture of ripe individuals prior to spawning (Berggren et al., 2016; Tibblin et al., 2016a, 2015). Pike is one of the most popular target species in recreational fisheries in Fennoscandia and pike fishing during late winter is particularly popular (Swedish Agency for Marine and Water Management, 2019). One reason for this is that large numbers of pike aggregate in shallow waters during winter and thereby become easily accessible for anglers. Also, this is prior to spawning and the females are then close to their maximum weight. Pike is considered to be relatively resilient to C&R fishing and previous studies have found low direct mortality (Arlinghaus et al., 2008, 2009; Baktoft et al., 2013; Klefoth et al., 2008; Muoneke and Childress, 1994; Stålhammar et al., 2014).

2.2. Study area

We conducted C&R fishing in three adjacent bays at the Baltic Sea shore of Öland, Sweden (Fig. 1). This area is known to harbour a population of anadromous pike that use the coastal habitat for foraging and, at time of spawning, migrate through a small stream (~350 m long, < 3 m wide and average depth of < 50 cm) to reach their spawning habitat: the wetland Harfjärden (N 56° 49′ 15.6″; E 16° 48′ 32.7″). We chose this study area based on low recreational fishing pressure such that pike will be naïve to prior C&R experience, in combination with extensive background knowledge on population dynamics and migratory behaviour from previous studies (Nordahl et al., 2019; Sunde et al., 2018a, 2018b, 2019). In addition, the small stream allows robust detection of migrating PIT-tagged fish and can be entirely closed off with a fyke-net. To confirm our assumption of low recreational fishing pressure in the area we performed continuous monitoring (35 visits) of the study area between October 2019 to February 2020. No pike fishing was observed in the study area during these visits. Throughout the sampling period, two temperature loggers (HOBO Pendant) were placed in the wetland at potential spawning grounds to hourly track the water temperature (Fig. 2b).

2.3. Catch-and-release treatment

We C&R a total of 87 female pike (total length 66.7 ±9.0 cm, mean ± s.d.) between 30 October 2019 to 18 February 2020 in 15 separate fishing efforts. We fished either from boat or the shore, by actively casting with spinning rod and reel, using artificial hard- or soft lures. All fish were captured in depths less than 1.5 m, thus excluding potential effects of barotrauma. C&R followed the common procedure regarding landing (Cooke and Suski, 2005); captured pike were landed swiftly (average landing time was 42 s) in a rubber net and, if possible, handled under water whilst unhooked with pliers.

Following unhooking, focal fish was handled above water to mimic the procedure of documentation (photographs and measurements of length and weight). The handling time was on average 2.5 min, which is similar (but in the higher end) to previous C&R studies on pike (Arlinghaus et al., 2009; Dubois et al., 1994). During this time, we also recorded length (total length, nearest cm) and inserted a PIT-tag (23.1 mm long and 3.85 mm in diameter, model HDX23, Biomark, Boise, Idaho, USA). To minimise the risk of damaging reproductive organs, PIT-tags were inserted under the pelvic girdle rather than in the body cavity, using a sterile needle mounted on an injector. After the marking

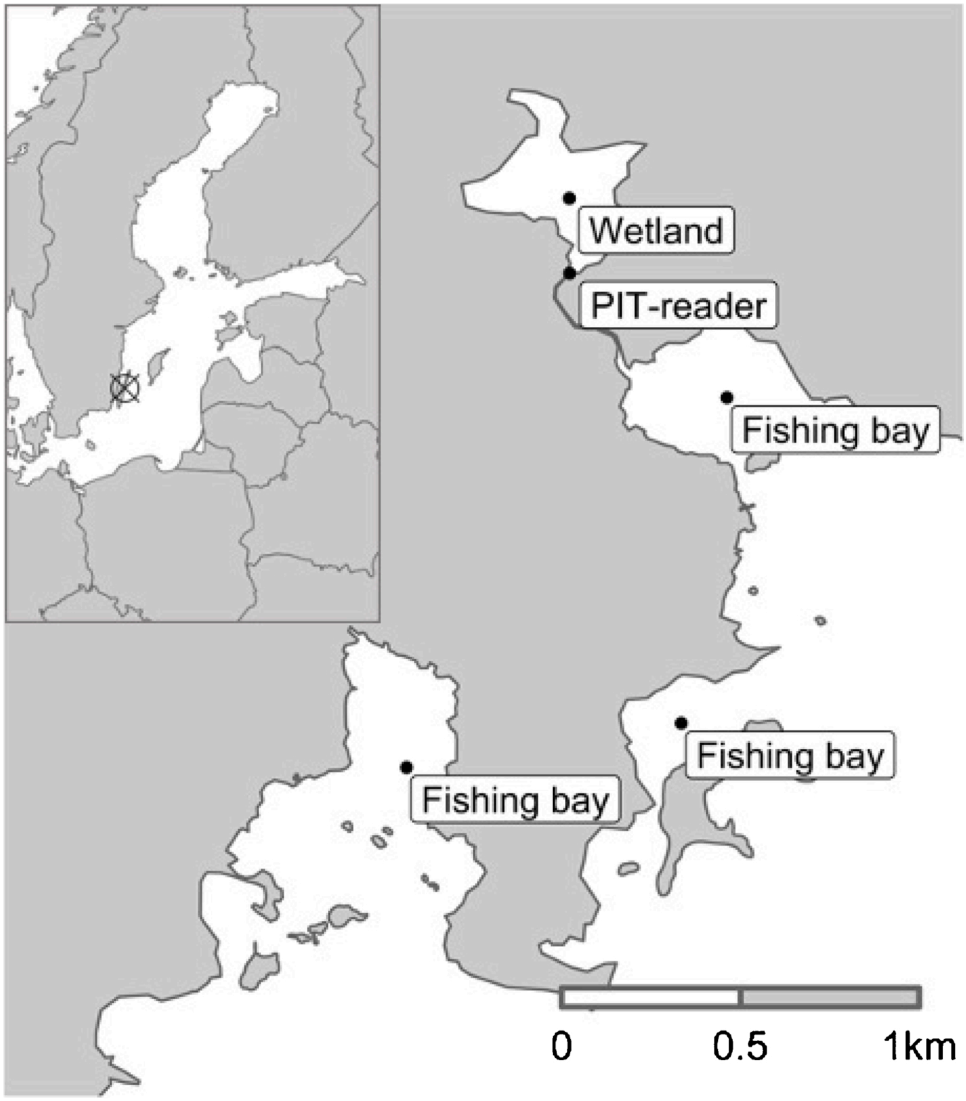

Fig. 1. Study site. Map of the study area at the Baltic Sea shore of Öland, Sweden. Map includes the three bays in which pike were caught-and-released, the freshwater wetland to which pike migrate and spawn as well as the outlet pool of the wetland were a swim-through PIT-tag reader was installed.

procedure all pike were released back to the water. There were cases of multiple C&R events for individual fish. Eight pikes were subjected to C&R twice and one pike was C&R three times. Out of the individuals C&R-treated twice, three were included in the analyses of migration timing and maturity stage, the rest were not detected at the wetland (except for one individual partially detected, see below for explanation). All other analyses were only based on single C&R individuals.

2.4. Swim-through PIT-tag reader to monitor spawning migratory timing

To evaluate influences of C&R on migratory timing, we placed a PIT-tag reader station directly downstream from the outlet pool of the wetland (Fig. 1). The PIT-tag reader was installed February 14, 2020, but a proportion (n = 20) of tagged and C&R-treated females had already migrated to the wetland or failed to be detected at arrival as evidenced by their subsequent downstream migration. The PIT-tag reader was removed April 24, thirteen days after the last upstream movement had been detected. To estimate timing of arrival of C&R-treated individuals, we included only females for which we could confirm an exact date of upstream migration (n = 39). The PIT-tag reader station consisted of two antennas that enabled determination of migration direction, however due to partial detections of fish (detected by only one of the two antennas), we know that an additionally 6 C&R-treated females migrated to the wetland during the spawning season but the direction of movement could not be determined, and they were subsequently not included in any comparisons.

Tagging of individuals has been conducted in the study area since 2017. Here, we take advantage of previously tagged female pike, with no recent (focal year) experience of C&R, to estimate timing of arrival in control fish (n = 32) during 2020.

2.5. Assessment of maturity stage and stripping of gametes

To capture focal fish for assessment of maturity stage and to strip gametes for egg quality assessment and the artificial fertilisation experiment (see below), we used a stream-wide fyke net that completely shut-off the outlet pool of the wetland between February 23 to March 27, 2020 (Fig. 1). Since a high proportion of females caught during upstream migration were not yet ovulating, the stream-wide fyke net were only used periodically. Additional fyke nets (n = 3) were placed inside the wetland, where the proportion of ovulating females were higher. Fyke nets were emptied daily. Maturity stage, categorised as either pre-spawn condition (not ovulating) or spawn (ovulating)/spent condition, was assessed for all females by applying a gentle pressure on the

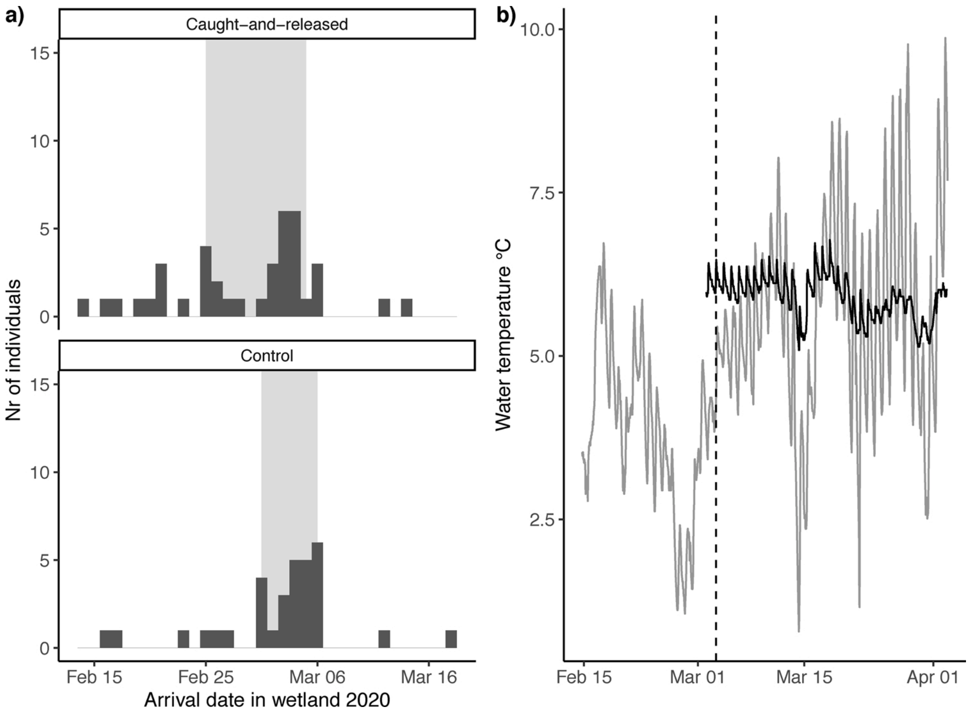

Fig. 2. a) Migration timing. Arrival of caught-and-released and control pike females to the spawning wetland according to PIT-tag detections. The grey background show 25-75 % quartile of arrivals. b) Water temperature. Hourly water temperature in the wetland (grey line) and in the incubation experiment (black line) during the study period. The hourly water temperature for each location is calculated as an average from two temperature loggers. Dashed vertical line show the median arrival date of all females to the wetland.

abdomen.

In total, 10 ovulating C&R-treated females were recaptured and stripped for eggs. Simultaneously to each recapture, ovulating C&R-naïve females (to be used as control) as well as C&R-naïve males were stripped for gametes to produce crossings by artificial fertilisation (details, see below). There was an incident of shortage of ovulating C&R-naïve females, resulting in one less stripped control female and male. Before release back to the wetland, all stripped fish were measured for body length (total length, nearest cm) and, if unmarked, PIT-tagged to ensure that no fish were stripped twice. Body length was similar in C&R-treated (n = 10, total length 69.3 ±10.0 cm) and control females (n = 9, total length 66.6 ±9.0 cm) stripped for artificial fertilisation (two sample t-test, $t_{16.3} = 0.62$, $p = 0.54$). The first batch of eggs from each female was discarded in order to avoid contact with water and a resulting premature opening of the micropyle. Eggs were collected in 10 mL Falcon tubes and milt in 1.25 mL Micro tubes that were put on ice and transported to the laboratory.

2.6. *Artificial fertilisation experiment and measurements of egg quality*

The fertilisation experiment to evaluate effects of C&R on egg viability was carried out at the Linnaeus University, Kalmar Sweden between March 2 to April 2 in a temperature-controlled room, set such that the water (tap water aerated for 48 h) temperature was ~6 °C to mimic natural conditions during spawning according to previous studies (Sunde et al., 2019). Fertilisation was conducted no more than three hours after gamete stripping. To account for potential effects of male sperm quality on fertilisation success and egg viability, milt from each individual male was used to fertilise eggs from both a C&R-treated and the respective control female, resulting in 19 crosses. Each cross was done in two replicates, which were produced by independent artificial fertilisations to reduce effects of random errors on fertilisation and incubation, resulting in a total of 38 experimental units. The fertilisation process for all experimental units followed the method established in Sunde et al. (2018, 2019) by placing ~30 eggs (31 ± 2 eggs) from the focal female in a small porcelain bowl, pipetting an excess of milt (~50 μl) from the focal male on top and adding 1 mL of water from the experimental system to the bowl. The gametes were mixed by a gentle whirl for 2 min, rinsed with water three times to remove excess milt and then immediately transferred to an 800 mL plastic cup filled with water. All cups/experimental units were randomly distributed within the room and two temperature loggers (Hobo Pendant) were placed in unused cups filled with water to get hourly measurements of water temperature during the experiment (Fig. 2b). Photographs of each experimental unit was taken immediately after fertilisation so that the exact number of eggs at start could be quantified. A partial water exchange (75 % of volume) was performed once a day across the experimental system by an automated water drip system and identification and removal of dead eggs were done daily in each replicate to avoid potential confounding effects through effects on the water quality. Dead pike eggs become opaque and are easy to discern, however, unfertilised eggs are discernible first after ~3−5 days when incubated in freshwater (Sunde et al., 2018a). Consequently, it is difficult to visually discriminate between unfertilised eggs and eggs that die during early development. Viability of incubated eggs (estimated as still being alive) was thus analysed by counting viable eggs from a second photograph taken 10–21 days post fertilisation, including also potential unfertilised eggs. Due to the paired design (a single male fertilising eggs from both control and C&R-treated females at same occasion/day) as well as replication within family crossings, this measurement captures the ability of the egg to be fertilised and subsequently develop for a defined period. Although the incubation time until the count of viable eggs varied between families there was no variation in incubation time between treatments due to the paired design.

Dry mass per egg, a proxy of nutrient content and egg quality (Berggren et al., 2016; Murry et al., 2008), was estimated by drying 1 mL of unfertilised eggs from each female in the fertilisation experiment overnight at 60 °C in a heating cabinet. However, two paired samples, one from each treatment, failed (resulting in 9 samples from C&R-treated females and 8 samples from control females). To increase the sample size and robustness of the comparison, eggs from additional C&R-naïve females (n = 9), sampled concurrently, was added resulting in a total of 17 control samples. Body length was similar in C&R-treated (n = 9, total length 67.7 ±8.9 cm) and control females (n = 17, total length 68.9 ±9.7 cm) used for estimating egg quality (two sample t-test, $t_{17.8} = 0.34$, $p = 0.74$). Before drying, eggs from each female were spread out in a single layer on an aluminium baking tin and photographed for quantification of number of eggs (1 mL of eggs amounted to 131 ± 22 eggs). Following drying, each sample of eggs was weighed to the nearest 0.1 mg (BL 210 S Analytical balance, Sartorius, Goettingen) and divided by the number of eggs to calculate dry mass/egg.

2.7. Data analysis and statistics

The software R 4.0.3 (R Core Team, 2020) was used for all statistical analyses. Figures were prepared in R using the packages ggplot2 (Wickham, 2016) and ggmap (Kahle and Wickham, 2013). Photographs of eggs for measurements of dry egg mass and egg viability were analysed using ImageJ software (1.52q) (Schneider et al., 2012). An alpha level of 0.05 was used for all statistical tests.

Timing of arrival to the wetland was examined using median, 25th and 75th percentiles of calendar date for C&R-treated and control females. In addition, a Kolmogorov-Smirnov (KS) test was used to evaluate if timing of arrival, measured as number of days from start of monitoring until arrival of focal fish, differed between C&R-treated and control females.

Contingency tables with Fisher's exact test for count data were used to determine whether stage of maturity, defined as either pre-spawn or spawn/spent, differed between C&R-treated and control females. Analyses were separated for females caught arriving to the wetland and females caught inside the wetland.

ANCOVA was used to test the possible effect of C&R treatment on resource allocation in eggs (dry mass per egg) with female body length treated as a covariate. The nonsignificant interaction term between treatment (C&R *vs* control) and body length was removed from the model. However, the covariate body length was significant and thus kept in the model (ANCOVA, effect of total length: $F_{1,23} = 5.09$, $p = 0.03$).

The influence of C&R treatment on egg viability was analysed using a generalised linear mixed model (GLMM) in the lme4 package with a binomial fit and a logit-link function. The response variable was the number of viable eggs at the end of incubation out of the total number of eggs at start of incubation. The treatment of females (C&R *vs* control) was treated as a fixed factor. To account for replication within family crossings, individual families were included in the model as a random effect. Parameter estimates and associated statistical significance levels of the random effect are not reported since we were not interested in quantifying these effects as such.

3. Results

3.1. Migration timing

In total, 60 out of 87 (69 %) C&R-treated females were confirmed by detection of their PIT-tags to arrive at their spawning habitat in the wetland. C&R-treated females had their peak arrival, *i.e.* the time period when 50 % of the individuals arrived, between February 25 to March 4, 2020 (n = 39, median = March 2) (Fig. 2a). In comparison, PIT-tagged females that had not been subjected to C&R in this study (control females) had an overlapping peak of distribution at March 1–5 (n = 32, median = March 4). There was no significant difference between C&R-treated and control females in time of arrival (two sample KS-test, $D = 0.25$, $p = 0.20$).

3.2. Maturity stage

The maturity stage of C&R-treated and control females did neither differ significantly at arrival to the wetland (C&R-treated: n = 10, 80 % pre-spawn, control: n = 66, 72 % pre-spawn, Fisher's exact test: odds ratio = 0.67, $p = 1$) nor inside the wetland (C&R-treated: n = 14, 7% pre-spawn, control: n = 74, 24 % pre-spawn, Fisher's exact test: odds ratio: 4.13, $p = 0.29$) (Fig. 3).

3.3. Egg quality

Egg quality, measured as dry mass per egg, of C&R-treated (~2.30 mg, confidence interval: 2.14–2.47 mg) and control female pikes (~2.28 mg, confidence interval: 2.16–2.39 mg) did not differ significantly (ANCOVA, effect of C&R: $F_{1,23} = 0.09$, $p = 0.76$) (Fig. 4a).

3.4. Egg viability

Egg viability was high in both C&R-treated (~93 % viable eggs,

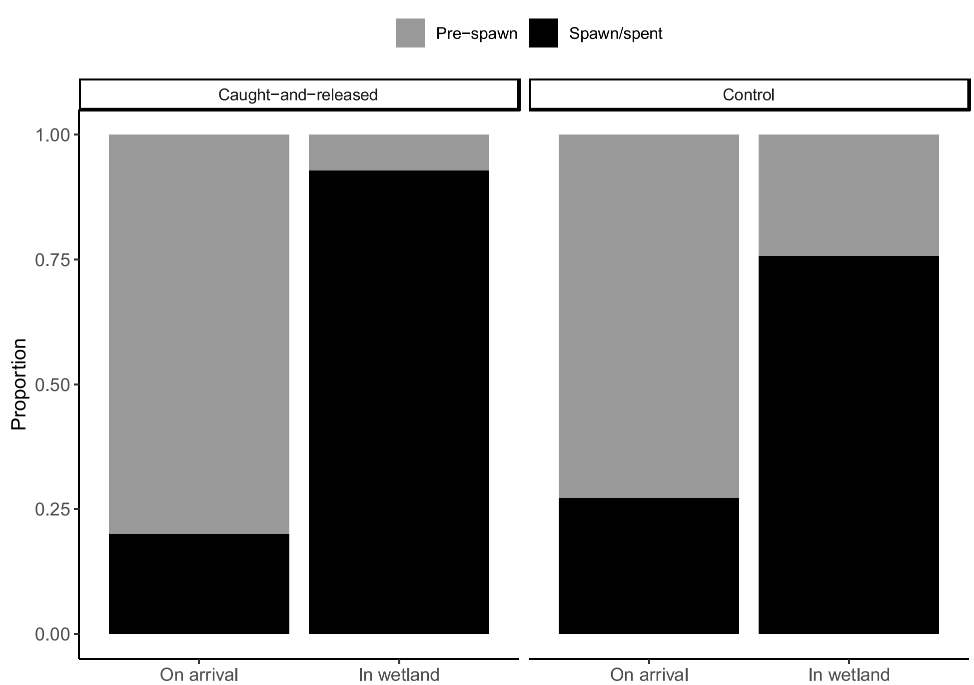

Fig. 3. Maturity stage. Proportion females in pre-spawn and spawn/spent condition, caught either on arrival to the wetland (C&R: n = 10, control: n = 64) or inside the wetland (C&R: n = 14, control: n = 74).

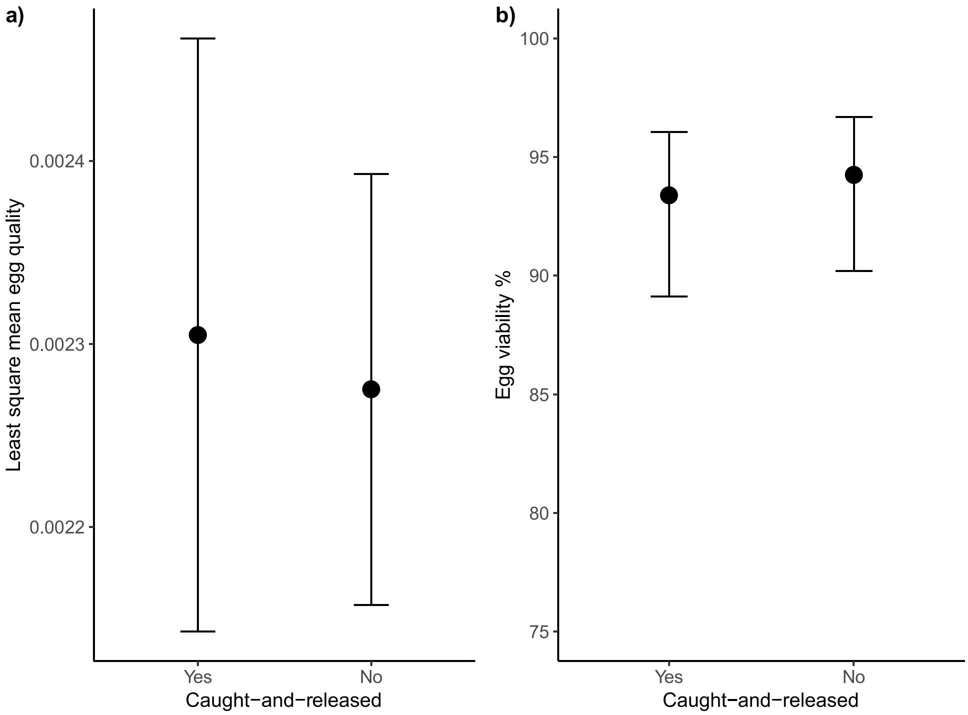

Fig. 4. a) Egg quality. Least square means (adjusted for female body length effect) of dry mass per egg from C&R and control females. Black point represents mean and error bar represents 95 % confidence interval. Note that the scale on the y-axis does not start at zero. b) Egg viability. Percentage egg viability for C&R and control females as predicted from the GLMM model fit, black point represents mean and error bar represents 95 % confidence interval. Note that the scale on the y-axis does not start at zero.

GLMM confidence interval: 89–96 %) and control females (~94 % viable eggs, GLMM confidence interval: 90–97 %). Egg viability did not differ significantly between the groups (GLMM, effect of C&R treatment: $z = 0.38$, $p = 0.71$ (Fig. 4b).

4. Discussion

Fish reproduction is sensitive to stress, accordingly researchers have advocated C&R fisheries to avoid capturing fish immediately before or during the spawning period, until there is firm evidence that there is no C&R-induced negative impacts on recruitment success (Arlinghaus et al., 2007; Cooke and Suski, 2005). Yet, to evaluate reproductive consequences of C&R-induced stress in natural settings is challenging, hence the knowledge and understanding on such effects are inadequate and, adding to the complexity, the few existing studies show disparate results. Our study provides unique and important knowledge by testing such long-term effects of authentic C&R in natural settings in pike during the period of vitellogenesis, whilst oocyte development is susceptible to stress. Although our results suggest that C&R did not impair any of the focal components of reproductive potential in pike, continued cautiousness is required in the implementation of these findings in management.

Arrival timing at spawning sites have clear bearings on the fitness of fish by influencing the survival of both juvenile and adult life-stages (Einum and Fleming, 2000; Tamario et al., 2019; Tibblin et al., 2016b). We anticipated C&R to alter arrival time and maturity stage in anadromous pike due to the anti-developmental and inhibitory reproductive effects of stress hormones. For example, rainbow trout (*Oncorhynchus mykiss*) exposed to acute stress by air exposure have been shown to delay ovulation several weeks (Campbell et al., 1992) and exposure to C&R in rainbow trout leads to a reduction in plasma levels of oestrogens (Pankhurst and Dedualj, 1994). Further, C&R have shown to induce downstream movement and delay upstream spawning migration in Atlantic salmon (*Salmo salar*). However, this is suggested to result from short-term effects on physical recovery, loss of orientation or escape behaviour rather than due to suspended gamete development (Havn et al., 2015; Thorstad et al., 2007). Our results show an overlapping peak arrival of C&R-treated and control females, without any tendency of C&R delaying spawning migration. Similarly, we found no evidence of delayed ovulation in C&R-treated females. Upon arrival to the wetland, 80 % of C&R-treated females were in pre-spawn condition, similar proportion as in control fish. Among fish caught in the spawning grounds only 7% of C&R-treated fish were found in pre-spawn condition, the rest were either ovulating or spent, as expected during a normal spawning event. Our results are in accordance with pond-based studies on Australian bass (*Macquaria novemaculeata*) and golden perch (*Macquaria ambigua*), demonstrating normal gonadal development following simulated C&R, with exception for harshly angled fish (Hall et al., 2017, 2009).

In oviparous (and viviparous) fish, all nutrients essential for embryonal development must be incorporated in the oocyte before ovulation, hence nutrient content of an egg together with the genetic material determines egg quality (Brooks et al., 1997). Rainbow trout exposed to acute stress experience reduced egg size and viability (Campbell et al., 1992). However, consequences of C&R-induced stress on egg nutrient content has prior to our study never been considered. Our results demonstrate no difference in egg dry mass, a proxy of nutrient content in pike eggs (Murry et al., 2008), between C&R-treated and control females. Egg dry mass from C&R-treated individuals was around 2.14–2.47 mg per egg (95 % confidence interval) compared to 2.16–2.39 mg in control females. The observed quality of eggs coheres to the results from our laboratory experiment of fertilised egg viability that showed over 90 % overall egg viability in both C&R-treated and control females. Previous studies on the effects of C&R on fertilised egg viability have been conducted in salmonids using simulated C&R which have generally demonstrated no impacts of C&R (Booth et al., 1995; Pettit, 1977; Smukall et al., 2019). By using authentic C&R in a natural setting rather than simulated C&R we provide additional and unique support of that neither quality nor viability of eggs seem to be significantly reduced by C&R.

Admittedly, the lack of significant statistical effects of C&R on the recruitment potential of pike, in combination with the focal sample sizes, require cautious inferences and implementation of the results. Still, that there were no significant negative effects in any of the investigated responses to C&R (arrival timing, maturity stage, egg quality and egg viability) points to that the negative effects of C&R on pike reproduction are minor although negative effects mediated through other pathways such as atresia cannot be excluded. Moreover, in experimental studies demonstrating reproductive consequences of stress, focal fish have been exposed to repeated acute stress (Campbell et al., 1992; Giesing et al., 2011). In our study only a few fish were captured multiple times and thus we cannot exclude potential additive effects of multiple C&R which may occur in intense C&R fisheries. In the same vein, it is important to note that fish handling in this study was conducted by experts and extreme caution was exercised when handling the fish. It is possible that different handling methods and/or prolonged retention time would have visible effects on reproductive traits.

A possible explanation to that C&R did not result in discernible reproductive impairments could be that female pike is capable of protecting embryos from negative effects of stress by regulating the transfer of stress hormones to oocytes during vitellogenesis, as demonstrated in zebrafish (*Danio rerio*) (Faught et al., 2016). Alternatively, stress induced by C&R might influence the trade-off between reproductive output and somatic growth such that C&R-treated females allocated energy to uphold their reproductive potential but deprioritised self-maintenance and growth (Schreck et al., 2001). To some extent this is supported by a whole-lake C&R experiment that showed reduced growth rates across seven months in C&R-treated pikes (Klefoth et al., 2011). However, such negative effects of C&R on the growth rates of pike could potentially also result in lowered fecundity (Berggren et al., 2016) which emphasis the need of further studies to disentangle the effects of C&R on the growth-reproduction trade-off.

From a fisheries management point of view, our results represent an important finding suggesting that C&R do not represent a stressor with substantial long-term negative consequences on the reproductive potential in pike and subsequent impacts on recruitment and population dynamics. However, such inference of our results rest upon that the direct mortality of C&R is low, that negative effects of somatic growth do not translate into effects on reproduction or that survival in later juvenile life-stages is impaired, and, finally, that there are no additive effects of multiple C&R events or unfavourable handling and must thus be implemented with caution. While pike has shown to be relatively resilient to C&R, there is considerable variation among species in the response to C&R fishing (Muoneke and Childress, 1994) that stress for species-specific management (Cooke and Suski, 2005). As an alternative to traditional catch-and-kill fishing, C&R can play an important role as management tool to aid sustainable fisheries, as shown in wild populations of Atlantic salmon where C&R-treated fish contributes significantly to the total reproductive output (Richard et al., 2013; Thorstad et al., 2003; Whoriskey et al., 2000). As participation in recreational fishing is popular and the practice of C&R increases in many countries (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005), future research on this topic is warranted. For successful management, there is a need to better understand sublethal effects of C&R in general, for example on reproductive traits not covered here such as total reproductive investment, absolute fecundity, spawning competition, hatching rate and fry performance. Future research should also address the effects of C&R on the trade-off between reproduction and somatic growth and try to disentangle how it changes depending on gonadal maturation in females during C&R exposure.

To conclude, we found no evidence of that C&R of pike during prespawn season cause alterations upon spawning in either arrival time, maturity stage, egg quality or egg viability. In combination, our results suggest that C&R-induced stress do not cause significant long-term effects on key reproductive traits. The results are of general interest because we, unlike related studies, exposed females to C&R during vitellogenesis while there is an additional demand of energy and oocytes are susceptible to hormonal impairment. In addition, the study reflects authentic C&R on wild fish in their foraging habitat and evaluates the consequences by field observations in the spawning ground as well as in a controlled laboratory experiment. Although our results are promising in the context of the sustainability of C&R, there is still large gaps of knowledge in our understanding of the consequences of C&R on recruitment, and species- and context-dependence thereof, that needs to be answered for C&R to be unconditionally implemented in fisheries management.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The laboratory was approved as research facility (Dnr 5.2.18–17988/18) and the study was granted ethical approvals (Dnr 168677-2018; Dnr 19359-2019) by the Ethical Committee on Animal Experiments, Swedish Board of Agriculture, in Linköping and Stockholm respectively.

CRediT authorship contribution statement

Henrik Flink: Conceptualization, Project administration, Methodology, Writing - original draft, Writing - review & editing, Formal analysis, Visualization, Investigation. **Oscar Nordahl:** Investigation, Writing - review & editing. **Marcus Hall:** Investigation, Writing - review & editing. **Anton Rarysson:** Investigation, Writing - review & editing. **Kristofer Bergström:** Investigation, Writing - review & editing. **Per Larsson:** Investigation, Resources, Writing - review & editing. **Erik Petersson:** Conceptualization, Writing - review & editing. **Juha Merilä:** Conceptualisation, Writing - review & editing. **Petter Tibblin:** Conceptualization, Project administration, Resources, Methodology, Writing - original draft, Writing - review & editing, Funding acquisition, Supervision, Investigation.

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.

Acknowledgements

We thank Jasper Münnich, Johanna Sunde, Per Koch-Schmidt, Robert Franzén and Jonas Jakobsson for excellent help in the field and the laboratory. We are grateful to the landowners granting us access to the spawning pike sampling site. We thank two anonymous reviewers för valuable comments on earlier drafts of the manuscript. This work was supported by funds kindly provided by the Swedish Research Council FORMAS(grant 2018-00605 to P.T.) the Crafoord Foundation (grant 20190636 to P.T.) and Göte Borgströms Foundation(grant to P. T.).

References

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., 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. Rev. Fish. Sci. Aquac. 15, 75–167. https://doi.org/10.1080/10641260601149432.

Arlinghaus, R., Klefoth, T., Kobler, A., Cooke, S.J., 2008. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. North Am. J. Fish. Manag. 28, 123–134. https://doi.org/10.1577/m06-263.1.

Arlinghaus, R., Klefoth, T., Cooke, S.J., Gingerich, A., Suski, C., 2009. Physiological and behavioural consequences of catch-and-release angling on northern pike (*Esox lucius* L.). Fish. Res. 97, 223–233. https://doi.org/10.1016/j.fishres.2009.02.005.

Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Koed, A., Pedersen, M.W., Svendsen, J.C., Skov, C., 2013. Effects of angling and manual handling on pike behaviour investigated by high-resolution positional telemetry. Fish. Manag. Ecol. 20, 518–525. https://doi.org/10.1111/fme.12040.

Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. 15, 129–154. https://doi.org/10.1007/s11160-005-2175-1.

Berggren, H., Nordahl, O., Tibblin, P., Larsson, P., Forsman, A., 2016. Testing for local adaptation to spawning habitat in sympatric subpopulations of pike by reciprocal translocation of embryos. PLoS One 11, 1–15. https://doi.org/10.1371/journal.pone.0154488.

Booth, R.K., Kieffer, J.D., Davidson, K., Btelak, A.I., Twpts, B.L., 1995. Effects of late-season catch and release angling on anaerobic metabolism, acid-base status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 52, 283–290. https://doi.org/10.1139/f95-029.

Brooks, S., Tyler, C.R., Sumpter, J.P., 1997. Egg quality in fish: what makes a good egg? Rev. Fish Biol. Fish. 7, 387–416. https://doi.org/10.1023/A:1018400130692.

Campbell, P.M., Pottinger, T.G., Sumpter, J.P., 1992. Stress reduces the quality of gametes produced by rainbow trout. Biol. Reprod. 47, 1140–1150. https://doi.org/10.1095/biolreprod47.6.1140.

Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodivers. Conserv. 14, 1195–1209. https://doi.org/10.1007/s10531-004-7845-0.

Donadi, S., Austin, N., Bergström, U., Eriksson, B.K., Hansen, J.P., Jacobson, P., Sundblad, G., Van Regteren, M., Eklöf, J.S., 2017. A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems. Proc. R. Soc. B Biol. Sci. 284 https://doi.org/10.1098/rspb.2017.0045.

Dubois, R.B., Margenau, T.L., Stewart, R.S., Cunningham, P.K., Rasmussen, P.W., 1994. Hooking mortality of northern pike angled through Ice. North Am. J. Fish. Manag. 14, 769–775. https://doi.org/10.1577/1548-8675(1994)014<0769:hmonpa>2.3.co;2.

Einum, S., Fleming, I.A., 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). Evolution 54, 628–639. https://doi.org/10.1111/j.0014-3820.2000.tb00064.x.

Eklöf, J.S., Sundblad, G., Erlandsson, M., Donadi, S., Hansen, J.P., Eriksson, B.K., Bergström, U., 2020. A spatial regime shift from predator to prey dominance in a large coastal ecosystem. Commun. Biol. 3, 1–9. https://doi.org/10.1038/s42003-020-01180-0.

Espmark, Å.M., Eriksen, M.S., Salte, R., Braastad, B.O., Bakken, M., 2008. A note on pre-spawning maternal cortisol exposure in farmed Atlantic salmon and its impact on the behaviour of offspring in response to a novel environment. Appl. Anim. Behav. Sci. 110, 404–409. https://doi.org/10.1016/j.applanim.2007.04.003.

Faught, E., Best, C., Vijayan, M.M., 2016. Maternal stress-associated cortisol stimulation may protect embryos from cortisol excess in zebrafish. R. Soc. Open Sci. 3 https://doi.org/10.1098/rsos.160032.

Ferter, K., Borch, T., Kolding, J., Vølstad, J.H., 2013. Angler behaviour and implications for management - catch-and-release among marine angling tourists in Norway. Fish. Manag. Ecol. 20, 137–147. https://doi.org/10.1111/j.1365-2400.2012.00862.x.

Forsman, A., Tibblin, P., Berggren, H., Nordahl, O., Koch-Schmidt, P., Larsson, P., 2015. Pike *Esox lucius* as an emerging model organism for studies in ecology and evolutionary biology: a review. J. Fish Biol. 87, 472–479. https://doi.org/10.1111/jfb.12712.

Giesing, E.R., Suski, C.D., Warner, R.E., Bell, A.M., 2011. Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. Proc. R. Soc. B Biol. Sci. 278, 1753–1759. https://doi.org/10.1098/rspb.2010.1819.

Hall, K.C., Broadhurst, M.K., Butcher, P.A., Rowland, S.J., 2009. Effects of angling on post-release mortality, gonadal development and somatic condition of Australian bass *Macquaria novemaculeata*. J. Fish Biol. 75, 2737–2755. https://doi.org/10.1111/j.1095-8649.2009.02474.x.

Hall, K.C., Broadhurst, M.K., Butcher, P.A., Cameron, L., Rowland, S.J., Millar, R.B., 2017. Sublethal effects of angling and release on golden perch *Macquaria ambigua*: implications for reproduction and fish health. J. Fish Biol. 90, 1980–1998. https://doi.org/10.1111/jfb.13282.

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. J. Fish Biol. 87, 342–359. https://doi.org/10.1111/jfb.12722.

Jensen, J.L.A., Halttunen, E., Thorstad, E.B., Næsje, T.F., Rikardsen, A.H., 2010. Does catch-and-release angling alter the migratory behaviour of Atlantic salmon? Fish. Res. 106, 550–554. https://doi.org/10.1016/j.fishres.2010.08.013.

Kahle, D., Wickham, H., 2013. Ggmap: spatial Visualization with ggplot2. R J. 5, 144–161.

King, H.R., Pankhurst, N.W., Watts, M., Pankhurst, P.M., 2003. Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. J. Fish Biol. 63, 153–167. https://doi.org/10.1046/j.1095-8649.2003.00137.x.

Klefoth, T., Kobler, A., Arlinghaus, R., 2008. The impact of catch-and-release angling on short-term behaviour and habitat choice of northern pike (*Esox lucius* L.). Hydrobiologia 601, 99–110. https://doi.org/10.1007/s10750-007-9257-0.

Klefoth, T., Kobler, A., Arlinghaus, R., 2011. Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius*) fishery. Knowl. Manag. Aquat. Ecosyst. 1–18. https://doi.org/10.1051/kmae/2011072.

Larsson, P., Tibblin, P., Koch-Schmidt, P., Engstedt, O., Nilsson, J., Nordahl, O., Forsman, A., 2015. Ecology, evolution, and management strategies of northern pike populations in the Baltic Sea. Ambio 44, 451–461. https://doi.org/10.1007/s13280-015-0664-6.

Lennox, R.J., Uglem, I., Cooke, S.J., Næsje, T.F., Whoriskey, F.G., Havn, T.B., Ulvan, E. M., Solem, Ø., Thorstad, E.B., 2015. Does catch-and-release angling alter the behavior and fate of adult Atlantic salmon during upriver migration? Trans. Am. Fish. Soc. 144, 400–409. https://doi.org/10.1080/00028487.2014.1001041.

Lennox, R.J., Cooke, S.J., Diserud, O.H., Havn, T.B., Johansen, M.R., Thorstad, E.B., Whoriskey, F.G., Uglem, I., 2016. Use of simulation approaches to evaluate the consequences of catch-and-release angling on the migration behaviour of adult Atlantic salmon (*Salmo salar*). Ecol. Modell. 333, 43–50. https://doi.org/10.1016/j.ecolmodel.2016.04.010.

Lennox, R.J., Havn, T.B., Thorstad, E.B., Liberg, E., Cooke, S.J., Uglem, I., 2017. Behaviour and survival of wild Atlantic salmon *Salmo salar* captured and released while surveillance angling for escaped farmed salmon. Aquac. Environ. Interact. 9, 311–319. https://doi.org/10.3354/AEI00235.

Ljunggren, L., Sandström, A., Bergström, U., Mattila, J., Lappalainen, A., Johansson, G., Sundblad, G., Casini, M., Kaljuste, O., Eriksson, B.K., 2010. Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift. ICES J. Mar. Sci. 67, 1587–1595. https://doi.org/10.1093/icesjms/fsq109.

Medford, B.A., Mackay, W.C., 1978. Protein and lipid content of gonads, liver, and muscle of northern pike (*Esox lucius*) in relation to gonad growth. J. Fish. Res. Board Canada 35, 213–219. https://doi.org/10.1139/f78-035.

Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. Aquac. 2, 123–156. https://doi.org/10.1080/10641269409388555.

Murry, B.A., Farrell, J.M., Schulz, K.L., Teece, M.A., 2008. The effect of egg size and nutrient content on larval performance: implications to protracted spawning in northern pike (*Esox lucius* Linnaeus). Hydrobiologia 601, 71–82. https://doi.org/10.1007/s10750-007-9267-y.

Nilsson, J., Andersson, J., Karås, P., Sandström, O., 2004. Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden. Boreal Environ. Res. 9, 295–306.

Nilsson, J., Engstedt, O., Larsson, P., 2014. Wetlands for northern pike (*Esox lucius* L.) recruitment in the Baltic Sea. Hydrobiologia 721, 145–154. https://doi.org/10.1007/s10750-013-1656-9.

Nilsson, J., Flink, H., Tibblin, P., 2019. Predator–prey role reversal may impair the recovery of declining pike populations. J. Anim. Ecol. 88, 927–939. https://doi.org/10.1111/1365-2656.12981.

Nordahl, O., Koch-Schmidt, P., Sunde, J., Yıldırım, Y., Tibblin, P., Forsman, A., Larsson, P., 2019. Genetic differentiation between and within ecotypes of pike (*Esox lucius*) in the Baltic Sea. Aquat. Conserv. Mar. Freshw. Ecosyst. 1–13. https://doi.org/10.1002/aqc.3196.

Pankhurst, N.W., Dedualj, M., 1994. Effects of capture and recovery on plasma levels of cortisol, lactate and gonadal steroids in a natural population of rainbow trout. J. Fish Biol. https://doi.org/10.1111/j.1095-8649.1994.tb01069.x.

Pettit, S.W., 1977. Comparative reproductive success of caught-and-released and unplayed hatchery female steelhead trout (*Salmo gairdneri*) from the Clearwater River. Idaho. Trans. Am. Fish. Soc. 106, 431–435. https://doi.org/10.1577/1548-8659(1977)106<431:crsoca>2.0.co;2.

R Core Team, 2020. R: a Language and Environment for Statistical Computing.

Richard, A., Dionne, M., Wang, J., Bernatchez, L., 2013. Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.)? Mol. Ecol. 22, 187–200. https://doi.org/10.1111/mec.12102.

Richard, A., Bernatchez, L., Valiquette, E., Dionne, M., 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 71, 1730–1739. https://doi.org/10.1139/cjfas-2014-0072.

Roff, D.A., 1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39, 1686–1698. https://doi.org/10.1139/f82-225.

Roth, C.J., Schill, D.J., Quist, M.C., High, B., Campbell, M.R., Vu, N.V., 2019. Effects of air exposure during simulated catch-and-Release angling on survival and fitness of yellowstone cutthroat trout. North Am. J. Fish. Manag. 39, 191–204. https://doi.org/10.1002/nafm.10262.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. https://doi.org/10.1038/nmeth.2089.

Schreck, C.B., Contreras-Sanchez, W., Fitzpatrick, M.S., 2001. Effects of stress on fish reproduction, gamete quality, and progeny. Aquaculture 197, 3–24. https://doi.org/10.1016/S0044-8486(01)00580-4.

Smukall, M.J., Shaw, A., Behringer, D.C., 2019. Effect of simulated catch-and-release angling on postrelease mortality and egg viability in sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 76, 2390–2395. https://doi.org/10.1139/cjfas-2018-0426.

Sopinka, N.M., Donaldson, M.R., O'Connor, C.M., Suski, C.D., Cooke, S.J., 2016. Stress indicators in fish. Fish Physiol. Biochem. https://doi.org/10.1016/B978-0-12-802728-8.00011-4.

Stålhammar, M., Fränstam, T., Lindstrom, J., Hojesjö, 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. Fish. Res. 157, 164–169. https://doi.org/10.1016/j.fishres.2014.04.002.

Stein, J.A., Philipp, D.P., 2015. Quantifying brood predation in Largemouth Bass (*Micropterus salmoides*) associated with catch-and-release angling of nesting males. Environ. Biol. Fishes 98, 145–154. https://doi.org/10.1007/s10641-014-0244-9.

Steinhart, G.B., Marschall, E.A., Stein, R.A., 2004. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Trans. Am. Fish. Soc. 133, 121–131. https://doi.org/10.1577/T03-020.

Sunde, J., Tamario, C., Tibblin, P., Larsson, P., Forsman, A., 2018a. Variation in salinity tolerance between and within anadromous subpopulations of pike (*Esox lucius*). Sci. Rep. 8, 1–11. https://doi.org/10.1038/s41598-017-18413-8.

Sunde, J., Tibblin, P., Larsson, P., Forsman, A., 2018b. Sex-specific effects of outbreeding on offspring quality in pike (*Esox lucius*). Ecol. Evol. 8, 10448–10459. https://doi.org/10.1002/ece3.4510.

Sunde, J., Larsson, P., Forsman, A., 2019. Adaptations of early development to local spawning temperature in anadromous populations of pike (*Esox lucius*). BMC Evol. Biol. 19, 1–13. https://doi.org/10.1186/s12862-019-1475-3.

Suski, C.D., Svec, J.H., Ludden, J.B., Phelan, F.J.S., Philipp, D.P., 2003. The effect of catch-and-release angling on the parental care behavior of male smallmouth bass.

Trans. Am. Fish. Soc. 132, 210–218. https://doi.org/10.1577/1548-8659(2003)132<0210:teocar>2.0.co;2.
Swedish Agency for Marine and Water Management, 2019. Recreational Fisheries in Sweden 2019. Statistical Report JO 57 SM 2001.
Tamario, C., Sunde, J., Petersson, E., Tibblin, P., Forsman, A., 2019. Ecological and evolutionary consequences of environmental change and management actions for migrating fish. Front. Ecol. Evol. 7, 1–24. https://doi.org/10.3389/fevo.2019.00271.
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. Fish. Res. 60, 293–307. https://doi.org/10.1016/S0165-7836(02)00176-5.
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. Fish. Res. 85, 316–320. https://doi.org/10.1016/j.fishres.2007.02.010.
Tibblin, P., Forsman, A., Koch-Schmidt, P., Nordahl, O., Johannessen, P., Nilsson, J., Larsson, P., 2015. Evolutionary divergence of adult body size and juvenile growth in sympatric subpopulations of a top predator in aquatic ecosystems. Am. Nat. https://doi.org/10.1086/681597, 000–000.
Tibblin, P., Berggren, H., Nordahl, O., Larsson, P., Forsman, A., 2016a. Causes and consequences of intra-specific variation in vertebral number. Sci. Rep. 6, 1–12. https://doi.org/10.1038/srep26372.
Tibblin, P., Forsman, A., Borger, T., Larsson, P., 2016b. Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. J. Anim. Ecol. 85, 136–145. https://doi.org/10.1111/1365-2656.12439.
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 Am. J. Fish. Manag. 39, 254–269. https://doi.org/10.1002/nafm.10267.
Whoriskey, F.G., Prusov, S., Crabbe, S., 2000. Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoi River, Kola Peninsula, Russian Federation. Ecol. Freshw. Fish 9, 118–125. https://doi.org/10.1034/j.1600-0633.2000.90114.x.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.