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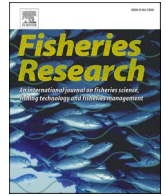
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Anatomical hooking location and bleeding occurrence in northern pike (*Esox lucius*) caught in recreational catch-and-release angling in a lake with reduced prey fish availability

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ABSTRACT

Catch-and-release (C&R) is a common practice in recreational angling for northern pike (*Esox lucius*), whereby the angler releases the fish back into the water after capture with the expectation that it will survive with negligible stress and physical injuries. This may not always be the case, as hooking in critical anatomical locations, such as gills, esophagus, and stomach, increases the frequency of bleeding at the hook wound and has been recognized as a key determinant of post-release mortality in pike. Several factors (e.g. bait type and size, hook characteristics, and fish length) can influence the risk of hooking in critical locations, and the fish's willingness to strike the fishing lure/bait may largely depend on previous feeding history and associated motivation to feed. In this respect, food deprivation and greater feeding motivation can be expected to result in an intensified response and more forceful attacks on fishing lures/baits, which could increase the risk of hooking injuries in sensitive tissues, as the fish may ingest the hook more deeply. Here, we assess the hooking location and bleeding occurrence in pike caught on soft plastic shads and baitfish in a shallow eutrophic lake. The prey fish density of this lake, primarily common roach (*Rutilus rutilus*), has been substantially reduced by seining as part of a lake restoration project. Experimental angling sessions took place at the end of 2020 and 2022, approximately 1–2 months and 25–26 months after the initial reduction in prey fish density, respectively. Removal of roach from the lake was also done regularly by seining after the angling sessions in 2020. Pike angled in 2022 had significantly lower body condition than individuals caught in 2020, indicating that mass removal of roach from the lake resulted in food shortage. The risk of hooking in critical locations (herein defined as hooking in gills and back of mouth) was not associated to angling year, body condition, or length of the pike. However, across the two angling years, the incidence of hooking in critical locations was higher for soft plastic shads compared to baitfish (24.2% versus 7.4%). Pike caught on soft plastic shads also bled more frequently than individuals caught on baitfish (19.7% versus 6.2%), most likely due to the fact that hooking in the gills almost exclusively occurred with soft plastic shads. Bleeding propensity was also not related to angling year, body condition, or fish length. Hence, the present study found no evidence that long-term reductions in food availability and resulting declines in body condition influence how pike strike and ingest fishing lures/baits, at least not in a manner that increases the risk of hooking injuries in sensitive locations. Instead, bait type seems to play the largest role for the observed bleeding patterns. We recommend that future studies investigate the potential effects of C&R angling on the post-release survival of pike with reduced body condition due to limited food availability.

1. Introduction

Recreational angling is widespread and can be a major factor in the exploitation of aquatic resources (Cooke and Cowx, 2006). Impacts of recreational angling on the target fish population may manifest as

reduction in total population abundance, age and size truncation, and even as evolutionary effects through selective harvest (Arlinghaus et al., 2010; Ayllón et al., 2018; Lewin et al., 2006; Post et al., 2002). Moreover, angling often targets predatory fish at the top of the food chain, which can induce trophic cascades and, ultimately, alter the structure

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and functioning of aquatic ecosystems (Altieri et al., 2012).

The northern pike (*Esox lucius*, hereafter termed pike) is a predatory freshwater fish with a circumpolar distribution in the Northern hemisphere (Craig, 1996). Recreational angling for pike is popular and has increasingly been implementing both mandatory and voluntary catch-and-release (C&R), whereby fish are returned to the water shortly after capture with the presumption that most or all released fish will survive and contribute to succeeding generations (Cooke et al., 2013; Jansen et al., 2013; Paukert et al., 2001; Pierce et al., 1995). Based on these premises, C&R has become a widely adapted practice to aid in the management and conservation of wild fish populations (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Cooke et al., 2016; Cooke and Suski, 2005). Previous research has shown that hooking mortality of pike is generally less than 10% in C&R angling (Hühn and Arlinghaus, 2011; Tomcko, 1997), with several studies reporting mortality rates below 5% (Arlinghaus et al., 2008; Burkholder, 1992; Burr, 1998; Trahan et al., 2021). Among other factors, hooking mortality has been associated to the intensity of bleeding during capture, and studies have shown that the anatomical hooking location is an important predictor of bleeding propensity (Arlinghaus et al., 2008; Stålhammar et al., 2014). For instance, bleeding at the hook wound is typically more frequent and severe when pike are hooked in critical locations (e.g. gills and esophagus) compared to hooking in the outer parts of the mouth (Burkholder, 1992; Stålhammar et al., 2014).

Several factors, such as bait type and size, angling technique, and hook characteristics, can influence hooking location and likelihood of bleeding in fish (Arlinghaus et al., 2008; Grixti et al., 2007; Lennox et al., 2015; Stålhammar et al., 2014). While the angler or local management regulations can control the type of terminal gear and angling technique, intrinsic factors (e.g. fish size and maturity status) associated with hooking injury and mortality are largely outside the realm of controllable variables in recreational angling (Arlinghaus et al., 2007; Kuparinen et al., 2010; Muoneke and Childress, 1994). Hunger can increase vulnerability to capture by hooks as hungry fish are usually more motivated to feed and thus easier to capture (Lennox et al., 2017a; Mogensen et al., 2014; Raat, 1991). In addition, fish often display enhanced risk-taking behaviour and food searching activity in response to low prey abundance (Stoner, 2004). Conversely, fish that are satiated may reduce foraging activity and become more selective of prey items (Gill, 2003; Stoner, 2004; Turesson et al., 2006), potentially decreasing capture vulnerability to angling gear. It is also possible that the level of hunger and associated feeding motivation influence how individual fish approach, attack and ingest fishing baits/lures (Fernö et al., 1986; Stoner, 2003). For instance, food deprivation can be expected to result in an intensified response and more forceful attacks towards fishing lures/baits, which could increase the risk of hooking injuries in vital locations due to the fish swallowing the hook more deeply. In this context, past studies have shown that food-deprived whiting (*Merlangius merlangus*) and Atlantic cod (*Gadus morhua*) are more prone to swallow baited hooks in longline fisheries, leading to higher rates of hooking in the esophagus and stomach (Fernö et al., 1986; Johannessen, 1983). However, despite food deprivation being a common stressor in wild fish populations (McCue, 2010), there has been surprisingly little effort to understand whether and to what extent limited food resources impact the fate of individual fish in C&R angling.

In this study, we explore the anatomical hooking location and incidence of bleeding in pike caught on soft plastic shads and baitfish. This research took place in a small eutrophic lake where the density of prey fish, mainly common roach (*Rutilus rutilus*, hereafter termed roach), was gradually reduced by seining as part of a large-scale lake restoration project since fall 2020. Specifically, angling sessions were conducted at the end of 2020 and 2022, approximately 1–2 months and 25–26 months after the initial reduction in prey fish density, respectively. Removal of roach by seining was also performed between the two angling years. We predicted that the continued mass removal of roach would impact the condition factor of pike, such that individuals angled in 2022 should

have lower body condition than those caught in 2020 as they were exposed to reduced food availability for a longer period. Accordingly, we hypothesized that pike in 2022 would be more motivated to feed and therefore attack and ingest the soft plastic shads and baitfish with less caution, which should increase the risk of hooking in critical locations and bleeding from the hook wound. We also expected higher rates of hooking injuries (i.e. bleeding) in sensitive tissues among pike caught on baitfish relative to soft plastic shads, as natural baits tend to hook fish deeper than artificial lures (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Hühn and Arlinghaus, 2011). To put our findings into context, we compared the rates of hooking in critical locations and bleeding observed in our study to those found in existing C&R studies on pike.

2. Methods

2.1. Study area

The study was conducted in Lake Ormstrup (56°19'34'' N, 9°38'21'' E), which is located in the central part of Jutland, Denmark (Fig. 1). It is a shallow eutrophic lake (maximum depth: 5.5 m, mean depth: 3.4 m) with a surface area of 11 ha. Coverage of submerged macrophytes is very low and dominated by curly-leaf pondweed (*Potamogeton crispus*). Lake Ormstrup has a small outlet stream at the western end. The water level in the stream varies seasonally and part of it occasionally dries out to form isolated pools during the summer months. The stream passes several physical barriers that prevent immigration of fish into Lake Ormstrup from downstream areas. The fish community is dominated by roach and pike, but the lake also holds European perch (*Perca fluviatilis*), and very low densities of European eel (*Anguilla anguilla*) and tench (*Tinca tinca*). A mark-recapture analysis, carried out in 2020, showed that the pike population was dominated by individuals larger than 50 cm in total length (TL) with an estimated population size of 384 individuals, corresponding to 29.5 individuals per ha (95% CI: 25.0–36.2). Due to its physical characteristics, the lake has a dynamic mixing regime and alternates between stratified periods and mixing events, especially throughout the summer (Søndergaard et al., 2023). The deterioration of the lake through eutrophication has been ongoing for decades. Initially, it was caused by agricultural runoff and later exacerbated by intensive stocking and subsequent feeding of ducks for hunting. A lake restoration project was initiated in fall 2020 which included removal of roach and tench (i.e. biomanipulation) in attempts to improve water quality.

2.2. Prey fish removal

Removals of roach and tench in Lake Ormstrup occurred between 2020 and 2022 by seining during four intensive sampling periods: fall 2020 (September 22–October 8), spring 2021 (April 12–23), fall 2021 (September 6–17) and summer 2022 (June 13–July 1). At each sampling period, 15–23 seine hauls were undertaken by towing the seine net at various positions in the lake. The seine net was capable of catching fish > 5–6 cm TL. All captured roach and tench were removed from the lake and later used for feed in zoos or energy production in biogas plants, whereas perch and pike were returned to the lake as quickly as possible. Before being released, pike were measured for total length (cm), and weight (g) was taken using a wet weight sling and a handheld scale. Untagged pike were also injected with a 23 mm PIT tag (Texas Instruments, Plano, Texas, USA) in the musculature immediately below the dorsal fin, allowing for individual identification in case of recapture.

Altogether, 6091 kg of roach were removed by 72 seine hauls between 2020 and 2022 (Table 1). Based on subsampling, total catches for different size-classes of roach were as follows: 210 kg (< 6 cm TL), 3497 kg (6–12 cm TL), 2101 kg (12–18 cm TL), 283 kg (> 18 cm TL). Total catches of roach varied between 385 and 4129 kg among the seine sampling periods, and the highest catch occurred in fall 2020. Apart from roach, 129 kg of tench were removed from the lake. A few days

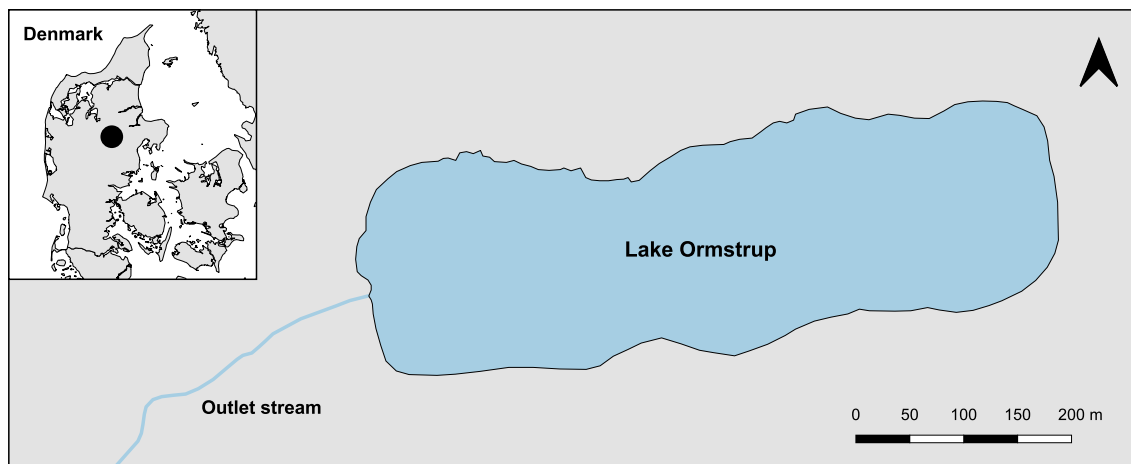


Fig. 1. Map of Lake Ormstrup, Denmark. The location of the lake is indicated by the black circle in the inset.

Table 1

Overview of removal of common roach (*Rutilus rutilus*) and tench (*Tinca tinca*) by seining between 2020 and 2022 in Lake Ormstrup. Number of seine hauls and total catches (kg) of roach and tench are shown for each of the four sampling periods (fall 2020, spring 2021, fall 2021, summer 2022). The percentages of PIT-tagged roach (> 12 cm TL) recaptured during seining are also shown. Associated values in parentheses represent the number of recaptured and PIT-tagged roach, respectively.

	Number of hauls	Roach				Sum	Tench	Recapture rate
		< 6 cm	6–12 cm	12–18 cm	> 18 cm			
Fall 2020	23	33	2707	1243	146	4129	122	66.7 (60/90)
Spring 2021	15	13	330	91	3	437	6	31.8 (42/132)
Fall 2021	17	163	160	706	111	1140	0	37.5 (75/200)
Summer 2022	17	1	300	61	23	385	1	5.7 (10/174)

before each seine sampling period, 90–200 roach (above 12 cm TL) were caught and subsequently tagged with a 23 mm PIT tag in the body cavity before they were released back into the lake. After each seine haul, all captured roach larger than 12 cm TL were scanned for the presence of PIT tags. This allowed us to estimate the proportion of roach that was removed from the lake by seining through mark-recapture analysis. Based on the number of recaptured roach, the estimated reduction in roach density varied from 5.7% to 66.7% among the four seine sampling periods (Table 1).

2.3. Experimental pike angling

Lake Ormstrup is located on a private property and according to the landowner, angling on the lake was very rare in the years before this study. Experimental angling sessions for pike took place at the end of 2020 (November 10–December 17) and 2022 (November 8–30) in boats throughout the lake. Anglers consisted of fisheries biologists and technicians from DTU Aqua with substantial recreational angling experience, and they followed the rules of best practice for C&R such as minimizing fight- and handling times (Brownscombe et al., 2017). In each boat, 2–4 fishing rods were used simultaneously with either artificial lure or natural bait. Artificial lure was a soft plastic shad (19 cm long) fished with a stinger treble hook (size 2 with barbs, Owner ST-36BC) attached to a steel wire. Roach (about 12–17 cm TL) sourced from the lake were used as natural bait. The roach were equipped with one treble hook (size 4 with barbs, Owner ST-36BC) in the snout. A fishing tackle consisting of a float and a lead weight was attached to the main fishing line, allowing the baitfish (i.e. roach) to be suspended at the desired depth. Floats were also used as visual bite indicators and the anglers aimed to set the hook immediately after a strike was detected to avoid artificially increasing the incidence of deep hooking due to the pike swallowing the baitfish. Soft plastic shads were fished by casting, whereas baitfish were slowly trolled behind the boat. Our choices of terminal gear and angling techniques were intended to reflect common

tactics used by anglers targeting pike (Arlinghaus et al., 2017; Bursell and Arlinghaus, 2018). Once hooked, each pike was landed as quickly as possible, either by hand under the opercular cover or using a rubberized fishing net. Hooks were removed from the pike using pliers.

The anglers recorded total length, weight, bait type, anatomical hooking location, and bleeding intensity for each capture. Hooking location was categorized as either non-critical (outer mouth, mouth corner, foul-hooked outside the mouth) or critical (back of mouth, gills) using similar criteria to those developed by Arlinghaus et al. (2008). Bleeding intensity at the hook wound was assigned into one of three categories: none (i.e. no blood), moderate (i.e. blood is present, but only single drops), or substantial (i.e. constant flow of blood). Duration of the fight (i.e. time in seconds from hooking the pike to landing it) was also recorded for all angled pike in 2022. All pike were scanned for PIT tags using a handheld reader, and untagged individuals were PIT-tagged as previously described. Following these procedures, pike were released back into the lake.

2.4. Literature review on hooking location and bleeding occurrence in angled pike

To compare the observed frequencies of hooking in critical locations and bleeding to values from previous C&R studies on pike, we searched candidate literature using standard search strings such as “pike AND angling”, “pike AND catch-and-release”, “pike AND hooking”, and “pike AND bleeding”. Literature searches were done using Clarivate Web of Science and Scopus database in March 2023. Additional searches were performed in Google Scholar, which can help to identify non-indexed literature published as technical reports, academic books, or dissertations (Haddaway et al., 2015). Apart from hooking location and bleeding occurrence, we also extracted information on other potential contributing variables, including bait type and size, hook characteristics, pike length, water temperature, and study site.

2.5. Data analysis

For all analyses, angling year (2020, 2022), hooking location (non-critical, critical), bait type (soft plastic shad, baitfish), and seine sampling period (fall 2020, spring 2021, fall 2021, summer 2022) were treated as categorical variables, while fish length was treated as a continuous variable. Because very few pike exhibited substantial bleeding from being hooked ($n = 2$), bleeding intensity was pooled into presence or absence of blood at the hooking location in the analyses. Thus, bleeding was considered as a categorical variable with two levels.

Length and weight measurements of individual pike captured during seining and angling were used to calculate Fulton's condition factor (K):

$$K = \left(\frac{\text{weight}}{\text{length}^3} \right) \times 100$$

Subsequently, we used a GLM (generalized linear model) with Gaussian distribution and identity link function, followed by Tukey's HSD multiple comparisons test, to assess differences in mean condition factor between pike captured during the seine sampling and angling events. This was done in order to evaluate whether the reduced density of prey fish resulted in food scarcity. If so, the body condition of pike was expected to vary among capture events with a decreasing trend over time. Condition factor was treated as a continuous variable.

A GLM, following a Bernoulli distribution with logit link function, was applied to determine the effects of angling year, bait type, and fish length on hooking location. All possible two-way interactions between these covariates were considered in the full model. Model selection was performed on the interaction terms by comparing nested models using the likelihood ratio test (LRT). By this procedure, non-significant interactions were progressively removed from the model in a backward fashion (i.e. the model was refitted after elimination of the least significant interaction term), but all main effects were retained in the final model, even if they were non-significant (Zuur et al., 2013). All interaction terms were non-significant, and the final model, therefore, included the main effects of angling year, bait type, and fish length on hooking location.

A second Bernoulli GLM was used to examine the effects of angling year, hooking location, and fish length on the risk of bleeding. The full model included all possible two-way interactions between the covariates, and model selection was performed as described above. Bait type was not included as a covariate in the model since exploratory data analyses revealed collinearity between bait type and hooking location. Consequently, the model was carried out separately for soft plastic shads and baitfish. For both bait types, the final model considered the main effects of angling year, hooking location, and fish length on the probability of bleeding. However, to compare bleeding propensity between bait types, we used another Bernoulli GLM with bait type as a covariate and bleeding as the response variable. Along similar lines, the condition factor of the angled pike was associated to angling year and therefore not included as a covariate in the above analyses on hooking location and bleeding. Instead, we used separate Bernoulli GLMs to quantify the

effects of condition factor on hooking location and bleeding probability. The relationship of fight time (treated as a continuous variable) with length and condition factor of the pike angled in 2022 was explored using Gaussian GLMs with identity link function (fight time was not recorded for pike angled in 2020). Lastly, Fisher's exact test was used to compare the incidence of hooking in critical locations and bleeding found in our study with those reported in previous C&R studies on pike. These analyses were conducted separately for pike caught on baitfish and artificial lures.

For individual pike caught and released multiple times within each angling year ($n = 11$ in 2020 and $n = 12$ in 2022), only data from the first capture event was included in the analyses. The reasoning behind this approach is that the first capture event might have altered the short-term behaviour of the pike following release (Arlinghaus et al., 2017, 2009; Baktoft et al., 2013; Stålhammar et al., 2012), which could influence how they subsequently strike and ingest the fishing lure/bait. However, data on individual pike caught in both 2020 and 2022 were maintained in the analyses, as we judged that the capture and release events in 2020 would not affect a similar event in 2022.

Assumptions of homoscedasticity and normality were ensured by graphical inspection of the residuals according to the protocol described in Zuur et al. (2010). Statistical analyses were performed using R version 4.1.2 (R Core Team, 2021). Significance level was set at $p < 0.05$. Results are presented as means \pm SD throughout.

3. Results

3.1. Angled pike

Pike were angled at mean water temperatures of 7.0 ± 2.1 °C (range: 4.5–9.2 °C) in 2020 and 8.7 ± 2.3 °C (range: 5.3–10.7 °C) in 2022. Mean Secchi depth was 2.2 ± 0.4 m and 2.3 ± 0.7 m during angling in 2020 and 2022, respectively.

In 2020, 79 individual pike were successfully angled (Table 2). Of these, 68 individuals were caught once (86%), ten individuals twice (13%), and one individual three times (1%). In 2022, we angled 68 individual pike of which 56 individuals were caught once (82%), eleven individuals twice (16%), and one individual three times (2%). Across bait types, the mean length of angled pike was 72.4 ± 6.8 cm (range: 61–88 cm) in 2020 and 67.1 ± 6.2 cm (range: 56–82 cm) in 2022.

3.2. Condition factor of pike

The analysis showed an overall difference in mean condition factor of pike captured during seining and angling ($F = 59.650$, $df = 5$, $p < 0.0001$). Pike angled in 2022 had significantly lower condition factor than those caught by angling in 2020 and seining in fall 2020, spring 2021, and fall 2021 (Fig. 2). However, the mean condition factor did not differ between pike caught by seining and angling in 2022. Furthermore, the condition factor of pike angled in 2020 was higher than that of conspecifics caught by seining in fall 2021 and summer

Table 2

Number, mean total length (cm), and Fulton's condition factor (K) of northern pike (*Esox lucius*) caught on soft plastic shads and baitfish in Lake Ormstrup during the angling sessions in 2020 and 2022. The table also shows the associated percentages of pike bleeding and hooked in non-critical (outer mouth, mouth corner, foul-hooked outside the mouth) and critical (back of mouth, gills) locations. Values in parentheses are number of pike. Variation in association with mean values is given as \pm SD.

	n	Total length	Condition factor (K)	Hooking location		Bleeding
				non-critical	critical	
2020						
Soft plastic shad	34	74.0 \pm 6.72	0.66 \pm 0.08	76.5 (26)	23.5 (8)	23.5 (8)
Baitfish	45	71.2 \pm 6.72	0.67 \pm 0.05	91.1 (41)	8.9 (4)	4.4 (2)
2022						
Soft plastic shad	32	67.0 \pm 5.08	0.52 \pm 0.10	75.0 (24)	25.0 (8)	15.6 (5)
Baitfish	36	67.2 \pm 7.04	0.55 \pm 0.10	94.4 (34)	5.6 (2)	8.3 (3)

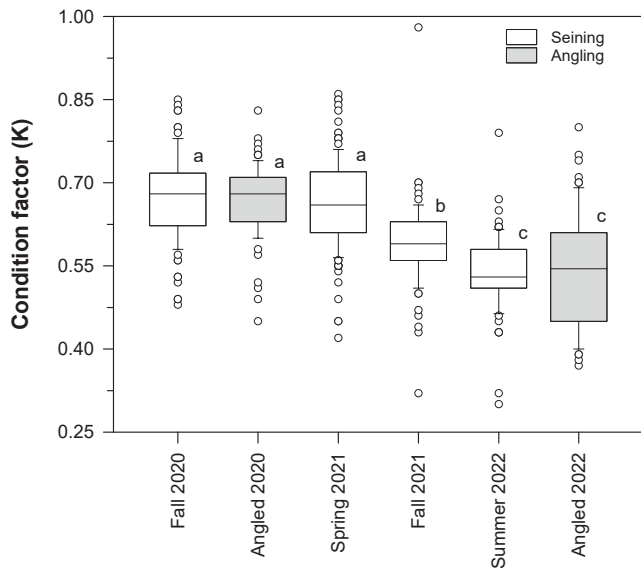


Fig. 2. Boxplot showing Fulton's condition factor (K) of northern pike (*Esox lucius*) caught by seining (fall 2020, spring 2021, fall 2021, summer 2022) and angling (angled 2020, angled 2022) in Lake Ormstrup. Horizontal lines within each box represent the median condition factor, ends of boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and open circles indicate values beyond the 10th and 90th percentiles. Boxes not sharing the same letter are significantly different at $p < 0.05$ (Tukey's HSD multiple comparisons test). Between 73 and 134 individual pike were captured during the four seine sampling periods and the mean lengths were as follows: 70.5 ± 10.0 cm (range: 29–98 cm, $n = 120$) in fall 2020; 71.2 ± 8.2 cm (range: 34–98 cm, $n = 134$) in spring 2021; 70.9 ± 6.5 cm (range: 58–85 cm, $n = 82$) in fall 2021; 70.2 ± 6.2 cm (range: 57–85 cm, $n = 73$) in summer 2022.

2022, while it was statistically similar to those caught by seining in fall 2020 and spring 2021 (Fig. 2).

3.3. Hooking location and bleeding in angled pike

The majority of pike were hooked in the outer mouth (64.6%) followed by mouth corner (18.4%), back of mouth (8.2%), and gills (6.8%) (Fig. 3). Foul-hooking was rare (2.0%) and only occurred with soft plastic shads. All instances of foul-hooking were in the lower jaw, outside the pike's mouth, and thus considered non-critical. The

probability of hooking in critical locations did not differ between angling years (LRT = 0.002, $df = 1$, $p = 0.968$), and was not related to length of the pike (LRT = 0.105, $df = 1$, $p = 0.746$). However, hooking location differed between bait types as pike caught on soft plastic shads were more likely to be hooked in critical locations, especially in the gills, than pike caught on baitfish (LRT = 7.989, $df = 1$, $p = 0.005$; Fig. 3, Table 2). Overall, the incidence of hooking in critical locations was 24.2% and 7.4% for pike caught on soft plastic shads and baitfish, respectively.

Pike caught on soft plastic shads bled more frequently from the hook wound than individuals caught on baitfish (LRT = 6.273, $df = 1$, $p = 0.012$; Fig. 3, Table 2). Bleeding occurred in 19.7% of the captures on soft plastic shads, compared to 6.2% of the pike caught on baitfish. For both bait types, the probability of bleeding was not affected by angling year (soft plastic shad: LRT = 2.029, $df = 1$, $p = 0.154$; baitfish: LRT = 1.699, $df = 1$, $p = 0.192$) or length of the pike (soft plastic shad: LRT = 1.422, $df = 1$, $p = 0.233$; baitfish: LRT = 3.696, $df = 1$, $p = 0.055$). In addition, hooking location was not associated to the probability of bleeding for pike caught on baitfish (LRT = 0.692, $df = 1$, $p = 0.405$). However, pike hooked in critical locations with soft plastic shads were more likely to bleed than conspecifics hooked in non-critical locations (LRT = 10.818, $df = 1$, $p = 0.001$). Condition factor of pike was not a significant predictor of bleeding probability (LRT = 0.189, $df = 1$, $p = 0.664$) or hooking location (LRT = 1.230, $df = 1$, $p = 0.254$). The mean fight time was 51 ± 23 s (range: 8–125 s) across bait types for pike angled in 2022. Fight time was unrelated to length ($F = 0.451$, $df = 1$, $p = 0.504$) and condition factor ($F = 2.545$, $df = 1$, $p = 0.115$) of the pike.

3.4. Literature review on hooking location and bleeding occurrence in angled pike

We identified eight studies on pike that reported hooking location and/or incidence of bleeding in relation to recreational angling (Table 3). Together, these studies included a variety of different bait types and sizes, angling techniques, as well as hook types, sizes, and numbers. Six studies were carried out in natural freshwater lakes and two in brackish water in the Baltic Sea. In two of these studies, pike were captured by ice angling on North American lakes using so-called "tip-ups", consisting of a wooden, plastic, or steel frame with a spool of line that allows the angler to suspend the baited hook at the desired depth below the ice. The spool is attached to a release mechanism that flips a flag above the ice once a fish strikes and swims off with the bait, alerting

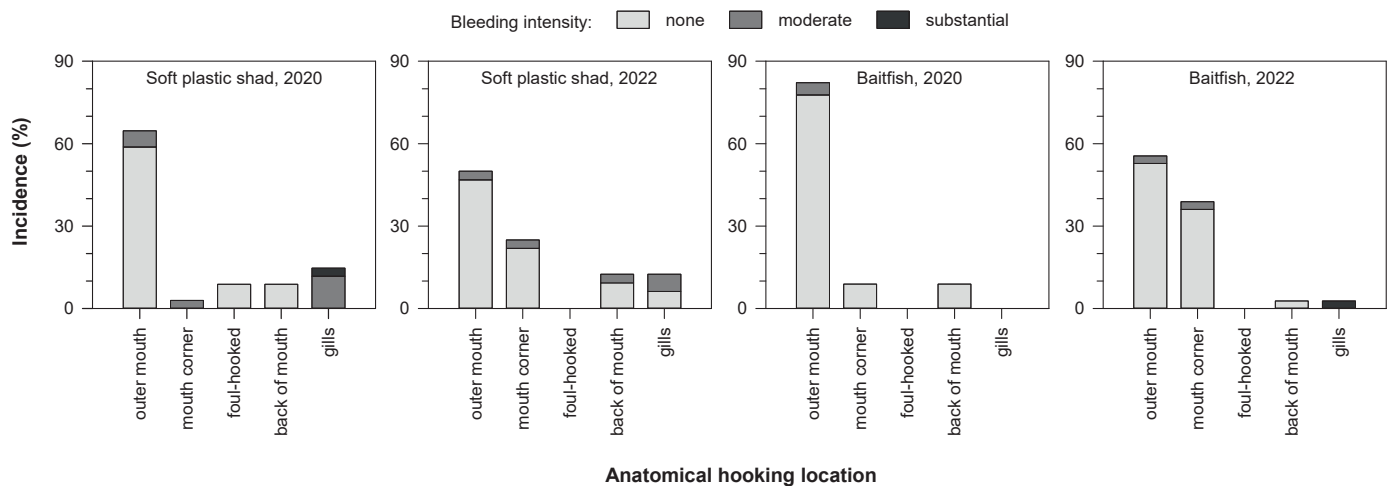


Fig. 3. Incidence (%) of different bleeding intensities at the hook wound in relation to anatomical hooking location among northern pike (*Esox lucius*) caught in Lake Ormstrup on soft plastic shads and baitfish during the angling sessions in 2020 and 2022. Across the two angling years, the incidence of hooking in critical locations (back of mouth, gills) and bleeding was significantly higher for pike caught on soft plastic shads relative to those caught on baitfish.

Table 3

Variables extracted from studies that reported anatomical hooking location and/or frequency of bleeding in angled northern pike (*Esox lucius*), including study site and timing, water temperature, sample size (N), fish length, bait type, and hook characteristics. Studies that did not have the associated data are marked by NA. Length of the pike is reported as total (TL) or fork (FL) length to the nearest cm, and number in brackets indicates the average length. Single hooks are abbreviated as “Single” and treble hooks as “Treble”. If reported, the number of hooks is also shown. NS denotes that hook number and size were not standardized within artificial lures. Definition of hooking in critical locations: a = gills, b= esophagus, c = stomach, d = aorta, e = back of mouth. Scientific names of baitfish species: common bream (*Abramis brama*), common roach (*Rutilus rutilus*), European perch (*Perca fluviatilis*), golden shiner (*Notemigonus crysoleucas*), and white sucker (*Catostomus commersonii*).

Reference	Country	Study site	Study timing	Water temperature (°C)	N	Fish length (cm)	Hook	Bait type	Bleeding (%)	Hooking in critical locations (%)	Characteristics of hook and bait/lure
Current study	Denmark	Lake Ormstrup	Nov-Dec	4.5–10.7	81	56–88 TL	1 Treble	Baitfish	6.2	7.4 ^{a,e}	Baitfish (~ 12–17 cm) and soft plastic shads (19 cm) were equipped with a size 4 and size 2 treble hook, respectively. Treble hooks had barbs. Common roach were used as baitfish.
					66	(70)	1 Treble	Soft plastic shad	19.7	24.2 ^{a,e}	
Althoff et al. (2020) [†]	USA	Lake Grand	Jan	0.9–3.3	65	35–75 TL (51)	Single/Treble	Baitfish	NA	12.3 ^{a,b}	Baitfish (~ 10 cm) were mounted with a treble hook (size 4) or Extra Wide Gap single hook (size 2/0). Golden shiners were used as baitfish.
Arlinghaus et al. (2008)*	Germany, Canada	Lake Kleiner Döllnsee, Lake Opinicon	Summer	NA	39	25–102 TL (51)	2 Treble	Baitfish	22.4	23.1 ^{a,b}	Hook numbers or sizes were not standardized within or across bait types. Lures were equipped with at least one treble hook. Some soft plastic shads and jigs were fished with a single hook and 1–2 treble hooks. Baitfish had two treble hooks. Baitfish species were common roach, European perch and common bream.
					35		NS	Spinner		11.4 ^{a,b}	
					103		NS	Spoon		18.4 ^{a,b}	
					76		NS	Soft plastic shad/jig		13.2 ^{a,b}	
85		NS	Wobbler		7.1 ^{a,b}						
Bursell and Arlinghaus (2018)* *	Denmark, Germany	Baltic Sea	Year round	NA	73	NA	2 Treble	Jerkbait/swimbait	13.7	NA	Size of all lures was 17 ± 3 cm. Lures used tradition hook mount or release-rig. Lures with traditional hook mount had large treble hooks (size 1/0–2/0) and lures with release-rig had small treble hooks (size 6–4). Treble hooks had barbs.
Burkholder (1992)	USA	George Lake	Jun	NA	60	27–94 FL	1 Single	Spoon	25.0	8.3 ^a	No information was available for specific hook sizes.
					60		1 Treble (large)	Spoon	31.7	6.6 ^a	
					62		1 Treble (small)	Spoon	62.9	12.9 ^a	
					60		2 Treble	Wobbler	23.3	1.7 ^a	
DuBois et al. (1994) [†]	USA	Long Lake, Lipsett Lake, Lake Mendota	Dec-Feb	NA	161	33–76 TL (46)	Treble	Baitfish	24.2	17.4 ^{a,b,c}	Size of baitfish was 11–19 cm. The study used barbed treble hooks (size 4). Information about the number of treble hooks is not available. Golden shiners and white suckers were used as baitfish.
Falk and Gillman (1975)* **	Canada	Beaver Lake, Stephanie minesite	Jun-Aug	< 19	94	37–88 FL	Treble	Spoon/wobbler/spinner	42.6	29.0 ^{a,b}	The study used different lures (spoon, wobbler, spinner), equipped with 1–2 treble hooks (with or without barbs).

(continued on next page)

Table 3 (continued)

Reference	Country	Study site	Study timing	Water temperature (°C)	N	Fish length (cm)	Hook	Bait type	Bleeding (%)	Hooking in critical locations (%)	Characteristics of hook and bait/lure
Klefoth et al. (2008)* ** *	Germany	Lake Kleiner Döllnsee	May-Oct	NA	12	48-49 TL (58)	2-Treble	Baitfish	16.7	8.3 ^a	Hook numbers or sizes were not standardized within or across bait types. Lures (8–16 cm) were equipped with at least one treble hook. Some soft plastic shads had a single hook and 1–2 treble hooks. Baitfish (9–23 cm) had two treble hooks. Baitfish species were common roach, European perch and common bream.
					2		NS	Spinner	50.0	0.0 ^a	Lures (8–16 cm) were equipped with at least one treble hook. Some soft plastic shads had a single hook and 1–2 treble hooks. Baitfish (9–23 cm) had two treble hooks. Baitfish species were common roach, European perch and common bream.
					1		NS	Spoon	0.0	0.0 ^a	Lures (8–16 cm) were equipped with at least one treble hook. Some soft plastic shads had a single hook and 1–2 treble hooks. Baitfish (9–23 cm) had two treble hooks. Baitfish species were common roach, European perch and common bream.
					6		NS	Soft plastic shad	0.0	0.0 ^a	Lures (8–16 cm) were equipped with at least one treble hook. Some soft plastic shads had a single hook and 1–2 treble hooks. Baitfish (9–23 cm) had two treble hooks. Baitfish species were common roach, European perch and common bream.
1		NS	Wobbler	0.0	0.0 ^a	Lures (8–16 cm) were equipped with at least one treble hook. Some soft plastic shads had a single hook and 1–2 treble hooks. Baitfish (9–23 cm) had two treble hooks. Baitfish species were common roach, European perch and common bream.					
Stålhamner et al. (2014)	Sweden	Baltic Sea	Mar-Jun	2–22	74	39–113 TL (67)	1-Treble	Bucktail	11.6	17.6 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).
					410		2-Treble	Glider	11.5	10.0 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).
					23		2-Treble	Softbait	4.3	13.0 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).
					198		1-Treble	Spinlyf	19.1	23.7 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).
					106		2-Treble	Tailbait	6.6	7.6 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).
51		2-Treble	Crankbait	7.8	9.8 ^{a,d}	Size of all lures was 18 ± 3 cm. Lures were mounted with barbed treble hooks (size 2/0).					

^aPike were caught by ice angling using so-called “tip-ups” (see main text for further details).

*Data for frequencies of bleeding and hooking in critical locations were extracted from Figure 4 and Table 1, respectively, in Arlinghaus et al. (2008). Bleeding frequency was pooled for artificial lures (i.e. spinner, spoon, soft plastic shad, jig, wobbler) and baitfish.

** Pike were not angled in the protective period (1 April–15 May). Furthermore, bleeding frequency was pooled for artificial lures (jerkbait and swimbait) with traditional hook mount and release-rig (see Bursell and Arlinghaus, 2018 for details). Frequency of bleeding was 33.3% and 4.1% for artificial lures with traditional hook mount and release-rig, respectively.

*** Bleeding frequency was pooled for artificial lures with barbed and barbless treble hooks. Frequency of bleeding was 40.0% and 52.6% for artificial lures with and without barbed hooks, respectively.

**** Data for frequencies of bleeding and hooking in critical locations were extracted from Table 1 in Klefoth et al. (2008), and are estimated for 22 capture events of 16 individual pike.

the angler. Then, the angler grabs the line, sets the hook and pulls the fish by hand through the hole drilled in the ice. Thus, angling with tip-ups is a passive technique. In the remaining studies, pike were targeted using standard rod and reel fishing gear fitted with baitfish or artificial lures (e.g. spoon, spinner, wobbler, soft plastic shad). Artificial lures were either fished by casting and reeling in or trolled behind moving boats, while baitfish were mainly fished passively. Artificial lures and baitfish were predominantly equipped with one or two barbed treble hooks (size 6–2/0). However, some of the larger soft plastic shads and jigs used up to three hooks: one single hook and two treble hooks. Baitfish species were roach, perch, common bream (*Abramis brama*), golden shiner (*Notemigonus crysoleucas*), and white sucker (*Catostomus commersonii*). Based on the accessible data, the size of baitfish ranged between 9 cm and 23 cm (present study: 12–17 cm), whereas the artificial lures measured from 8 cm to 21 cm (present study: 19 cm). However, the study by Arlinghaus et al. (2008) also included artificial lures and baitfish smaller than 7.5 cm.

The mean length of the captured pike was reported in five studies and ranged from 46 cm to 67 cm TL (present study: 70 cm TL across angling year and bait type). Across the different types and sizes of artificial lures, bleeding rates varied between 0% and 62.9% with a grand mean value of 19.4% (present study: 19.7%), and hooking in critical locations (here defined as gills, esophagus, stomach, aorta, and back of mouth) ranged between 0% and 29% with a grand mean value of 13.3% (present study: 24.2%). Fisher’s exact test showed that the risk of hooking the pike in critical locations was significantly higher for the soft plastic shads used in the present study relative to the artificial lures used in the existing studies ($p = 0.017$), whereas no difference was found for bleeding occurrence ($p = 0.999$). For baitfish, the incidence of bleeding ranged from 16.7% to 24.2% with a grand mean value of 23.7% (present study 6.2%), while the rates of hooking in critical locations varied from 8.3% to 23.1% with a grand mean value of 15.9% (present study: 7.4%). The analysis showed that the pike caught on baitfish in our study were less likely to bleed from the hook wound when compared to those caught on different species and sizes of baitfish in the previous studies ($p < 0.001$). However, the risk of hooking in critical locations was not statistically different ($p = 0.094$).

4. Discussion

This study found no evidence that prolonged declines in prey fish availability influence the anatomical hooking location and occurrence of bleeding from the hook wound in pike caught on soft plastic shads and baitfish. Mass removals of roach from Lake Ormstrup most likely resulted in food scarcity as pike angled in 2022 had overall lower body condition relative to individuals caught in 2020. On this basis, we expected that pike in 2022 would exhibit higher motivation to feed and therefore attack and ingest the soft plastic shads and baitfish with less caution, which could increase the rate of hooking injuries in sensitive tissues. However, regardless of bait type, the incidence of hooking in critical locations (i.e. gills and back of mouth) and bleeding was not statistically different for pike angled in 2020 and 2022. In addition, the condition factor of pike was not related to hooking location or bleeding occurrence across the two angling years. These results collectively suggest that extended periods of food scarcity, and resulting declines in body condition, do not cause pike to approach, strike, and ingest fishing lures/baits in a manner that increases the risk of hooking-related bleeding.

Contrary to our expectations, we found that soft plastic shads caused bleeding more frequently than baitfish, most likely due to their increased propensity to hook the pike in critical locations, especially in the gills. Indeed, hooking in the gills was 11.3 times higher for soft plastic shads than baitfish, and 80.0% of the gill-hooked pike bled across both bait types. These results also contradict the general notion that natural baits tend to be ingested more deeply compared to artificial lures, which increases the rates of hooking injuries in sensitive locations

(Arlinghaus et al., 2008, 2007; Bartholomew and Bohnsack, 2005). Natural bait is typically fished passively with a relatively slacked line, giving the fish more time to swallow the bait before the angler sets the hook (Arlinghaus et al., 2007). The striking fish may also recognize the natural bait as a food source, which is thought to induce deep hooking (Arlinghaus et al., 2008). On the other hand, artificial lures are usually fished actively on tight lines and the hook is set instantly after a fish strike, thereby increasing the odds of hooking the fish superficially in the mouth (Brownscombe et al., 2017). However, in our study, the soft plastic shads were fished quite passively as they were allowed to sink towards the bottom before the angler started to retrieve the lure slowly. Moreover, short pauses were regularly added during the retrieve, such that the soft plastic shad dropped slightly back towards the bottom. It is possible that this angling technique enhanced the risk of gill hooking and associated bleeding, since slower moving lures are likely easier for the pike to strike efficiently and swallow. In any case, the anglers noted that some of the pike took the soft plastic shad on the fall rather than during the retrieve. Arlinghaus et al. (2008) also showed that soft plastic shads were more likely to hook pike in critical locations relative to spinners and wobblers, presumably because they were retrieved more passively as well. The authors further suggested that soft plastic shads resemble natural prey more closely than lures made of wood, hard plastic, or metal, which could be an additional aspect facilitating deep hooking. However, another study by Stålhammer et al. (2014) noted that softbaits (i.e. artificial lures made of soft plastic) tended to hook pike in non-critical locations (lip and palate) and reduced the risk of bleeding in comparison to other types of similar-sized lures, especially bucktails (i.e. artificial lures with feather or bucktail hair added to the hook) and spinfly (i.e. artificial fly fished with regular spinning gear). This discrepancy was probably because the softbaits were retrieved at a relatively fast and steady pace. Taken collectively, these results suggest that the angling technique, such as retrieval speed and pattern, with artificial lures may be important for the anatomical hooking location and severity of tissue injuries.

The incidence of hooking in critical locations and bleeding in pike caught on baitfish was at the lower end relative to the values reported in the existing literature. In total, we identified four studies during the literature search that reported hooking location and/or bleeding occurrence in pike caught on baitfish (Althoff et al., 2020; Arlinghaus et al., 2008; DuBois et al., 1994; Klefoth et al., 2008). The fishing gear and angling techniques used in these studies vary from the present study in ways that could help explain the discrepancies in bleeding rates and proportion of critically hooked pike. More specifically, Arlinghaus et al. (2008) included smaller baitfish (< 7.5 cm) than the present study (12–17 cm), which could have increased the frequency of deep hooking, since smaller baits are likely more easily swallowed by pike. Klefoth et al. (2008) used two treble hooks on their baitfish (one placed in the dorsal region and one in the pectoral region), whereas the roach were equipped with one treble hook through the snout in our study. Larger numbers of hook points could increase the risk of hooking the pike in sensitive tissues and therefore offer a potential explanation for the higher bleeding rate reported by Klefoth et al. (2008). In the last two studies, pike were captured through the ice using tip-ups rigged with baitfish (Althoff et al., 2020; DuBois et al., 1994). The wait time from a pike strike until the angler set the hook and started to retrieve the fish was quite long in both of these studies, on average 89 s and 143 s in the studies by DuBois et al. (1994) and Althoff et al. (2020), respectively. This contrasts the angling technique used in our study where the anglers aimed to set the hook immediately after a bite was detected, which probably reduced the incidence of hooking in critical tissues and bleeding from the hook wound.

As noted above, Stålhammer et al. (2014) caught pike on different types of similar-sized artificial lures. The authors found that larger pike were more likely to exhibit substantial bleeding from the hook wound, even though the risk of hooking in critical locations was unrelated to fish size. Based on these results, it was proposed that larger pike fought more

vigorously than smaller individuals, which could have inflicted increased trauma and bleeding of the tissue penetrated by the hook. The present study could not confirm this pattern as the length of the angled pike did not influence fight time or bleeding occurrence regardless of the bait type used. However, our result aligns with Arlinghaus et al. (2008), who also observed no association between bleeding and length of pike caught on baitfish or different types and sizes of artificial lures.

Mortality was not included as an endpoint in our study. However, all angled pike vigorously swam away upon release, except for one individual that died shortly after capture in 2022, suggesting an overall low immediate hooking mortality of 0.7%. The pike that died was not able to maintain an upright orientation and floated at the water surface after release. It was hooked in the corner of the mouth using baitfish and exhibited minor bleeding, i.e. only a few drops of blood were present at the hook wound. Bleeding was, therefore, an unlikely cause of mortality in this case. Notably, the body condition of the pike was very low ($K = 0.42$), belonging to the lowest 10th percentile of all angled individuals. A capture and release event inevitably causes some level of physiological disturbance for fish (Arlinghaus et al., 2007; Kieffer, 2000), and individuals in poor body condition may be more susceptible to such additional stressors (Cook et al., 2012). For instance, capture and handling of fish elicit a glucocorticoid stress response of varying magnitude and can impose significant disturbances in the metabolic, acid-based, osmotic and electrolyte balances (Holder et al., 2022; Kieffer, 2000). This is particularly true if the hooked fish is subjected to physical exhaustion during the landing process and/or longer durations of air exposure before release (Arlinghaus et al., 2007). In some cases, these physiological disturbances can be so severe that the fish fails to restore homeostasis following capture, ultimately causing death (Ferguson and Tufts, 1992; Holder et al., 2022; Wood et al., 1983). While earlier studies have suggested that pike are relatively resilient to physiological stressors associated to angling (Arlinghaus et al., 2009; Ison et al., 2017; Schwalm and Mackay, 1985), it is reasonable to assume that individuals with a very low body condition may be less likely to recover from such disturbances. Hence, we suppose that the specific pike most probably died of capture-induced stress. It should also be noted that even if a fish swims away upon release, this does not necessarily imply that it will survive the capture event. Numerous studies have reported delayed mortality of captured fish following release across a diverse range of species, such as Atlantic salmon (*Salmo salar*) (Lennox et al., 2017b), largemouth bass (*Micropterus salmoides*) (Sylvia and Weber, 2019), bluegill sunfish (*Lepomis macrochirus*) (Gingerich et al., 2007), and rainbow trout (*Oncorhynchus mykiss*) (Schill, 1996). Post-release delayed mortality has also been observed for pike (DuBois et al., 1994; Falk and Gillman, 1975), and the closely related muskellunge (*Esox masquinongy*) (Margenau, 2007). Hence, we recommend that future studies assess the potential consequences of C&R angling on the post-release mortality of pike with a decreased body condition due to food scarcity. In this respect, it would be highly relevant to look beyond the effects of physical injuries associated to hooking and quantify the role of physiological disturbances arising from the capture event.

Our study has some other potential limitations that should be acknowledged. Firstly, angling for pike was not carried out prior to the first reduction in prey fish density by seining in fall 2020. It is therefore plausible that pike already experienced increased hunger and feeding motivation during the angling sessions in 2020, occurring 1–2 months after the initial prey fish removal. If so, however, this was not reflected by changes in their body condition as the analysis showed no difference in condition factor of pike captured by seining in fall 2020 and angling 1–2 months later. It is also important to keep in mind that the density of roach was further reduced after the angling sessions in 2020, which probably lead to additional declines in feeding opportunities for pike as illustrated by the reduction in body condition from fall 2021 onwards. Consequently, if prey fish availability and the level of hunger were important drivers for the strike behaviour of pike towards fishing lures/baits, we would have expected to see differences in hooking location and

bleeding rates between pike angled in 2020 and 2022, everything else being equal. Secondly, sex of the pike was not determined in the present study. Because the energetic needs to gamete production are higher for female than male pike (Diana, 1983), the behavioural responses to food shortage may differ between sexes, which could translate into differences in strike behaviour towards fishing lures/baits. For instance, it is possible that the higher energetic cost of female gonad development and related food demand may increase the risk of deep hooking, ultimately leading to an overrepresentation of females among the group of pike with hooking injuries in vital areas. If this is the case, the sex ratio of pike could play an important role in determining the consequences of C&R angling at the population level. Finally, our study only included one type of artificial lure (i.e. soft plastic shad) and one baitfish species (i.e. roach). This may limit the generalizability of the present results since bait type and size can affect hooking location and severity of tissue injuries in pike as previously noted (Arlinghaus et al., 2008; Stålhammar et al., 2014), along with other lure/bait characteristics including tackle configuration as well as hook type, number and size (Burkholder, 1992; Bursell and Arlinghaus, 2018; Falk and Gillman, 1975).

5. Conclusion

The present results show no evidence that long-term reductions in prey fish density and related declines in body condition alter how pike strike and ingest artificial lures or natural baits, at least not in a way that increases the risk of hooking injuries in sensitive tissues. Consistent with previous research, we found higher bleeding propensity from the hook wound when the pike were hooked in critical locations, especially in the gills. Our study also supports the notion that bait type is an important predictor for hooking location and level of bleeding in angled pike. However, contrary to our initial expectations, soft plastic shads caused bleeding more frequently than baitfish, most likely because they had higher tendency to hook the pike in the gills. It should be emphasized that the majority (85.0%) of hooking locations encompassed non-critical areas across bait types, and the proportion of pike exhibiting moderate (10.9%) and substantial (1.4%) bleeding was relatively low. Nonetheless, bleeding from the hook wound has been shown to increase the mortality of pike following release in previous studies. On top of this, it is possible that pike with a very low body condition may be more susceptible to physical injuries and physiological stress associated to angling than conspecifics in better condition. Thus, further research is needed to assess the potential impacts of C&R angling on pike populations exposed to prolonged reductions in food availability before unambiguous recommendations to sustainable fisheries management can be provided.

CRedit authorship contribution statement

Martin H. Larsen: Writing – original draft, Formal analysis, Data curation, Funding acquisition, Methodology. **O. Jonas Palder:** Writing – review & editing, Data curation. **Casper Gundelund:** Writing – review & editing. **Nicolas Azana Schnedler-Meyer:** Writing – review & editing. **Henrik D. Ravn:** Writing – review & editing, Data curation. **Christian Skov:** Conceptualization, Funding acquisition, Writing – review & editing, Methodology.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Ethics

Fish were sampled and tagged in according to the guidelines described in permission (2017–15-0201–01164) from the Danish Experimental Animal Committee.

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