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Predator responses in recreational fishing: Assessing selective pressure of bait types on behavioral diversity in northern pike (*Esox lucius*)

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ABSTRACT

This study investigated the predatory behavior of northern pike in response to trolling with natural and artificial baits using underwater cameras. Predator types of 32 captured pike were identified based on their coping style under altered environmental conditions by measuring latency to forage in individual novel net enclosures. Fast-attacking pike during angling were more likely to forage in the enclosures than slow-attacking conspecifics. Bait type influenced attack latency, with soft plastic baits being attacked faster than natural baits. Pike biting the artificial bait exhibited a faster defensive response compared to the natural bait; however, the likelihood of capture was not affected. The results suggest that wild pike exhibit variability in coping styles, i.e. different responses to environmental changes, which are related to their vulnerability to angling. In consequence, bait selectivity, due to more proactive predators attacking soft plastic baits less hesitantly than their reactive counterparts, may influence pike populations even within the same fishing technique. Recreational fishery management should consider the behavioral diversity within pike populations to maintain genetic integrity and contribute to both angler satisfaction and ecosystem function.

1. Introduction

Fishing is a widespread human activity that provides an important source of food and recreation (Arlinghaus and Cooke, 2009; Cooke et al., 2018; Cooke and Cowx, 2006). Recreational fishing, predominantly angling, is enjoyed by approximately 220 million people worldwide, five times more than are employed in the commercial fishing sector (Arlinghaus et al., 2019), and contributes substantially to the global economy (Arlinghaus et al., 2012; Kelleher et al., 2012). As well as providing food, the activity offers benefits such as social benefits, competitive interaction, and contact with nature (Arlinghaus, 2006; Birdsong et al., 2021; Cooke et al., 2018; Hunt et al., 2013).

The impact of angling, used hereafter as a synonym for recreational fishing, goes beyond the economic and recreational dimensions, with potential for direct and indirect effects on fish populations, resulting in a complex interplay of ecological effects (Lewin et al., 2006). If the goal is harvest, which is a legal requirement in some parts of the world, angling has direct effects via the removal of individuals from a population. However, even with catch-and-release angling, where the primary goal is recreational, the captured fish are exposed to various stressors, such as hooking, physical exhaustion and dehydration, which can lead to immediate or delayed mortality (Arlinghaus et al., 2007; Cooke and Schramm, 2007; Cooke and Suski, 2005). Both harvest and delayed release mortality may unintentionally reduce the population size and affect the life history of the target species (Coble, 1988; Erisman et al., 2011).

In addition to the direct effects of fishing mortality on population size, there is increasing awareness that capture is not random and can exert selective pressure on traits in the fish population (Lewin et al., 2006; Paul et al., 2003). This selection effect is most obvious in the removal of large fish through gear selectivity and/or angler preference (Arlinghaus et al., 2014, 2008). More recently, however, consideration has been given to the possibility that certain behavioral traits may predispose some individuals in the target population to greater vulnerability to fishing (Alós et al., 2012; Cooke et al., 2007; Wilson et al., 2015). Behavior in animals is often categorized along the axes of variation in aggression, boldness, activity, exploration, and/or sociability (Conrad et al., 2011; Réale et al., 2007), and these can be linked to physiological traits (Réale et al., 2010). Consistent variation in these traits amount to a behavioral strategy. For example, members of a

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population may exhibit coping styles in response to particular challenges or stressors, whereby proactive individuals are less likely to be dissuaded from their natural behavior than their reactive conspecifics (Coppens et al., 2010; Koolhaas et al., 1999). In this context, bolder, more active, stress-resilient, or less stress-responsive individuals of target species highly valued by anglers are likely to show highest vulnerability to fishing. Such species include northern pike (*Esox lucius*) (Monk et al., 2021), muskellunge (*Esox masquinongy*) (Bieber et al., 2023a), common carp (*Cyprinus carpio*) (Klefoth et al., 2017), rainbow trout (*Oncorhynchus mykiss*) (Koeck et al., 2019), and largemouth bass (*Micropterus salmoides*) (Louison et al., 2017; Wilson et al., 2015). Behavioral strategies such as coping styles not only show consistency over time, but they also are likely heritable, with implications for individual fitness and the reproductive success of future generations of the target species (Biro and Stamps, 2008; Cooke et al., 2007; Philipp et al., 2015). Consequently, in addition to its motivation (hunger state), the frequency of encountering fishing gear, the characteristics of the gear and learning (Beukemaj, 1970; Lennox et al., 2017), the likelihood of an individual being captured is also influenced by its behavioral strategy. This link between behavioral strategies and vulnerability to fishing must be taken into account when assessing the impact of fishing. Thus, understanding behavioral responses to angling is critical in anticipating both short- and long-term effects of angling on fish populations.

As a passive fishing technique, angling attempts to deceive target fish into attacking a bait, often by imitating species-typical aspects of natural food or prey (Lennox et al., 2017; Nannini et al., 2011). Hooks are equipped with natural or artificial bait to elicit a feeding response from a fish, resulting in the hook being lodged in the fish upon strike. Unlike other passive (e.g., gillnets) or active (e.g., trawls) methods that collect fish passively or through external forces, angling relies on the fish's decision to bite. The mere presence of the hook does not guarantee a strike, making fish behavior critical to successful capture (Løkkeborg et al., 2014). Susceptibility to this kind of fishing is thus likely to be influenced by variation in individual foraging strategies within the target species (Lennox et al., 2017). Traits that influence likelihood of capturing prey or ability to discriminate bait from natural prey may be affected by the selective pressure of recreational angling (Nannini et al., 2011). These factors may include trade-offs between the time taken to recognize prey (Hughes, 1979) and the speed of response required for successful prey capture (Domenici, 2002). This selection may also affect systems related to prey detection and handling, such as sensory biases (Mazur and Beauchamp, 2006), nociception (Sneddon, 2019), and metabolic performance (Louison et al., 2018; Metcalfe et al., 2016; Redpath et al., 2010; Uusi-Heikkilä et al., 2008). Based purely on frequency of foraging or attack behavior, fish possessing a more proactive coping style may be at higher risk of capture by anglers than those possessing a more reactive coping style. It is therefore important to understand how angling-induced selection acts on foraging behavior within populations.

The northern pike (*Esox lucius*) is of special interest for analyzing long-term effects of angling on their foraging behavior, as it is a highly valued predator species for recreational fishing throughout the northern hemisphere, including Europe, and anglers have targeted its populations for decades. Nowadays pike anglers have a wide variety of baits to choose from, ranging from natural ones, such as baitfish, to more recently developed artificial baits, including soft plastics that are often, but not exclusively, designed to mimic prey species (Arlinghaus et al., 2017; Raison et al., 2014). The popularity of fishing for top predators also serves as a significant economic driver, with expenditure on equipment, travel, and related services contributing substantially to local economies (Fromherz et al., 2024; Strehlow et al., 2023). Pike play a key ecological role as stalking apex predators in freshwater ecosystems (Hobson, 1979). Their predation on lower trophic levels has a cascading effect on the entire aquatic ecosystem (Craig, 2008; Grimm and Backx, 1990; Mehner et al., 2004; Nicholson et al., 2015; Nilsson et al., 2019). Understanding how angling affects pike behavioral traits, such as foraging behavior, is crucial for managing pike populations, impacting both angler satisfaction (stability of catch rates) and overall ecosystem sustainability.

In a laboratory study, it was found that northern pike exhibit consistent traits in foraging behavior (Lucas et al., 2023). In experiments that tested responses towards prey items in the presence of a stressor, individuals were categorized into fast-responding (proactive) or slow-responding (reactive) predator types. Moreover, testing vulnerability to angling revealed that proactive pike are more likely to attack any presented bait than their reactive counterparts (Lucas et al., 2023). However, whether these predator types could also be detected in the field remained an open research question. In the context of the findings of the laboratory study and the literature, the current study aimed to determine whether wild pike would exhibit individual differences in their hunting behavior on artificial or natural baits during angling and determine how this behavior is related to their coping style. The following hypotheses were postulated: (1) wild pike exhibit individual coping styles in their foraging behavior; and (2) wild pike with differing predator types respond differently to two bait types (natural dead bait and artificial soft plastic bait).

2. Materials and methods

2.1. Ethics approval

The experiments were conducted according to the German Animal Welfare Act (TierSchG), and ethical permission was granted by the animal experimentation administration, the Regierungspräsidium Tübingen, Referat Tierschutz (animal experiment application: LAZ 04/21 G), Germany. Pike were continuously monitored, and all fish were caught according to current fishery law (LFischVO).

2.2. Study concept

The experimental design was based on previous research indicating that animals show individually consistent responses to environmental changes. This variability considered in terms of opposites: fast (proactive) coping individuals who adjust rapidly to circumstances and return to habitual behaviors, displaying a tendency toward risk-taking, and slow (reactive) coping individuals who take more time to adapt, and tend towards greater risk avoidance (Coppens et al., 2010; Koolhaas et al., 1999). Individuals that quickly adapt to stressors tend to exhibit more active and bold behaviors, and such behaviors include foraging proactively after a predator attack (Bell, 2005).

This study aimed to differentiate between coping styles in the foraging behavior of pike, which have been demonstrated to be repeatable traits in a previous study conducted on northern pike (Lucas et al., 2023) and to connect these coping styles to their individual predatory behavior during trolling-angling with different bait types. As a proxy for predator type, the coping style of captured wild pike was determined as foraging under the influence of a stressor (*sensu* Martins et al., 2011; Øverli et al., 2002). As an environmental stressor, the pike were placed in a net enclosure after capture, followed by the introduction of roach as a forage fish. The terms "coping styles" and "predator types" are used to indicate specific measurements of behavior in the net enclosures, namely, the delay in foraging in the response to a stressor. The term "predatory behavior" is used to describe the behavior of the pike towards the baits during angling.

2.3. Experimental site

The experiments took place at lake Mindelsee in southern Germany. Mindelsee lies between the two parts of Lake Constance (47° 45′ 16″ N, 9° 1′ 20″ E) (Fig. 1) and is characterized as a mesotrophic glacial lake of approximately 115 ha (ha) with a maximum depth of 13.5 meters (m) and a mean depth of 8.5 m. It is 2170 m long and 560 m wide. The

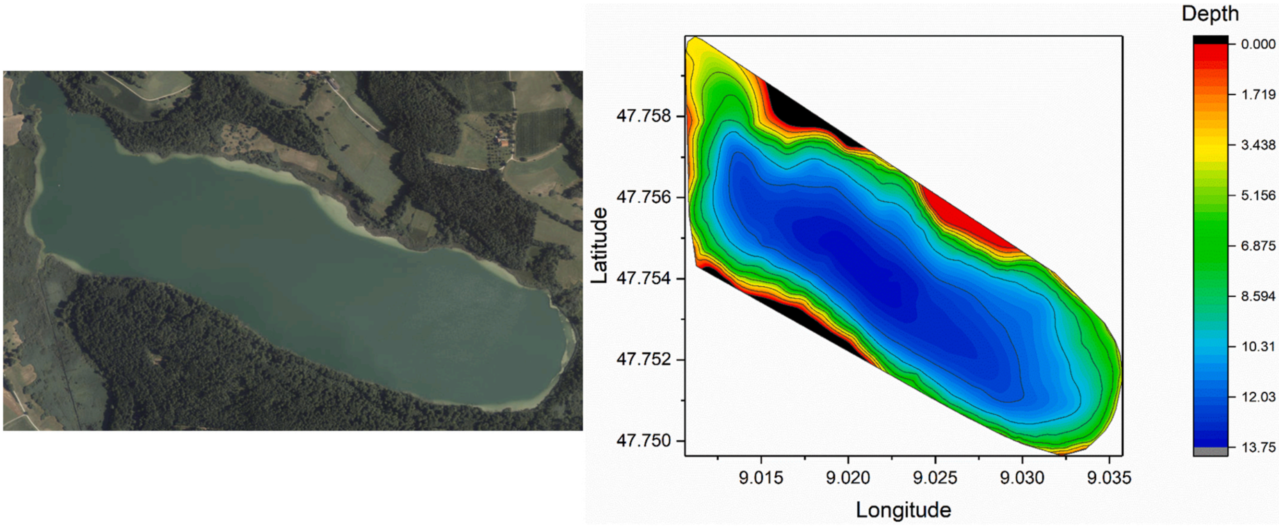

Fig. 1. Aerial view (left) and depth chart (m) (right) of lake Mindelsee. Trolling-angling was conducted around the lake in a depth of ca. 8 m.

southern shore is steeply sloping; otherwise, the Mindelsee is surrounded by moorland. Macrophytes are limited in the lake. Its main tributaries are the Fällgraben in the west and the Krebsbach and Adernbach in the east. The Mühlbach river drains some of the water into Lake Constance. The shores were declared nature reserves in 1938 and now cover an area of approximately 400 ha. There are also landscape and water conservation areas in the catchment, amounting to 2543 ha in area. Anthropogenic use is low, with only one bathing access, and a single commercial fishing license. The fish fauna comprises mainly northern pike (*Esox lucius*), perch (*Perca fluviatilis*), stocked whitefish (*Coregonus wartmanni*), tench (*Tinca tinca*), bream (*Abramis brama*), roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*) and European catfish (*Silurus glanis*) (data from regular monitoring of lakes, Fisheries Research Station Langenargen).

2.4. Angling for northern pike

Angling started in spring 2023 after the spawning season of the northern pike. Trolling was the angling method of choice, being a commonly applied and effective technique for this species (Arlinghaus et al., 2008). In trolling, baits are towed behind a moving boat. In this case, freshly killed roach provided by the commercial license holder were used as natural baits alongside "Westin Ricky the Roach" rubber shads in the color "Lively Roach" (Fairpoint Outdoors A/S, Denmark) as the artificial alternative. The bait size was standardized to 14 cm. Both baits were fished on a size 1.5 "Stocker" trolling system. The rig was equipped with three barbless treble hooks (Fig. 2). Interactions between pike and baits were recorded on video using a fishing camera (see video recording and analysis section), which was connected to the bait between two 50 cm long wire leaders. In addition, a 30-gram (g) trolling lead was attached behind the camera. The fishing line used was a strong multicolor multifilament, “STROFT GTP Type E” (Waku GmbH, Germany), with a 19 kg breaking strain. This line has color markings every 5 m so that the baits could always be set at the same distance of 30 m from the boat. After each capture or missed bite (escape), the baits were visually inspected for damage and replaced if necessary. Fishing was conducted from a boat using two rods, with the tips of the rods at least 5 m apart, each equipped with one of the two baits. Thus, the baits were spaced farther apart than the maximum recorded Secchi depth (>3.5 m). Trolling speed was monitored using a "Deeper Smart Sonar Pro" fish finder (Deeper, Lithuania), and averaged 3 km/h. At this speed, the depth of the baits was 5–6 m (controlled with a "G5 DST" depth logger: Cefas Technology, UK), corresponding to 2–3 m above the bottom. At this depth, the water has little to no structure throughout the

Fig. 2. Both bait types mounted on the “Stocker” trolling-rig: (top) natural bait, a freshly killed roach and (bottom) artificial bait, a soft plastic shad in the color "Lively Roach". Both baits had a standardized length of 14 cm and were equipped with three barbless treble hooks.

lake, so fishing was always conducted in a similar habitat. According to the approved animal experiment application (see Ethics approval), 16 northern pike were caught per bait type, resulting in a total of 32 test individuals.

At 12:00 noon on each fishing day, measurements were recorded for air temperature (°C), air pressure (hPA) and visibility depth (m) using a Secchi disk. Following an attack on one of the baits, the pike was brought to the boat as quickly as possible and caught with a landing net made of knotless rubberized netting material. The barbless hooks were carefully removed while the pike was still in the water. Each fish was then measured (total length, TL, to the nearest cm), weighed (to nearest ten g), and photographed. A wet unhooking mat or weighing bag was always used as a support to avoid damaging the mucus layer of the pike (Barthel et al., 2003; Colotelo and Cooke, 2011). Any injuries and bleeding in the mouth were documented. The captured pike were then carefully transferred individually into a net enclosure (see: Behavioral experiments) in a sheltered area of the northwestern part of the lake. The photographs were used for non-invasive identification of individuals to avoid double testing in the experiments, using the method of (Kristensen et al., 2020) to identify and compare individual markings on a section of the body using the software I³S Pattern^{+} (version 4.1).

2.5. Behavioral experiments

A floating construction made of PVC pipes (Pokorný - Sítě s.r.o., Czech Republic) was used for each net enclosure. The net enclosures measured 1.20 m × 1.20 m × 6.70 m (L × W × D), had a mesh size of 10 mm and an underwater volume of approximately 8.64 m^3. Seven strips (50 cm × 10 cm) of green plastic foil and cork material were attached to the bottom of the enclosures to mimic shelter provided by aquatic plants as environmental enrichment. In addition, a frame made of aluminum rods (cross-section 2.5 cm × 2.5 cm) from the company Alusteck, Germany, was installed inside the net enclosures so that the volume available for each pike did not change when the "walls" moved due to wind and water movement. The bottom of the net enclosures was set at one to two meters from the lake bottom. This allowed the pike to reach their preferred temperature at the depth at which they were caught. The enclosures were anchored in the water at a minimum distance of 5 m apart to avoid visual contact and other interactions between the test individuals. Each individual was then given three 14 cm long roach as forage fish, and seven days to acclimatize to the new environment. After seven days, the remaining forage fish were counted and removed, and a dead 14 cm roach serving as bait was attached to a hookless ice fishing system with a tip-up flag (Frabill, USA) at a depth of 5 m. The baitfish was connected to a 0.12 mm monofilament line "STROFT GTM" (Waku GmbH, Germany) with a loop, which would open if the pike attacked the bait. An additional 5 g fishing weight was connected to the line to submerge the bait. GoPro Hero 8 cameras were installed on top of the net enclosures and were programmed to take images every 15 minutes. The intention was to provide the pike in the test with a fresh, dead baitfish over a period of seven days and to record bites using the trigger flag of the ice fishing rod at a resolution of 15 minutes. Unfortunately, none of the test individuals fed on the dead roach. Fortunately, however, the acclimatization period before the "dead baitfish experiment" could be used as a basis for assessing the behavior of the pike in the net enclosures. During the entire trial period, the pike were monitored daily using a GoPro Hero 8 camera attached to a long pole from the outside of the net enclosures so that any behavioral abnormalities or injuries could be identified. None of the test individuals died during the testing period. At the end of the trial period, each pike was checked for health and carefully released at the point of initial capture before the next pike was caught and placed in the now empty net enclosure until 32 pike had been tested. No significant effects of order of capture were found in the results of the behavioral trials in the net enclosures ($p > 0.10$; data not shown).

2.6. Video recording and analysis

The interactions between pike and baits were recorded on video using a fishing camera (Water Wolf 2.0; Savage-Gear, Denmark). The recorded video material (1920 × 1080 pixels at 30 fps) was initially screened using the free video tool Lossless Cut (version 3.49.0, Windows 10). This program made it possible to cut the video files into frame accurate segments for later analysis. Episodes where a snagged twig or algae affected the natural movement of the baits were not included in the analysis of the total fishing time. The definitions for the events that were determined on the video files and used for the analysis are given in Table 1. The hook shedding response was a typical response to hooking and was consistently identifiable for each pike as they tried to remove the foreign object by opening their mouth wide, spreading their gill plates and shaking their head intensely. The total fishing time per bait was determined as the sum of fishing time when neither lake debris nor a pike on the hook interfered with the bait. The total trolling distance per bait was calculated by multiplying total fishing time per bait with the average trolling speed of 3 km/h.

Table 1
Summary of the methods for video analysis of the behavior of northern pike during angling.

Behavior/Outcome Definition	Recorded timeframe	Measured parameter
Approach: Pike was clearly distinguishable and reacted to bait. The interaction could result in capture / escape / follow	First frame at which pike appeared	• Event* * all pike were actively responding to bait
Capture: Pike approached and attacked a bait and was captured	First frame at which pike appeared until frame at which pike was caught in the net	Predatory Behavior • Latency to attack: duration from first sight until bite (including biting point on bait) • Latency to react: Bite until hook shedding response • Duration of fight (end in net)
Escape: Pike approached and attacked a bait and was not captured	First frame at which pike appeared until frame at which pike was off the hook	Predatory Behavior • Latency to attack: duration from first sight until bite (including biting point on bait) • Latency to react: Bite until hook shedding response
Follow: Pike approached and followed a bait and did not attack	First frame at which pike appeared until frame at which pike disappeared	Predatory Behavior • Duration to follow: duration from first sight until cessation of approach
Attack: Pike approached bait and bit hook, bait or both	First frame at which pike appeared to the last frame of the bite (closed mouth)	• Latency to attack
Bite (or Hooking): Pike bite hook or bait or both	First frame at which pike bites hook or bait or both	• Event • Bite point on the baits
Hook shedding response: The defensive response to biting/hooking	Last frame of the bite (closed mouth) to the first frame in which the pike began to open its mouth and spread its gill plates	• Latency to react • Event

2.7. Data analysis and statistical methods

Statistical tests used the software package JMP (JMP®Pro, Version 17, SAS Institute, Inc., US). Parametric statistics were used for normally distributed variables. Two variables, attack latency (time taken to attack the bait) and defensive response to hooking, were log-transformed to correct for the skew in their distributions. Differences between two groups were tested using Student's t tests with pooled variances (F tests were non-significant). The standard least squares platform of JMP was used to analyze linear models (LM) testing group differences in continuous variables. If the response variable was ordinal or nominal, a logistic regression analysis (GLM) was performed (binomial with logit link), and least square statistics are reported. Significant deviations from the expected distribution in contingency tables were tested using Fisher's exact test for 2×2 tables or chi-square test for more complex tables. A measure of variance explained by the predictor variable (effect size) was calculated from the sum of squares in the LM using Eta squared (H^2). For logistic regression and contingency tables the odds ratio (OD) was calculated as a measure of effect size.

3. Results

It took 28.52 hours and 87 km of trolling to catch 16 pike with the artificial soft plastic bait, while the same number of pike was caught with the natural bait in 15.08 hours and about 45 km. Capture rates per hour angling were significantly lower ($t[33] = 2.64$, $p = 0.012$) for the artificial soft plastic bait (0.55 ± 0.55 pike/h; N = 29 h; mean ± SD) than for the natural dead bait (1.04 ± 0.64 pike/h; N = 15 h; mean ± SD). An overview of the behavior of the 122 recorded northern pike during trolling-angling is shown in Fig. 3. The artificial bait was approached by 90 of the 122 pike. Fifty-three pike attacked this bait type, while a further 27 pike followed the artificial bait but did not attack. Ten fish bit the camera instead of the artificial bait. Of the 53 attacks on the artificial bait, 37 fish were not successfully hooked and escaped, while the remaining 16 were successfully captured. The natural bait was approached by the remaining 32 of the 122 northern pike. Of these, 25 attacked the natural bait, five followed it without attacking, and two fish attacked the fishing camera instead. Of 25 attacks on the natural bait, nine fish were not successfully hooked and escaped, while the remaining 16 were successfully captured. Pike that bit the camera were excluded from further analysis.

3.1. Predatory behavior of caught pike during angling

No significant differences were found in the size or weight of the pike caught by the artificial or natural baits (total length: $t[30] = 0.41$, $p = 0.69$; body weight: $t[30] = 0.044$, $p = 0.96$). Pike caught with the artificial bait had a total length of 68 ± 13.8 cm and a body weight of 2.19 ± 1.33 kg (N = 16; mean ± SD), while pike caught with the natural baits had a total length of 70 ± 12.0 cm and a body weight of 2.21 ± 1.05 kg (N = 16; mean ± SD). The average duration of fighting for the 32 pike was 54 ± 10.9 s, with body length predicting approximately 62 % of variation in fighting time (LM, adjusted $R^2 = 0.62$, $F[1,30] = 48.88$, $p < 0.001$). Mild bleeding from the mouth due to hooking injury was observed in 50 % of the pike caught, but no significant difference in bleeding was found between pike caught by the artificial or natural bait (Fisher's exact test $p = 0.29$, OD = 2.78). Severe bleeding from gill damage was not observed.

The predatory behavior of caught pike during angling and the defensive response to hooking showed clear differences in fish attacking the two different types of bait (Table 2). Bait type explained 13 % of the latency to attack the bait (LM bait type: $F[1,28] = 4.31$, $p = 0.047$, $H^2 = 0.13$). Pike attacked the artificial bait significantly quicker (latency to attack: 0.79 ± 0.99 s) than the natural bait (latency to attack: 1.56 ± 1.55 s). Neither Secchi depth nor the interaction between bait type and Secchi depth had a significant effect on the latency to attack the bait (LM Secchi depth main and interaction effect with bait type: $F[1,28] < 0.70$, $p > 0.41$, $H^2 < 0.024$). The defensive response latency of pike that were hooked after biting was explained by bait type in 59 % of cases (LM bait type $F[1,28] = 41.77$, $p < 0.0001$, $H^2 = 0.595$). This latency was 7.9 times lower for pike hooked by artificial bait than pike hooked by natural bait (latency to react 0.23 ± 0.14 s *vs.* 1.82 ± 1.67 s). Neither individual body length of pike nor the interaction between bait type and body length had a significant effect on the latency of the defensive response to the hooking event (LM length main and interaction effect with bait type: $F[1,28] < 0.13$, $p > 0.72$, $H^2 < 0.0045$).

3.2. Foraging of captured pike in experimental enclosures

After capture, the 32 pike were transferred to individual net enclosures and fed three roach as natural prey fish. Within one week, 14 captured pike had foraged in the enclosure, while 18 had not (Table 3). Logistic regression was used to analyze whether pike related factors (length, bleeding, and latency to attack during the angling event) were related to the likelihood of foraging in the enclosure (two levels: yes, no; N = 32; model significance, $X^2[6] = 13.45$, $p = 0.0364$). The likelihood of foraging in the enclosure was significantly related to the latency to attack ($X^2[1] = 10.90$, $p = 0.0010$), showing an 8.2 % decrease in odds ratio with every second before the end of the attack (OD = 8.23 / s). The likelihood of foraging in the enclosure was not significantly related to bleeding after capture ($X^2[1] = 2.56$, $p = 0.11$, OD = 6.45) or pike length ($X^2[1] = 0.17$, $p = 0.67$, OD = 1.02 / cm).

3.3. Escaped pike during angling

Of 78 recorded attacks on both bait types (N = 53 on artificial bait and N = 25 on natural bait), 59 % (N = 46) of pike came off the hook and escaped. 68 % of bites on the artificial bait resulted in an escape, while 32 % of bites on natural dead baits resulted in an escape (Fisher's exact test $p = 0.0066$, OD = 4.1). For the 46 pike that escaped, predatory behavior in terms of latency to attack did not differ between individuals that bit the artificial bait and those that bit the natural bait (LM log-transformed, $F[1,40] = 1.75$, $p = 0.19$; in 2 cases, the latency to attack could not be determined). Neither Secchi depth nor the interaction between bait type and Secchi depth had a significant effect on latency to attack in pike that were not caught (LM, $F[1,40] < 1.29$,

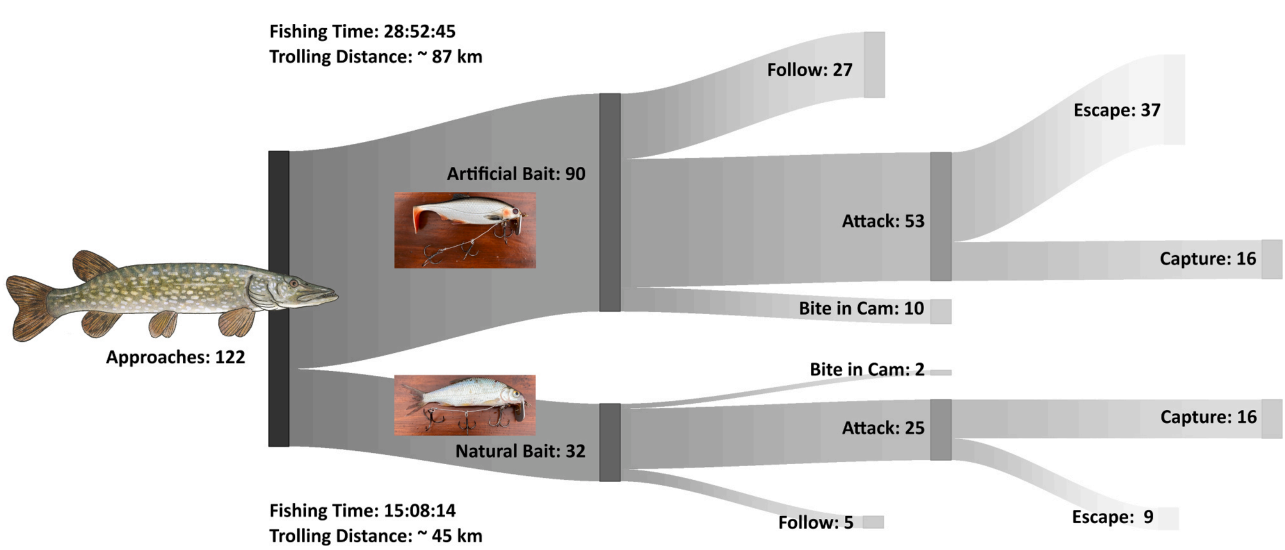

Fig. 3. Detailed overview of all pike-bait-interactions during trolling from the video recordings throughout the process of capturing all 16 pike per bait.

Table 2
Pike behavior during capture and morphometric parameters of pike separated by bait type (N = 32). * indicates a significant difference.

		Behavior during capture			Morphometric parameters		
Bait type	N	Latency to attack (s)*	Latency to react (s)*	Duration of fight (s)	Total length (cm)	Body weight(kg)	Condition(K)
artificial	16	0.79 ± 0.99	0.23 ± 0.14	52.9 ± 12.1	68.0 ± 13.8	2.19 ± 1.33	1.02 ± 0.10
natural	16	1.56 ± 1.55	1.82 ± 1.67	54.7 ± 9.9	70.0 ± 12.0	2.21 ± 1.05	1.00 ± 0.08

Table 3
Pike behavior during capture and morphometric parameters of pike separated by foraging behavior in the enclosure (N = 32). * indicates a significant difference.

		Behavior during capture			Morphometric parameters		
Foraging in enclosure	N (captured on bait type)	Latency to attack (s)*	Latency to react (s)	Duration of fight (s)	Total length (cm)	Body weight (kg)	Condition (K)
yes	10 artificial4 natural	0.55 ± 0.55	0.70 ± 0.89	54.8 ± 11.6	69.0 ± 13.9	2.22 ± 1.32	1.02 ± 0.10
no	6 artificial12 natural	1.66 ± 1.57	1.29 ± 1.71	53.1 ± 10.6	69.0 ± 12.3	2.28 ± 1.10	1.00 ± 0.08

$p > 0.26$).

The latency of the defensive response to hooking did not differ between captured and escaped pike (LM, $F[1,74] = 0.039$, $p = 0.84$; interaction with bait type $F[1,74] = 0.0021$, $p = 0.96$). As for the captured pike, the escaped pike also exhibited a much lower defensive hooking response latency (factor 5.7) after biting the artificial bait compared to the natural bait (latency of 0.31 ± 0.50 s *vs.* 1.79 ± 1.24 s; $t[44] = 4.90$, $p < 0.001$).

The location of the bite on the bait significantly affected whether the pike was caught or not ($X^2[3] = 9.27$, $p = 0.026$). A post hoc analysis of the contingency table showed that the largest deviation from expectation was for pike that attacked any part of the bait without a hook and thus had a 100 % chance of escaping (0 out of 10 captured *vs.* 4.1 expected, cell $X^2[1] = 4.103$, $p < 0.05$). Also in terms of odds-ratios, the largest change was at this location of bite (OD: bait and hook *vs.* entire bait = 1, hook *vs.* bait and hook = 0.33, hook *vs.* bait = 0). After removing this location from the contingency table, no further significant differences between attack locations were found ($X^2[2] = 1.86$, $p = 0.40$), with an average of 53 % of attacking fish escaping from biting either a hook, a part of the bait with one of the three hooks or the entire bait (Fig. 4).

An ordinal logistic regression was used to test whether the predatory behavior of all 78 recorded pike attacks differed by bait type or biting location (bait type, latency to attack) during the angling event. Latency to attack had a significant effect on biting location ($X^2[1] = 9.02$, $p = 0.0027$), with the likelihood of swallowing more of the bait showing a 2.2 % decrease in odds ratio with every second of duration of the attack (OD = 2.2 / s). Moreover, the natural bait showed a 3 times higher odds ratio in respect of being swallowed more entirely than the artificial bait ($X^2[1] = 4.06$, $p = 0.044$; OD = 3.0). There was no significant interaction effect ($X^2[1] = 3.05$, $p = 0.081$).

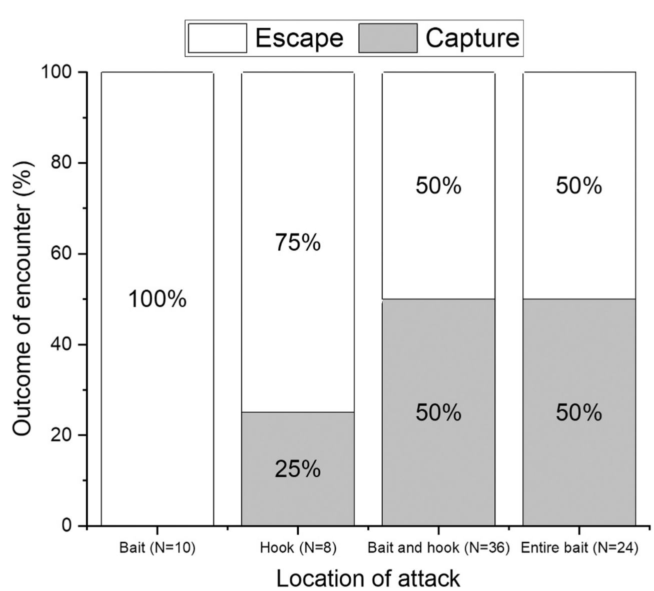

Fig. 4. The location of the bite on the bait significantly affected the outcome of the attack (N = 78). The largest deviation from expectations was for pike that attacked parts of the bait without a hook and therefore had a 100 % chance of escaping (first bar on the left). No further significant differences were found.

3.4. Followers

Thirty-two pike followed the baits without engaging in further interaction. Bait type did not affect the number of these followers significantly: 27 followers out of observed 80 pike (34 %) approached the artificial bait, while 5 followers out of 30 observed pike (17 %) approached the natural bait (Fisher's exact test, $p = 0.10$). The duration of bait-following (stalking) did not differ significantly between the two bait types (LM, $F[1,28] = 0.25$, $p = 0.62$). Furthermore, neither Secchi depth (LM, $F[1,28] = 0.46$, $p = 0.50$) nor the interaction between bait type and Secchi depth had a significant effect on the duration of following the baits ($F[1,28] = 0.018$, $p = 0.89$).

4. Discussion

The main aim of the study was to verify whether different predator types exist in a natural population of northern pike. Pike were captured using different bait types using trolling as a common angling technique. More effort was required to capture pike with the artificial bait (28.52 hours and 87 km of trolling for 16 pike) than with the natural bait (15.08 hours and about 45 km for 16 pike). The video recordings showed that the caught pike attacked the artificial soft plastic bait faster than the natural bait. Subsequent behavioral tests in the net enclosures showed that the faster attacking individuals during capture were also more likely to forage in the novel environment than slow attacking individuals. Furthermore, pike biting the natural bait took longer to enact a defensive response to the hooking event than those attacking the artificial bait. The location of the bite on the bait significantly influenced whether the pike was captured, whereas the defensive response latency did not affect this outcome. Overall, the artificial soft plastic bait was approached more often (~74 % *vs.* ~26 % of all recordings) - but subsequently attacked less often than the natural bait (~59 % *vs.* ~78 % (Table 4, Fig. 3). Compared to the soft plastic bait, attacks on the natural bait happened quickly and resulted in swallowing more of the bait.

4.1. Predator types in wild northern pike

Pike that were captured were individually placed in a net enclosure in which they were supplied with natural prey. Of the 32 pike captured, 14 individuals foraged in the net enclosures, while 18 did not. This

Table 4
Summary of the results.

Results	Effect
A. General angling Results	**Higher in**
Pike Approaches / Captured Pike	Artificial Bait
Pike Attacks / Captured Pike	Artificial Bait
Fishing Effort / Captured Pike	Artificial Bait
Capture Rate (Pike / Hour)	Natural Bait
B. Behavior during Angling	**Higher in**
Escape Rate after Attack	Artificial Bait
Latency to Attack Bait	Natural Bait
Latency to React to Bait	Natural Bait
Duration of Fight	No Significant Difference
C. Parameters after Capture	**Higher in**
Bleeding after Capture	No Significant Difference
Mortality after Capture	None reported
Captured Pike Length	No Significant Difference
Captured Pike Weight	No Significant Difference
D. Behavior in Net Enclosures	**Higher in**
Foraging (fast coping)	Artificial Bait
E. Behavior of Pike that Escaped	**related to bait**
Latency to React to Bait	Natural Bait
Follow / Capture	No Significant Difference
	related to capture success
Latency to React to Bait	No Significant Difference
Bite Location including Hook	captured

foraging behavior in the presence of a stressor was used as a proxy for determining the predator type as this has been found to be a robust repeatable trait (Lucas et al., 2023). Pike that foraged in the net enclosure were defined as having a more proactive coping style than those (reactive) individuals that did not (*sensu* Coppens et al., 2010; Koolhaas et al., 1999), as confinement in this novel net enclosure was considered a stressor to the wild pike (Øverli et al., 2002). Moreover, prior to being placed in the enclosure, all pike had fought against capture on the angling rod, which in itself is a relevant source of distress (Gustaveson et al., 1991). Additionally, fast recovery of food intake in a novel environment has been shown to be related to an active coping style in fish (Martins et al., 2011; Øverli et al., 2002). Relating the latency to attack of the 32 caught pike during capture (latency to bite the bait) to their corresponding behavior in the net enclosures revealed that proactive pike were also less hesitant than reactive individuals were when attacking an angling bait in the field under natural conditions.

By selecting a soft plastic bait that resembled the natural bait and using the same angling technique for both baits, the intention was to target the natural foraging behavior of the pike. No bait was used that resembled conspecifics, as this might have elicited aggressive, cannibalistic or even territorial behavior (Craig, 2008; Eklöv, 1992; Tanaka et al., 2011). Similarly, lures classed by anglers as irritating, for example those with unnatural colors, shapes, swimming movements or with loud noises that might induce behavior different from that of natural foraging were avoided (Wilson et al., 2015). Furthermore an appraisal of condition was carried out in order to test whether energy demand might explain susceptibility to angling (Lennox et al., 2017). However, the pike captured with the different bait types had similar size-corrected condition factors, and all pike were supplied with a standardized number of prey items in the net enclosures. Therefore, it can be assumed that all 32 pike caught during angling had a similar requirement for nutrients. This provides additional certainty that the results of the subsequent trials in the net enclosures were indicative of individual coping styles of the pike and not of other motivating factors (Bieber et al., 2023b).

Some caution is warranted when using the results of the foraging experiment in the net enclosures to estimate the relative proportions of the two predator types in the natural population. Several factors might have influenced this proportion in captured individuals. For example, injuries inflicted by angling can have short-term effects on foraging in pike (Stålhammar et al., 2012). However, injuries recorded in the current study were minor, and did not differ in severity between pike that foraged and pike that did not forage. In addition, the size of the pike did not differ between the two groups. Nevertheless, it is very likely that pike with a highly reactive coping style being more responsive to stressors might be more likely to be deterred by the fishing gear alone than proactive pike. As these predator types could only be determined for those pike that were captured, the results only address a subpopulation and may have limited validity for estimating the overall distribution of predator types in a natural population. To be able to make such an estimate, it would be necessary to establish links between these predator types and genetic markers in pike (Schjolden and Winberg, 2007) and then apply a method to randomly sample the entire population.

In conclusion, our results confirm that it is possible to detect different predator types, having proactive and reactive coping styles, in northern pike in the field, as was predicted by a laboratory study (Lucas et al., 2023). The selectivity of the angling and the hunting behavior of the pike are thus further discussed in the context of these predator types.

4.2. *Selective pressure of bait type on predator types*

No evidence was found for size or weight selectivity for angling with different bait types. This suggest that different bait types did not exert different selective pressures on the morphological traits of northern pike in the field. In contrast, a size-selective effect of angling was found in a study by Arlinghaus et al. (2008), in which bait size was correlated with the size of the pike caught. However, given that the two baits used in the current study did not differ in size, our results remain consistent with that finding. Another possibility is that bait type may be selective for body condition, as indicated by previous research using different species of natural bait (Aydin, 2011). However, no evidence was found for such a selective effect in the current study.

In addition to the overall relation between predator type and latency to attack in the caught pike, also pike caught on the soft plastic bait were more likely to forage in the net enclosures and more quickly attacked the soft plastic bait during angling than were pike caught on the natural bait. This indicates a selective bait effect on predator type, with fast-coping, proactive individuals more likely to be captured on the artificial bait. This result was unexpected, as in an earlier laboratory study, fast- and slow-coping pike did not differ in their response to angling with different bait types (Lucas et al., 2023). It may be pertinent that the present study used a different fishing method (trolling) to the lab trial. Moreover, recent research on several other apex predator species relevant to recreational fishing revealed possible bait and gear selectivity within a target species (Wilson et al., 2015).

Apparently, some aspects of natural and artificial baits elicit different responses in pro- and reactive pike. In the present study, the two baits were very similar in shape, color, and size, and the trolling rig imparted both with similar movement underwater. With the wide variety of baits available for anglers, this similarity was intentional, in order to determine whether pike would already react to differences that appear very minor from the human perspective (Pander et al., 2022; Raison et al., 2014). Apart from chemical cues and texture, the most obvious difference between bait types was the paddle tail of the soft plastic bait, which slightly emphasized the movement of the tail section compared to the natural dead bait. This visual cue, paired with the possible potential of emitting slightly more pressure waves underwater, might have provoked the proactive pike to attack the bait. It could also be the case that reactive conspecifics were more hesitant because of this slightly exaggerated movement (Wilson et al., 2015).

4.3. *Overall hunting behavior of pike during angling*

Models to describe the hunting behavior of predatory fish range from actively running down prey at continuously high speed (pelagic swimming predators) to on-the-spot ambushing (benthic species) or stalking (Hobson, 1979). The northern pike is considered as a typical stalking predator, in which the predation sequence begins with orientation toward the prey, followed by an approach in which the pike attempts to close the distance to one from which it can initiate a fast start and capture its prey (Harper and Blake, 1991; Hobson, 1979). A similar orientation-approach-bite (strike) method has been described for other species, including stickleback (Lucas et al., 2021; Parrish, 1993). In most cases in the present study, the fishing camera missed the orientation phase, which likely occurred outside the field of view. However, the approach/attack phase and defensive response to hooking were recorded in detail. After the bait was captured, the pike showed a rejection response, which appears to be a reflex to remove foreign objects or unsuitable prey from the mouth to reduce injury or other harm (Hobson, 1979). The predator-bait interactions of captured and non-captured pike are discussed further below.

From an angler's perspective, it is interesting as to why not all "successful" attacks on the two baits, where the pike was able to bite the bait, resulted in capture. The latency of the defensive response of the pike to hooking did not differ between caught and escaped individuals. Therefore, in trolling at least, response latency does not appear to affect the probability of capture. However, the location of the attack on the bait did significantly affect the outcome, as pike engulfing all or most of the bait were more likely to be caught than those with a smaller proportion of the bait in their mouth when closing it after an attack. Since the defensive mechanism of the pike followed a consistent pattern and was not related to their pro- or reactive behavior in the net enclosures, this mechanism seems to be highly based on reflex-like motor patterns (Barlow, 1977; Brown and Colgan, 1985).

By analyzing the location of bite on the bait by both captured and non-captured individuals, it was found that the natural bait was swallowed more often completely than the soft plastic bait, which was usually only partly swallowed. Fast-attacking pike swallowed the bait more often than hesitant conspecifics did. The artificial bait, therefore, attracted relatively more attention in percentage terms but subsequent attacks were less frequent and less committed in terms of swallowing, which ultimately resulted in a capture bias towards fast-responding pike when using the soft plastic bait. The natural bait, on the other hand, was probably identified as a "real" prey item and, therefore, was attacked in a routine manner to minimize the risk of escape. This would suggest that pike in a natural ecosystem possess some ability to differentiate artificial baits from natural prey, even when they are very similar in appearance. A laboratory study previously determined a similar ability in juvenile pike (Lucas et al., 2023).

The susceptibility of an individual to capture is, among other factors, affected by the spatial overlap of bait and target species (Matthias et al., 2014). While this was the case for some pike recorded following the bait, other factors, such as the level of satiation, could have affected motivation and the likelihood of a given individual continuing from approach to bite (attack) (Bieber et al., 2023b; Raat, 1991). Corrected for time, the current study recorded 1.4 times more approaches to the soft plastic bait than the natural dead baitfish. The soft plastic bait potentially stimulated slightly more interest due to the movement of the paddle tail, provoking pike to make a closer inspection, while the natural bait was more often attacked or ignored (*e.g.*, detected as natural food but not stalked due to satiation levels). Furthermore, the selective impact of bait type might relate to differences between predator types in the approach phase, as a proportion of reactive pike inspecting the soft plastic bait may have been deterred from biting by its exaggerated tail movement. Reactive pike might have to reach a higher motivational threshold before enacting a bite than proactive pike. Even a slight increase in latency to attack might improve the ability of pike to discern prey from non-prey but this may trade off against a lower success rate in capturing potential prey.

A final consideration is the potential for learning to influence the attack behavior of pike but this was not testable in the present study. Experience of escaped or released individuals and even social learning have previously been considered critical factors affecting the catchability of fish. As none of the 32 tested pike was caught a second time, this might indicate a potential learning effect in released individuals (Askey et al., 2006; Lennox et al., 2017; Lovén Wallerius et al., 2020; Lucas et al., 2023).

4.4. *Angling success with artificial and natural baits*

A goal of recreational fisheries management is to maintain angler satisfaction, which can be partly explained by the effort required to catch preferred target species (Beardmore et al., 2015). In this study, effort can be described in terms of time and trolling distance and this differed between the two baits, with twice the effort required to catch a pike using the artificial bait compared to the natural bait. Approximately one pike per hour was caught with the natural bait, and 0.5 pike per hour was caught with the artificial bait. This was within the upper range of values reported in the literature for pike angling: 0.2–0.4 pike/hour depending on the month in a European lake (artificial bait: Arlinghaus et al., 2017) and 0.52 pike/h in lakes in the USA (open water angling, bait unknown: Pierce et al., 1995). For muskellunge, a related esocid species, capture rates of 1.1 juvenile age-0 fish/h were reported (0.04 ha ponds, 140 individuals stocked, artificial baits: Bieber et al., 2023b). The factors that might have resulted in this high capture rate were season, high density of pike, turbidity, food availability, previous moderate fishing pressure and some parameters specific to the fishing technique, such as constantly moving to another area or the speed with which the baits were trolled. From the studies of Pierce et al. (1995) and Bieber et al. (2023b) it can be deducted that density of pike alone is not a good predictor of capture rates. Nevertheless, density and other factors are not likely to be mutually exclusive, and the contributions of combinations of these factors can be evaluated only on a large sample set that includes several lakes with good knowledge of possible covariates. From a management perspective, these results suggest anglers using trolling might lose some efficiency when fishing with artificial baits compared to natural baits, which would lead to lower angler satisfaction (Beardmore et al., 2015). However, this loss of satisfaction might be partially offset by the increased availability, durability and storability of artificial baits compared to natural bait (Legault et al., 2023). Overall angler satisfaction shapes preferences for regulations, compliance, and general angler behavior such as participation rates or even expenditures, which in turn can benefit management (Birdsong et al., 2021)

To maintain catch rates of pike, it is also important to minimize post-release mortality, as pike are often released after capture for legal or voluntary reasons. No critical tissue injuries, such as those to the gills or esophagus, were observed, though light bleeding occurred with both bait types. A previous study found a higher probability of bleeding with natural and soft plastic baits compared to artificial metal baits (Stålhammar et al., 2014). The trolling method used in this study may have reduced injuries, as the immediate tension on the line limited how deeply the pike could take the bait into critical areas. The use of barbless hooks also reduces injury (Meka, 2004). Despite the direct tension, pike that attacked the natural bait exhibited a longer defensive response than those that attacked the artificial bait. This is consistent with previous research comparing attacks on natural baits and soft plastic lures (Lucas et al., 2023). The delayed response could be due to the familiar texture and smell of freshly killed roach, a common prey species for pike in this lake.

5. Implications for the management of pike populations

Successful management of recreational fisheries has as priorities the preservation of ecosystem function and the maintenance of angler satisfaction (Beardmore et al., 2015). If only one of the here described predator types within the population is targeted by angling, both priorities might be negatively affected. Against a backdrop of a changing environment, the existence of different predator types may be important in the resilience of a population, and the maintenance of such behavioral diversity should thus be integral to recreational fisheries management.

Since proactive pike seem less hesitant toward a fishing bait overall, they are possibly more prone to both removal through harvest or post-release mortality and to learned avoidance behavior. Furthermore, proactive pike seem less disrupted by a stressor and more likely to continue natural hunting behavior as circumstances change. In a natural ecosystem, each individual is repeatedly exposed to stressors in the form of environmental changes (*e.g.*, the appearance of alien species or the effects of the climate crisis (McBryan et al., 2013; Strayer, 2010)); therefore, it can be expected that proactive pike contribute slightly more to maintaining ecosystem function than their reactive counterparts. Thus, the removal of proactive pike can have multiple consequences including impaired ecosystem function, declining catch rates and decreased angler satisfaction. From a fisheries management perspective, it can also result in biased estimates of population variables and recreational fishing impact if assessments are based on catch rates.

Management to counteract selective removal of a specific pike predator type should involve the application of best-known fishing practices, including the reduction of air exposure, the application of rubberized net materials, minimizing damage to the mucus layer of the fish through contact with dry surfaces, and avoiding fishing during periods with high temperatures and low oxygen levels (Brownscombe et al., 2017). Furthermore, it is recommended that appropriate gear strength be used to prevent line breakage and reduce fighting time, that baits be appropriately sized, and that barbless hooks be considered if the fish is to be returned for voluntary or legal reasons. If they are not already in place, closed seasons throughout the spawning season could be implemented to reduce cumulative mortality effects through stress and a suppressed immune response. When best-known fishing practices are applied, pike mortality rates have been reported to be less than 10 % (Klefoth et al., 2008).

In particular, despite the similar appearance of the natural bait and the soft plastic lure, the latter selectively caught proactive pike. This bait selectivity provides an interesting basis for further research, testing bait types with more drastic differences in appearance, movement or trialing them with other angling techniques. A further essential consideration is the extent to which angling vulnerability and predator type in northern pike are heritable traits, as has been previously shown for largemouth bass, where vulnerability to angling is heritable and partly related to their foraging behavior (Cooke et al., 2007; Nannini et al., 2011; Philipp et al., 2015). Recent studies of this bass species have proposed methods to support the management of recreational fisheries to maintain angler satisfaction by implementing (rotating) protected areas (Cooke et al., 2017). It follows that decisions regarding the management of recreational pike fishing should consider the behavioral diversity of pike populations as a component to conserve their genetic integrity, with the aim of maintaining angler satisfaction and ultimately maintaining, or even promoting, ecosystem function in the future.

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CRediT authorship contribution statement

Brinker Alexander: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. **Geist Juergen:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Ros Albert:** Writing – review & editing, Methodology, Conceptualization. **Lucas Jorrit:** Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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.

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Data availability

Data will be made available on request.

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