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# Hook retention but not hooking injury is associated with behavioral differences in Bluegill

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ABSTRACT

Recreational catch-and-release angling (C&R) is prevalent and growing in popularity, along with concerns over the welfare of released fish. Although there have been many studies quantifying post-release mortality in fish exposed to C&R, there is growing interest in understanding and minimizing any sublethal consequences of recreational fisheries interactions with the aim of improving fish health and welfare. Short-term fish behavior has been explored as an endpoint for C&R, but effects of hooking injury have not been examined independently of other angling stressors. We used Bluegill (*Lepomis macrochirus*) as a model to assess whether immediate injuries from hooking or the retention of a hook influenced fish behavior compared to unhooked controls using Z-maze and flight initiation distance tests. Fish that retained a hook were less likely to leave a refuge-emergence chamber than fish that were hooked–unhooked or unhooked controls. Moreover, when fish with the hook retained did leave the refuge, they were less exploratory than fish in the other two treatments. Unhooked control fish and fish that were hooked-unhooked did not significantly differ in their overall behavioral patterns outside the refuge. This suggests that fish are resilient to the acute tissue damage associated with minor hooking injuries and that reported behavioral impairments in fish after release are driven more by hook retention, physiological exhaustion from the fight, landing, and/or subsequent handling and air exposure.

## 1. Introduction

Hooks have been used to capture fish for thousands of years (Fujita et al., 2016) and are the primary means of capture via rod and line in modern recreational angling. Although many fish captured by recreational anglers are harvested for food (Cooke et al., 2018), many are also released to comply with fisheries-specific regulations or voluntarily as a result of conservation ethics (i.e. catch-and-release angling, hereafter referred to as C&R; Arlinghaus et al., 2007). Cooke and Cowx (2004), for example, estimated that of ~47 billion fish caught by anglers around the globe annually, more than 30 billion were subsequently released. From a fisheries management perspective, C&R has been an important strategy for maintaining sustainable and responsible recreational fisheries (Wydoski, 1977; Cooke et al., 2019). Fisheries managers generally focus at the population level and thus are concerned with terminal endpoints (mortality), whether from intentional harvest or unintended post-release mortalities (Coggins et al., 2007). In the context of C&R, post-release outcomes are usually only of concern to the extent that sub-lethal impacts may result in decreased reproductive fitness (Cooke et al., 2002a), but there is growing recognition that animal welfare aspects of sub-lethal effects of C&R demand greater consideration and prioritization (Cooke and Sneddon, 2006).

Fish exposed to a C&R event can experience a range of injuries and physiological stressors ranging from the hooking injury itself (where the hook or hooks intersect with the fish), handling injury during landing and hook removal, and physiological exhaustion from the fight and subsequent air exposure during handling (reviewed in Arlinghaus et al., 2007). Such injuries and physiological disturbances have the potential to impact post-release behaviors (Cooke and Schramm, 2007; Klefoth et al., 2008, 2011) and may reduce individual reproductive fitness (Cooke et al., 2002a). Injury to captured fish is unavoidable in recreational angling when using hook and line, as hook penetration will always inflict some degree of tissue damage. Several factors including types of bait (e.g. live vs. artificial), the size of bait, and hook influence

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the likelihood of more severe injuries being incurred (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007). Of note, barbless hooks generally reduce hooking injury and handling times relative to barbed hooks, with improved outcomes for survival of released fish (Bartholomew and Bohnsack, 2005; Brownscombe et al., 2017). As not all hooked fish are successfully landed (e.g. due to line breaks) and anglers may decide to release captured fish without removing the hook(s), understanding the outcomes for fish with retained hook(s) remains of great importance (Tsuboi et al., 2006; Robert et al., 2012; Stein et al., 2012; Weltersbach et al., 2016). For instance, Tsuboi et al. (2006) and Stein et al. (2012) observed no mortalities occurring due to hook retention with hook expulsion rates between 32–46 % in White-Spotted Charr (*Salvelinus leucomaenis*) and Bonefish (*Albula vulpes*), respectively. Pullen et al. (2019) compared the movements and long-term behavioral consequences of hook retention in released Northern Pike (*Esox Lucius)* by inferring that hook retention was associated with decreased movement in spatial telemetry studies. By contrast, Robert et al. (2012) and Weltersbach et al. (2016) observed some mortality attributed to hook retention (27–60 %) and lower hook expulsion rates (0–40 %) in Bluegill (*Lepomis macrochirus*) and European Eel (*Anguilla anguilla*), respectively, indicating that hook retention can have negative consequences including death. However, little is known about how hooking injury or hook retention independent of other angling-related stressors (e.g. air exposure) influence short-term, fine-scale fish behavior.

Research to date has revealed that modified fish behavior following C&R can include differences in movement (Cooke et al., 2002b; Klefoth et al., 2008, 2011), increased susceptibility to predation (Raby et al., 2014, 2018; Lennox et al., 2017), and reduced foraging behavior (Fobert et al., 2009; Stålhammar et al., 2012). However, these studies hold the assumption that behavioral alterations are related to physiological disturbances from the fight, landing, and/or subsequent handling, and not directly from the hook and hooking injuries *per se*. Although the use of topical analgesics at the site of hooking prior to release has been suggested (Mettam et al., 2011), to our knowledge besides experiments by Eckroth et al. (2014) on Atlantic Cod (*Gadus morhua*), there have not been any other controlled laboratory studies published that explicitly tested whether hooking injury or presence of the hook itself alter short-term behaviors independent of physiological stressors of the fishing event (i.e. fight duration, landing, handling, and air exposure). Fish behaviors have been used as proxy measurements to study fish welfare (Eckroth et al., 2014), including what some have interpreted as pain (Sneddon et al., 2003a,b), though these interpretations are contested (see Rose et al., 2014; Key, 2015), thus evaluating fine-scale behavioral differences between hooked and unhooked fish represent important topics for exploration to link survival and welfare considerations within the C&R context.

The goal of this study was to identify any acute behavioral effects resulting from physical hooking and hook retention in the absence of additional C&R stressors such as physical exertion and air exposure. Bluegill are an ideal focal species as they are a common target in recreational fisheries, are relatively easy for inexperienced anglers to catch, and tend to be caught using live bait techniques (Cooke et al., 2003) that make them especially vulnerable to hooking injury (Kerr et al., 2017). Bluegill also have small mouths with limited gape capacity, rendering hook removal relatively difficult and thus favoring the use of smaller hooks to facilitate removal. We evaluated behavioral responses of Bluegill that had either been hooked and unhooked (hooked-unhooked) or hooked and left hooked (hook-retained) versus unhooked controls via two behavioral assays, flight initiation distance (FID) from a novel object, and exploration and movement in a Z-maze arena. Identifying how behavioral patterns may differ immediately following hooking events and/or hook removal in the absence of other C&R stressors within a recreational fishery context will provide valuable information for fish welfare guidelines, conservation and management agencies, hook and angling gear manufacturers, and recreational anglers to improve C&R practices.

## 2. Methods

### 2.1. Fish collection and holding conditions

Size-matched Bluegill (total length = 133 ± 2 mm, mean ± SD) were collected using a beach seine (20m × 1m) in Opinicon Lake, Elgin, ON, Canada (44.5590 °N, 76.3280 °W) during August 2018. Capture sites were limited to shallow, sandy bays (~1 m depth) with low to moderate aquatic macrophyte coverage. Every fish collection technique suffers from sampling bias. As such, our collection method could lead to bias considering that we chose to collect fish using seine nets which have been shown to be size selective and lead to higher catch efficiency in habitats with higher macrophyte biomass (Pierce et al., 1990). Once collected, a maximum of 18 Bluegill ($n = 56$ total) were held for a 24 h acclimation period in two outdoor tanks (110 L; 9 per tank) covered with netting to exclude predators and prevent escape. Holding tanks were supplied with a continuous flow of fresh lake water and were kept at a stable temperature (23.2 ± 0.3 °C; DO ≥ 80 % saturation). All experimental procedures complied with the guidelines for the care and use of research animals of the Canada Council on Animal Care and all applicable Canadian laws under approval by the Carleton University Animal Care Committee (AUP #104281).

### 2.2. Experimental treatments

To quantify how fish behavior was influenced by hooking events, Fish were carefully netted out of the holding tank and quickly transferred to a 15 L treatment tank for 1 min, then removed from the treatment tank for 20 s by an experimenter with wet hands and exposed to one of the three treatments (unhooked controls, hooked-unhooked, or hook-retained). An unmanipulated control group (unhooked controls; $n = 18$) were held out of water with wet hands for 20 s and 15 cm longnose pliers were inserted into the mouth to simulate the mechanical process used to hook individuals in the experimental treatments. To simulate a hooking event, a hook (size 6 barbless octopus-style hooks, Gamakatsu, Normark Inc, Oshawa, ON, Canada) was held with the pliers, inserted into the mouth, and pierced through the soft tissue of the upper jaw behind the lip (~5 mm from the anterior end of the fish). Hooks were removed within the 20 s holding time in the hooked-unhooked ($n = 18$) treatment fish or left in place in the hook-retained ($n = 20$) treatment fish. A new hook was used for each individual, and used hooks were discarded. All fish were air exposed for a total of 20 s, a duration shown to be tolerable to Bluegill (Gingerich et al., 2007) and a fraction of the 180 s needed to elicit a maximal stress response for this species at this water temperature (~23 °C; Cook et al., 2012).

### 2.3. Behavioral assays

We used two separate behavioral assays (FID; Z-maze novel arena) to evaluate the effects of hooking and hook retention compared to unhooked controls. Flight initiation distance is a common behavioral assay used to evaluate individual reactiveness and propensity to flee from an approaching novel object simulating a predator or other negative disturbance (Stankowich and Blumstein, 2005), while Z-maze assays provide estimates of individual propensity to enter and explore a novel environment (Chapman et al., 2010). We chose this combination of behavioral tests as they provide complementary, ecologically relevant information on potential post-release effects of hooking as an isolated stressor in C&R fishing. The order of the tests (either Z-maze or FID first) was randomized prior to experimentation to avoid trial biases. Once a fish had completed one behavioral test, it was transferred immediately to the holding area of the second test without a recovery period between assays. Immediate testing prevents cumulative stress from multiple handling and hooking treatments. Accordingly, we chose to assess each individual only once per behavioral assay as truly repeated measurers would require multiple simulated capture events for each fish, which was not the intention of the study. Additionally, Bluegill behaviors related to boldness and exploration have been shown to be repeatable within individuals within 1–3 months of the original observation (Wilson and Godin, 2009; Conrad et al., 2011), suggesting that similar patterns may also be expressed over shorter (minutes) timescales. Each test was recorded using GoPro Hero3 cameras (GoPro, Inc., San Mateo, California) mounted overhead and behavioral data were transcribed from the videos. The maximum number of fish tested on any given day was $n = 18$, comprising $n = 6$ per treatment group, with testing taking a total of five days. Trial arenas were drained and rinsed thoroughly to remove any semiochemical artefacts between each trial.

The FID arena consisted of a rectangular fiberglass raceway tank (156 cm length x 27.7 cm width, ~130 L volume) filled with unfiltered lake water to a depth of 30 cm. A measuring tape was fixed lengthwise at the bottom of the tank to record FID (Stankowich and Blumstein, 2005; Wilson and Godin, 2009). Focal fish were transferred to the arena and allowed to swim freely for a 2 min acclimation period, after which the novel object (a 3.2 cm red and white spherical bobber mounted on one end of a 1.98 m long plastic rod) was lowered into the arena to below the water surface and moved towards the head of the fish at a steady speed (~0.2 m $s^{-1}$). The approach was stopped as soon as the fish moved to avoid the bobber. Nearest distance between approaching novel object and focal fish (FID) was measured from the video and binned into 5 cm increments to account for sub-optimal accuracy of measurements.

The Z-maze consisted of a rectangular arena (80cm × 100cm) constructed out of black plexiglass with a covered and gated refuge (40cm × 20cm) at one end. The rest of the arena was divided by three staggered partitions 20 cm apart from each other and arranged to form three corridors in a switchback or a Z–pattern (Fig. 1). Every 20 cm interval along the corridors was marked to form 18 identical squares (refer to Chapman et al., 2010) and the maze was filled with unfiltered lake water to a depth of 15 cm. Prior to the start of each trial, a focal fish was placed in the refuge with the gate down and the lid replaced for a 5 min acclimation period. After 5 min, video recording started and the gate was removed to allow the fish 10 min to emerge and explore the Z–maze. Fish that left the covered refuge were allowed to return to the refuge throughout the 10 min trial period (Lawrence et al., 2018). We recorded: i) time to emerge from the refuge, ii) total time spent in the maze, iii) furthest distance reached within the maze (furthest square; max = 18), and iv) total number of line crosses, this includes both forward travel away from the refuge and backwards travel towards the refuge (a proxy for total distance traveled) from the video files. After behavior trials, hooks were removed, and fish were released back to the lake.

### 2.4. Statistical analysis

Data generated from both behavioral trials were analyzed and visualized using RStudio Version 1.3.959 (RStudio, 2015) for R v4.0.0 (R Core Team, 2020) and 'ggplot2' v3.3.1 (Wickham, 2016). Reactivity measurements (FID), as described above, were binned to the nearest 5 cm and counts of individuals observed at each distance per treatment were determined. The discrete distribution was assessed using 'fitdistrplus' v1.1-1 (Delignette-Muller and Dutang, 2015) and a Poisson Generalized Linear Model (GLM) with hooking treatment and binned distances as interacting categorical factor were used to determine if treatment affected fish reactiveness.

Z-maze behavioral metrics (time to emerge from the refuge chamber, total time spent in the maze, furthest distance traveled, total of number of lines crossed) were all dependent variables while the independent variable was hooking treatment per each statistical test. Data were assessed for normality using kurtosis, skewness, and distribution fit ('moments' v0.14; Komsta and Novomestky, 2015; 'fitdistrplus' v1.1-1; Delignette-Muller and Dutang, 2015), while homoscedasticity was assessed using Levene's test ('car' v 3.0-8; Fox and Weisberg, 2019). The behavioral metric data for the Z-maze were all non-normally distributed and transformations did not correct for normality, thus Kruskal-Wallis (K-W) tests were used to assess overall differences between treatment groups for each of the four behavioral metrics. If the K-W tests were significant, we performed a Dunn's post hoc test with False Discovery Rate adjustment (Benjamini and Hochberg, 1995) to identify pairwise differences between individual treatments. Fish that emerged from the refuge during the 10 min trials were classified as '1', while fish that did not emerge were classified as '0'. We evaluated binomial fish emergence data using GLM with hooking treatment as a categorical factor against a binomial error distribution. A post hoc multiple comparisons of means test with Tukey contrasts from the 'multcomp' package v1.4-13 (Hothorn et al., 2008) was used to identify pairwise differences between treatments. Statistical significance was accepted at a level of $\alpha < 0.05$ for all tests.

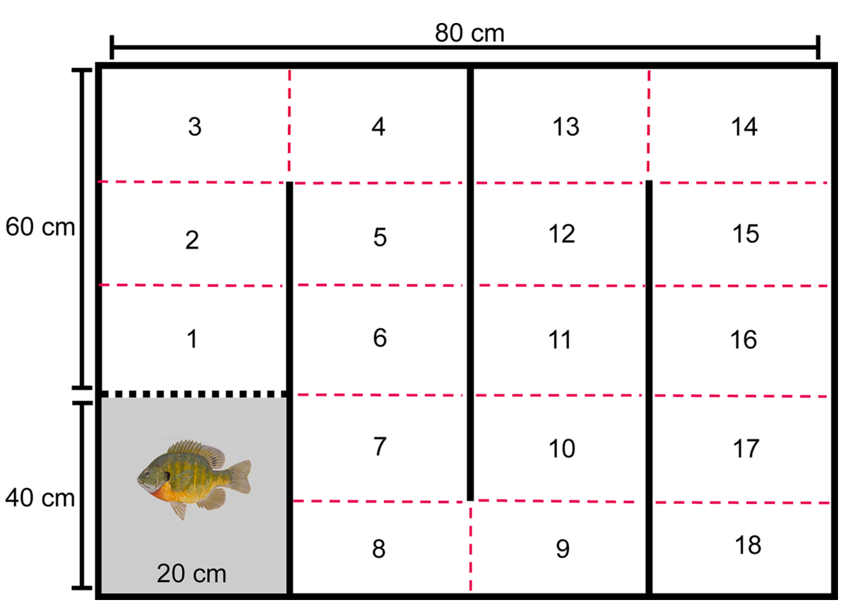


**Fig. 1.** Schematic diagrams of the behavioral assay consisting of a Z-maze novel arena used to assess behavioral differences in Bluegill (*Lepomis macrochirus*) in different hooking treatments. In the Z-maze assay, black plexiglass partitions make up a Z like pattern (solid bolded black lines), while a grid pattern consists of 18 identical squares (20 cm × 20 cm, red dashed lines, numbered 1–18), and the grey box represents the refuge and emergence chamber. The refuge (40cm × 20cm) was equipped with a pulley-mounted rising gate (dotted black line) that was left closed until the start of each trial.

**Table 1**
A summary of the percentage of individuals observed per treatment per flight initiation distance (cm). No significant differences were observed between treatments (Poisson GLM; Likelihood-Ratio $\chi$ 2 = 7.40, df = 11, α = 0. 0.766).

| Treatment | Flight Initiation Distance (cm) | Percentage of Individuals Observed |
|---|---|---|
| Control | <5 | 40 |
| Control | 5 | 10 |
| Control | 10 | 15 |
| Control | 15 | 15 |
| Control | 25 | 10 |
| Control | 30 | 5 |
| Control | 35 | 5 |
| Hooked-Unhooked | <5 | 19 |
| Hooked-Unhooked | 5 | 19 |
| Hooked-Unhooked | 10 | 5 |
| Hooked-Unhooked | 15 | 19 |
| Hooked-Unhooked | 20 | 10 |
| Hooked-Unhooked | 25 | 14 |
| Hooked-Unhooked | 30 | 5 |
| Hooked-Unhooked | 40 | 5 |
| Hooked-Unhooked | 70 | 5 |
| Hook-Retained | <5 | 33 |
| Hook-Retained | 5 | 10 |
| Hook-Retained | 10 | 19 |
| Hook-Retained | 15 | 5 |
| Hook-Retained | 20 | 14 |
| Hook-Retained | 25 | 5 |
| Hook-Retained | 35 | 5 |
| Hook-Retained | 45 | 5 |
| Hook-Retained | 60 | 5 |

## 3. Results

Regardless of hooking treatment, majority of individuals were observed to have FID values of <5 cm (40 % controls; 19 % hooked-unhooked; 33 % hook-retained; Table 1). Hooking treatment did not influence FID, with fish in all treatments demonstrating similar variation in reactive responses to the approaching novel object (Poisson GLM; Likelihood-Ratio $\chi^2 = 7.40$, df = 11, α = 0. 0.766).

We did, however, detect differences in behaviors in the Z–maze, with hooking treatments significantly influencing the time it took to emerge from the refuge chamber (K–W $\chi^2 = 8.12$, df = 2, α = 0.017). Bluegill in the hook-retained treatment took significantly longer to emerge than control fish, while there was no difference between control and hooked-unhooked fish or hooked-unhooked and hook-retained fish (Table 2; Fig. 2A). Total time spent in the maze overall differed significantly between hooking treatments (K–W $\chi^2 = 10.35$, df = 2, α = 0.006) with hook-retained fish spending significantly less time in the maze compared to control fish (Table 2; Fig. 2B). Furthest square reached did not differ significantly between treatments (K–W $\chi^2 = 5.82$, df = 2, α = 0.055; Fig. 2C) nor did the total number of lines crossed (exploratory behavior; K–W $\chi^2 = 4.89$, df = 2, α = 0.087; Fig. 2D).

Assessments of fish emergence from the refuge chamber differed significantly between treatments (binomial GLM; Likelihood-Ratio $\chi^2 = 9.117$, df = 2, α = 0.011) with hook-retained fish less likely to emerge from the refuge for the entire duration of the test compared to control fish, and no apparent differences between hook-retained and hooked-unhooked or control and hooked-unhooked fish (Table 3). In total, 39 % of control fish did not leave the refuge compared to 67 % hooked-unhooked and 80 % hook-retained fish.

## 4. Discussion

Simulated angling (hooking) of Bluegill revealed that fish that were hooked-unhooked did not differ in their immediate behaviors from unhooked control fish, while Bluegill that retained a hook (hook-retained) demonstrated behaviors consistent with inhibition relative to unhooked controls. We observed that most (80 %) Bluegill with retained hooks did not emerge from the refuge chamber (Table 3), and when they did exit, they demonstrated inhibited exploratory behavior by not traveling as far into the maze, spending less total time in the maze, and crossing fewer lines in the maze than control fish (Fig. 2). Reactivity (FID) assays did not reveal differences between hooking treatments, suggesting that while hook-retained Bluegill demonstrate decreased exploration and activity for some behavioral metrics compared to the other treatments, the physical damage associated with hooking is not of sufficient degree to impair avoidance or reactivity responses. Thus,

**Table 2**
Dunn's post hoc test results of pairwise hooking treatment comparisons for two behavioral measures demonstrated by Bluegill (*Lepomis macrochirus*) in a Z–maze assay. Bold font indicates statistically significant differences (α < 0.05). Summary statistics below are the following for treatment comparisons: Behavioral Metric of interest, treatment comparison, degrees of freedom (df), Z value, and α.

| Behavioral Metric | Comparison | df | Z | α |
|---|---|---|---|---|
| *Emergence time* | control : hook-retained | (16, 18) | −2.789 | **0.016** |
| *Emergence time* | control : hooked-unhooked | (16, 16) | −0.928 | 0.353 |
| *Emergence time* | hooked-retained : hooked-unhooked | (18, 16) | 1.836 | 0.099 |
| *Total time in maze* | control : hook-retained | (16, 18) | −3.177 | **0.004** |
| *Total time in maze* | control : hooked-unhooked | (16, 16) | −2.069 | 0.058 |
| *Total time in maze* | hooked-retained : hooked-unhooked | (18, 16) | 1.054 | 0.292 |

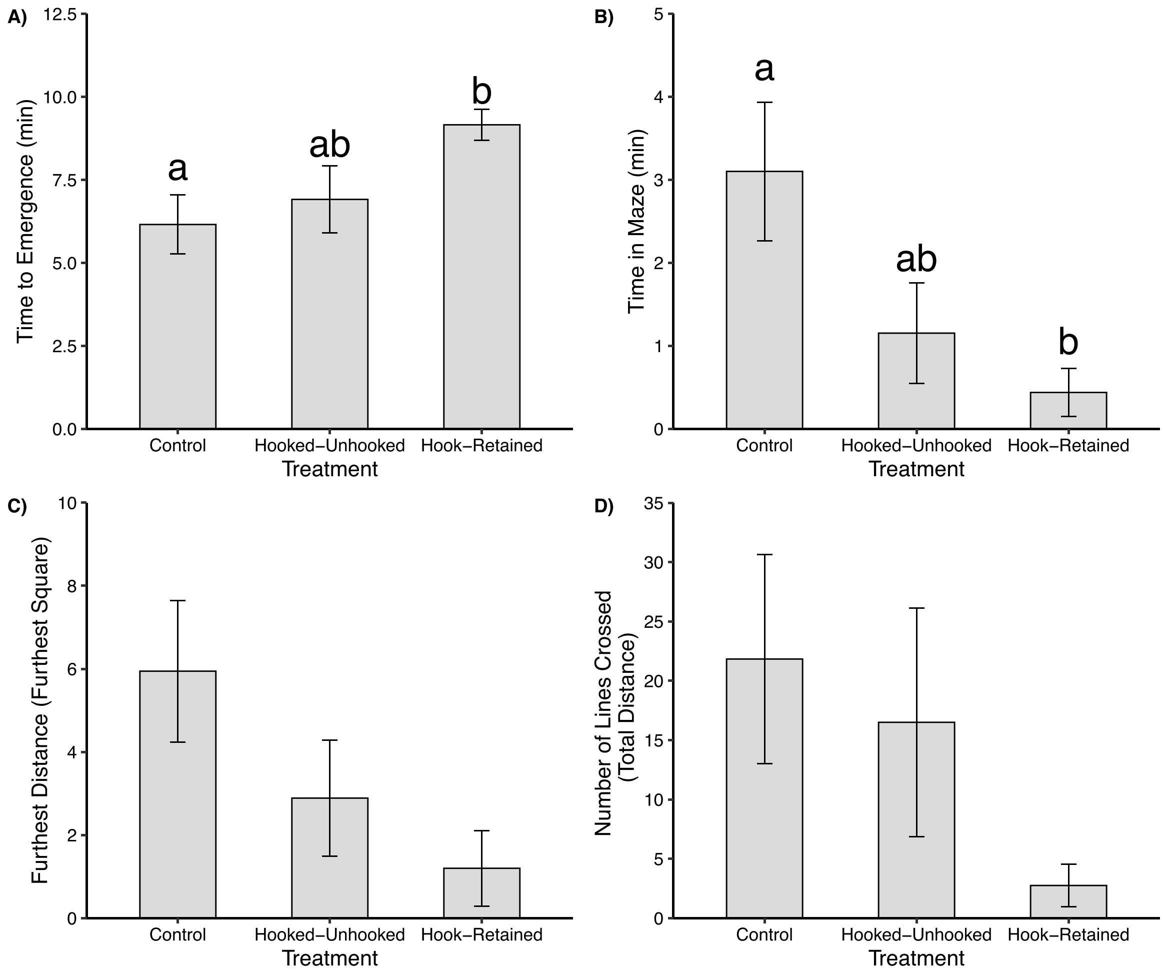


**Fig. 2.** The effects of hooking treatments (unhooked controls, hooked-unhooked, hook-retained) on A) time (min) to emerge from the refuge, B) total time (min) spent in the maze C) furthest distance (square) traveled, and D) number of line crosses by Bluegill (*Lepomis macrochirus*) in a Z-maze behavioral assay. Each bar represents the mean plus or minus the standard error of the mean (error bars). Different letters indicate significant pairwise differences between treatment groups at alpha (α) = 0.05. Behavioral metrics that were not found to be overall significant do not have letters indicating pairwise differences between treatment groups.

**Table 3**
Multiple comparison of means (Tukey's post-hoc test) for pairwise comparisons of different hooking treatments effect on Bluegill (*Lepomis macrochirus*) emergence from the refuge of a Z–maze. Bold font indicates statistically significant differences (α = 0.05). Summary statistics below are the following for treatment comparisons: degrees of freedom (df), estimate of the parameter (estimate), standard error of the estimate (std error), z value for the estimate, and alpha (α).

| Treatment | df | estimate | std error | z value | α |
|---|---|---|---|---|---|
| control : hook-retained | (16, 16) | −2.187 | 0.791 | −2.764 | **0.016** |
| control : hooked-unhooked | (16, 18) | −1.145 | 0.696 | −1.646 | 0.225 |
| hook-retained : hooked-unhooked | (18, 16) | −1.041 | 0.801 | −1.300 | 0.394 |

hooks themselves may not impose short-term survival costs arising from inhibited predator avoidance or escape abilities. More reactive fish, as inferred from greater demonstrated FIDs, may have greater success at avoiding foraging predators (Stankowich and Blumstein, 2005) and experience with elevated predation risk (Dill, 1974). Collectively, these observations from both behavioral assays indicate that the effects of hooking in a simulated angling context do not manifest in detectable differences in exploratory or activity-related behaviors, whereas leaving the hook in place (hook-retained) resulted in significant decreases in exploration and activity.

Although we did not detect FID differences between hooking treatments, the Z-maze metrics suggest that hook-retained fish are more likely to occupy physical refugia for some period of recovery, leaving them less exposed or vulnerable to predation attempts from which flight or escape may be necessary. Raby et al. (2018) quantified the post-release behavior of four reef fish species in the Great Barrier Reef after a simulated catch-and-release event (i.e., no hooking). The study found Spanish flag snapper spent more time immobile when exposed to high stress during simulated catch-and-release. Behavioral responses to being hooked in recreational angling contexts have been reported and generally described as immediate reductions in movement and exploration in some species, although these studies also included real or simulated landing fights involving physical exertion on the fish (Arlinghaus et al., 2008; Henry et al., 2009; Pullen et al., 2017). Our results indicate that hooking followed by quick removal (< 20 s; Meka, 2004; Meka and McCormick, 2005; Gutowsky et al., 2017) of the hook had no significant effects on Bluegill behaviors, suggesting that current C&R recommendations to remove the hook from captured fish as quickly as possible improves fish welfare outcomes and minimizes negative effects of the hooking event (Brownscombe et al., 2017). Although not included in this study, minimizing fight times, landing, subsequent air exposure, and handling are other vital approaches to improve welfare and survival outcomes of fish involved in C&R (reviewed in Arlinghaus et al., 2007).

Bluegill in the hook-retained treatment adopted behavioral patterns consistent with decreased exploration and activity along with increased refuging, consistent with reported behaviors of wild fish released with hooks or lures retained in their mouths during post-C&R angling experiments (Arlinghaus et al., 2008; Henry et al., 2009). Reducing exploratory behavior following tissue damage from a hooking event may be beneficial in providing an interval for an individual to resume an ideal position and location, recover physiologically after exhaustive exercise, and to recuperate from acute injury. Additionally, fish in the hook-retained treatment may be acting to dislodge or remove the hook (Lennox et al., 2015) while their nociceptors are detecting a foreign object or noxious stimulus (Sneddon et al., 2003a,b, Eckroth et al., 2014). This may in turn be facilitated by occupying a physical refuge. Indeed, some hook-retained fish did appear to try to dislodge the hook by using the floor and/or walls of the refuge, in behavior similar to the lateral head shaking observed in hooked Atlantic Cod (Eckroth et al., 2014). Interestingly, Eckroth et al. (2014) found that besides head shaking, hooked Atlantic Cod exhibited no significant behavioral or physiological differences compared to control fish injected with saline, consistent with our observations in the present study of no apparent differences between the behavior of controls and hook-unhooked fish. However, in contrast to the present study, Eckroth et al. (2014) found that Atlantic Cod exposed to presumed noxious treatments (injections with 2 % acetic acid and 0.1 % capsaicin) displayed reduced use of shelter, while hook retained Bluegill in the present study exhibited behavior consistent with increased shelter use, as observed in fishes in the wild (Arlinghaus et al., 2008; Henry et al., 2009). These inconsistencies between fish behaviors in different studies suggest these sorts of behavioral criteria may be species and/or context specific, bringing their broader utility for study of presumed noxious events for fish into question (Rose et al., 2014), and highlighting a need for further studies in this field.

A general assumption when practicing C&R is that the fish survives capture and is largely unaffected by the capture event (Arlinghaus et al., 2007), but post-release mortality, behavioral changes, physiological stress responses, reduced reproductive fitness, and increased vulnerability to predation have been reported in released fish following recreational angling (reviewed in Arlinghaus et al., 2007; Brownscombe et al., 2017), attracting ethical and animal welfare concerns about the practice. Our findings demonstrate that when practicing C&R, removing the hook as opposed to leaving the hook in place, will result in significantly shorter periods of behavioral impairments. We suggest that, in addition to minimizing fight times, landing, air exposure, and handling, hooks be removed as quickly as possible to facilitate recovery as brief hooking events themselves do not appear to influence the behaviors of hooked-unhooked fish relative to unhooked controls. However, if fish are deeply hooked, research clearly demonstrates that survival is higher if the line is cut and hook left in place (Fobert et al., 2009; Cooke and Danylchuk, 2020). Future welfare-driven angling regulations should focus on best practices in terms of fishing gear and handling techniques, and not on the act of C&R itself, to maximize the welfare of species targeted in recreational fisheries and human stakeholders who engage in the activity (Diggles, 2016).

## Author contributions

All authors contributed to the design of the experiment. The experimental trials were conducted by B.L.H, D.M.G, A.D.C, B.S.E. Data analyses and figures were done by B.L.H. The manuscript was written by B. L.H with all authors contributing to revisions.

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## 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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