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Synergistic and interactive effects of angler behaviour, gear type, and fish behaviour on hooking depth in passively angled fish

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ABSTRACT

Despite a growing body of literature on the impacts of recreational fisheries on wild populations, surprisingly little is known regarding how individual differences in fish behaviour and their interaction with a baited hook influences hooking injury. We used an underwater video camera, fixed to the fishing line, to record the behaviour of wild sunfishes (*Lepomis* spp.) as they approached and attacked one of four treatments of baited hook used under a passive angling scenario. Angler reaction time was measured as the difference between the fish strike and hook set. Length-corrected hooking depth was evaluated as a function of multiple putative explanatory variables. Angler performance (hooksets/min) varied over the two day study, where hooksets/min decreased with small hooks and increased with large hooks. Model selection and model averaging revealed the top models included the terms: angler reaction time, approach to bait (cautious, deliberate, aggressive), hook size (small or large), and the interaction between approach to bait and hook size. The model-averaged fitted values indicated that length-corrected hooking depth increased most dramatically with angler reaction time when fish aggressively attacked a baited hook. A cautious approach to a large baited hook led to a deeper length-corrected hooking depth than a similar approach to a small baited hook. These results illustrate synergistic and interactive relationships among factors known to influence impairment, injury, and mortality in caught and released fish. Of particular novelty was our ability to assess the variation in how fish behaviour influences injury in a catch-and-release fishery using underwater cameras, which suggests that this approach holds promise in fisheries science.

1. Introduction

Across the globe, millions of fish are released annually by recreational anglers as a result of conservation ethics or to comply with fishing regulations—an activity called "catch-and-release" (herein termed C&R; Arlinghaus et al., 2007). The premise of C&R is that released fish survive with negligible injury and sublethal physiological and behavioural alterations (Cooke and Schramm, 2007; Wydoski, 1977). Despite the good intentions of anglers and managers, C&R exposes fish to injuries and stressors that potentially decrease their chances of survival (Arlinghaus et al., 2007; Cooke and Suski, 2005). C&R science has largely been directed toward understanding endpoints (e.g., injury, impairment and mortality) in an effort to minimize the negative consequences of C&R and maximize the likelihood that fish survive. The result has been a growing body of literature that forms the scientific basis for best angling practices (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994).

For C&R angling studies that examine injury, statistical variance is often explained with controllable variables that originate from the angler and the environment (Arlinghaus et al., 2007). For instance, hooking depth, eye injury and the amount of bleeding varies according to multiple factors such as hook type, angler experience, and hook-set behaviour (Bacheler and Buckel, 2004; Cooke et al., 2003, 2001; Dunmall et al., 2001; Lennox et al., 2015). While C&R science often focuses on angler behaviour and the environment, fish behaviour is increasingly being considered as a largely uncontrollable, though nonetheless important, component of the C&R process (Brownscombe et al., 2014; Thorstad et al., 2003; Vainikka et al., 2016; Wilson et al., 2015). However, given that impairment, injury and mortality manifest from several sources in C&R fisheries (Cooke et al., 2013), understanding the contribution of fish behaviour to any potential endpoint requires the investiga-

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tion be inclusive and capable of decoupling the influence of fish behaviour from those well-known and independent factors.

Determining or manipulating angler behaviour is a relatively straightforward exercise. For instance, participation, knowledge and skill can be used to define angler experience while hook types can be easily incorporated as experimental treatments (Dunmall et al., 2001; Lennox et al., 2015; Rapp et al., 2008). Given that wild fish are cryptic by nature and often strike angling gear without warning, there are few appropriate techniques for evaluating fish behaviour prior to hooking. However, underwater action cameras (Struthers et al., 2015) provide the opportunity to study fish behaviour as they approach, inspect and interact with baited hooks (e.g., Alós et al., 2014; Alós et al., 2015). When examined in conjunction with angler behaviour, underwater videography techniques provide the ability to evaluate the potential influence of multiple factors on injury or mortality in C&R fish immediately prior to capture.

In this study, we use newly available underwater video cameras and an information theoretic analytical framework to better understand the influence of fish behaviour on hooking depth in wild-caught sunfishes (Lepomis spp.). The study was performed by novice anglers using four hook and bait configurations. Fish were captured from their natural environment using passive angling where the only indication of a strike was through the movement of a bobber (i.e., fishing float). This technique simulated real angling situations for these species while enabling us to simultaneously measure angler reaction time, record fish behaviour and control gear type. Using underwater cameras and model selection, our objectives were to reveal: 1) synergistic and interactive effects from multiple explanatory variables and; 2) the putative influence of fish behaviour on hooking depth in a C&R fishery.

2. Methods

2.1. Study site and sample collection

The study was performed at the Queen's University Biological Station on Lake Opinicon in the Rideau Lakes area of Eastern Ontario (44° 34′N, 76° 19′W). Angling took place between approximately 14:00 to 16:00 h on 7 May and 8 May 2015. Lake Opinicon is shallow (<10 m deep), mesotrophic, and contains a diverse fish community including but not limited to largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*) and two species of sunfish [Pumpkinseed, *Lepomis gibbosus* (Ps) and Bluegill, *Lepomis macrochirus* (Bg)]. Two novice participants (i.e., no previous angling experience) were employed to angle over the brief span of days. Participants were selected based on their similar lack of angling experience whereas the brief span of days helped reduce confounding influences of increasing water temperatures during the spring sampling period. Each of the two participants were outfitted with a medium action rod (198 cm) and reel, light-weight monofilament line (3.5 kg), and a Water Wolf underwater camera (Svendsen Sport, Gadstrup, Denmark). Cameras were tied between the main line and a leader that was approximately 60 cm long from the camera lens to the baited hook. A weight near the lens of the camera ensured it was oriented vertically and faced toward the baited hooks below (Fig. 1A, B). A small bobber was attached above the camera to provide additional buoyancy (Fig. 1B). Cameras were optimized for low-light conditions and able to internally record a series of 20-min videos for up to four hours (12 video files × 20 min/video file; resolution: 720 p).

From the camera it was possible to assess fish behaviour such as the approach and post-strike movement. Fish approach and attack was categorized as cautious (no clear forward motion with only buccal cavity suction to engulf the bait), deliberate (slow forward motion [approx. ≤1 body length s^{-1}] and buccal cavity suction), and aggressive (rapid forward motion [approx. >1 body length s^{-1}] to engulf the bait). During passive angling of sunfish, post-strike behaviour prior to hook setting usually involved rapid pivoting (e.g., a unidirectional head shake and 45° turn) with little lateral movement. As this was a common behaviour among angled sunfishes, post-strike and pre-hook set fish behaviour was assessed as the number of these movements. All research activities were conducted in accordance with guidelines from the Canadian Council on Animal Care at Carleton University, and under a scientific collection permit obtained from the Ontario Ministry of Natural Resources and Forestry (License no. 1079391).

Gear treatments included: a large baitholder hook (6/0) and large bait (3 cm piece of cut dew worm); a small baitholder hook (8/0) and small bait (1 cm piece of cut dew worm); a large hook and small bait; a small hook and small bait. Each angler used one hook size per day and changed bait sizes after capturing 10 fish for a total of 20 fish/day/angler. Anglers were instructed on how to set the hook by sharply pulling the bait away from a detected strike (Fig. 1C). Anglers were not permitted to sight fish their bait (i.e., the ability to observe fish while handling the bait), thus hook setting was only influenced by observing bobber movement. Once captured, fish body size (TL to the nearest mm) and hooking depth (mm) were measured. If the hook was not visible (i.e., lodged in the esophagus or stomach), the fishing line was cut and a new line retied. The depth to the eye of the hook plus the total length of the hook was used to estimate deep-set hooking depth. Length-corrected hooking depth was calculated as the ratio of hooking depth to fish total length (Dunmall et al., 2001). Anatomical hooking location was recorded prior to hook removal. From the recorded videos, angler reaction time was measured as the difference in time (to the nearest millisecond) between the hook set and fish strike.

3. Analyses

3.1. Angler performance and deeply hooked fish

We first explored the data for outliers, collinearity, and two-way relationships using various plotting functions in the R statistical environment (R Core Development Team, 2012). For this study we were interested in three possible response variables: angler performance, the number of deeply hooked fish, and length-corrected hooking depth. Although hooking depth may differ with hook type for Ps and Bg (Cooke et al., 2003), initial data exploration indicated no species-related differences in length-corrected hooking depth for the two baitholder hook sizes. Thus Ps and Bg catches were pooled for analysis. Angler performance was assessed by calculating the number of attempted hook sets per minute while the bait was submerged. This metric was calculated for each video file which was approximately 20 min in length. Hook sets/min served to illustrate trends related to angler behaviour. In addition, variation in performance (e.g., improvements by the novice anglers) would suggest that statistical models may be further explained using fixed or random effects for individual angler over time. The number of deeply hooked fish was plotted as a function of angler reaction time and length-corrected hooking depth. This plot was further used to illustrate the apparent minimum angler reaction time and length-corrected hooking depth to observe a deeply hooked sunfish.

3.2. Length-corrected hooking depth

Akaike information criterion was used to determine how angler behaviour, gear type, and fish behaviour may explain length-corrected hooking depth (Akaike, 1974). Models (n = 23) were *a priori* specified and compared using second-order AIC where mod-

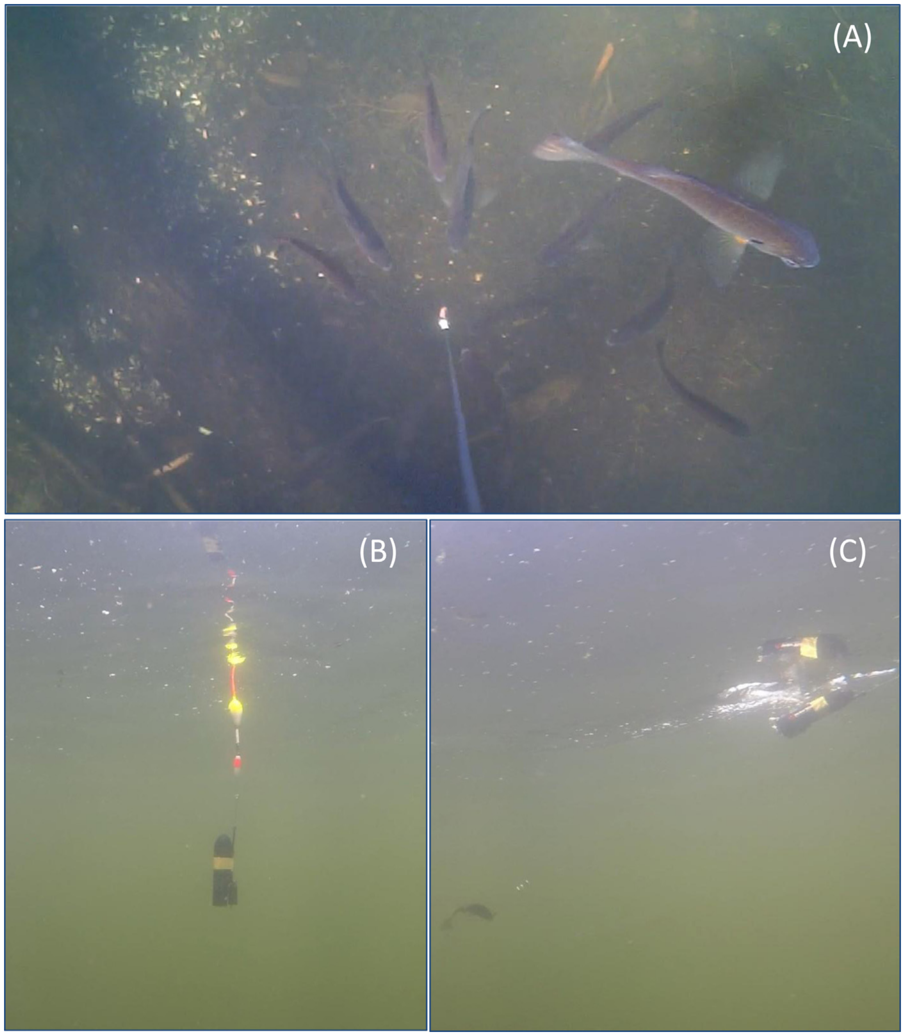

Fig. 1. (A) An image from the underwater camera footage used to record angler reaction time and fish behaviour while passively angling sunfishes in Lake Opinicon, Ontario. (B) The underwater camera is fixed to the line and suspended below a fishing float. (C) Setting the hook following the detection of a strike.

els with ΔAICc < 2 were considered the most parsimonious. Fixed effects could include angler behaviour [reaction time (continuous covariate)], gear type [hook size (categorical factor), bait size (categorical factor)], and fish behaviour [approach (categorical factor), number of sharp movements (continuous covariate)]. Anatomical hooking location was excluded as a covariate due to the highly uneven number of observations per hooking location category. Models included random effects for angler and sampling day. The choice to test the importance of these terms (i.e., using AIC, Zuur et al., 2009) was based on study design, as estimates for the variance associated with angler and sampling day would be based on two levels and would therefore add little to the overall model estimates (Gelman and Hill 2006). Length-corrected hooking depth was log-transformed to obtain heterogeneity of variance in the residuals. Model averaging was performed on the top models (Barton, 2016; Symonds and Moussalli, 2011). The relative importance (RI) of the predictor variables in the top models was assessed by taking the sum of the Akaike weights over all of the models in which the parameter of interest appeared (Barton, 2016). The fit (marginal R^2) of the top model(s) was assessed following Nakagawa and Schielzeth (2013). Candidate models were validated by plotting the residuals against the fitted values and all possible explanatory variables (Zuur et al., 2009). One extreme observation (angler reaction time = 66.02 s) was identified as an outlier and removed for this analysis.

Table 1
Summary statistics for angled sunfish that were recorded with an underwater camera while striking a baited hook. The study occurred 7 May–8 May 2015 in Lake Opinicon, Ontario.

	Median (TL mm)	Min (TL mm)	Max (TL mm)	N
Angler 1—Day 1	147.5	125	193	20
Angler 2—Day 1	152.0	122	186	20
Angler 1—Day 2	139.0	101	202	20
Angler 2—Day 2	145.0	118	198	20

4. Results

Over the two study days, 80 sunfishes (Ps = 36; Bg = 44) were captured (Table 1). Contrary to our expectations, angler performance varied between individuals on a given day (Fig. 2). On day 1, both anglers managed to capture 20 fish each in ≤120 min whereas on day two, under the same environmental conditions and time of day, anglers caught 20 fish each in 160 min. Hook sets/min increased as the anglers fished using small hooks. Conversely, the number of hook sets/min tended to decrease while using large hooks (Fig. 2). Fish approached baited hooks cautiously (n = 23), deliberately (n = 27), and aggressively (n = 30). Following handling of a baited hook and prior to hooking, sunfish ranged in the number of sharp movements, which was highly correlated with angler reaction time (median = 3; range = 0–21; r = 0.8). Most

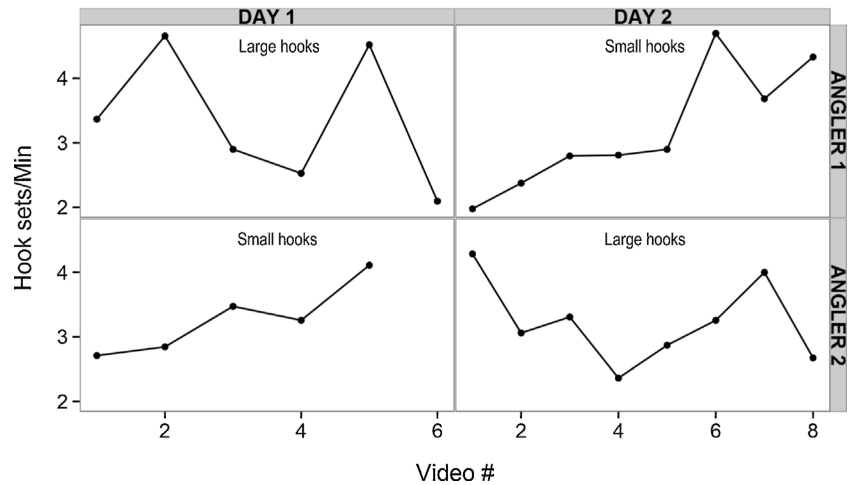

Fig. 2. Hook sets/min during each approximately 20 min video shown by day, angler, and hook size.

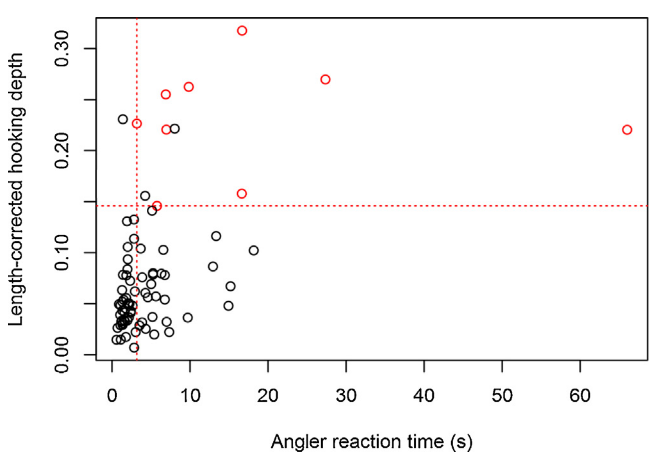

Fig. 3. Length-corrected hooking depth relative to angler reaction time for all passively angled sunfishes captured in Lake Opinicon, Ontario. Observations include hooks that were removed (black open circles) and hooks that were considered deep such that the line was cut (red open circles). Red hashed lines indicate the apparent thresholds for deeply-hooked sunfishes in this study (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

hooks were embedded in the upper jaw (n = 48). All other anatomical hooking locations included: eye (n = 11), corner lip (n = 9), side of mouth (n = 8), lower lip (n = 3), roof (n = 1). Except for two captured fish, angler reaction time was less than 15 s when hooks were the large size. For the small hook size, angler reaction time was up to approximately 27 s. Neither bleeding nor immediate mortality was observed in any sunfish.

Of the eighty sunfish captured, 9 (11.25%) were deeply hooked. Eight of these fish were caught using small hooks baited with either large (n = 4) or small pieces of worm (n = 4). A single sunfish (196 mm TL) was deeply hooked when the treatment included a large hook and worm. Deep hooking occurred as quickly as 3.182 s and at a minimum length-corrected hooking depth of 0.146 (Fig. 3). Three fish were above this apparent threshold where the hook was removed without injury to the fish. Two of these fish had a length-corrected hooking depth of 0.200. Hooks were removed in fish where a length-corrected hooking depth of 0.231 was achieved in 1.392 s and when a fish held bait for up to 18.16 s yet achieved a length-corrected hooking depth of only 0.102 (Fig. 3).

AIC model selection indicated that crossed random effects (i.e., Angler and Sampling day) were the most appropriate extension to the candidate set of models ($AIC_{randomeffects}$ = 180.2; $AIC_{interceptonly}$ = 186.9). The top models (where ΔAICc was <2) included angler reaction, hook size, approach, and a two-way interaction between hook size and approach (M12 and M14, Table 2). The model-averaged fitted values showed that length-corrected hooking depth increased rapidly with angler reaction time when a fish aggressively attacked a baited hook (Fig. 4). A cautious approach to the bait led to a deeper length-corrected hooking depth when the hook was large. For example, when angler reaction time was 14 s, the length-corrected hooking depth was 40% deeper for large hooks compared to small hooks (Fig. 4). According to model averaging, the most important factors were approach (RI = 1.0), reaction time (RI = 1.0), and hook size (RI = 1.0), followed by approach*hook size (RI = 0.49). Fixed factors in model M12 explained approximately 31.8% of the variance whereas those from model M14 explained approximately 36.5% of the variance.

5. Discussion

By using underwater cameras affixed to fishing lines we were able to observe fish behaviour prior to hooking. As expected, length-corrected hooking depth was explained by fish behaviour together with other well-known sources of injury in C&R fisheries (Arlinghaus et al., 2007; Cooke et al., 2013; Muoneke and Childress, 1994). While hooking depth is not the only end-point worth exploring in this context, the negative consequences associated with hooking depth make it important to understand (Arlinghaus et al., 2007; Cooke et al., 2012). The results of the current study illustrate that potential injury in C&R angling originates from a complex process that includes synergistic and interactive relationships among well-studied factors, as well as the lesser-studied individual behaviour of wild fish.

Injury in C&R fish is related to a number of variables originating with the angler (Dunmall et al., 2001; Gutowsky et al., 2011; Lennox et al., 2015). One such example is by Dunmall et al. (2001) who found that experienced anglers hooked smallmouth bass (*Micropterus dolomieu*) more deeply than novice anglers; a relationship attributed to the jig fishing techniques employed among different skill levels of angler. Because both participants in the current study were novices who used the same techniques, traditional thought may have ignored angler influence as a factor (fixed or random) of hooking depth. However, the underwater camera footage revealed the number of hooks sets per minute varied greatly within individual anglers and over time, despite the abundance of sunfishes and similarity in environmental conditions during the sampling period (Fig. 1 and 2). These results indicate that

Table 2
Model selection statistics for models on length-corrected hooking depth. AICc is the bias-corrected Akaike Information Criterion; ΔAICc is the difference in bias-corrected AIC between a given model and the top ranked model; wAICc is the relative weight of the bias-corrected AIC; Log(L) is the log-likelihood of the models; K is the number of parameters. All models contain angler and sampling day as crossed random effects. ART is angler reaction time, HS is hook size, BS is bait size, APP is fish approach to the baited hook, NST is number of sharp turns made by a fish.

Model name	Fixed Effects	*K*	AICc	ΔAICc	AICc Wt	Cum Wt	Log(*L*)
M12	ART + HS + APP	9	170.2	0	0.3	0.3	−74.77
M14	ART + HS * APP	11	170.2	0.06	0.29	0.59	−72.13
M10	ART + BS + HS	8	172.2	2.01	0.11	0.7	−77.05
M18	ART + BS + HS + APP	10	172.6	2.45	0.09	0.78	−74.68
M13	ART * HS + APP	10	172.8	2.62	0.08	0.87	−74.77
M21	ART + BS * HS + APP	11	173.7	3.54	0.05	0.92	−73.87
M9	ART	6	174	3.89	0.04	0.96	−80.44
M15	ART + BS * HS	9	174.4	4.23	0.04	0.99	−76.88
M23	ART * BS * HS + APP	14	180.2	10.08	0	1	−72.83
M17	ART * BS * HS	12	180.6	10.48	0	1	−75.95
M20	ART * HS * APP	16	182.1	11.93	0	1	−70.65
M2	NST + APP	8	184.6	14.42	0	1	−83.25
M1	APP	7	184.7	14.58	0	1	−84.57
M4	NST	6	184.9	14.71	0	1	−85.84
M11	NST + BS + HS	8	185.5	15.35	0	1	−83.72
M8	BS	6	186.5	16.31	0	1	−86.65
M5	HS	6	186.9	16.75	0	1	−86.86
M16	NST + BS * HS	9	187.1	16.99	0	1	−83.26
M19	NST + BS + HS + APP	10	187.1	16.99	0	1	−81.95
M6	HS + BS	7	187.3	17.16	0	1	−85.86
M22	NST + BS * HS + APP	11	187.6	17.43	0	1	−80.82
M3	NST * APP	10	188.8	18.62	0	1	−82.76
M7	HS * BS	8	188.9	18.73	0	1	−85.41

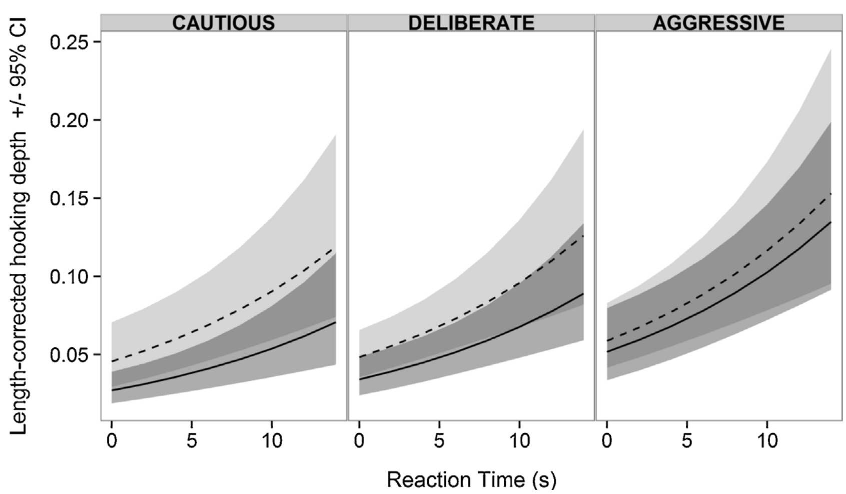

Fig. 4. Model-averaged estimates (±95% CI) of length-corrected hooking depth as a function of angler reaction time, fish approach and hook size. Estimates for large hooks and small hooks are demarcated with hashed and solid lines, respectively. Shaded regions are 95% confidence intervals. The darkest regions of shading illustrate confidence interval overlap.

capture efficiency and indeed hooking depth should be considered in light of individual angler behaviours. However, estimating the influence of individual angler behaviour on C&R fish injury requires a larger sample size of participants, possibly covering a range of skill levels.

Hook type, design and size are each related to injury and impairment in numerous C&R fisheries (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994). However, in their review that included the influence of hook size on mortality, Muoneke and Childress (1994) found inconsistent research findings (e.g., hook size may be positively or inversely related to mortality) which may result from interspecific differences (Arlinghaus et al., 2007). In addition, many C&R studies are not designed to simultaneously evaluate the influence of multiple factors, making it likely that unaccounted covariates commonly confound results. In the current study, the overall mean length-corrected hooking depth was greatest for small hooks (small hooks: 0.84; large hooks: 0.79), however the inclusion of additional covariates showed the relationship was more complicated. We found the interaction between hook size and fish behaviour was important. With angler reaction time included, the estimates for hooking depth were greatest for large hooks when fish approached cautiously whereas no appreciable difference in hooking depth was estimated when fish aggressively attacked either baited hook size (Fig. 3). While the exact mechanisms are unclear, in several sunfish, length-corrected hooking depth remained shallow for small hooks despite poor angler reaction times. Sunfish may have engulfed and handled small hooks whereas large hooks were engulfed and then partially embedded before the angler reacted. However, testing this hypothesis requires further controls (e.g., sample sizes) and the measurement of additional putative covariates, related to fish behaviour, to explain length-corrected hooking depth.

It is largely impossible to control the intrinsic characteristics that affect the fate of an angled fish. For instance under most circumstances anglers indiscriminately target both sexes, all body sizes, and all stages of maturity. Nevertheless, intrinsic characteristics have an influence on the fate of angled fish. Measuring physiological impairment and fight metrics of angled largemouth bass (*Micropterus salmoides*), Brownscombe et al. (2014) found that body size was positively correlated with blood glucose which was also highest in impaired fish. Fish size influences the duration of angling because larger fish require more time to land (Brownscombe et al., 2014; Meka and McCormick, 2005; O'Toole et al., 2010). In the current study, we focused on pre-strike fish behaviour which, when the method (i.e., passive or active, live bait or artificial lures) remains constant, is an uncontrollable factor during angling. Although the reasons that angled sunfishes approached baited hooks at different rates are speculative (e.g., level of satiation, personality, intraspecific competition), simultaneously examining intrinsic and extrinsic factors illustrated the complexity and challenge of understanding how endpoints are reached for C&R fish (Arlinghaus et al., 2007).

It is important to consider why the influence of fish behaviour on injury is relevant to C&R anglers and fisheries managers. Well-intending C&R anglers may employ best angling practices only to see their catch meet an undesirable endpoint. For example, vigilant bobber fishing with gears designed to reduce impairment or mortality will occasionally result in deep hooking because of uncontrollable factors, e.g., body condition and tolerance to stress (Cook et al., 2012; Meka and McCormick, 2005). By knowing that intrinsic factors affect the fate of fish, anglers and managers are further informed about the causes of impairment and mortality in C&R fisheries. Responsible fisheries are formed by a community of informed anglers and managers (Arlinghaus et al., 2007; Nguyen et al., 2012). Additionally, fish behaviour explains variance that would otherwise not be considered in models designed for improving estimates on a given endpoint (e.g., impairment, mortality). Accounting for the variance associated with intrinsic factors will lead to accurate estimates that are indispensable when, for example, C&R mortality is used to establish fishing regulations (Cooke et al., 2013; Gutowsky et al., 2015; Pollock and Pine, 2007).

Quantitative studies commonly isolate explanatory variables rather than investigate them together during the C&R process (Cooke et al., 2013). We found that controllable (i.e., angler behaviour and gear choice) and uncontrollable (i.e., fish behaviour) factors affect injury in a passive C&R fishery. While anglers have the ability to choose practices and gears that minimize the likelihood that fish sustain injury, fish behaviour is an uncontrollable though nonetheless important consideration in evaluating endpoints. Future research will be able to build on these findings to explore additional relationships among explanatory variables and C&R endpoints. It is our view that anglers, researchers, and managers benefit from knowing all of the sources that contribute to impairment, injury and mortality in C&R fisheries.

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