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Short communication

Consequences of fishing lure retention on the behaviour and physiology of free-swimming smallmouth bass during the reproductive period

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ABSTRACT

When break-offs occur during recreational angling, lures may be retained by the fish. To date, there have been few studies on the consequences of lure retention on sportfish. This study evaluated how the retention of three different types of lures (i.e., crankbait, jig and plastic worm—all with barbed hooks) influenced the behaviour, physiology and reproductive success of nesting, male smallmouth bass (*Micropterus dolomieu*) relative to controls released after lure removal. Bass were angled from their nests and subjected to a simulated lure retention scenario in which one of three lure types was placed in the upper middle jaw. Males were subsequently released and their behaviour (time to return to nest, parental care behaviour) was monitored. Immediately after release, fish with retained lures exhibited altered behaviour relative to control fish, attempting to expel the lure. However, these differences in behaviour were no longer apparent after 24 h even for those fish that retained the lures. Rates of nest abandonment did not differ between treatment and control fish in the short term. Fish were rarely able to liberate themselves from the retained lure in the several days post-treatment. Physiological sampling conducted on jig treatment fish and angled controls revealed elevated blood glucose concentrations in fish that had retained lures for 24 h, while lactate concentrations and hematocrit did not differ between treatment and control fish. These results demonstrate that lure retention in the short-term influences both the behaviour and physiology of smallmouth bass. Given that lures were generally retained throughout the study period, there may be merit in anglers using barbless hooks that may be more readily shed by fish that break the line, reducing the welfare impacts associated with lure break-offs on wild fish. Additional studies are needed to understand the longer term consequences of lure retention in free-swimming fish.

1. Introduction

Globally, recreational angling is a popular activity that provides important economic benefits for regional and national economies (Cowx, 2002). Many of the captured fish are released, either in response to regulations or conservation ethic, with the assumption that released fish will survive (Cooke and Schramm, 2007). Several hundred studies have been published that evaluate the biological consequences of catch-and-release angling (reviewed in Arlinghaus et al., 2007). Most of these studies have focused on fish that have been landed by anglers and intentionally released. However, a component of those fish that are hooked break the line before being landed and are usually referred to as “break-offs”. Arlinghaus et al. (2008) defined a “break-off” as an event that occurs during angling when the hook/lure, leader and line or any combination thereof become detached from the angler or their rod and reel assembly and are retained by the fish. Break-off occurs as the result of many events but is common in fish with sharp dentition, gill rakers, bony structures (e.g., sharp opercular plates) or scales, such as northern pike (*Esox lucius*; Arlinghaus et al., 2008), muskellunge (*E. masquinongy*), great barracuda (*Sphyraena barracuda*) and sharks. Anglers may experience break-offs more frequently when fishing in areas of submerged vegetation, debris, or other structures such as fallen trees, coral, or rocks that can tangle or cut the line. Angler experience level may also contribute to break-off through improper knot tying or drag adjustment. Lure retention may also occur without break-off as a result of deep hooking in situations when the lure cannot be removed without extensive injury and the fish is released after capture with the lure still in place. Whatever the cause, the end result remains the same; a fish swims away with a lure or hook(s) in place. With increased interest in fish welfare (Davie and Kopf, 2006; Cooke and Sneddon, 2006), and a need to provide anglers and managers with knowledge to enhance the sustainability of recreational fisheries (Cooke and Schramm, 2007), there is a need to understand the consequences of break-off on fish (Arlinghaus et al., 2007).

Research conducted to date on this subject has focused mainly on the consequences of deeply embedded single hooks (e.g., Warner, 1979; Schill, 1996; Dubois and Kuklinski, 2004; Tsuboi et

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al., 2006) typically used when fishing with organic bait (e.g., worms, baitfish). In those studies, hook retention was evaluated in the context of fish being deeply hooked and the angler having to cut the line in order to facilitate release although the data are also relevant to break-offs. To date, only a single study (i.e., Arlinghaus et al., 2008) has investigated the consequences of lure retention in a recreational angling context. Arlinghaus et al. (2008) used northern pike as a model to investigate the behaviour and survival of fish with retained lures. In the short term (i.e., hours) the authors used floating visual tags to study behaviour of control and treatment fish (released with a plastic shad in the lower jaw) and in the longer term (days to weeks), the authors used radio transmitters to study the post-release behaviour and survival. No mortality was observed after monitoring fish for a 3-week period and although there were some behavioural alterations in fish with retained lures relative to controls, they were short lived (Arlinghaus et al., 2008). Collectively, their results indicated that lure retention does indeed influence the behaviour of pike, at least in the short term, justifying further research into the behavioural, physiological and reproductive success outcomes of lure retention in all fish (Arlinghaus et al., 2008).

The current study used nest guarding male smallmouth bass (*Micropterus dolomieu*) as a model to investigate behavioural, physiological and reproductive consequences of lure retention. Smallmouth bass are popular and economically important sportfish in North America. Male bass provide sole parental care for their brood for a period as long as a month (Ridgway, 1988; Cooke et al., 2006) during which time they engage in a variety of behaviours including active defense against predators and fanning of pectoral fins to prevent silt accumulation while ensuring proper gas exchange for the brood (Kramer and Smith, 1962). Parental care supplied by the male is energetically demanding and further compounded by greatly reduced feeding effort during nesting (Cooke et al., 2002). Because parental care requires the integration of behaviour and physiology and is relevant to fitness, it provides a unique opportunity to experimentally evaluate lure retention in fish. Moreover, because the fish remain in a relatively defined area and conduct a suite of easily quantifiable behaviours, parental care providing bass serve as a useful model for exploring lure retention and the possible sublethal impacts in wild free-swimming fish. Here we sought to determine whether the behaviour (measured as parental care behaviour), physiology (blood glucose, blood lactate and hematocrit as indicators of physiological stress), and reproductive success (a fitness proxy) of fish were influenced by retained lures. We compared three lure types including crankbaits (positively buoyant lure with multiple barbed treble hooks), jigs (weighted, single barbed hooks) and unweighted plastic worms (unweighted single barbed hook) to determine the role of lure type on lure retention and associated endpoints.

2. Materials and methods

This study was conducted in southeastern Ontario on Indian Lake (mean depth = 10 m, maximum depth = 26 m, 44°36′00″N, 76°20′00″W) from May 20 to 24, 2008. To assess the consequences of lure retention on parental care providing male smallmouth bass, nests with males present were located using snorkel surveys in the littoral zone surrounding four small islands. Only nests with males present, guarding broods, consisting of fresh eggs, with an egg score (categorical estimate of the number of eggs in a nest from 1 to 5, low = 1, high = 5) (Kubacki, 1992) from 3 to 4 were included in the study. All accepted nests were marked with individually numbered polyvinyl chloride tiles for easy identification (Kubacki, 1992). The 67 nests included in the study were randomly assigned to one of five experimental groups: (I) non-angled control (herein called "control") fish which consisted of individuals that were observed but never angled from the nest ($n = 11$), (II) angled controls (herein called "sham") that were angled from their nest but did not receive lure treatment ($n = 15$) and the remaining groups, (III) crankbait ($n = 11$; Fig. 1A), (IV) jig ($n = 20$; Fig. 1B) and (V) plastic worm ($n = 10$; Fig. 1C) represented simulated break-off conditions. Detailed descriptions and images of the lures can be found in Fig. 1.

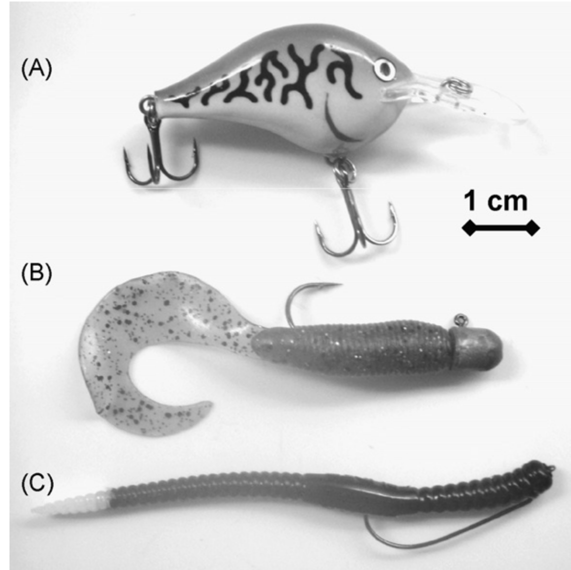

Fig. 1. Lures experimentally placed in the mouths of smallmouth bass to simulate break-offs. Lures used included crankbaits (A; floating, total mass of lure 12.3 ± 3.7 g; total lure length 8.8 ± 1.5 cm), jigs (B; lead dart style jig with a 1/0 barbed hook with a soft plastic twister tail, total mass of lure 13.6 ± 0.2 g; total lure length 6.4 ± 0.1 cm) and plastic worms (C; 1/0 worm hook with a soft plastic worm, total lure mass 3.4 ± 0.1 g; total lure length 11.9 ± 0.6 cm).

Sham controls and lure treated groups were angled from within 5 m of their nests in <20 s using heavy-action recreational fishing gear. All fish were initially captured using barbless jigs and we restricted our efforts to fish that were shallowly hooked (i.e., jaw) and exhibited no bleeding and minimal tissue damage (just the hook penetration site). Fish were then placed in a padded v-shaped trough filled with fresh lake water where the lure was removed and total length of fish recorded (to the nearest cm). Crankbait treated fish were released with a positively buoyant, double number four sized treble hook crankbait with a single posterior hook placed in the jaw of the fish using pliers. Fish in the jig treatment were released with a lead dart style jig with a 1/0 barbed hook with a soft plastic twister tail. Worm treatments consisted of a 1/0 worm hook with a soft plastic worm. Pliers were used to place the lures in the upper jaw. Processing time from landing to release of fish was completed within 2 min in all cases, while a diver remained near the nest preventing brood loss through predation. Air exposure was limited because all sampling and handling occurred in water thus emulating the lack of air exposure that would occur in a break-off scenario.

To assess the behaviour of treatment fish relative to shams we first evaluated the time taken for the fish to return to the nest when released from a standardized distance from the nest (i.e., 5 m) to the nearest second. A fish was deemed to have returned to the nest once it was positioned immediately above the nest and staying in position using a combination of pectoral and caudal fin activity. Upon return to the nest, a 5-min observational behavioural assay at 30 s intervals was employed on a subset of each group (control $n = 8$, sham $n = 6$, crankbait $n = 7$, jig $n = 8$, worm $n = 8$). Possible scores for each time period ranged from 1 to 3 with the final value (behavioural sum) being a sum of each intervals score (maximum value 33). Behaviours were categorized as (1) parent not within 3 m of the nest, (2) parent within 3 m of the nest but not attempting to provide parental care for their brood, and (3) parent positioned within 3 m of the nest and actively providing parental care (i.e., fanning or predator defense) (Suski et al., 2003). The higher the number indicated greater parental vigilance. Measurements of time to return to nest for non-angled control fish were not possible but the behavioural assay was conducted in the same manner as the other treatment groups. Anecdotal observations related to attempts to expel the lure (e.g., jumping, head shaking, rubbing) were also recorded.

Twenty-four hours after initial experimentation and behavioural measurements, nests were revisited to evaluate abandonment (nest empty and male absent), lure presence, and behaviour. Males present following the 24 h interval were evaluated for the presence of the lure and then presented with a model predator (bluegill, *Lepomis macrochirus*) in a large mason jar (5 L) placed on the nest. For 1 min, the number of aggressive responses (number of times the male bass made contact with the jar) toward the predator by the parental male was scored as per Gravel and Cooke (2009). Predator defense scores were then recorded as a single value, number of hits per minute.

To assess the physiological impact of lure retention we focused our sampling efforts on jigs that were retained 24 h after treatment ($n = 7$) and sham treated males ($n = 8$) 24 h after initial capture and release. Efforts were focused on jig fish because the jigs did not interfere with our ability to angle or handle the fish a second time. Fish were brought on-board and placed in the v-shaped water-filled trough in supine position for collection of 1 mL of blood by caudal venipuncture (Cooke et al., 2005). Blood was collected in a vacutainer containing lithium heparin anticoagulant (Becton Dickson, Inc., Franklin Lakes, NJ) using a 1.5″ 21 g needle. Immediately after blood sampling, the vacutainer was placed in a water-ice slurry. All blood samples were obtained in <2 min after hooking the fish. During this time jigs were removed from the mouth of lure treated fish. After sampling, 10 μL of whole blood was added to a handheld glucose meter (Accu-chek, Compact Plus, Roche Diagnostics Corp., Indianapolis, IN) and lactate meter (Lactate Pro LT-1710 Analyzer. Arkay, Inc., Kyoto, Japan) to determine concentrations (mmol/L) of glucose and lactate in the whole blood samples. Use of these meters has been validated in previous studies with results being comparable to those derived from laboratory assays (Morgan and Iwama, 1997; Cooke et al., 2008). Some of the remaining blood was then placed in microhematocrit (Iris International Inc., Westwood, MA) tubes and centrifuged for 6 min at 10,000 times gravity and the fraction of red blood cells to entire blood volume determined (i.e., hematocrit).

The mean of behavioural sum, predator defense assays, and time to return to nest were compared among treatments using a one-way analysis of variance (ANOVA) and Dunnett's post hoc test (where applicable; Zar, 1999). Mean concentrations of metabolites (glucose and lactate) and hematocrit were compared between jig and sham controls using a student's t-test (Zar, 1999). Rates of nest abandonment and lure retention were compared using chi-square analysis (Zar, 1999). All statistical tests were performed using JMPIN version 5.1 (SAS Institute) with α for all tests being 0.05. Fish in each treatment (including shams and estimates of control fish size) were of similar size (One-way ANOVA, $F = 2.078$, $P = 0.096$; control = 367 ± 25 cm; sham = 382 ± 19 cm; crankbait = 410 ± 20 cm; jig = 412 ± 15 cm; worm = 411 ± 21 cm).

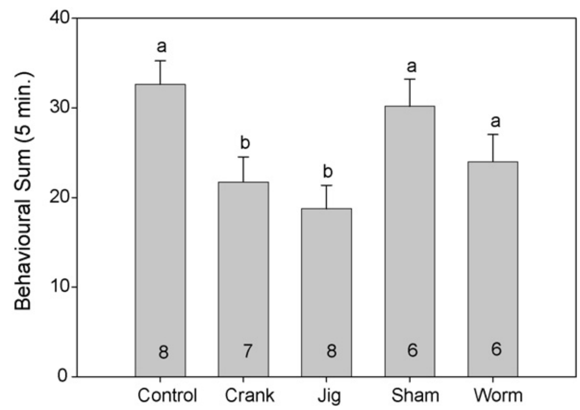

Fig. 2. Comparison of behavioural assay scores (immediately after returning to nest post-release) of treatment fish (crankbait—angled with crankbait placed in upper middle jaw, jig—angled with a jig and worm placed in upper middle jaw and worm—angled with hook and plastic worm in upper middle jaw) to controls. Bars represent mean ± S.D. Letters denote significant differences between group means as per Dunnett's post hoc test with sample sizes in bars.

3. Results

Once returned to the water following angling and simulated lure retention, the mean time required for fish to return to their nests did not differ significantly between sham controls and lure treated fish ($F = 0.131$, $P = 0.941$; Table 1). Upon return to the nest, observation of parental care behaviour (behavioural sum over 5 min span) revealed that treatment influenced parental care behaviour ($F = 4.61$, $P = 0.005$; Fig. 2). Both jig ($P = 0.003$) and crankbait ($P = 0.030$) treated fish showed significantly reduced parental care behaviours compared to non-angled controls. This difference in mean behavioural sum was not significant between non-angled controls and both the angled controls ($P = 0.933$) or plastic worm treated ($P = 0.126$) fish (Table 1).

Following 24 h of resumed nesting activity, rates of nest abandonment was observed in three treatment groups with jig treatments having the highest abandonment rate (% abandonment, 17.6%, 3 of 17) compared to crankbait and non-angled controls (9.1%, 1 of 11). However, abandonments rates were not statisti-

Table 1
Results of behavioural assays and statistical analysis amongst smallmouth bass subjected to simulated break-off conditions (non-angled control [control]—not angled with no lure treatment, angled controls [sham]—angled with no lure treatment, crankbait—angled with crankbait placed in upper middle jaw, jig—angled with a jig and worm placed in upper middle jaw and worm—angled with hook and plastic worm in upper middle jaw).

Treatment	Time to return to nest (s)		Behavioural sum (index)		Hits/min	
	n	Mean ± S.D.	n	Mean ± S.D.	n	Mean ± S.D.
Control	N/A	N/A	8	32 ± 2.6	10	16.3 ± 3.2
Sham	11	297 ± 83	6	30 ± 3.0	15	13.5 ± 2.6
Crankbait	11	300 ± 83	7	22 ± 2.8	10	14.4 ± 3.2
Jig	20	256 ± 62	8	19 ± 2.6	14	8.2 ± 2.7
Worm	10	241 ± 88	6	24 ± 2.8	8	16.8 ± 3.6
F-ratio	0.131		4.613		1.363	
P-value	0.941		0.005		0.296	
Power	0.072		0.907		0.395	

Table 2
Comparison of nest abandonment and lure retention for smallmouth bass subjected to simulated break-off conditions (crankbait—angled with crankbait placed in upper middle jaw, jig—angled with a jig and worm placed in upper middle jaw and worm—angled with hook and plastic worm in upper middle jaw) and control fish.

Treatment	Abandonment		Retention	
	n	*n* abandoned	*n*	*n* retained
Control	11	1	N/A	N/A
Sham	15	0	N/A	N/A
Crankbait	11	1	11	9
Jig	17	3	17	15
Worm	10	0	10	8
χ^2 critical	9.488		5.991	
P-value	0.911		0.842	

Table 3
Comparison of blood-borne indicators of stress 24 h following angling event from individuals in jig ($n=7$) and sham ($n=8$) treatments.

Response variable	Glucose (mmol/L)		Lactate (mmol/L)		Hematocrit (%)	
Treatment	Sham	Jig	Sham	Jig	Sham	Jig
Mean	2.3	2.8	1.3	1.1	24.9	23.7
S.D.	0.30	0.57	0.51	0.50	3.60	3.60
t-Statistic	−2.466		0.270		0.772	
P-value	0.029		0.792		0.455	
Power	0.620		0.057		0.110	

cally different among treatments ($\chi^2=9.488$, $P=0.911$; Table 2). Abandoned nests were subject to heavy brood predation and in all cases no eggs remained in the nests. Treatment males that had not abandoned their nests showed no significant difference in mean predator defense (hits per minute) compared to controls ($F=1.363$, $P=0.260$; Table 1). Of the fish remaining on their nests, the majority of fish retained the lures for 24 h with no significant difference in lure retention among treatment groups ($\chi^2=5.991$, $P=0.842$; Table 2). In general, lure retention at 24 h was high (>80% in all treatment groups).

Blood sampling of sham and jig treated fish revealed no significant differences in blood lactate ($t=0.27$, $P=0.792$) although statistical power was low (Table 3). However, whole blood glucose concentrations were significantly higher in jig than sham treated fish ($t=-2.466$, $P=0.029$; Table 3). Hematocrit fractions did not differ between sham and jig treatments ($t=0.772$, $P=0.455$; Table 3).

4. Discussion

Lure retention due to break-off and deep hooking can occur during recreational angling. Research conducted to date on this subject has focused mainly on changes in behaviour and the fate of fish that have been deeply hooked or retained gear (e.g., Arlinghaus et al., 2008). Arlinghaus et al. (2008) found short-lived changes in northern pike behaviour subjected to simulated lure retention. Fish with plastic shads in the upper middle jaw showed reduced mobility compared to controls when released (Arlinghaus et al., 2008). In this study we used nesting smallmouth bass as a model because of their attentiveness to the nest during the parental care period, enabling us to monitor wild free-swimming fish through time (including targeted blood sampling post-treatment). Moreover, parental care requires an integration of behaviour and physiology and is directly related to fitness. Hence, the use of nesting fish as a model proved to be a logistically simple and a powerful means of investigating the biological consequences of break-offs. Our choice of study model does not imply that there is a specific break-off issue with nesting bass although we do occasionally see lures in the mouths of bass during routine nest snorkeling (Cooke, personal observations). In addition, jigs and plastic worms have the potential to be deeply hooked preventing removal of the lure by the angler.

When male smallmouth bass were released within 5 m from their nests the time taken to return did not differ between treatments and controls. However, once the fish were on their nests anecdotal evaluation of behaviour indicated that jig and crankbait treatment groups showed significantly reduced parental care activity. We noted that these fish (jig and crankbait treated) appeared distracted by the retained lure and were observed breaching, rubbing the lure on surrounding debris, shaking their heads and exhibiting other behaviours that were perceived to be related to attempting to remove the retained lure. Such behaviours were not observed in worm treatments (the closest treatment to neutral buoyancy) or either control conditions. The quantitative behavioural assays (sum) revealed altered behaviour in parental care providing bass. Specifically, lower behavioural sums indicate greater time away from the nest and associated reductions in guarding and fanning effort. During the period when fish were exhibiting low behaviour scores (e.g., not on the nest) we observed predators eating eggs. Changes in the behaviour of male bass actively guarding nests may therefore influence brood size and reproductive success. Indeed, nests that have been subject to predation have been shown to be at a higher probability for male abandonment, resulting in zero reproductive output for that year (Philipp et al., 1997). Although changes in jig and crankbait treated fish behaviour were present immediately following return of the male to the nest, these changes were not evident when nest defense assays were performed 24 h later.

Blood sampling during this experiment was used to determine if any physiological changes arise from the retention of lures. Sampling of metabolic byproducts of anaerobic activity (lactate and glucose) and hematocrit are used frequently as a means to characterize the physiological condition of fish (e.g., Wendelaar Bonga, 1997; Barton, 2002). Blood lactate concentrations rise in response to anaerobic metabolic activity (e.g., bursting locomotion and recruitment of glycolytic white muscle fibres) associated with intense exercise (Barton, 2002). In our study we did not note any differences in lactate concentrations between jig and control fish suggesting that they were not engaged in more anaerobic activity, at least by 24 h post-treatment. Blood glucose concentrations were elevated in jig treated fish when compared to controls, implying that there was some physiological stress resulting from lure retention. Elevated blood glucose concentrations in the absence of elevations in lactate may occur as a result of cortisol action stimulating gylconeogenesis (Barton, 2002). Although we would have expected the initial angling event to have resulted in elevation of lactate, cortisol, and glucose, in most conditions these parameters will return to baseline levels within about 4 h (Suski and Philip, 2004). Because we sampled fish 24 h later and noted elevated glucose in fish with retained jigs, it is suggestive that the physiological disturbance is the result of chronic stress (i.e., the persistent burden of the lure) rather than the acute angling stressor. Hematocrit fractions were measured as indicators of several disturbances including stress and injury (e.g., blood loss). However, there was no indication that hematocrit differed between jig and control fish.

Catch-and-release angling of smallmouth bass during the reproductive season has been shown to induce nest abandonment in instances when the male is removed from the nest for extended periods, enabling brood predation (e.g., Philipp et al., 1997; Suski et al., 2003). If a stressor such as a retained lure causes enough physiological disturbance that future reproductive output is compromised, the nest may be abandoned (Philipp et al., 1997). Our results indicate that at least in the short term this was not the case as relatively few fish abandoned their broods. Furthermore, by 24 h after treatment and presuming the male stayed with his brood while retaining a lure, the aggressiveness of brood defense to a model predator was not significantly altered compared to controls. However, it is possible that although bass were willing to engage predators with the same vigor, that their effectiveness is reduced. In the long term the presence of the lure would also have the potential to influence feeding, although during parental care bass typically exhibit voluntary anorexia (Hinch and Collins, 1991). Elevated glucose indicates the potential for a higher cost to parental care with a retained lure in the long term.

In the present study, some short-term changes in nesting behaviour were noted among fish that retained lures. In addition, 24 h after treatment, glucose concentrations were elevated in response to a retained jig. These results indicate that while short-term behavioural changes are evident, nest defense and the rate of abandonment is unaltered when a male decides to stay and defend his brood. From a fish welfare perspective (i.e., Cooke and Sneddon, 2006; Davie and Kopf, 2006), changes in both behaviour and physiology arise from lure retention. Comparison of lure types indicated that neutrally buoyant lures (e.g., the plastic worm and hook with no weight) may have the least effect on the behaviour of fish. Although such an observation is intuitive, it provides no reasonable management response. From a management perspective, the use of proper gear such as wire leaders when angling for fish with sharp morphological features (Arlinghaus et al., 2008), tying of proper knots, selection of appropriate line and gear, and the awareness of submersed objects may reduce the number of fish with retained lures. In addition, given that the majority of the fish still retained lures after 24 h, there may be merit in using barbless hooks that may be more easily liberated by the fish. Understanding and reducing the impacts of break-offs is a neglected but important component of recreational fishing; one that has the potential to improve fish welfare if strategies can be developed to reduce incidences of break-off or increase a fishes ability to liberate a lure. Clearly there is a need for additional research on this topic with a focus on long-term consequences of lure retention.

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References

Arlinghaus, R., Cooke, S.J., Lyman, J.L., Policansky, D., Schwab, A., Suski, C., Sutton, G., Thorstad, E.B., 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev. Fish. Sci. 15, 75–167.

Arlinghaus, R., Klefoth, T., Gingerich, A.J., Donaldson, M.R., Hanson, K.C., Cooke, S.J., 2008. The behaviour and survival of pike (*Esox lucius* L.) with a retained lure in the lower jaw. Fish. Manage. Ecol. 15, 459–466.

Barton, B.A., 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integr. Comp. Biol. 42, 517–525.

Cooke, S.J., Philipp, D.P., Weatherhead, P.J., 2002. Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. Can. J. Zool. 80, 756–770.

Cooke, S.J., Crossin, G.T., Patterson, D., English, K., Hinch, S.G., Young, J.L., Alexander, R., Healey, M.C., Van Der Kraak, G., Farrell, A.P., 2005. Coupling non-invasive physiological and energetic assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. J. Fish Biol. 67, 1342–1358.

Cooke, S.J., Schramm Jr., H.L., 2007. Catch-and-release science and its applications to conservation and management of recreational fisheries. Fish. Manage. Ecol. 14, 73–79.

Cooke, S.J., Philipp, D.P., Wahl, D.H., Weatherhead, P.J., 2006. Parental care energetics of six syntopic centrarchid fishes. Oecologia 148, 235–249.

Cooke, S.J., Sneddon, L.U., 2006. Animal welfare perspectives on catch-and-release angling. Appl. Anim. Behav. Sci. 104, 176–198.

Cooke, S.J., Suski, C.D., Danylchuk, S.E., Danylchuk, A.J., Donaldson, M.R., Pullen, C., Bulte, G., O'Toole, A., Murchie, K.J., Schultz, A., Brooks, E., Goldberg, T.L., 2008. Effects of capture techniques on the physiological condition of bonefish (*Albula vulpes*) evaluated using field physiology diagnostic tools. J. Fish Biol. 73, 1351–1375.

Cowx, I.G., 2002. Recreational fisheries. In: Hart, P., Reynolds, J. (Eds.), Handbook of Fish Biology and Fisheries, vol. II. Blackwell Science, Oxford, pp. 367–390.

Davie, P.S., Kopf, R.K., 2006. Welfare of fish during recreational fishing and after release. N. Z. Vet. J. 54, 161–172.

Dubois, R.B., Kuklinski, K.E., 2004. Effect of hook type on mortality, trauma, and capture efficiency of wild stream trout caught by active bait fishing. N. Am. J. Fish. Manage. 24, 617–623.

Gravel, M.-A., Cooke, S.J., 2009. Influence of inter-lake variation in natural nest predator burden on the parental care behaviour of smallmouth bass (*Micropterus dolomieu*). Ethology 115, 608–616.

Hinch, S.G., Collins, N.C., 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observation. Trans. Am. Fish. Soc. 120, 657–663.

Kramer, R.H., Smith, L.L., 1962. Formation of year classes in largemouth bass. Trans. Am. Fish. Soc. 91, 29–41.

Kubacki, M.R., 1992. The Effectiveness of a Closed Season for Protecting Nesting Largemouth and Smallmouth Bass in Southern Ontario. MSc thesis. Urbana, IL, USA: University of Illinois at Urbana-Champaign, p. 86.

Morgan, J.D., Iwama, G.K., 1997. Measurements of stressed states in the field. In: Iwama, G.K., Pickering, A.D., Sumpter, J.P., Schreck, C.B. (Eds.), Fish Stress and Health in Aquaculture. Cambridge University Press, Cambridge, pp. 247–268.

Philipp, D.P., Toline, C.A., Kubacki, M.F., Philipp, D.F., Phelan, F.J.S., 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. N. Am. J. Fish. Manage. 17, 557–567.

Ridgway, M.S., 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieu*). Can. J. Zool. 66, 1722–1728.

Schill, D.J., 1996. Hooking mortality of bait-caught rainbow trout in an Idaho trout stream and hatchery: implications for special-regulation management. N. Am. J. Fish. Manage. 16, 348–356.

Suski, C.D., Philip, D.P., 2004. Factors affecting the vulnerability of angling of nesting male largemouth and smallmouth bass. Trans. Am. Fish. Soc. 133, 1100–1106.

Suski, C.D., Svec, J.H., Ludden, J.B., Phelan, F.J.S., Philipp, D.P., 2003. The effect of catch-and-release angling on the parental care behaviour of male smallmouth bass. Trans. Am. Fish. Soc. 132, 210–218.

Tsuboi, J., Morita, K., Ikeda, H., 2006. Fate of deep-hooked white-spotted charr after cutting the line in a catch-and-release fishery. Fish. Res. 79, 226–230.

Warner, K., 1979. Mortality of landlocked Atlantic salmon hooked on four types of fishing gear at the hatchery. Prog. Fish-Cult. 41, 99–102.

Wendelaar Bonga, S.E., 1997. The stress response in fish. Physiol. Rev. 77, 591–625.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice-Hall, NJ.