Fisheries Research 99 (2009) 38–46

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Cut the line or remove the hook? An evaluation of sublethal and lethal endpoints for deeply hooked bluegill

Emily Fobert[a], Patrick Meining[a], Alison Colotelo[a], Constance O'Connor[a], Steven J. Cooke[a,b,*]

[a] Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6
[b] Institute of Environmental Science, Carleton University, Ottawa, ON, Canada K1S 5B6

ARTICLE INFO

Article history:
Received 9 February 2009
Received in revised form 30 March 2009
Accepted 16 April 2009

Keywords:
Recreational fishing
Hooking mortality
Deep hooking
Injury
Stress

ABSTRACT

Research on a wide range of fish species has revealed that deep hooking is perhaps the single most important determinant of injury and post-release mortality in recreational fisheries. However, there is little information on the best option for dealing with deeply hooked fish that are to be released; should the line be cut or should the hook be removed? Using bluegill sunfish (*Lepomis macrochirus*) as a model we investigated sublethal (e.g., swimming performance, physiological condition, injury levels) and lethal consequences associated with removal of deeply ingested hooks versus cutting the line and leaving the hook embedded in the esophagus, relative to shallowly hooked controls. Neither hook retention nor deep hook-removal altered the swimming performance of the fish in this study relative to controls. However, there was evidence of short-term physiological disturbance. For example, hematocrit was reduced for fish that had hooks removed, consistent with visual observations of bleeding. In addition, blood glucose levels tended to be higher and plasma Na^+ levels tended to be lower in deeply hooked fish that had hooks removed indicating stress and ionic imbalance even 24 h after capture. During holding experiments we noted the highest mortality levels in fish for which the hook was removed (33% after 48 h and 44% after 10 days). Mortality rates were lowest for the controls (0% after 48 h and 4% after 10 days) and intermediate for the line-cut treatment (8% after 48 h and 12.5% after 10 days). After 48 h, 45.5% of the fish from the line-cut treatment group were able to expel the hook originally embedded in their esophagus, and at the end of the 10 day study, 71.4% had expelled the hook. Even with the hook left in the esophagus, fish were able to feed although at lower rates than controls during the first 48 h of holding. By 10 days post-capture, there were no differences in feeding rates as evidenced by growth patterns among the treatment groups, nor were there differences in the hepatosomatic index. Collectively, the findings from this study demonstrate that cutting the line is a more effective release method than removing the hook when fish are deeply hooked. As such, angler education efforts should focus on disseminating this message to anglers as well as encouraging the use of gear and techniques that minimize incidences of deep hooking (e.g., circle hooks, non-organic bait).

1. Introduction

Recreational angling is a popular activity around the globe (Cooke and Cowx, 2004; Arlinghaus et al., 2007), and many of the fish caught are immediately released after capture (Cooke and Suski, 2005). A fundamental assumption of catch-and-release angling is that the released fish survive hooking, landing, and handling (Cooke and Schramm, 2007), but studies have revealed that a proportion of released fish die as a result of the angling event (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007). One of the primary factors that has been determined to influence the post-release mortality of fish is deep hooking (e.g., Pelzman, 1978; Taylor and White, 1992; reviewed in Bartholomew and Bohnsack, 2005). Deep hooking, characterized by the hook penetrating the esophagus, gills or other sensitive tissue beyond the mouth cavity (e.g., pericardial cavity, stomach, liver), can inflict more substantial physical injury than shallow hooking. There are a number of factors that influence incidences of deep hooking. For example, studies have revealed that live or organic bait results in a significantly higher incidence of deep hooking than flies or artificial lures (Taylor and White, 1992). Moreover, smaller lures or baits are more likely to be deeply ingested than larger baits (Arlinghaus et al., 2008). Hook design can also influence deep hooking. Circle hooks have been shown to generally result in shallower hooking relative to conventional "J" style hook designs (reviewed in Cooke and Suski, 2004). Angler experience also has the potential to influence deep hooking rates as novice anglers may be less able to detect strikes (Dunmall et al., 2001).

* Corresponding author. Tel.: +1 613 520 2600; fax: +1 613 520 3539.
E-mail address: Steven_Cooke@Carleton.ca (S.J. Cooke).

0165-7836/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2009.04.006

Schill (1996) reported that fishing method (tight line versus slack line) also influenced incidences of deep hooking. The attempted removal of a deeply ingested hook can influence air exposure duration (due to protracted time to remove hook; Cooke et al., 2001) and can cause significant damage to vital organs (Pelzman, 1978; Aalbers et al., 2004), thus increasing the probability of mortality following release. Based on the above data, researchers, management agencies, and outdoor media outlets have been advocating the use of gear and strategies that reduce incidences of deep hooking (e.g., Pelletier et al., 2007). Nonetheless, deep hooking still occurs, particularly when using single baited hooks, and it is unlikely that innovations in gear or angling techniques will completely eliminate deep hooking.

So what should an angler do when they have captured a fish that is deeply hooked? Assuming that the fish is to be released (e.g., conservation measure, management regulation, culling), an angler can either cut the line and leave the hook in place or use pliers, their fingers, or some other hook removal device to manually remove the hook. Some studies have indicated that fish mortality is reduced when deep hooks are not removed (Mason and Hunt, 1967; Warner, 1979) or that there is no difference in survival between fish released with or without hooks in place (e.g., Wilde and Sawynok, 2009). Other studies have shown that some fish are capable of expelling hooks that are left in (Schill, 1996; Diggles and Ernst, 1997; Aalbers et al., 2004; Tsuboi et al., 2006; Dubois and Pleski, 2007) although the time between deep hooking and evaluation of retention varies widely among studies. Collectively, the evidence from these disparate studies suggests that injuries resulting from hook removal may be a greater threat to survival than the consequences of line-cutting and hook retention. However, cutting the line and leaving hooks in place may affect food consumption and growth (Schisler and Bergersen, 1996; Aalbers et al., 2004), and have a number of pathological consequences (e.g., Borucinska et al., 2001, 2002). Incidences of deep hooking can be high when using organic baits (e.g., 17% of rainbow trout, Schill, 1996; 14% of striped bass, Nelson, 1998; 12% of white spotted char, Tsuboi et al., 2006; 26% for brook and brown trout combined, Dubois and Kuklinski, 2004; 2–10% for eight species of tropical reef fish, Mapleston et al., 2007; 16% for black bream, Grixti et al., 2008). Given that mortality rates of deep hooked individuals are often high (e.g., 73% in cutthroat trout, Hunsaker et al., 1970; 6–29% for brook trout, Dubois and Kuklinski, 2004; 36% of sand flathead (*Platycephalus bassensis*), Lyle et al., 2007; 70% of painted comber (*Serranus scriba*), Alós, 2008; 16% of black bream, Grixti et al., 2008) and that significant post-release mortality has the potential to negatively influence fish populations (Coggins et al., 2007; Cooke and Schramm, 2007), there is a need to provide anglers and managers with better information on whether to cut the line or remove the hook when fish are deeply hooked. This is particularly timely given the growing recognition that animal welfare considerations are relevant to the recreational fishing sector (Davie and Kopf, 2006; Cooke and Sneddon, 2007; Arlinghaus et al., 2007). Clearly there is need for a comprehensive study that incorporates a combination of endpoints (lethal and sublethal) to evaluate the risks and benefits of the two strategies for dealing with deep hooking.

The purpose of this study was to determine the least damaging catch-and-release practice—hook removal or line cutting in deeply hooked fish. In particular, this study assessed the effects of hook removal or retention on physical injury, feeding, swimming performance, physiological condition, and survival. For all experiments we compared these two treatments to shallowly hooked control fish from which the hook was easily removed. The combination of lethal and sublethal endpoints used here range from whole organism locomotor ability to the hepato-somatic index, and provide a unique opportunity to understand the complete range of consequences of each hook removal technique from an integrated short and long-term perspective. Previous studies have tended to focus primarily on salmonids (e.g., Warner, 1979; Schill, 1996; Dubois and Kuklinski, 2004; Tsuboi et al., 2006) and usually evaluated only one endpoint (e.g., mortality), which had made interpretation difficult given the complexity of the issue. For example, although short term survival could be higher in deeply hooked fish for which the line is cut and the hook left in, there could be longer term impacts on fish condition. Conversely, hook removal may result in immediate death to a proportion of deeply hooked fish and influence feeding in the short term, but in the longer term they may be able to recover.

The present study focused on adult bluegill sunfish (*Lepomis macrochirus*) as a freshwater model species. Bluegill were chosen as the study species because they are an important recreational fish in North America and have a high tendency of deeply ingesting hooks given that they are often targeted by anglers using small hooks and organic bait (Cooke et al., 2003) and are a popular quarry of inexperienced anglers. In fact, because bluegill have a small mouth, hook removal can be difficult such that deeply hooked fish either have the line cut or have the hook pulled out. Although harvest rates for bluegill can be high, anglers will often “cull” smaller individuals to select larger fish for harvest, in some cases as a result of management regulations. From a pragmatic research perspective, bluegill can be readily captured in large numbers based on their abundance and adjust quickly to captive holding facilities. Because of their relatively small body size, it is also possible to standardize other aspects of the angling event (e.g., air exposure, water temperature). To effectively manage bluegill and other recreational fisheries and to maintain welfare status, it is necessary to provide anglers and mangers with credible guidance for handling deeply hooked fish. To that end, the results of this study will be useful for providing management agencies, conservation organizations, and ultimately anglers with direction for determining the best angling practices.

2. Materials and methods

2.1. Field site and fish capture

All experiments were conducted at Queen’s University Biological Station on Opinicon Lake, Ontario. Opinicon Lake is a mesotrophic natural lake with abundant populations of rock bass *Ambloplites rupestris*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, pumpkinseed *Lepomis gibbosus* and, in particular, bluegill sunfish *L. macrochirus*. Experiments were conducted between May 8 and July 5, 2008. Water temperatures during this time ranged from 12 °C to 23 °C. Cooke et al. (2003) and Gingerich et al. (2007) reported that mortality rates for angled bluegill were uniformly low for bluegills at various temperatures below 26 °C in Opinicon Lake provided that there were not prolonged periods of air exposure. Therefore, water temperature was not considered to be a factor in bluegill mortality rates in this study. Individual study components (e.g., the swimming performance assessment, physiological assays) were conducted across a narrow (1 or 2 °C) thermal range because of the influence of temperature on swimming ability. Other study components (e.g., growth evaluations) involved exposing treatment and control fish to the same thermal environment simultaneously so temperature variation across a study period was not relevant.

All fish were angled using rod and reels and all angling was conducted either from a fishing boat or from docks that extend out into the lake to a depth of at least 1 m. Commercially available barbed J-hooks (Jeros Brand, Rahway, NJ; model K5BH10, snelled baitholder style, bronze material, thin wire, size 10 with a 6 mm gape) were used for angling. These hooks were appropriate to target bluegill (Cooke et al., 2005) and are routinely used by anglers. Organic bait – small worm pieces measuring approximately

5 mm × 5 mm – were used by all anglers. Air exposure duration for all fish caught, whether deep or shallow (controls) was standardized at 60 s, including removal of hook and enumeration, to control for the negative impacts of air exposure and to eliminate differential handling times and air exposure durations as a factor in the analysis. Previous research on bluegill in Opinicon Lake revealed that there was negligible mortality as a result of air exposure of this duration at the temperatures observed in this study (Gingerich et al., 2007). Angler expertise ranged from novice to expert, however, all handling (e.g., once the angler had landed the fish) was conducted by experienced research staff to eliminate the influence of angler expertise on fish handling. Our intention was not to characterize deep hooking rates. Instead, we intentionally let fish "nibble" for sufficiently long periods to ensure that some fish were deeply hooked. Experiments focused on fish that were >130 mm in total length and were carefully balanced across all treatment groups and experiments such that there were no significant ($P < 0.05$) differences in size (overall mean total length ± SEM = 167 ± 3 cm). All experiments were conducted in accordance with the guidelines of the Canadian Council on Animal Care as administered by the Carleton University and Queen's University Animal Care Committees and with scientific collection permits provided by the Ontario Ministry of Natural Resources.

2.2. Experimental treatments

For all experiments, fish were classified upon capture as either shallowly hooked (hooked in the lip), deeply hooked (hooked in the gullet), or hooked in other locations (e.g., roof of mouth, gills, eye). Fish in the shallow and deeply hooked groups were individually marked with small numbered anchor tags (Floy Manufacturing, WA) while fish hooked in other locations had the hook removed and were released. The shallowly hooked fish were designated the control group, and the hook was carefully removed. The deeply hooked fish were randomly assigned to one of two treatment groups; one in which the hook was removed with surgical hemostats using a steady pull on the line or hook (the hook-removal treatment group), and one in which the line was cut about 1 cm from mouth of the fish and the hook was left in place (the line-cut treatment group). Following hook removal or line cutting, the fish was examined for injury in the mouth and presence of blood was determined to be "none," "moderate" (less than 0.1 ml), or "severe" (more than 0.1 ml). All fish were then placed into a 1 m^3 round tank holding approximately 700 l of water and held for further experimentation (see below).

2.3. Short term feeding, injury, and survival

To test the effects of hook retention or hook removal on short-term feeding behaviour and survival, 44 bluegills were angled within a 12 h period. Each fish was numbered and assigned to one of the three treatment groups; 12 fish were assigned to the line-cut group, 12 fish were assigned to the hook-removal group, and 20 fish were controls. The fish were then placed in a single 1 m^3 round tank holding approximately 700 l of water and held for 48 h. Tanks were flow through and were housed outside under natural photoperiod. Fish experienced diel fluctuations in water temperature consistent with water temperatures in the lake. Every 6 h, mortalities were recorded and the deceased fish were removed from the tank. Approximately 24 h after capture the fish were fed approximately 50 g of frozen blood worms. They were fed again the following morning, 1 h prior to the end of the 48 h holding period. At the completion of the holding period, the mortality rate was assessed and recorded. Fish were then removed one at a time from the holding tank and their stomachs were emptied with gastric lavage using a syringe. The stomach contents were transferred to individual vials for freezing and later analysis (see below). Immediately following the flushing process, each fish was weighed. Before flushing commenced, the fish belonging to the line-cut treatment group were visually examined to determine hook location. Fish in which the hook was not visible from the mouth were euthanized and a necropsy was performed to determine the internal location of the hook and to verify that the hook did not affect stomach flushing.

In the lab, stomach content samples were defrosted and distilled water was used to wash stomach contents from the vials into a crucible. The samples were then dehydrated in a drying oven for 2 h at 60 °C. The dried samples were weighed and the final dry weight was used to calculate the mass corrected stomach contents of each fish (i.e., stomach content mass was expressed as a percentage of fish mass).

2.4. Long term feeding, injury, and survival

To test the effects of hook retention or hook removal on long-term feeding behaviour and survival, 75 bluegills were angled within a 3 h period. Upon capture, each fish's initial weight and total length were recorded. The fish were numbered and assigned to one of the three previously described treatment groups; 24 fish were assigned to the line-cut group, 25 fish were assigned to the hook-removal group, and 23 fish were controls. The fish were then placed in a single round tank (as above) and held for 10 days. During the holding period, the fish were checked every 6 h for mortalities, and deceased fish were recorded and removed from the tank. The fish were fed approximately 25 g of frozen blood worms twice daily, with the exception of the last 2 days where they were fed 3 times daily.

On the tenth day of holding, the bluegill were removed from the tank and euthanized for necropsy using cerebral percussion. Their final weight was recorded and their liver was harvested and weighed to determine their hepato-somatic index (HSI). During necropsy, the presence or absence of a hook in the line-cut treatment group was determined, and the hook location, when present, was recorded.

2.5. Swimming performance challenge

To test the effects of hook removal or retention on sustained exercise and swimming performance, fish were caught and assigned to each of the three previously described treatment groups (as above). Fish were held for either 1, 6, or 24 h in tanks (as above) supplied with fresh lake water before commencement of experimental trials. Fish mortalities were recorded during the holding period. For the line cut treatment, only fish that retained their hook were used in the experiment.

For experimentation, one fish at a time was moved from the common holding tank to an annular flume (Nixon and Gruber, 1988)—a circular tank (approximately 60 cm in diameter), painted white for visibility, with black marks dividing the tub into eight equal parts, and sufficient water to generate a depth of 10 cm. A round plastic coated metal cage was placed in the middle of the tank such that it created an external ring to which the fish were restricted. A video camera (Sony HDD 2000) secured to a tripod was positioned directly above the annular flume to record fish swimming performance. Ten seconds after the fish were placed in the annular flume, the swimming challenge commenced whereby the fish were chased by hand until they no longer responded to three consecutive gentle tail pinches, signifying exhaustion (Kieffer, 2000). The distance travelled (number of lines crossed) and the time to reach exhaustion was recorded for each fish. Following recovery, fish were released back into the lake.

2.6. Physiological experimentation

To evaluate the sublethal physiological consequences of hook retention and hook removal, we conducted a laboratory study to monitor blood biochemistry and hematology over a 24 h period. Fish were angled and categorized into three treatment groups as above. Approximately 13 fish were angled per treatment per time interval (0, 1, 6, and 24 h for the control group and at 1, 6, and 24 h for both experimental groups), equating to 129 fish. After capture, fish were placed into black rectangular sensory deprivation chambers (18 cm × 90 cm) that were continuously supplied with fresh lake water. Lights were shut off to help maintain sensory deprivation and access to the holding room was restricted. Water temperatures were taken daily and averaged 22.8 °C (±0.5 °C) over the six-day experimental period. At the appropriate sampling period, fish were quickly removed from their holding chamber and placed supine in a water filled trough. Blood samples from the caudal vessel(s) were taken using a heparinized syringe (1 ml) using a 25 gauge needle. Only blood samples that were obtained in less than 1 min were considered valid and used in the analysis. Glucose concentrations were immediately determined on whole blood using a field glucose meter (Accu-Chek Compact Plus, Roche, Basal, Switzerland) that was recently calibrated and that had previously been validated for use on fish (i.e., Cooke et al., 2008). Hematocrit was determined using a micro-hematocrit centrifuge (Crit Spin Micro-Hematocrit Centrifuge, IRIS International, CA). The remaining blood was centrifuged using a Micro-Fuge (Fischer Scientific, MA) at 2000× gravity, and the plasma labelled and frozen in a liquid nitrogen dewar until it was transferred to a −80 °C freezer for storage and later analysis. Plasma ion (Na^+, Cl^- and K^+) concentrations were quantified using the Roche Hitachi 917 analyzer (Roche, Basal, Switzerland) and relevant Roche reagents.

2.7. Statistical analysis

The chi-square contingency table analysis was used to evaluate differences in the mortality rates between treatment groups. Because fish size has the potential to influence the outcome of most variables examined here, we conducted a variety of analysis of variances (ANOVAs) to test for size differences between treatment groups. Across all analyses there were no significant differences so we do not provide further details in Section 3. One-way ANOVA was used to test for differences between treatments for the feeding experiments (gut content and growth), as well as HSI. Two-way ANOVAs were used to evaluate the influence of treatment and sampling time period on various physiological parameters (including swimming performance, blood biochemistry and hematology). Because different fish were used for each time period, repeated measures approaches were not needed. Where significant differences were noted in the ANOVA model, we used a Tukey honestly significant difference (HSD) test to identify where those specific differences occurred. Time zero controls for the biochemistry and hematology analyses were only collected for one group (as it would be redundant to obtain time zero for all treatments), which precludes the possibility of including time zero in the two-way ANOVA model. Hence, time zero control values are provided as a baseline for qualitative comparison and context. All analyses were conducted using JMP v7.0 or SAS v10.0 (both, Carey, NC) and significance was evaluated at an alpha of 0.05.

3. Results

3.1. Short term injury, mortality, and condition

After 48 h, mortality rates were highest for the hook removal treatment ($\chi^2 = 8.996$, $P = 0.011$; Table 1). All 20 control fish survived until the end of the experiment and only one fish of the line-cut treatment group died before the end of the 48-h holding period. The fish that did not survive the experiment had observed bleeding from the gills upon capture, and died after about 18 h in the holding tank. From the hook-removal treatment group, 33% (4 fish) died before the end of the experiment. Three of the fish died within 1 h after capture, two of which exhibited pulsatile blood flow (PBF) immediately following hook removal. The fourth fish, which also exhibited PBF after hook removal, died after about 12 h in the holding tank. Most of the mortalities occurred immediately after capture, with 60% occurring within 1 h following hooking. All mortalities recorded in the short-term study occurred within 18 h after hooking. It was not possible to statistically resolve temporal patterns of mortality between fish in the line-cut and hook removal groups.

Table 1
Summary of short-term and long-term bluegill mortalities and bleeding (moderate to severe combined) across treatments. Note that the experiments were conducted in sequence so that we could evaluate hook retention and placement in deep hooked fish. Bleeding was only evaluated in the short term holding experiment.

Treatment	*N*	Mortality (%)	Bleeding (%)
Short Term (48 h)			
Control	20	0	0
Line-cut	12	8	2.8
Hook-removal	12	33	35.6
Long Term (240 h)			
Control	26	4	NA
Line-cut	24	12.5	NA
Hook-removal	25	44	NA

Levels of bleeding observed upon capture differed significantly among treatments ($\chi^2 = 57.464$, $P < 0.001$). Of the fish from the hook-removal treatment group, 35.6% showed moderate to severe bleeding upon capture (Table 1), which was much higher than the levels of bleeding observed in the line-cut (2.8%) or control treatment fish (0%). Incidence of bleeding was also a predictor of mortality, with 57% of fish that showed moderate to severe bleeding upon capture resulting in mortality. Conversely, less than 6% of fish that failed to show any signs of bleeding died. At the end of the short-term holding experiment, 11 fish survived from the line-cut treatment group of which 45.5% (5 fish) were able to expel the hook within the 48 h period. For those that retained the hook, they were located in the esophagus for all but one individual which was hooked in the stomach.

Analysis of the mass corrected stomach contents of the bluegill after 48 h in a holding tank revealed a difference in the feeding activity between the three treatment groups (Table 2). The mean mass corrected weight of the stomach contents was highest in the control group and lowest in the hook-removal group despite no differences in the mean size of fish in each treatment. The difference between the control group and the hook removal group was statistically significant ($F = 5.108$, $P = 0.011$).

3.2. Long-term injury, mortality and condition

As with the short term holding period, after 10 days in the holding tank significantly more fish died in the hook removal

Table 2
Summary of mass corrected stomach contents collected after 48 h relative to treatment. SEM indicates standard error of the mean.

Treatment	*N*	Mean mass corrected stomach contents (%)	SEM
Control	20	0.222	0.028
Line-cut	11	0.152	0.028
Hook-removal	9	0.081	0.034

Table 3
Summary of bluegill mass change and hepatosomatic index (HSI) after 10 days relative to treatment. SEM indicates standard error of the mean.

TREATMENT	N	Mean mass change (%)	SEM of mass change	Mean HSI	SEM of HSI
Control	22	−8.740	2.247	1.135	0.052
Line-cut	21	−0.898	4.670	1.183	0.073
Hook-removal	14	−10.099	3.819	0.984	0.060

group (44%) than in the line cutting (12.5%) or control groups (4%) ($\chi^2 = 14.202$, $P < 0.001$; Table 1). None of the fish in the control treatment or line cutting treatment had any obvious injuries or indication of possible causes of death. As noted with the short-term holding experiment, most mortality occurred immediately after capture, with 46.7% occurring within the first 2 h, 60% occurring within the first 4 h, and 66.7% occurring within 12 h after hooking. At the end of the long-term holding experiment, 21 fish remained from the line-cut treatment group of which 71.4% (15 fish) had expelled the hook within the 10-day period. Only 19.0% (4 fish) were still hooked in the esophagus, and the hook was found in the stomach of two fish.

There was no significant difference in the mass change of the fish held for a period of 10 days ($F = 1.804$, $P = 0.175$; Table 3). Our estimates of ration size were apparently low as all fish including controls lost weight (Table 3) despite the fact that the bluegill quickly habituated to captivity. Although the mass reduction of the line-cut treatment fish was generally less than the control or hook-removal treatment groups, the difference was not significant. Following the 10 day holding period, 57 fish (22 controls, 21 line-cut, 14 hook-removed) were necropsied to determine their HSI. The mean HSI for the fish from which the hook was removed was generally lower than the fish belonging to the control or line-cut treatment groups (Table 3). However, statistically none of the treatment groups differed with respect to HSI ($F = 2.227$, $P = 0.118$).

3.3. Swimming performance

There were no significant differences in the swimming performance of fish that had the hook removed, fish that had the line cut and retained the hook, or the control fish (P's > 0.05; Fig. 1A and B). However, all three treatment groups performed significantly better 6 h post capture than at 1 or 24 h post-capture, in both distance swam ($F = 11.60$, $P < 0.001$; Fig. 1A) and time to exhaustion ($F = 4.767$, $P = 0.011$; Fig. 1B). It should be noted that 23%, 17% and 25% of the hook-removal fish that were being held died before swim testing at 1, 6, and 24 h post-capture, respectively. Therefore the fish with fatal hooking injuries and severe bleeding were often excluded from the swimming tests.

3.4. Hematology and blood biochemistry

Blood glucose concentrations varied by treatment and sampling period and exhibited a significant interaction ($F = 4.330$, $P = 0.003$; Fig. 2A). All groups after a 1 h holding period showed uniformly elevated glucose concentrations relative to the baseline mean concentration (defined by the control group 0 h). At the 6 h period, all treatment groups were significantly different with the control returned to baseline levels, the hook removal group the most elevated, and the line cut group at an intermediate level. By 24 h, fish in the hook removal group still had elevated glucose levels whereas all other groups had returned to pre-treatment levels (Fig. 2A).

The hematrocrit values differed by treatment group ($F = 3.841$, $P = 0.024$) and time period ($F = 10.951$, $P < 0.001$), but there was no significant interaction (Fig. 2B). Overall, significant differences in hematocrit were observed between the 1 and 6 h ($P < 0.001$) period

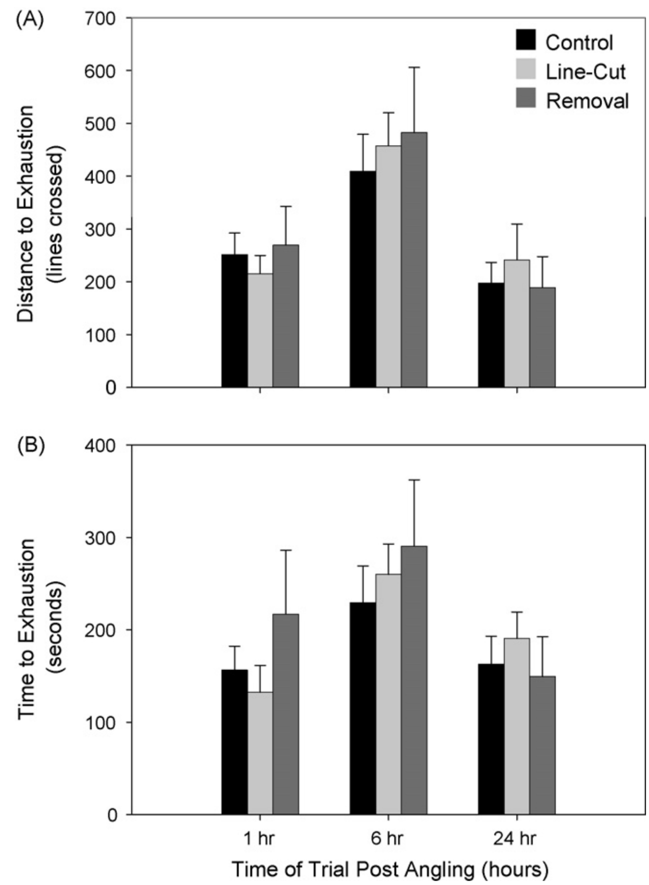

Fig. 1. Distance swam before reaching exhaustion during swimming performance tests at 1, 6, and 24 h after capture for control fish, line-cut treatments, and hook removal treatments (A). Time to reach exhaustion during swimming performance tests at 1, 6, and 24 h after capture for control fish, line-cut treatments, and hook removal treatments (B). All bars represent means and whiskers represent 1 standard error of the mean.

and the 6 and 24 h period ($P < 0.001$). In addition, the hook removal treatment group consistently yielded significantly lower hematocrit levels than control group ($P < 0.001$) while the line cut group was intermediate and not significantly different from the other two treatments.

Plasma ion concentrations responded differently from one another (Fig. 2C, D and E). Plasma Na^+ concentrations differed between treatments ($F = 7.665$, $P < 0.001$), but not for holding periods. In addition, there was no interaction. Significantly lower Na^+ concentrations were observed when deeply embedded hooks were removed when compared to the control groups ($P < 0.001$). Analysis of plasma K^+ concentrations revealed that only the recovery period yielded a significant difference ($F = 8.432$, $P < 0.001$). After the 6 and 24 h holding periods, the K^+ levels were significantly lower than compared to the 1 h levels ($P = 0.001$ and $P = 0.003$, respectively). Plasma Cl^- levels differed by treatment group ($F = 3.578$, $P = 0.032$) and holding period ($F = 3.662$, $P = 0.029$) and lacked an interaction between the two. The Cl^- concentrations were significantly lower at 6 h than at 24 h ($P = 0.036$). Among the treatment groups, significantly lower Cl^- levels occurred for bluegill when the hooks were removed as opposed to simply cutting the line or relative to controls (both $P < 0.001$).

4. Discussion

A fundamental assumption of catch-and-release angling is that the released fish survive. However, there is a growing body of

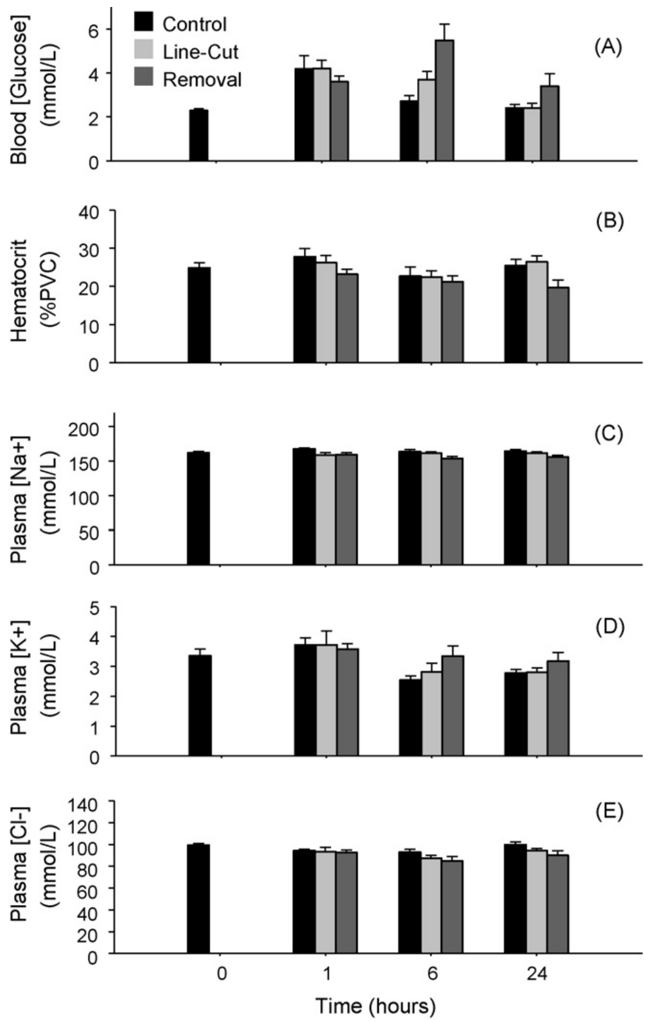

Fig. 2. Mean glucose concentrations (A), hematocrit (B), Na^+ (C), K^+ (D), and Cl^- (E) for control fish, line-cut treatments, and hook removal treatments across a time course. Glucose was measured on whole blood whereas ions were measured in plasma. All bars represent means and whiskers represent 1 standard error of the mean. Details on significant differences can be found in Section 3. Note that the time 0 control values are provided only for context and were not used in statistical analysis.

evidence that gear and angler behaviour can influence the outcome of a catch-and-release fishing event (e.g., Cooke and Suski, 2005; Arlinghaus et al., 2007). Given that deep hooking has been repeatedly implicated in the mortality of released fish, there is a need for research to both reduce incidences of deep hooking and to determine what should be done when an angler lands a deeply hooked fish that will be released. In this study we focused on the later issue in an effort to provide anglers with guidance as to whether they should cut the line and release the fish or leave the hook in place when fish are deeply hooked. We used bluegill as a warmwater fish model and evaluated sublethal and lethal endpoints. Collectively, the data suggested that mortality rates were consistently lower for fish that had hooks left in place relative to those for which the hook was removed. In addition, deeply hooked fish that had the hooks removed tended to exhibit more sublethal disturbances. By ten days post captured, more than 60% of the deeply hooked fish had expelled their hooks. Hence, if a fish is deeply hooked and the hook cannot be easily and safely removed, then the hook should be left in place. However, because shallowly hooked control fish experienced negligible mortality and experienced minimal sublethal disturbance, we suggest that additional efforts should focus on strategies to minimize incidences of deep hooking in the first place.

4.1. Injury, mortality and condition

Many factors can affect the post-release mortality of angled fish (e.g. Muoneke and Childress, 1994), but it has been demonstrated repeatedly that anatomical location (i.e., deep hooking in areas such as gills, esophagus, and stomach) is one of the strongest contributing factors across a range of species (Murphy et al., 1995; Diodati and Richards, 1996; Taylor et al., 2001; Carbines, 1999; Hulbert and Engstrom-Heg, 1980; Diggles and Ernst, 1997; Aalbers et al., 2004; summarized in Bartholomew and Bohnsack, 2005). Mortality usually occurs as a result of the hook penetrating vital organs or other tissues often associated with the circulatory, hepatic, or digestive systems. Such mortality can occur quite rapidly if the circulatory system is compromised and the fish experience significant blood loss. However, mortality can also happen hrs, days or weeks later as a result of injury to tissues that do not immediately affect the survival of the fish but that have long-term pathological effects (Borucinska et al., 2001). When an angler captures a deeply hooked fish and if that fish is to be released (for whatever reason) then the angler is faced with a decision—to cut the line and leave the hook in place or attempt to remove the hook. Both scenarios have the potential to create additional problems for the fish. A hook that is left in place could block the alimentary canal and prevent feeding or lead to longer-term pathological problems. Conversely, while removing a deep hook further injury may occur resulting in more severe injury and blood loss. When bluegills are shallowly hooked at moderate water temperatures (below 26 °C), mortality rates are quite low (typically less than 3%; Cooke et al., 2003, 2005; Barthel et al., 2003; Gingerich et al., 2007). This study occurred on the same system where the aforementioned studies were conducted (i.e., Opinicon Lake, Ontario) at temperatures between 14 and 23 °C and we also observed negligible mortality in the shallowly hooked control fish (0% after 48 h and 2.5% after 10 days). Provided that environmental conditions are benign (e.g., not extreme temperatures, sufficient oxygen) and that the fish are angled and handled quickly and appropriately (e.g., not fought to exhaustion, minimal air exposure), we would expect similar low levels of mortality across a range of game fish species when they are shallowly hooked.

Consistent with existing literature on salmonids other fish (summarized in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005) we found that deep hooking resulted in elevated mortality relative to shallowly hooked controls. The highest levels of mortality were noted for fish in the treatment where hooks were removed. We always attempted to first remove the hooks with surgical hemostats, however, when we were unsuccessful in removing the hook we used steady pressure to pull the hook from the fish, undoubtedly resulting in tearing of the esophagus and potentially underlying vasculature and tissue. Many anglers fishing for bluegill or other panfish may not have hemostats or pliers that fit within the mouth of these relatively small fish so we believe that most deeply hooked bluegills have the hook removed by pulling (Cooke, personal observations). We were successful with removing the hook with hemostats about 25% of the time. Mortality rates that we observed following hook removal exceeded the level (i.e., 20%) deemed to be “high” in a synthesis by Muoneke and Childress (1994). In fact, by 10 days after hook removal, more than 40% of the fish for which the hooks were removed had died. Mortality rates for fish that had the hook left in place (i.e., line cut) experienced mortality levels that were intermediate to the controls and hook removal treatment. Previous research has also revealed that leaving the hook in place appears to be a better strategy than attempting to remove a hook if it is deeply embedded. Hulbert and Engstrom-Heg (1980) and Mason and Hunt (1967) both found a 3-fold increase in mortality when deep hooks were removed from brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss*, respectively, compared to when the line was cut. Interestingly, the actual mortality rates that we observed for deeply hooked bluegill that had the hooks left in were much lower than those that have been reported for salmonids (e.g., 57% mortality in Atlantic salmon, Warner, 1979; 47% mortality in rainbow trout, Schill, 1996) although there are several exceptions (e.g., 16% for brook trout and 8% for brown trout, Dubois and Kuklinski, 2004). Our mortality rates for deeply hooked fish that had hooks removed, although high (40%), were still lower than the mortality observed in most salmonid studies (90% for Atlantic salmon, Warner, 1979; 76% for rainbow trout, Schill, 1996).

More than half of the mortality that occurred for deeply hooked fish was within hours of capture suggesting that injuries to vital organs or the cardiovascular system was a primary contributor to mortality. Indeed, we noted high levels of bleeding after hook removal in 35.6% of the deeply hooked fish after removal and the fish that exhibited significant bleeding died at higher rates (i.e., 57.6% then those fish that bled minimally or not at all after hook removal, consistent with observations on a number of other studies, e.g., Aalbers et al., 2004; Cooke et al., 2005; Jenkins, 2003). Aalbers et al. (2004) found 41% of mortalities in juvenile white seabass exhibited moderate to heavy bleeding upon capture. Even during the 10-day holding period, the majority of the mortality occurred towards the beginning of the holding period. Although the time period that we selected for the longer-term assessment (i.e., 10 days) was shorter than periods used in other studies (e.g., Tsuboi et al., 2006 studied deep hooking in white-spotted char over an entire season), the evidence from our study suggests that mortality occurs rapidly and has more to do with immediate severe injury rather than longer-term chronic pathological effects (e.g., mechanical injury, lesions, bacterial esophagitis and gastritis; Borucinska et al., 2002).

After holding fish for either 48 h or 10 days, or at time of death, we euthanized fish to examine the hooking locations and associated injury for fish with the line cut and to assess tissue damage in fish that had the hook removed. Because we used reasonably small hooks, no injuries to organs such as the liver and heart were apparent. Conversely, Mason and Hunt (1967) found that deeply hooked rainbow trout that died during their experiment had hooking damage to a range of organs including the stomach, liver, heart, kidneys, spleen and pyloric caeca. Hence, hook size, hook type, bait type and/or inter-specific morphological and anatomical variation appear to influence the severity and type of injury when deeply hooked.

We did note that fish that had the line cut were able to expel the hooks. By 10 days post-capture, more than 70% of fish had expelled the hooks. Of the hooks that were still retained, there were twice as many in the esophagus as in the stomach. No hooks were observed in other locations. In other studies, hook expulsion rates have also tended to be high. Tsuboi et al. (2006) found the probability of a hook remaining in white-spotted charr 70 days after cutting the line was 0%, and the average time to hook expulsion was 53.3 ± 36.3 days after line-cutting. These rates are highly variable both within and between species, but proportions of hook expulsion are substantial and show that most fish are capable of hook expulsion over weeks or months (Dubois and Pleski, 2007; Hulbert and Engstrom-Heg, 1980; Schill, 1996; Schisler and Bergersen, 1996; Tsuboi et al., 2006) and bluegill appear to be able to expel hooks more rapidly than some other species.

The mechanism of actual hook expulsion was not explicitly evaluated in this study, however, given that we found no hooks in digestive system posterior to the stomach, it is likely that the majority of these hooks were expelled via the mouth. Gastric digestion, direct passage via the opercular aperture, or movement through either end of the digestive tract have all been previously suggested as possible mechanisms of hook loss in fish (Mason and Hunt, 1967; Hulbert and Engstrom-Heg, 1980). Gastric digestion is an unlikely mechanism used by the bluegill in this study, as the study period was relatively short. In marine water, Aalbers et al. (2004) 130 days were required for juvenile white seabass to completely digest the hooks. Moreover, we found several intact hooks at the bottom of the tank at the end of the experiment.

Hulbert and Engstrom-Heg (1980) argued that a retained hook in the esophagus would have an adverse affect on foraging and digestion, as it could impede the passage of food down the digestive tract. As such, we evaluated the impacts of different treatments on fish feeding rates and condition. After 48 h the fish that had the hook removed had less food in their stomachs than fish that had the line cut or were shallowly hooked. Apparently the presence of the hook in line-cut fish did not impede ingestion of chironomids whereas the injury arising from hook removal was sufficient to either reduce competitive ability (but see below for discussion of swimming performance) or ability to mechanically process or ingest food. By 10 days post capture there were no differences in the growth or HSI (an index of fish nutritional condition). Although we failed to provide an adequate ration to yield positive growth, the extent of weight loss did not differ between groups. Hence, for the purposes of this paper the lack of relative difference in mass loss is sufficient to conclude that long-term growth and condition are not impaired by hook retention or hook removal. Line-cut treatment group fed slightly less then the control group, however, the majority of fish had full stomachs, indicating that food consumption was not problematic. It was the hook-removal group whose foraging activity was significantly reduced, and this difference in feeding behaviour could be a result of higher stress levels experienced by the hook-removal fish. Of the few studies that have investigated sublethal metrics such as growth or condition when comparing hook retention versus hook removal, most found that fish that have had the line cut grew less than fish that had the hook removed (e.g. Jenkins, 2003; Mason and Hunt, 1967; Hulbert and Engstrom-Heg, 1980). In this study, however, the line-cut treatment fish experienced the least decrease in mass compared to the other treatment groups. These contradictory findings could simply be a result of inter-specific variation (in mouth morphology and feeding). In addition, bluegill were fed dehydrated blood worms during our study which are small and could likely be easily passed around a hook that is in the alimentary canal relative to other food items that adult bluegill would normally eat while in the wild (e.g., terrestrial insects, caddis fly larvae, large zooplankton, small fish; Sadzikowski and Wallace, 1976; Keast, 1985).

4.2. Swimming performance

Swimming performance is a sensitive indicator of overall organismal health and physiological condition. Swimming performance is also ecologically relevant, as swimming is essential for crucial behaviours such as evasion of predators, feeding, and nest guarding (Schreer et al., 2005; Plaut, 2001). Although we noted sublethal changes in blood biochemistry, we did not observe any differences in the swimming performance between fish in the different treatment groups. Although the hook-removal treatment group performed equally well during the swim tests, rapid mortality within this group may have biased the results. Almost one quarter of all hook-removal treatment fish died before they were subjected to the swimming performance tests suggesting that we were biased towards the use of fish that were more likely to survive. Nonetheless, if we focus on this metric as an indicator of sublethal impairment, there is no influence of treatment on fish swimming performance. To date few studies have used swimming performance for evaluating catch-and-release fishing (e.g., examination of air exposure impacts on swimming ability of brook trout; Schreer et al., 2005) and to our knowledge none have evaluated deep hooking or hook removal versus retention.

4.3. Hematology and blood biochemistry

In addition to evaluating injury and mortality, we also compared the physiological consequences of the three different treatments. Consistent with other time-course studies on the physiological responses of shallowly hooked freshwater fish, bluegill experienced elevated glucose and some loss of ions 1 h after disturbance but most parameters had returned to resting levels by 6 h. The rapid rise of glucose as a result of an acute stress (e.g., angling) is mediated predominantly by cortisol and functionally is intended to provide the fish with the energetic substrates needed to deal with a stressor (Barton, 2002). Frequently accompanying elevations of cortisol and glucose are changes in ionic status. When freshwater fish are exposed to stress, they typically respond by losing ions. Interestingly, there was also a trend in the control fish again exhibiting indicators of stress by 24 h after capture. Previous studies have noted that confinement, as occurs during sensory deprivation as part of time course physiology experiments, can itself be stressful (Barton, 2002). Relative to shallowly hooked controls, fish that had the hooks removed exhibited significant physiological disturbance. Glucose levels remained elevated relative to controls throughout the monitoring period. Even at 24 h glucose levels in fish that had the hook removed were nearly twice that of control fish indicating that the stress associated with hook removal was significant. Indeed, even following a number of severe stressors in competitive fishing tournaments, walleye and largemouth bass are physiologically recovered by 6 h after capture (Suski et al., 2004; Killen et al., 2006). Hence, the prolonged physiological disturbance in fish that had the hook removed indicates chronic stress.

One factor contributing to the prolonged physiological disturbance in fish that had the hook removed may be blood loss. We measured hematocrit which can be used as an indicator of blood loss as well as physiological disturbance. Consistent with observations noted above (i.e., fish bleeding after hook removal), hematocrit levels were low. Although hematocrit can vary quickly and for different reasons (e.g., increasing as a result of splenic contractions which release more red blood cells or because of erythrotic swelling and erythropoiesis (Wendelaar-Bonga, 1997) or decreasing because of osmotic shifts and hemodilution as a result of changes in gill permeability (Gustaveson et al., 1991) or blood loss), hematocrit is regarded is a good indicator of the relative oxygen carrying capacity and the general condition of fish (Barton, 2002). Even by 24 h the hematocrit levels of the hook removal group were significantly lower than shallowly hooked controls. In general, leaving the hook in place resulted in physiological disturbance that was intermediate but not significantly different from the other two treatments, particularly for glucose and hematocrit.

An important consideration in the interpretation of our physiological findings is that we standardized the level of handling associated with each treatment (e.g., we exposed all fish to air for 1 min). In reality, hook removal usually takes longer when fish are deeply hooked (Grixti et al., 2008) and this can result in more severe physiological alterations (Cooke et al., 2001). As such, under scenarios where an angler were to capture a fish in the wild, the level of physiological stress experienced by deeply hooked fish would presumably be greater than for controls or line-cut fish which could be handled and returned to the water more quickly.

4.4. Management implications and conclusion

Mortality among fish that are released after angling has the potential to negatively affect fish populations and make harvest regulations ineffective or counterproductive (Coggins et al., 2007). Given that deep hooking has been repeatedly identified as a critical factor in post-release mortality (Bartholomew and Bohnsack, 2005), efforts are needed to reduce incidences of deep hooking and to provide anglers and management agencies with information on what to do when a fish is deeply hooked. Such efforts have the potential to increase the sustainability of recreational fisheries (Cooke and Schramm, 2007) and are consistent with maintaining the welfare status of angled fish (Davie and Kopf, 2006; Cooke and Sneddon, 2007; Arlinghaus et al., 2007). Consistent with a growing body of literature on salmonids (e.g., Warner, 1979; Schill, 1996; Dubois and Kuklinski, 2004; Schisler and Bergersen, 1996; Tsuboi et al., 2006) and several marine fish (red drum, Jordan and Woodward, 1994; snook, Taylor et al., 2001), using bluegill as a model we revealed that when warmwater fish from inland waters are deeply hooked and the hook cannot be easily removed, the line should be cut and the fish released. Because we held fish in captivity, it is difficult to determine if our mortality rates are comparable to what would be observed in the wild. Although our tanks were void of predators and food was provided regularly, holding fish in captivity can also result in mortality. However, our control fish experienced negligible mortality during the holding period suggesting that the mortality we did observe was attributable to the treatments and that mortality would likely be higher in the wild. Fish that are deeply hooked and are released after hook removal will likely experience high levels of mortality and experience significant sublethal physiological alterations and short term feeding impacts. When the line is cut and the hook is left in place, mortality is much lower and sublethal impacts are similar to those observed in shallowly hooked controls. Management agencies should also consider effort control over size or bag limits in instances where deep hooking levels are high, thus enabling anglers to harvest deeply hooked fish. Alternatively, angler education programs should emphasize gears available to minimize deep hooking (e.g., circle hooks, non-organic baits) and to cut the line when fish are deeply hooked.

A recent review of catch-and-release guidelines provided by state and provincial management agencies in North America revealed that 90% of them recommended cutting the line when the fish was too deeply hooked to enable safe removal (Pelletier et al., 2007). However, it is unknown the extent to which these guidelines are followed or adopted by anglers. Two natural resource agencies recommended removing the hook and only leaving the hook in place if removal efforts fail (Pelletier et al., 2007). There is obviously inherent risk in this approach if the attempts to remove the hook cause significant injury whether successful with hook removal or not. In addition, long periods of time spent attempting to remove the hook from deeply hooked fish will also lead to more severe physiological disturbances due to the longer air exposure and handling (Cooke et al., 2001). Some authors have advocated for the use of dehooking tools to remove deep hooks (Malchoff and MacNeill, 1995), however, to our knowledge there is no quantitative evaluation of the many different dehooking tools. As such, we would advise caution when using these tools and encourage research on that topic. Simple tools such as hemostats or needlenose pliers (appropriately sized for the fish) should be used when angling as they are likely the most effective tool for reaching deep hooks, given the caveat that removal attempts could cause more severe injury. Future research should evaluate different hook materials (e.g., bronze, stainless steel), sizes (overall hook size and gape size), gauges of the hook material, designs (e.g., aberdeed, octopus, baitholder) and configurations (e.g., barbed versus unbarbed) and evaluate how these factors influence whether the line should be cut or the hook left in place as those factors may influence the ability of fish to expel the hook.

Acknowledgements

We thank Marie-Ange Gravel, Cody Dey, Chris Pullen, Jake Davis, Claire Yick, Caleb Hasler, and Lianne Nowell for assistance in the field, and we thank Kyle Hanson for his guidance with statistical analyses. Scott Smithers of the Ontario Ministry of Natural Resources kindly provided scientific collection permits. All research was conducted in accordance with the Canadian Council on Animal Care as administered by Carleton University and Queen's University. This research was supported by Carleton University, the Ontario Ministry of Research and Innovation, the Ontario Research Fund, and the Canada Foundation for Innovation. The lead author (E. Fobert) was also supported by an NSERC URSA.

References

Aalbers, S.A., Stutzer, G.M., Drawbridge, M.A., 2004. The effects of catch-and-release angling on the growth and survival of juvenile white seabass captured on offset circle and J-type hooks. North Am. J. Fish. Manage. 24, 793–800.

Alós, J., 2008. Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (*Serranus scriba*) released by recreational anglers. ICES J. Mar. Sci. 65, 1620–1625.

Arlinghaus, R., Klefoth, T., Kobler, A., Cooke, S.J., 2008. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for Northern Pike: the influence of type and size of bait. North Am. J. Fish. Manage. 28, 123–134.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C.D., Sutton, S.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.

Barthel, B.L., Cooke, S.J., Suski, C.D., Philipp, D.P., 2003. Effects of landing net mesh type on injury and mortality in a freshwater recreational fishery. Fish. Res. 63, 275–282.

Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish. Biol. Fisher. 15, 129–154.

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.

Borucinska, J., Kohler, N.E., Natanson, L.J., Skomal, G.B., 2002. Pathology associated with retained fishing hooks in blue sharks (*Prionace glauca*) (Linnaeus 1758) with implications for their conservation. J. Fish Dis. 25, 515–521.

Borucinska, J., Martin, J., Skomal, G., 2001. Peritonitis and pericarditis associated with gastric perforation by a retained fishing hook in a blue shark. J. Aquat. Anim. Health 13, 347–3354.

Carbines, G.D., 1999. Large hooks reduce catch-and-release mortality of blue cod *Parapercis colias* in the Marlborough Sounds of New Zealand. North Am. J. Fish. Manage. 19, 992–998.

Coggins, L.G., Catalano, M.J., Allen, M.S., Pine III, W.E., Walters, C.J., 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. 8, 196–210.

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

Cooke, S.J., Barthel, B.L., Suski, C.D., Siepker, M.J., Philipp, D.P., 2005. Influence of circle hook size on hooking efficiency, injury, and size selectivity of bluegill with comments on circle hook conservation benefits in recreational fisheries. North Am. J. Fish. Manage. 25, 211–219.

Cooke, S.J., Suski, C.D., Barthel, B.L., Ostrand, K.G., Tufts, B.L., Philipp, D.P., 2003. Injury and mortality induced by four hook types on bluegill and pumpkinseed. North Am. J. Fish. Manage. 23, 883–893.

Cooke, S.J., Phillipp, D.P., Dunmall, K.M., Schreer, J.K., 2001. The influence of terminal tackle on injury, handling time, and cardiac disturbance of rock bass. North Am. J. Fish. Manage. 21, 333–342.

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

Cooke, S.J., Sneddon, L.U., 2007. Animal welfare perspectives on recreational angling. Appl. Anim. Behav. Sci. 104, 176–198.

Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodivers. Conserv. 14, 1195–1209.

Cooke, S.J., Cowx, I.G., 2004. The role of recreational fishing in global fish crises. BioScience 54, 857–859.

Cooke, S.J., Suski, C.D., 2004. Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? Aquat. Conserv. 14, 299–326.

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

Diggles, B.K., Ernst, I., 1997. Hooking mortality of two species of shallow-water reef fish caught by recreational angling methods. Mar. Freshwater Res. 48, 479–483.

Diodati, P.J., Richards, R.A., 1996. Mortality of striped bass hooked and released in salt water. Trans. Am. Fish. Soc. 125, 300–307.

Dubois, R.B., Pleski, J.M., 2007. Hook shedding and mortality of deeply hooked brook trout caught with bait on barbed and barbless hooks. North Am. J. Fish. Manage. 27, 1203–1207.

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

Dunmall, K.M., Cooke, S.J., Schreer, J.F., McKinley, R.S., 2001. The effect of scented lures on the hooking injury and mortality of smallmouth bass caught by novice and experienced anglers. North Am. J. Fish. Manage. 21, 242–248.

Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish. Fish. Res. 86, 169–178.

Grixti, D., Conron, S.D., Morison, A., Jones, P.L., 2008. Estimating post-release survival and the influential factors for recreationally caught black bream (*Acanthopagrus butcheri*) in the Glenelg River, south eastern Australia. Fish. Res. 92, 303–313.

Gustaveson, A.W., Wydoski, R.S., Wedemeyer, G.A., 1991. Physiological response of largemouth bass to angling stress. Trans. Am. Fish. Soc. 120, 629–636.

Hulbert, P.J., Engstrom-Heg, R., 1980. Hooking mortality of worm-caught hatchery brown trout. N. Y. Fish Game J. 27, 1–9.

Hunsaker, D.II., Marnell, L.F., Sharpe, P., 1970. Hooking mortality of Yellowstone cutthroat trout. Prog. Fish Cult. 32, 231–235.

Jenkins, T.M., 2003. Evaluating recent innovations in bait fishing tackle and technique for catch and release of rainbow trout. North Am. J. Fish. Manage. 23, 1098–1107.

Jordan, S.R., Woodward, A.G., 1994. Hooking mortality of worm-caught brown trout. N. Y. Fish Game J. 27, 1–10.

Keast, A., 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Environ. Biol. Fish. 12, 119–129.

Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A 126, 161–179.

Killen, S.S., Suski, C.D., Cooke, S.J., Philipp, D.P., Tufts, B.L., 2006. Factors contributing to the physiological disturbance in walleyes during simulated live-release angling tournaments. Trans. Am. Fish. Soc. 135, 557–569.

Lyle, J.M., Moltschaniwskyj, N.A., Morton, A.J., Brown, I.W., Mayer, D., 2007. Effect of hooking damage and hook type on post-release survival of sand flathead (*Platycephalus bassensis*). Mar. Freshwater Res. 58, 445–453.

Malchoff, M.H., MacNeill, D.B., 1995. Guidelines to increase survival of released sport fish, released fish survival sport fish fact sheet. Cornell cooperative extension, Sea Grant.

Mapleston, A., Welch, D., Begg, G.A., McLennan, M., Mayer, D., Brown, I., 2007. Effect of changes in hook pattern and size on catch rate, hooking location, injury and bleeding for a number of tropical reef fish species. Fish. Res. 91, 203–211.

Mason, J.W., Hunt, R.L., 1967. Mortality rates of deeply hooked rainbow trout. Prog. Fish. Cult. 29, 87–91.

Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. 2, 123–156.

Murphy, M.D., Heagey, R.F., Neugebauer, V.H., Gordon, M.D., Hintz, J.L., 1995. Mortality of spotted seatrout released from gill-net or hook-and-line gear in Florida. North Am. J. Fish. Manage. 15, 748–753.

Nelson, K.L., 1998. Catch-and-release mortality of striped bass in the Roanoke River North Carolina. North Am. J. Fish. Manage. 18, 25–30.

Nixon, A.J., Gruber, S.H., 1988. Diel metabolic and activity patterns of the lemon shark (*Negaprion brevirostris*). J. Exp. Zool. 248, 1–6.

Pelletier, C., Hanson, K.C., Cooke, S.J., 2007. Do catch-and-release guidelines from state and provincial agencies in North America conform to scientifically based best practices? Environ. Manage. 39, 760–773.

Pelzman, R.J., 1978. Hooking mortality of juvenile largemouth bass Micropterus salmoides. Calif. Fish. Game 64, 185–188.

Plaut, I., 2001. Critical swimming speed: its ecological relevance. Comp. Biochem. Physiol. A 131, 41–50.

Sadzikowski, M.R., Wallace, D.C., 1976. A comparison of the food habits of size classes of three sunfish (*Lepomis machrochirus* Rafinesque, *L. gibbosus* Linnaeus, and *L. cyanellus* Rafinesque). Am. Midl. Nat. 95, 220–225.

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

Schisler, G.J., Bergersen, E.P., 1996. Post-release hooking mortality of rainbow trout caught on scented artificial baits. North Am. J. Fish. Manage. 16, 570–578.

Schreer, J.F., Resch, D., Gately, M., Cooke, S.J., 2005. Swimming performance of brook trout following simulated catch-and-release angling: looking for air exposure thresholds. North Am. J. Fish. Manage. 25, 1513–1517.

Suski, C.D., Killen, S.S., Cooke, S.J., Kieffer, J.D., Philipp, D.P., Tufts, B.L., 2004. Physiological significance of the weigh-in during live-release angling tournaments for largemouth bass. Trans. Am. Fish. Soc. 133, 1291–1303.

Taylor, R.G., Whittington, J.A., Haymans, D.E., 2001. Catch-and-release mortality rates of common snook in Florida. North Am. J. Fish. Manage. 21, 70–75.

Taylor, M.J., White, K.R., 1992. A meta-analysis of hooking mortality of nonanadromous trout. North Am. J. Fish. Manage. 12, 760–767.

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.

Wilde, G.R., Sawynok, W., 2009. Effect of hook removal on recapture rates in 27 species of angler-caught fishes in Australia. Trans. Am. Fish. Soc. 138, 692–697.