

Effects of different angling practices on post-release behaviour of nest-guarding male black bass, *Micropterus* spp.

K. C. HANSON

Center for Aquatic Ecology and Conservation, Illinois Natural History Survey, Champaign, IL, USA

S. J. COOKE

Institute of Environmental Science and Department of Biology, Carleton University, Ottawa, ON, Canada

C. D. SUSKI

Aquatic Ecosystems Research Branch, Ontario Ministry of Natural Resources, Peterborough, ON, Canada

D. P. PHILIPP

Center for Aquatic Ecology and Conservation, Illinois Natural History Survey, Champaign, IL, USA

Abstract This study evaluated how different angling practices affect the short-term post-release behaviour of nest-guarding male black bass, *Micropterus* spp. Male largemouth bass, *M. salmoides* (Lacepède), and smallmouth bass, *M. dolomieu* (Lacepède), were angled from their nests and subjected to treatments designed to simulate a variety of common angling practices associated with catch-and-release angling, including fishing tournaments. In addition, some nests had broods reduced (removal of the majority of the eggs or fry from the nest) during the angling treatments to simulate predation of offspring during the angling event. Fish subjected to procedures simulating fishing tournaments (including a 1-h livewell confinement and release 100 m from the nest) exhibited significantly longer rest periods prior to returning to their nest than did other treatment groups. This rest period was longer for largemouth bass than smallmouth bass. Brood removal and air exposure increased abandonment rates compared with controls. These results show that sublethal stressors inherent in some angling practices (such as air exposure and livewell confinement) may delay the return of male black bass to their nest. In the presence of nest predators, the delay in return time could result in increased nest abandonment.

KEYWORDS: angling, catch-and-release, nest abandonment, parental care, tournaments.

Introduction

Recreational angling is a globally popular activity that has also developed into a vital component of regional and national economies (Cowx 2002). Recognising that recreational fishing may be contributing to global fish declines (Cooke & Cowx 2004), research efforts have been initiated to evaluate the sustainability of recreational fishing activities. Much current work is

focused on understanding the impact of sublethal stressors on fish that are captured and subsequently released by anglers (Cooke & Suski 2005). Recent studies have shown that both freshwater and marine fishes subjected to catch-and-release angling can experience various negative impacts including physical injury (Muoneke & Childress 1994), physiological responses (Cooke, Schreer, Dunmall & Philipp 2002b; Suski, Killen, Morrissey, Lund & Tufts

Correspondence: Kyle Hanson, Ottawa-Carleton Institute of Biology, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6 (e-mail: khanson2@connect.carleton.ca)

2003b; Suski, Svec, Ludden, Phelan & Philipp 2003a), altered behaviour (Cooke & Philipp 2004), elevated mortality (Muoneke & Childress 1994; Cooke & Suski 2005) and possibly decreased fitness (Cooke *et al.* 2002b).

Largemouth bass, *Micropterus salmoides* (Lacepède), and smallmouth bass, *M. dolomieu* (Lacepède), are popular sportfish species in North America. The reproductive ecology and parental care behaviours of black bass make them especially vulnerable to angling during the reproductive period (Jennings 1997; Philipp, Toline, Kubacki, Philipp & Phelan 1997; Suski & Philipp 2004). When water temperatures reach approximately 14 °C, male black bass move into shallow water (usually 2 m or less) and construct large, saucer-like depressions in the substrate (Kramer & Smith 1962). Male bass court female bass to the nest where egg deposition and fertilisation occur; and, following spawning, the female departs (Kramer & Smith 1962). Male bass then provide sole parental care to the brood for a period that can last more than one month (Ridgway 1988). Parental care involves not only fanning eggs and fry to prevent silt deposition on the nest and to provide oxygenated water to the progeny, but also aggressive nest defense to protect the developing brood from potential predators (Kramer & Smith 1962). All of these activities are energetically demanding, particularly considering that food consumption by nest-guarding males is greatly reduced during this period (Hinch & Collins 1991; Mackereth, Noakes & Ridgway 1999; Cooke, Philipp & Weatherhead 2002a).

With the intent of increasing reproductive output, several jurisdictions have implemented regulations to restrict angling during the spawning period (Quinn 2002); unfortunately, compliance is often poor (Kubacki 1992). Both conventional catch-and-release angling and competitive angling events can impose sublethal stressors on angled bass (Cooke, Schreer, Wahl & Philipp 2002c). In conventional catch-and-release angling, males that are removed from the nest even for short periods of time often are exposed to air, increasing the likelihood of physiological impairment (Kieffer, Kubacki, Phelan, Philipp & Tufts 1995; Cooke, Philipp, Schreer & McKinley 2000), increased brood predation (Kieffer *et al.* 1995; Philipp *et al.* 1997) and subsequent nest abandonment (Kieffer *et al.* 1995; Philipp *et al.* 1997; Suski *et al.* 2003a). During competitive angling events, in addition to the stressors indicated above, fish can be further stressed during livewell confinement, transport and weigh-in procedures (Cooke *et al.* 2002c; Suski *et al.* 2003b). Removal of a nest-guarding male bass for as little as 1 min or release far from the nest (thereby increasing

the time a brood is unguarded) have been shown to increase the likelihood of nest abandonment as a result of nest predators in the area consuming some portion of the unguarded broods (Philipp *et al.* 1997). Exercise due to angling has also been shown to increase heart rate (Cooke, Bunt, Ostrand, Philipp & Wahl 2004) and impair locomotory activity (Cooke *et al.* 2000). It has been proposed that energy lost through exercise due to angling increases the potential for the reduction in parental care and, hence, nest abandonment (Cooke *et al.* 2000). It has also been shown that males with the largest broods and most developed offspring are the most aggressive brood defenders (Sargent & Gross 1986; Ridgway 1988, 1989;) and, therefore, the most vulnerable to angling (Suski & Philipp 2004). Nest abandonment by these males has been postulated to promote population-scale alterations in reproductive success that translate into reduced year class strength (Suski & Philipp 2004).

This study investigated the effect that sublethal stressors associated with recreational angling events has on both the short-term post-release behaviour of nest-guarding male black bass and nest abandonment. Because air exposure has been repeatedly identified as a major sublethal physiological stressor (e.g. Ferguson & Tufts 1992; Cooke *et al.* 2002c; Cooke & Suski 2005), extended air exposure of nesting males was expected to cause them to take more time to return to the nest, resulting in increased abandonment rates. Similarly, because release distance from the nest has been shown to impact return times of male bass (Philipp *et al.* 1997), individuals displaced longer distances would be more likely to abandon the brood. Because previous work illustrated that fish with reduced broods showed increases in nest abandonment (Kieffer *et al.* 1995; Suski *et al.* 2003a), fish with reduced broods were also predicted to experience higher nest abandonment rates than controls.

Materials and methods

Study site and experimental procedures

This study was conducted in eastern Ontario, Canada, between 10 May and 10 June 2004. Largemouth bass were sampled from Lake Opinicon (827.4 ha) and Warner Lake (8.3 ha), whereas smallmouth bass were sampled from Wolfe Lake (998.1 ha) and Devil Lake (1129.7 ha). Snorkel surveys were used to locate largemouth and smallmouth bass guarding nests with eggs or newly hatched egg sac fry (<4 d old). Once a suitable male was located, his nest was marked with a numbered PVC marker, and the nest depth, male total

length and number of eggs in the nest (visual categorical assessment ranging from low of 1 to high of 5; Kubacki 1992; Suski & Philipp 2004) were estimated. A total of 81 largemouth bass and 93 smallmouth bass were used for this study, and each nest-guarding male was randomly assigned to one of seven treatment groups.

1. Non-angled control fish were subjected to the snorkelling survey (including marking with PVC nest tags) but were otherwise undisturbed.

2. No-float control fish were collected by hook-and-line angling using standard gear from a nearby boat, with time of angling kept under 1 min (Suski & Philipp 2004). After capture, the fish was immediately placed in a cooler of fresh lake water, a small piece of upper caudal fin was removed as a mark and total length (nearest mm) was measured rapidly (< 5 s) to minimise air exposure time during processing. After 5 min total holding and processing time, the fish was released into the water approximately 5 m from its nest. While males were off their nest, snorkellers stayed in the area to make sure that the nest was not subjected to brood predation and to determine visually when the male returned to its nest and resumed guarding its brood.

3. Catch-and-release treatment fish were angled, put into a cooler of water, and measured as described for no-float control fish. While the fish was in the cooler, a visual float was attached at the posterior insertion of the dorsal fin using 2–4 m of 1.8-kg test monofilament fishing line. The visual float consisted of a 5 cm × 2 cm cylindrical foam bobber attached to a size 8 bait holder fish hook (Cooke & Philipp 2004). Floats of this size have been used in a previous study to monitor the post-release movements of fish with no effects on the mobility or behaviour (Cooke & Philipp 2004). After 5 min total holding and processing time, the fish was then released 5 m from its nest.

4. Catch-and-release with brood removal treatment fish were subjected to the same treatment as the catch-and-release treatment group, but approximately 90% of their eggs or offspring were removed from their nest by a snorkeller while the fish was held in the cooler. After 5 min total holding time, the fish was released into the water approximately 5 m from its nest. This treatment simulated the heavy brood loss that can occur while nest-guarding males are away from their nest (Philipp *et al.* 1997).

5. Air exposure treatment fish were subjected initially to the same treatment described for the catch-and-release treatment group, but the 5 min holding period included 2 min of air exposure in which the fish were held out of water prior to release approximately 5 m from its nest.

6. Air exposure with brood removal treatment fish were subjected to the same treatment described for the air exposure treatment group, but approximately 90% of their offspring were removed from their nest by a snorkeller while they were being held in the cooler. After 5 min total holding, the male was released into the water approximately 5 m from its nest.

7. Simulated tournament treatment fish were subjected to the same treatment described for the catch-and-release treatment group, except these fish were confined in a livewell for 1 h, air-exposed for 2 min, and then released approximately 100 m from the nest. In addition, approximately 90% of their offspring were removed from their nest by a snorkeller while they were being held in the cooler.

Following release, bass fitted with visual floats were tracked by an observer in a boat. Routes and distances travelled by the fish while they were returning to their nests were recorded for fixed intervals of time following release as described by Cooke & Philipp (2004). Briefly, observers drew a map of all movements (with accompanying times) to facilitate determining the movement distances, as well as the amount of time that fish spent swimming vs resting while returning to their nest. Unless the float submerged and was lost from view when the fish dove into deep water or the float broke off on some subsurface structure, fish were tracked until they returned to their nest. Fish without floats could not be tracked from a boat, but a snorkeller near the nest verified the time at which the fish returned to the nest. After each fish returned to the nest, snorkellers immediately assessed parental care behaviour of the fish (*viz.* whether they actively guarded their nest, as evidenced by axial turning, or they simply rested nearby). At 0.5 h, 1 h and 24 h after return to the nest, snorkellers determined presence or absence of each male, as well as assessed its behaviour at the nest. The behaviours observed were divided into three categories: (i) positioned within 0.5 m of their nest and actively engaging in brood defense or brood maintenance (fanning); (ii) positioned within 3 m of their nest, but not attempting to defend or provide parental care for their brood; or (iii) not positioned within 3 m of a nest during subsequent snorkelling surveys, apparently having abandoned their broods.

Statistical analyses

The effects of the different angling treatments on distance travelled by each male during its return to the nest, swimming time while returning to the nest, resting time while returning to the nest, and total time required to return to the nest for both smallmouth and

largemouth bass were evaluated with a two-way ANOVA and Tukey's HSD *post-hoc* test (Zar 1999). During the analysis of return time, swimming time and rest time, treatments with and without brood removal were combined because the male had no knowledge that brood removal occurred until returning to the nest. Nest abandonment rates were analysed by Chi-square contingency table analysis (Zar 1999); pairwise comparisons were performed to determine significant differences in abandonment rates between treatment groups. To minimise Type II error, significance for all tests was assessed at $\alpha = 0.10$. All analyses were performed using the statistical package JMP IN 4.0 (SAS Institute, Cary, NC, USA) except for comparisons of proportions, which were performed using a spreadsheet.

Results

Short-term behaviour

Subjecting fish of both species to simulated tournament conditions increased the return times (Fig. 1a, Table 1). Smallmouth bass in the simulated tournament treatment required an average of 38 min to return to their nests, which was approximately 20 times longer than any of the other treatments. Largemouth bass of this treatment group took an average of 50 min to return to their nests, which was five times longer than largemouth bass of any other treatment group. Smallmouth bass in the simulated tournament treatment group swam for longer time periods (10–25 times longer) than did any other smallmouth treatment group (Fig. 1b). Largemouth bass of the simulated tournament treatment group also swam for longer time periods than largemouth bass in other treatment groups. Also, largemouth bass spent more time actively swimming than did smallmouth bass across all treatments. The simulated tournament treatment fish also had greater resting times after release for both species (Fig. 1c), and largemouth bass spent roughly twice as much time resting as smallmouth bass. The distance travelled by smallmouth bass returning to their nest following the simulated tournament treatment was approximately 10 times greater than smallmouth bass in other treatment groups (Fig. 2). Simulated tournament-treated largemouth bass travelled more than 2.9 times farther than other largemouth bass treatment groups.

Abandonment rates

At the multiple levels that brood abandonment was analysed, a pattern of increasing abandonment for certain treatment groups emerged. Largemouth bass in

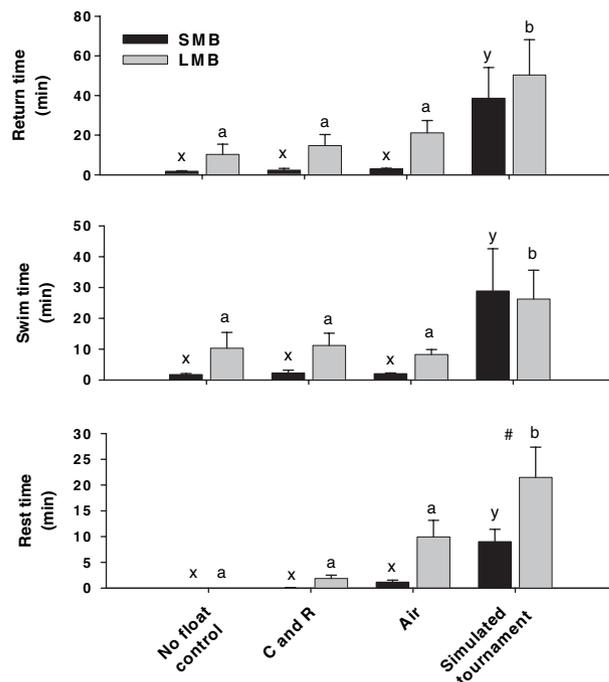


Figure 1. Effects of handling treatments on the time taken to return to a nest (a), amount of time spent swimming (b), and amount of time spent resting (c) while returning to a nest for nest-guarding male largemouth bass and smallmouth bass after angling. Treatments are described in the text. Letter assignments of 'a' and 'b' denote significant ($P < 0.10$) differences among treatment groups for largemouth bass, letter assignments of 'x' and 'y' denote significant differences among treatment groups for smallmouth bass and number sign (#) denotes significant differences between species within a particular treatment. Error bars show ± 1 SE. Sample sizes are 66 for largemouth bass and 73 for smallmouth bass distributed approximately equally across treatments.

the catch-and-release brood removal, air exposure, air exposure brood removal and simulated tournament treatments showed significantly greater abandonment at the 30-min ($\chi^2 = 36.567$, d.f. = 6), 1-h, ($\chi^2 = 43.675$, d.f. = 6) and 24-h ($\chi^2 = 30.784$, d.f. = 6) time intervals than fish in the no-angling control group (Fig. 3). The especially high abandonment rates of any fish subjected to brood removal indicates that this factor contributed substantially to nest abandonment. Also of note, almost every angling practice simulated by treatments in this study caused increased abandonment in largemouth bass compared with non-angled control fish. The same general trend was observed in smallmouth bass subjected to the various treatments, but this pattern was only statistically significant at the 24-h interval ($\chi^2 = 28.571$, d.f. = 6). For smallmouth bass at the 24-h interval, abandonment rates for the catch-and-release brood removal, air exposure, air exposure brood removal, and distance treatments were

Table 1. Two-way ANOVA results for behaviours of nest-guarding male largemouth bass and smallmouth bass subjected to different angling events. Treatments are described in the text

Response variable	Source	Sum of squares	d.f.	F	P
Return time	Treatment	6122083	5	7.1468	< .0001
	Species	10634508	1	9.3592	0.0028
	Treatment × Species	3944352	5	0.4605	0.8048
Swim time	Treatment	31502980	5	4.7239	0.0006
	Species	5682675	1	4.2606	0.0415
	Treatment × Species	306034	5	0.4538	0.8097
Rest time	Treatment	6374757.9	5	26.6055	< .0001
	Species	427011.8	1	8.9108	0.0035
	Treatment × Species	457580.3	5	1.9097	0.0990
Distance travelled	Treatment	262401.24	4	9.9050	< .0001
	Species	15826.50	1	2.3896	0.1265
	Treatment × Species	10226.83	4	0.3860	0.8180

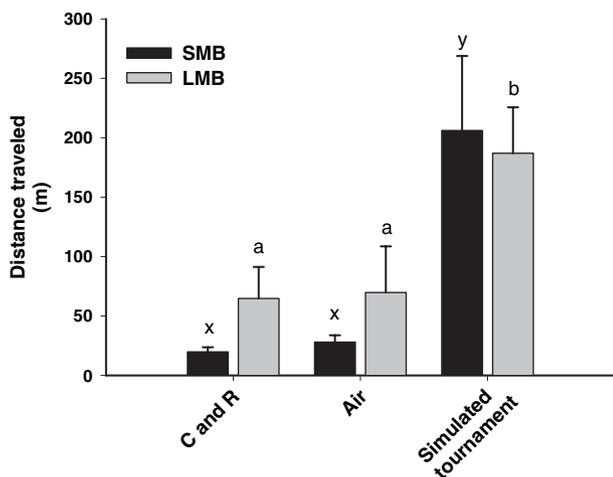


Figure 2. Effects of handling treatments on the distance travelled to return to a nest by nest-guarding male largemouth bass and smallmouth bass. Treatments are described in the text. Letter assignments of 'a' and 'b' denote significant ($P < 0.10$) differences among treatment groups for largemouth bass and letter assignments of 'x' and 'y' denote significant differences among treatment groups for smallmouth bass. Error bars show ± 1 SE. Sample sizes are 66 for largemouth bass and 73 for smallmouth bass distributed approximately equally across treatments.

increased above the levels of the control treatments. Again, brood removal was an important factor for smallmouth bass nest abandonment.

Discussion

The short-term behaviours of male largemouth and smallmouth bass were altered in response to angling treatments. All angled and released male bass eventually returned to their nest, although simulated tournament-treated individuals did not return as rapidly and efficiently as individuals from other treatments; these

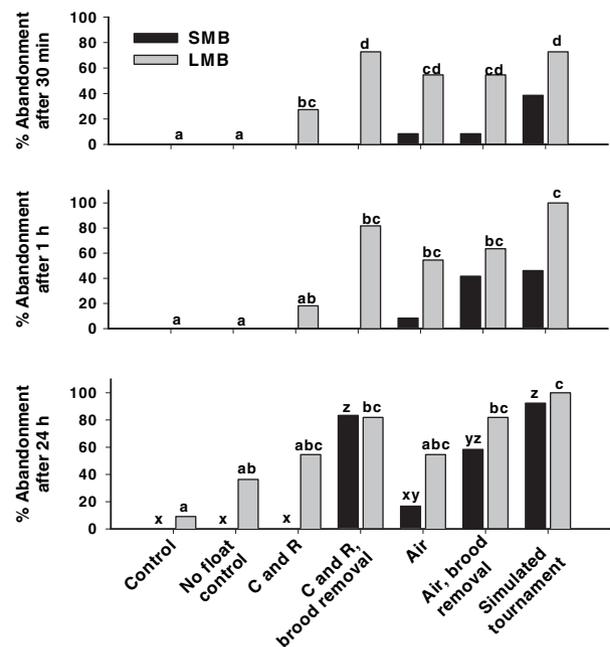


Figure 3. Abandonment rates at time intervals of (a) 30 min, (b) 1 h, and (c) 24 h for nest-guarding male largemouth and smallmouth bass subjected to various angling treatments. Treatments are described in the text. Letter assignments of 'a', 'b', and 'c' denote significant ($P < 0.10$) differences among treatment groups for largemouth bass, and letter assignments of 'x', 'y', and 'z' denote significant differences among treatment groups for smallmouth bass. Sample sizes are 81 for largemouth bass and 93 for smallmouth bass distributed approximately equally across treatments.

fish tended to swim longer distances than required to return, often in wandering circuitous patterns albeit in close proximity to the nest. This behavioural pattern may be a result either of the physiological changes associated with the exhaustive exercise of an angling event, as has been shown in previous studies (Gustaveson,

Wydoski & Wedemeyer 1991; Ferguson & Tufts 1992), or of displacement and temporary disorientation. Other fish species subjected to catch-and-release angling have been shown to exhibit altered post-release behaviour (Thorstad, Næsje, Fiske & Finstad 2003; Cooke & Philipp 2004; Gurshin & Szeldmayer 2004) consistent with our findings. Bass in the simulated tournament group were released 20 times farther from their nests than were fish in all the other treatment groups, and one would expect these fish to travel 20 times as far while returning to the nest as compared with other treatment groups. In actuality, largemouth bass in the simulated tournament treatment group travelled about two times farther than required, whereas males in other treatment groups displaced much shorter distances travelled five to six times farther than necessary, possibly indicating that largemouth bass may be able to find the general area of their nest quickly but have difficulty homing in on the exact location. Smallmouth bass generally travelled twice the distance required to return to the nest for all treatment groups. Further studies into the mechanisms used by nest-guarding bass to return to their nest site post-displacement may shed light upon this topic.

In general, largemouth bass seemed to be more severely affected by the various treatments than were smallmouth bass, as shown by slower movement rates and longer resting times when returning to the nest. This may be explained by differences in normal activity rates between species. Using electromyogram telemetry, Demers, McKinley, Weatherly & McQueen (1996) determined that during daytime smallmouth bass frequently travelled large distances, including movements in the pelagic areas of the lake, whereas largemouth bass movements were generally confined to small areas of the littoral zone. Consistent with the work of Demers *et al.* (1996), smallmouth bass have higher critical swimming speeds (e.g., Peake & Farrell 2004) than largemouth bass (e.g., Kolok 1991), suggesting greater aerobic capacity.

Smallmouth and largemouth bass showed a similar pattern of abandonment among treatments. In this study, brood loss associated with simulated brood removal caused marked increases in nest abandonment rates in males of both species, as has been shown in a previous study (Philipp *et al.* 1997). Exposing fish to air also elevated nest abandonment among largemouth bass during the first hours after an angling event. Angling may lower a male's overall energy stores at a time when the fish is already involved in an energetically costly behaviour (Hinch & Collins 1991; Mackereth *et al.* 1999; Cooke *et al.* 2002a), which may then hinder its ability to raise the

current brood effectively. As such, males that abandon their nest may be making the evolutionary decision to invest in future reproduction at the expense of the current brood by foregoing the continuance of energetically costly parental care that may inhibit future reproductive events (Trivers 1972; Sargent & Gross 1986).

Various angling and fish-handling practices can affect the reproductive output of largemouth and smallmouth bass differently, particularly if nest predators are present. It is also clear from this study that angling practices that remove male bass from their nests for extended periods of time, such as tournaments that require a weigh-in at the end of the event to determine a winner, can have substantial negative effects on the reproductive success of those fish. Some jurisdictions have enacted closed seasons that prohibit fishing for black bass during the reproductive period (Quinn 2002), and the results of this study indicate that such regulations may increase bass reproductive output. By-catch of nesting males by anglers targeting other fish, however, might limit the effectiveness of closed seasons. Alternatively, properly managed fish sanctuaries that prohibit all angling in certain portions of a water body may be more effective in protecting bass during the reproductive period (Suski, Phelan, Kubacki & Philipp 2002). In any case, if catch-and-release angling for black bass is allowed during the reproductive period, angling practices such as using barbless hooks and artificial lures, minimising playing time while the fish is on the line, avoiding exposing fish to air (Cooke & Suski 2005) and quick release following capture would serve to minimise any negative effects of angling.

The potential for catch-and-release angling to impact the reproductive success of an individual nesting male bass has been demonstrated here and elsewhere (Kieffer *et al.* 1995; Philipp *et al.* 1997; Cooke *et al.* 2000; Suski *et al.* 2003a; Steinhart, Leonard, Stein & Marschall 2005). A direct relationship between the cumulative annual reproductive success of all male bass in a population and the strength of the year class produced that year has not been assessed. If there is such a relationship, however, any activity that decreases the reproductive success of individuals (including angling) and concomitantly results in a decrease in the annual reproductive success of the population as a whole would result in decreased year-class strength. Because that potential outcome has such wide-ranging implications for bass management, studies to assess that relationship are needed and should be encouraged.

Acknowledgments

The authors would like to thank the numerous individuals who contributed to the collection of data for this study. Brandon Barthel, John Epifanio, Kevin Esseltine, Anne Readel, and Jeff Stein assisted with fish capture. This study was carried out at the Queen's University Biology Station. We thank the Biology Station staff, in particular Frank Phelan, Floyd Connor and Raleigh Robertson, for facilitating this research. Permits were provided by the Ontario Ministry of Natural Resources. Financial support was provided by the University of Illinois, Illinois Natural History Survey, Illinois Department of Natural Resources, and the Natural Sciences and Engineering Research Council. KCH and other aspects of this research project were partially supported by the Ron Ward Memorial Scholarship from the Champaign-Urbana Bass Club.

References

- Cooke S.J. & Cowx I.G. (2004) The role of recreational fisheries in global fish crises. *BioScience* **54**, 857–859.
- Cooke S.J. & Philipp D.P. (2004) Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biological Conservation* **118**, 599–607.
- Cooke S.J. & Suski C.D. (2005) Do we need species-specific guidelines for catch-and-release recreational angling to conserve diverse fishery resources? *Biodiversity and Conservation* **14**, 1195–1209.
- Cooke S.J., Philipp D.P., Schreer J.F. & McKinley R.S. (2000) Locomotory impairment of nesting male largemouth bass following catch-and-release angling. *North American Journal of Fisheries Management* **20**, 968–977.
- Cooke S.J., Philipp D.P. & Weatherhead P.J. (2002a) Parental care patterns and energetics of smallmouth bass, *Micropterus dolomieu*, and largemouth bass, *M. salmoides*, monitored with activity transmitters. *Canadian Journal of Zoology* **80**, 756–770.
- Cooke S.J., Schreer J.F., Dunmall K.M. & Philipp D.P. (2002b) Strategies for quantifying sublethal effects of marine catch-and-release angling – insights from novel freshwater applications. *American Fisheries Society Symposium* **30**, 121–134.
- Cooke S.J., Schreer J.F., Wahl D.H. & Philipp D.P. (2002c) Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. *American Fisheries Society Symposium* **31**, 489–512.
- Cooke S.J., Bunt C.M., Ostrand K.G., Philipp D.P. & Wahl D.H. (2004) Angling-induced cardiac disturbance of free-swimming largemouth bass (*Micropterus salmoides*) monitored with heart rate telemetry. *Journal of Applied Ichthyology* **20**, 28–36.
- Cowx I.G. (2002) Recreational fisheries. In: P. Hart & J. Reynolds (eds), *Handbook of Fish Biology and Fisheries*, Volume II. Oxford, UK: Blackwell Science, pp. 367–390.
- Demers E., McKinley R.S., Weatherly A.H. & McQueen D.J. (1996) Activity patterns of largemouth and smallmouth bass determined with electromyogram biotelemetry. *Transactions of the American Fisheries Society* **125**, 434–439.
- Ferguson R.A. & Tufts B.L. (1992) Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Onchorhynchus mykiss*): implications for catch-and-release fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1157–1162.
- Gurshin C.W.D. & Szeldmayer S.T. (2004) Short-term survival and movements of Atlantic sharpnose sharks captured by hook-and-line in the north-east Gulf of Mexico. *Journal of Fish Biology* **65**, 973–986.
- Gustavson A.W., Wydoski R.S. & Wedemeyer G.A. (1991) Physiological response of largemouth bass to angling. *Transactions of the American Fisheries Society* **120**, 629–636.
- 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 observations. *Transactions of the American Fisheries Society* **120**, 657–663.
- Jennings M.J. (1997) Centrarchid reproductive behavior: implications for management. *North American Journal of Fisheries Management* **17**, 493–495.
- Kieffer J.D., Kubacki M.R., Phelan F.J.S., Philipp D.P. & Tufts B.L. (1995) Effects of catch-and-release angling on nesting male smallmouth bass. *Transactions of the American Fisheries Society* **124**, 70–76.
- Kolok A.S. (1991) Photoperiod alters the critical swimming speed of juvenile largemouth bass, *Micropterus salmoides*, acclimated to cold water. *Copeia* **1991**, 1085–1090.
- Kramer R.H. & Smith L.L. (1962) Formation of year classes in largemouth bass. *Transactions of the American Fisheries Society* **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, 86pp.
- Mackereth R.W., Noakes D.L.G. & Ridgway M.S. (1999) Size based somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes* **56**, 263–275.
- Muoneke M.I. & Childress W.M. (1994) Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* **2**, 123–156.

- Peake S.J. & Farrell A.P. (2004) Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). *The Journal of Experimental Biology* **207**, 1563–1575.
- Philipp D.P., Toline C.A., Kubacki M.F., Philipp D.B.F. & Phelan F.J.S. (1997) The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. *North American Journal of Fisheries Management* **17**, 557–567.
- Quinn S. (2002) Status of seasonal restrictions on black bass fisheries in Canada and the United States. *American Fisheries Society Symposium* **31**, 455–465.
- Ridgway M.S. (1988) Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Zoology* **66**, 1722–1728.
- Ridgway M.S. (1989) The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieu*). *Ethology* **80**, 47–54.
- Sargent R.C. & Gross M.R. (1986) Williams' principle: an explanation of parental care in teleost fishes. In: T.J. Pitcher (ed.) *The Behavior of Teleost Fishes*. Baltimore, USA: Johns Hopkins University Press, pp. 275–293.
- Steinhart G.B., Leonard N.J., Stein R.A. & Marschall E.A. (2005) Effects of storms, angling, and nest predation during angling on smallmouth bass (*Micropterus dolomieu*) nest success. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2649–2660.
- Suski C.D. & Philipp D.P. (2004) Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Transactions of the American Fisheries Society* **133**, 1100–1106.
- Suski C.D., Phelan F.J.S., Kubacki M.F. & Philipp D.P. (2002) Use of sanctuaries to protect nesting bass from angling. *American Fisheries Society Symposium* **31**, 371–378.
- Suski C.D., Svec J.H., Ludden J.B., Phelan F.J.S. & Philipp D.P. (2003a) The effect of catch-and-release angling on the parental care behavior of male smallmouth bass. *Transactions of the American Fisheries Society* **132**, 210–218.
- Suski C.D., Killen S.S., Morrissey M.B., Lund S.D. & Tufts B.L. (2003b) Physiological changes in largemouth bass caused by live-release angling tournaments in southeastern Ontario. *North American Journal of Fisheries Management* **23**, 760–769.
- Thorstad E.B., Næsje T.F., Fiske P. & Finstad B. (2003) Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research* **60**, 293–307.
- Trivers R.L. (1972) Parental investment and sexual selection. In: B. Campbell (ed.) *Sexual Selection and the Descent of Man*. London: Heinemann Press, pp. 139–179.
- Zar J.H. (1999) *Biostatistical Analysis*, 4th edn. Englewood Cliffs, USA: Prentice-Hall, 663pp.