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[Article]

Latitudinal Variation in Physiological and Behavioral Responses of Nest-Guarding Smallmouth Bass to Common Recreational Angling Practices

KYLE C. HANSON,* MARIE-ANGE GRAVEL, TARA REDPATH, AND STEVEN J. COOKE

Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute of Biology, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, Canada

MICHAEL J. SIEPKER

Missouri Department of Conservation, Resource Science Division, 551 Joe Jones Boulevard, West Plains, Missouri 65775, USA

Abstract.—Management policies related to catch-and-release (CR) angling of smallmouth bass *Micropterus dolomieu* vary widely across the geographic distribution of the species. Some jurisdictions, principally in the northern latitudes, prohibit or limit angling efforts that target nesting male smallmouth bass, whereas angling during the nesting period is generally unregulated in southern jurisdictions. Existing studies of individual-level angling impacts on nesting smallmouth bass have primarily been conducted in the north; thus, the extent to which these findings are relevant to other regions is unknown. In the current study, we sought to systematically evaluate the rates of nest abandonment by nesting smallmouth bass subjected to common angling practices (CR treatment: brief angling and no exposure to air; air exposure [AE] treatment: exhaustive angling and 3 min of AE) and tournament practices (simulated tournament [ST] treatment: exhaustive angling, 2 h of live-well retention, and 3 min of AE prior to release) across a latitudinal gradient encompassing virtually the entire south–north range of smallmouth bass (i.e., southern Missouri [MO], southern Ontario [SON], and northern Ontario [NON]) and compared these treatment groups with nonangled controls. We also quantified the extent to which physiological disturbance associated with angling varied across latitudes (peripheral populations [MO and NON] versus the intermediate-latitude population [SON]). Whole-blood lactate and glucose levels were highest in fish subjected to ST conditions, indicating increased stress; this pattern was conserved across all latitudes (although there was some evidence of intraspecific variation in stress response). Additionally, the pattern of brood abandonment was similar among fish at all three latitudes; ST fish exhibited the highest rates of nest abandonment (MO: control = 9.1%, CR = 0%, AE = 9.1%, ST = 100%; SON: control = 10%, CR = 10%, AE = 10%, ST = 50%; NON: control = 7.7%, CR = 0%, AE = 9.1%, ST = 50%). Interestingly, fish from the most southerly latitude, where regulations are the most liberal, abandoned nests at higher rates than did fish from the other latitudes. Collectively, these data reveal that the reproductive success of individual smallmouth bass can suffer from interaction with anglers, particularly in a tournament context, regardless of the region. Further study is needed to determine the extent to which individual nest success is relevant to recruitment and how this relationship varies across latitudes.

Across the endemic range of black basses *Micropterus* spp., there is disparity among management agency policies regarding angling during the reproductive period. Some jurisdictions strictly regulate angling during this period and prohibit the intentional targeting of nesting black bass by anglers, while other jurisdictions allow angling during this period but either require the release of all individuals or have reduced bag limits (Quinn 2002). Other jurisdictions allow anglers to fish for and harvest black bass during this period, and live-release competitive angling events are also allowed (i.e., there are no regulations specific to the reproductive period; Quinn 2002). In general, regulations that limit angling of nesting black bass tend to be more conservative in northern clines and more liberal in the south. Although the basis for this difference is unclear, there is some suggestion that productivity in southern clines is sufficiently high that any potential negative effects on individuals are compensated for at the population level (e.g., Beamesderfer and North 1995). Furthermore, there is no clear evidence of a stock–recruitment relationship for black basses, even though one has been sought for some time (see Philipp and Ridgway [2002]). As a result, anglers, fisheries managers, and scientists continue to debate the need for angling restrictions during the black bass nesting period.

In jurisdictions where regulations are conservative, the premise for the regulations is that angling during

* Corresponding author: khanson2@connect.carleton.ca

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the reproductive period is detrimental to individuals and potentially to populations (Cooke and Suski 2005). In black basses, spawning commences when water temperatures reach approximately 14°C, and the male provides sole parental care for periods of up to 6 weeks (Coble 1975; Ridgway 1988; Cooke et al. 2006). During this time, the male expends significant energy while fanning eggs and defending the nest and offspring from brood predators (Hinch and Collins 1991; Mackereth et al. 1999; Cooke et al. 2006). Because of their heightened vigilance during the nesting period, parental males are extremely vulnerable to capture by anglers (Suski and Philipp 2004). A large body of research has been focused on the physiological or behavioral effects of angling on black bass during the reproductive period (Kieffer et al. 1995; Cooke et al. 2000), and a number of studies have examined angling-associated nest abandonment (Kieffer et al. 1995; Philipp et al. 1997; Hanson et al. 2007). However, a population-level effect of angling for nesting black bass has not been demonstrated. Indeed, factors such as predator burden (Steinhart et al. 2005), storms (Steinhart et al. 2005), and male size and condition (Suski and Philipp 2004) all contribute to differential reproductive success among individuals.

Although there is a mounting body of evidence that the angling of nesting black bass affects individual reproductive success and fitness of parental males (summarized by Cooke et al. [2002] and Siepker et al. [2007]), much of the work to date has been conducted in northern clines. In fact, the majority of studies have been conducted in two lakes located in southeastern Ontario (SON; i.e., Lakes Opinicon and Opeongo), and several other studies have been conducted in Michigan and New York. However, to our knowledge, there are no studies that have systematically evaluated the effect of angling on the rate of black bass nest abandonment across a latitudinal gradient. Furthermore, there is a need to understand the extent to which physiological disturbances associated with common catch-and-release (CR) angling practices vary among populations (i.e., latitudes; see Cooke and Suski [2005] and Arlinghaus et al. [2007]). Previous work on black basses has noted that populations distributed across short geographical distances are locally adapted to environmental conditions and exhibit differences in physiological processes, such as swimming performance, activity, and routine oxygen consumption (Philipp and Claussen 1995; Cooke et al. 2001). These patterns of local adaptation point to the possibility that common angling practices could elicit differing stress responses in populations of smallmouth bass *M. dolomieu* located in different portions of the species' range. Indeed, there is evidence that populations living on the periphery of a given species' range have greater responses to a standardized stressor, as was documented for lizards (Dunlap and Wingfield 1995) and birds (Wingfield et al. 1998). However, similar data are unavailable for fish.

Here, we present results of a comparative study in which nesting male smallmouth bass were angled from Bull Shoals Lake (southern Missouri–northern Arkansas; hereafter, MO), Lake Opinicon (hereafter, SON), and Rainy Lake (northwestern Ontario–northern Minnesota; hereafter, NON). We systematically varied angling disturbance and retention times to mimic a range of angling and tournament conditions while evaluating physiological disturbance and nest abandonment rates; results were compared among study sites. We predicted that as intensity of simulated angling increased (i.e., angling duration and retention time), physiological disturbance and subsequent nest abandonment rates would increase. Furthermore, we expected that the response to an angling stressor would be greater in the peripheral MO and NON populations than in the intermediate-latitude SON population.

Methods

Experimental procedures.—The three sampling locations (MO: 36°25′00″N, 92°45′00″W, sampled April 30–May 4, 2007; SON: 44°33′00″N, 76°20′00″W, sampled May 18–19, 2007; and NON: 48°38′00″N, 93°15′00″W, sampled June 11–13, 2007) represented almost the entire latitudinal range of smallmouth bass in North America (Scott and Crossman 1973). The surface area and mean depth were 18,390 ha and 20.4 m at the MO site; 787 ha and 2.5 m at the SON site; and 92,100 ha and 9.8 m at the NON site. Each lake contained a population of resident, naturally reproducing smallmouth bass and was representative of lakes within its particular region with respect to angling for this species. Angling regulations during the study varied between jurisdictions. In MO, there were no restrictions on black bass fishing during the spawning period aside from a 381-mm minimum length limit and a six-fish daily creel limit. In addition, competitive angling events occurred throughout the spawning season in MO. In SON, it was illegal to target black bass during the reproductive period; consequently, competitive black bass angling events were prohibited during this period. However, angling pressure for northern pike *Esox lucius* in the shallows was quite high, and previous work in this system revealed that compliance with regulations designed to protect spawning black bass was low (Philipp et al. 1997). Historically, the closed season was effective from late fall to the last week in June. In NON, there was no closed season but there was a 350-mm maximum length limit and a two-fish daily creel limit. However, because of an abundant population of walleyes *Sander vitreus*, very few anglers target smallmouth bass during the nesting period (D. McLeod, Ontario Ministry of Natural Resources, personal communication).

Smallmouth bass nests with young eggs (<4 d old) were located during daily snorkeling surveys of the littoral zone in each lake. Although the actual spawn timing varied across lakes, water temperatures at the time of spawning and during sampling were similar among the sites (MO = 15.4°C; SON = 14.7°C; NON = 15.0°C). Upon location of a nest, the snorkeler marked the nest with a numbered polyvinyl chloride tile for identification purposes and recorded nest depth, approximate male size, and egg score (a categorical assessment of the number of eggs in a nest; scale of 1–5, where 1 = low and 5 = high; Suski et al. 2003; Hanson et al. 2007). Fish were then randomly assigned to a control group or one of three treatment groups (i.e., CR, air exposure [AE], or simulated tournament [ST]) designed to mimic common angling practices throughout North America. Control fish were not disturbed beyond the initial snorkel survey and a follow-up assessment (see below). For the CR treatment, each fish was angled from its nest, landed within 30 s (mean $\pm$ SE = 18.6 $\pm$ 1.8 s), and transferred to a foam-lined sampling trough filled with fresh, oxygenated lake water for hook removal and blood sampling. After the hook was removed, the fish was held supine so that blood (~1 mL) could be collected via caudal venipuncture (Houston 1990) using a 3-mL Vacutainer (lithium heparin anticoagulant; 21-gauge, 38.1-mm [1.50-in] needle; Becton, Dickinson, and Co., Franklin Lakes, New Jersey). The filled Vacutainer was immediately placed in an ice slurry until analysis (described below). The fish was then measured for total length (mm) and released within 10 m of the nest location. In the AE treatment, each fish was angled exhaustively (duration = 78.7 $\pm$ 5.6 s) prior to landing. When landed, the fish was exposed to air for 3 min prior to blood sampling, length measurement, and release as described above. For the ST treatment, each fish was angled to exhaustion (duration = 40.9 $\pm$ 4.6 s) and landed. Upon landing, the fish was confined (confinement period = 1.7 $\pm$ 0.1 h) in a 40-L live well filled with lake water that was refreshed frequently. Additionally, to avoid water quality degradation due to overcrowding, no more than two individuals were confined in a live well at the same time. At the end of the confinement period, each fish was removed from the live well, exposed to air for 3 min, immersed in the sampling trough, and sampled as described above. The fish was then released into the littoral zone along the same shoreline as the nest, in an area that was 1 km (as determined using a portable Global Positioning System unit) from the nesting site. The release sites were chosen to mimic typical tournament conditions in which fish are released at a central location (and thus the tournament capture sites vary in distance from the release location). Each nest was visited 24 h after treatment to assess the presence or absence of the male (identifiable by a fin clip). Similar studies of simulated angling treatments have indicated that nest abandonment in response to treatment occurs primarily within the first 24 h (Hanson et al. 2007; M. J. Siepker unpublished data). Additionally, the 24-h interval was chosen to avoid confounding the effects of simulated angling with the effects of brood predation or decreased numbers of hatched embryos, which can result in natural abandonment.

Within 5 min of collecting the blood sample from an individual, the Vacutainer was removed from the ice slurry and whole-blood lactate and glucose levels were measured in the field by adding 10 μL of blood to a handheld glucose meter (Roche Diagnostics Corp., Indianapolis, Indiana; Accu-Chek) and lactate meter (Arkray, Inc., Kyoto, Japan; Lactate Pro LT-1710). Blood glucose and lactate values are commonly used indicators of stress and anaerobic activity in fish (Milligan and Wood 1986; Gustaveson et al. 1991; Ferguson and Tufts 1992). Prior to sampling, all meters were calibrated according to manufacturer instructions. Portable glucose and lactate meters have been shown to produce results that are comparable with those of laboratory studies and are particularly useful for evaluating relative differences between treatments (Morgan and Iwama 1997; Mizock 2002; Venn Beecham et al. 2006).

Statistical analyses.—Analyses were conducted with the statistical package JMP-IN version 4.0 (SAS Institute, Cary, North Carolina), and significance was assessed at an α-value of 0.05 unless otherwise noted. The effects of the different angling practices on glucose and lactate were evaluated by one-way analyses of variance (ANOVAs) and Tukey's honestly significant difference post hoc tests for each lake (Zar 1999). To determine whether there was a latitudinal influence indicative of intraspecific variation in stress response, one-way ANOVAs were used to evaluate the effect of latitude on the response of whole-blood glucose and lactate levels within each treatment group (Zar 1999). Nest abandonment rates within lakes were evaluated by chi-square contingency table analysis followed by pairwise comparisons to identify significant differences among treatment groups and among latitudes (Zar 1999).

TABLE 1.—Mean (±SD) total length (TL, mm) and egg score (1 = low number of eggs in nest; 5 = high number of eggs) of nest-guarding male smallmouth bass from Bull Shoals Lake (southern Missouri–northern Arkansas), Lake Opinicon (southern Ontario), and Rainy Lake (northwestern Ontario–northern Minnesota), 2007. Fish were subjected to one of three angling treatments (catch and release [CR], air exposure [AE], or simulated tournament [ST]; see Methods) or belonged to a control group; they were used in physiological sampling and were monitored for nest abandonment.

Lake	Treatment group	N	TL (mm)	Egg score
Bull Shoals	Control	22	328.1 ± 6.0	3.0 ± 0.1
	CR	11	347.6 ± 13.9	3.0 ± 0.1
	AE	11	342.2 ± 9.8	3.1 ± 0.1
	ST	11	351.4 ± 16.0	2.9 ± 0.2
Opinicon	Control	20	382.8 ± 6.4	3.0 ± 0.2
	CR	10	375.3 ± 10.9	3.3 ± 0.2
	AE	10	379.3 ± 12.1	2.9 ± 0.2
	ST	10	393.9 ± 9.4	3.0 ± 0.2
Rainy	Control	13	396.9 ± 7.6	3.3 ± 0.1
	CR	11	395.3 ± 8.2	3.2 ± 0.2
	AE	11	405.3 ± 8.2	3.1 ± 0.2
	ST	10	428.0 ± 8.6	3.2 ± 0.2

Results

Total lengths of male smallmouth bass did not differ among treatment groups within MO (one-way ANOVA: $F_{3,51} = 1.16$, $P = 0.34$; Table 1) or SON ($F_{3,56} = 0.54$, $P = 0.65$; Table 1). In NON, fish in the ST treatment group were significantly larger than fish in the other treatment groups (one-way ANOVA: $F_{3,41} = 3.25$, $P = 0.03$; Table 1). Additionally, egg score did not vary among treatment groups within lakes (MO: $\chi^2 = 3.27$, df = 6, $P = 0.77$; SON: $\chi^2 = 3.97$, df = 6, $P = 0.68$; NON: $\chi^2 = 3.34$, df = 6, $P = 0.76$; Table 1).

Across all lakes, the various angling practices induced significant physiological disturbances. Whole-blood glucose concentration was significantly higher for ST treatment fish than for CR or AE treatment groups, and this result was consistent across all lakes (Table 2; Figure 1B). Additionally, whole-blood lactate concentration increased with the increasing severity of the angling practices: the lowest value was observed in CR fish and the highest value was observed in ST fish across lakes (Table 2; Figure 1). Intraspecific variation in stress response was noted for all three treatment groups (Table 3; Figure 1). For a given treatment, whole-blood glucose and lactate concentrations were highest within the NON population (northernmost latitude) and lowest within the SON population (intermediate latitude; glucose: Table 3, Figure 1A; lactate: Table 3, Figure 1B). In general, whole-blood glucose and lactate concentrations for the NON treatment groups were roughly twice those for the SON treatment groups (Figure 1).

Corresponding to the gradation in physiological disturbance elicited by various angling practices, nest abandonment also varied among treatment groups. Nest abandonment was highest for ST fish in MO ($\chi^2 = 40.63$, df = 3, $P < 0.05$; Figure 2) and NON ($\chi^2 = 10.66$, df = 3, $P < 0.05$; Figure 2); the rate of nest abandonment by ST-treated fish was 10 times higher than that of any other treatment group in MO and 5 times higher than that of any other treatment group in NON. Abandonment rates across treatments in SON followed the same pattern as described above, but the differences were not significant ($\chi^2 = 9.19$, df = 3, $P > 0.05$; Figure 2). In comparisons among sites (latitudes), the rate of nest abandonment by ST fish in MO (100%) was twice the rate observed in SON (50%) or NON (50%; $\chi^2 = 8.23$, df = 2, $P < 0.05$; Figure 2). No significant differences in abandonment rate among

TABLE 2.—Results of one-way analyses of variance used to detect angling treatment-based differences in mean (±SE) blood glucose and lactate levels (mmol/L) among nest-guarding male smallmouth bass sampled at three latitudes (Bull Shoals Lake, Missouri; Lake Opinicon, southern Ontario; Rainy Lake, northwestern Ontario–northern Minnesota) during 2007. Fish were subjected to one of three angling treatments (catch and release, air exposure, or simulated tournament; see Methods).

Lake	Variable	Mean value (mmol/L)	df	F	P
Bull Shoals	Glucose	5.14 ± 0.70	2, 27	9.85	<0.001
	Lactate	4.20 ± 0.54	2, 30	13.16	<0.001
Opinicon	Glucose	4.30 ± 0.57	2, 26	82.74	<0.001
	Lactate	2.60 ± 0.35	2, 27	13.20	<0.001
Rainy	Glucose	8.89 ± 1.39	2, 29	21.91	<0.001
	Lactate	5.80 ± 0.57	2, 28	14.41	<0.001

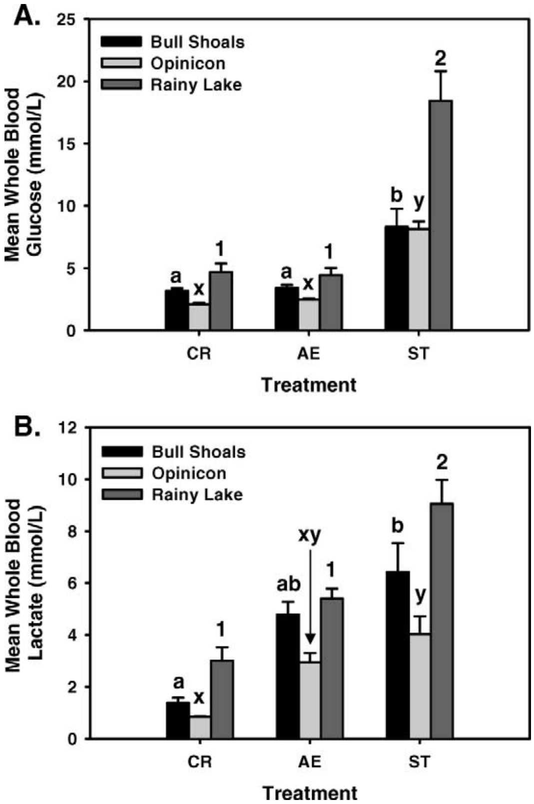

FIGURE 1.—Effects of common angling practices on mean (±SE) whole-blood concentrations of **(A)** glucose and **(B)** lactate in nest-guarding male smallmouth bass angled at three different latitudes (Bull Shoals Lake, southern Missouri–northern Arkansas; Lake Opinicon, southern Ontario; Rainy Lake, northwestern Ontario–northern Minnesota) during 2007 and subjected to one of three treatments prior to blood sampling (catch and release [CR], air exposure [AE], or simulated tournament [ST]; see Methods). Within a site, differing letters or numbers (a and b for Bull Shoals Lake; x and y for Lake Opinicon; 1 and 2 for Rainy Lake) indicate significant differences among treatment groups ($P < 0.05$).

latitudes were noted for control fish ($\chi^2 = 0.07$, df = 2, $P > 0.05$), the CR treatment ($\chi^2 = 1.12$, df = 2, $P > 0.05$), or the AE treatment ($\chi^2 = 0.01$, df = 2, $P > 0.05$; Figure 2).

Discussion

The goal of this study was to determine whether patterns in physiological disturbance and nest abandonment observed in northern systems were consistent across latitudes. In three systems spanning nearly the entire latitudinal range of smallmouth bass in North America, fish exhibited significant physiological disturbance associated with common angling practices. In particular, ST fish had the highest levels of lactate and glucose among treated fish; levels were lowest in CR fish and intermediate in AE fish. Lactate and glucose are indicators of stress and anaerobic activity in fish (Milligan and Wood 1986; Gustaveson et al. 1991; Ferguson and Tufts 1992). Fish from the AE and ST groups were angled to exhaustion, which would have involved burst anaerobic swimming and the associated tissue energy store depletion and metabolite production (e.g., Ferguson and Tufts 1992; Kieffer et al. 1995). Additionally, fish from both groups were also exposed to air for 3 min; AE occurring after exhaustive exercise has been shown to exacerbate physiological disturbance in teleost fishes (Ferguson and Tufts 1992). The water in which fish are held during live-well confinement can be of low quality depending on the rate of recirculation. Decreases in water quality (especially from lowered dissolved oxygen or accumulation of nitrogenous wastes) during live-well retention can be harmful to fish (Hartley and Moring 1993; Kwak and Henry 1995; Suski et al. 2006). In our study, water was exchanged frequently and water temperature and live-well density were low; thus, the stress associated with the tournament procedures was probably not reflective of poor water quality. Additionally, live-well retention can induce stress due to mechanical rocking of the boat in rough water conditions; sloshing of water in the live well forces the fish to constantly swim to maintain position in the center of the live well and to avoid colliding with the container's sides (Suski et al. 2005). When live-well water quality was properly maintained, largemouth bass *M. salmoides* recovered from physiological disturbances imparted by an initial angling event, as shown by clearance of metabolites and recovery of tissue energy stores (Suski et al. 2006).

Intraspecific variation in stress response has been noted in other fish species, such as Atlantic cod *Gadus morhua* (Nelson et al. 1994) and salmonids (Barton 2002). However, to our knowledge, there have been no studies on stress response in fish across such a large latitudinal gradient. Indeed, we noted variation in stress response (whole-blood lactate and glucose concentrations) between populations located at different latitudes. Specifically, whole-blood glucose and lactate levels in all treatment groups were consistently highest at the northernmost site, NON. Additionally, whole-blood glucose and lactate levels in all treatment groups were consistently lowest at the mid-latitude site, SON. This pattern is consistent with our prediction that smallmouth bass populations on the periphery of the species' range (i.e., NON and MO) would have a greater stress response than a more-central population (e.g., SON). To our knowledge, this is the first report of a latitudinal pattern (i.e., peripheral versus central

TABLE 3.—Results of one-way analyses of variance used to detect latitude-based differences in mean (±SE) blood glucose and lactate levels (mmol/L) among nest-guarding male smallmouth bass subjected to three angling treatments (catch and release [CR], air exposure [AE], and simulated tournament [ST]; see Methods) during 2007. Fish were sampled at three latitudes (Bull Shoals Lake, Missouri; Lake Opinicon, southern Ontario; Rainy Lake, northwestern Ontario–northern Minnesota).

Treatment group	Physiological variable	Mean value (mmol/L)	df	F	P
CR	Glucose	3.37 ± 0.32	2, 27	8.37	0.002
	Lactate	1.73 ± 0.24	2, 28	12.53	<0.001
AE	Glucose	3.50 ± 0.27	2, 27	5.98	0.007
	Lactate	4.42 ± 0.30	2, 29	9.15	<0.001
ST	Glucose	11.52 ± 1.26	2, 28	17.66	<0.001
	Lactate	6.5 ± 0.64	2, 28	2.31	0.004

populations) of stress response in fish. However, this pattern is well known among other vertebrates (Wingfield et al. 1998). Variation in stress response may be a product of localized adaptation to different abiotic and biotic conditions (e.g., predator burden or thermal regime) and differential investment in parental care activity. Populations of the congeneric largemouth bass exhibited localized adaptations across geographical distances that were much shorter than the entire range examined here for smallmouth bass (Philipp and Claussen 1995; Cooke et al. 2001). Intraspecific variation in stress response has been shown to lead to differential fitness among individuals in multiple vertebrate species (Blas et al. 2007; Cabezas et al. 2007). However, within the current study, variation in stress response among populations did not correspond to differences in fitness as evidenced by variation in nest success. Within the CR and AE treatment groups, significant differences in stress response were not reflected in differences in nest abandonment among populations (i.e., within a given treatment, the highest levels of physiological disturbance and nest abandonment were observed at different sites rather than at a single site). Also, among ST fish, the greatest stress response was observed at NON but the greatest nest abandonment rate was observed at MO. Clearly, the magnitude of the stress response alone is not an accurate predictor of subsequent nest abandonment by smallmouth bass.

In combination, the effects of these common angling practices can cause considerable pre- and postrelease physiological disturbance that has the potential to result in nest abandonment. After release, individuals enter a recovery period in which the body eliminates metabolites associated with anaerobic activity (Milligan and Wood 1986). During this recovery period, which can last multiple hours, nesting fish exhibit a reduction in the locomotory activity associated with nest defense and aeration (Cooke et al. 2000). If swimming performance declines, an individual is less able to employ burst swimming to protect the offspring from brood predators. Brood devaluation caused by nest predation has been shown to elicit increased abandonment among nest-guarding black bass (Philipp et al. 1997; Suski et al. 2003; Hanson et al. 2007). Brood devaluation is directly related to the amount of time the nest-guarding male is absent from (and thus unable to defend) the nest (Philipp et al. 1997), and previous work has shown that male black bass removed from the nest for long time periods and displaced for long distances will eventually return to the nest (Hanson et al. 2007). As such, nest-guarding male black bass subjected to tournament angling situations are the most likely to be removed from the nest for long time periods, experience high physiological disturbance, suffer major brood predation and devaluation, and subsequently abandon the nest upon return. This was the case in our study; ST fish, which had the highest

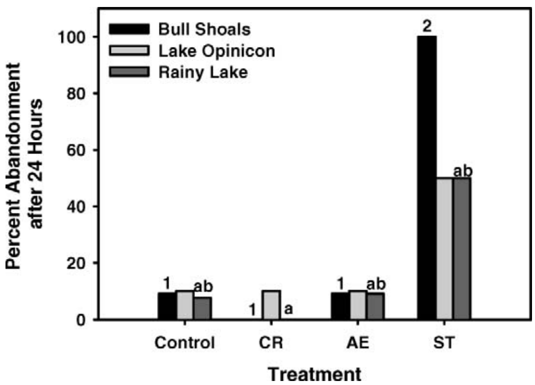

FIGURE 2.—Nest abandonment rates at 24 h posttreatment for nest-guarding male smallmouth bass subjected to one of three angling treatments (catch and release [CR], air exposure [AE], or simulated tournament [ST]; see Methods) at three different latitudes (Bull Shoals Lake, southern Missouri–northern Arkansas; Lake Opinicon, southern Ontario; Rainy Lake, northwestern Ontario–northern Minnesota) during 2007. Control fish were allowed to continue parental duties without experimental intervention. Within a site, differing letters or numbers (1 and 2 for Bull Shoals Lake; a and b for Rainy Lake) indicate significant differences among treatment groups ($P < 0.05$).

levels of physiological disturbance across all three latitudes, abandoned their nests at the highest rates relative to fish from AE and CR treatments. If the goal of a management plan in any one of these latitudes is to preserve individual nest success, common angling practices associated with tournament situations will clearly counteract that goal. Interestingly, there seems to be a threshold between stress level and nest abandonment within each lake, as there was no relationship between the magnitude of stress response (whole-blood indicators of stress) and the abandonment rate within the CR and AE treatments.

Multiple studies have indicated that the duration of absence from the nest is a major factor in individual nest abandonment (Philipp et al. 1997; Hanson et al. 2007). It is generally believed that as the time of absence increases, more brood predation will occur; the potential reproductive output of the current nest then decreases relative to future opportunities, resulting in brood abandonment (Philipp et al. 1997; Hanson et al. 2007). In the current study, all ST fish were removed from the nest for the same amount of time in each lake, but their nest abandonment rate was greater at the southernmost site (MO) than at SON and NON. Brood predator burden alone cannot explain this phenomenon, as this burden would have been highest in SON, intermediate in MO, and lowest in NON (M.A.G., unpublished data) and therefore does not conform to the pattern of nest abandonment across latitudes. Although untested, the pattern in brood abandonment rates could have been related to management strategies in effect at the study sites. Interestingly, brood abandonment rates were highest in MO, where there is currently no legal protection of black bass from angling during the reproductive period. Abandonment rates were similar between SON, which had a closed season, and NON, which had an open but rarely exploited fishery. However, further work examining the effects of management practices on nest success would be required to determine whether there is a causal relationship between management regulations and stress response or nest abandonment.

Although we did not measure recruitment, the pattern in physiological responses of nesting smallmouth bass to common angling practices was consistent across latitudes in that the ST treatment was more stressful than the CR or AE treatment. Additionally, nest abandonment rates of the different treatment groups also followed a pattern that was consistent across latitudes. If a relationship between recruitment and individual nest success exists and is consistent across latitudes, certain CR practices that occur during the reproductive period could be detrimental to sustainable management of wild fish populations, but this will require further research into black bass stock–recruitment dynamics. Some management jurisdictions have opted to protect existing nesting individuals through regulation of recreational angling during the parental care period (Quinn 2002); fishing (even CR) during the reproductive period is generally regarded as having inherent risk (Cooke and Suski 2005). Given the findings of this study and other studies, any management plan that focuses on protecting individual nest success should consider the potential for common recreational angling practices to (1) affect the physiological status of the individual and (2) cause nest abandonment. At a minimum, given the consistently high abandonment rates noted in fish subjected to the ST treatment (especially in southern areas, where tournament angling for nesting smallmouth bass occurs), fisheries managers may consider dissuading or prohibiting tournaments during the reproductive period. Our findings suggest that smallmouth bass across the species' range (and in multiple jurisdictions) exhibit physiological disturbance and nest abandonment in response to CR practices. In light of this information, there is clearly a need to determine whether there are system productivity differences that compensate for such individual-level impacts; this would permit identification of the most appropriate management strategies.

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References

Arlinghaus, R., S. J. Cooke, J. Lyman, D. Policansky, A. Schwab, C. D. Suski, S. G. Sutton, and E. B. Thorstad.

2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Reviews in Fisheries Science 15:75–167.

Barton, B. A. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integrative and Comparative Biology 42:517–525.

Beamesderfer, R. C. P., and J. A. North. 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North American Journal of Fisheries Management 15:688–704.

Blas, J., G. R. Bortolotti, J. L. Tella, R. Baos, and T. A. Marchant. 2007. Stress response during development predicts fitness in a wild, long lived vertebrate. Proceedings of the National Academy of Sciences of the United States of America 104:8880–8884.

Cabezas, S., J. Blas, T. A. Marchant, and S. Moreno. 2007. Physiological stress levels predict survival probabilities in wild rabbits. Hormones and Behavior 51:313–320.

Coble, D. W. 1975. Smallmouth bass. Pages 21–33 *in* R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Cooke, S. J., T. A. Kassler, and D. P. Philipp. 2001. Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management. Journal of Fish Biology 59:248–268.

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

Cooke, S. J., J. F. Schreer, D. H. Wahl, and D. P. Philipp. 2002. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Pages 489–512 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

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

Dunlap, K. D., and J. C. Wingfield. 1995. External and internal influences on indices of physiological stress. I. Seasonal and population variation adrenocortical secretion in free- living lizards. Journal of Experimental Zoology 271:36–46.

Ferguson, R. A., and B. L. Tufts. 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.

Gustaveson, A. W., R. S. Wydoski, and G. A. Wedemeyer. 1991. Physiological response of largemouth bass to angling. Transactions of the American Fisheries Society 120:629–636.

Hanson, K. C., S. J. Cooke, C. D. Suski, and D. P. Philipp. 2007. Effects of different angling practices on post-release behavior of nest-guarding male black bass, *Micropterus* spp. Fisheries Management and Ecology 14:141–148.

Hartley, R. A., and J. R. Moring. 1993. Observations of black bass (Centrarchidae) confined during angling tournaments: a cautionary note concerning dissolved oxygen. Aquaculture and Fisheries Management 24:575–579.

Hinch, S. G., and N. C. Collins. 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.

Houston, A. H. 1990. Blood and circulation. Pages 273–334 *in* C. B. Schreck and P. B. Moyle, editors. Methods in fish biology. American Fisheries Society, Bethesda, Maryland.

Kieffer, J. D., M. R. Kubacki, F. J. S. Phelan, D. P. Philipp, and B. L. Tufts. 1995. Effects of catch-and- release angling on nesting male smallmouth bass. Transactions of the American Fisheries Society 124:70–76.

Kwak, T. J., and M. G. Henry. 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. North American Journal of Fisheries Management 15:621–630.

Mackereth, R. W., D. L. G. Noakes, and M. S. Ridgway. 1999. Size based somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*. Environmental Biology of Fishes 56:263–275.

Milligan, C. L., and C. M. Wood. 1986. Tissue intracelluar acid-base status and the fate of lactate after exhaustive exercise in the rainbow trout. Journal of Experimental Biology 123:123–144.

Mizock, B. A. 2002. Point-of-care testing of blood lactate. Laboratoriums Medizin 26:77–81.

Morgan, J. D., and G. K. Iwama. 1997. Measurements of stressed states in the field. Pages 247–268 *in* G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B. Schreck, editors. Fish stress and health in aquaculture. Cambridge University Press, Society for Experimental Biology Seminar Series 62, Cambridge, UK.

Nelson, J. A., Y. Tang, and R. G. Boutilier. 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations from different environments. Physiological Zoology 67:330–354.

Philipp, D. P., and J. E. Claussen. 1995. Fitness and performance differences between two stocks of largemouth bass from different drainages within Illinois. Pages 236–243 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Use and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Philipp, D. P., and M. S. Ridgway. 2002. B2K: taking black bass biology and management into the 21st century. Pages 1–3 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Philipp, D. P., C. A. Toline, M. F. Kubacki, D. B. F. Philipp, and F. J. S. Phelan. 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. Pages 455–465 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Ridgway, M. S. 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieui*). Canadian Journal of Zoology 66:1722–1728.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa.

Siepker, M. J., K. G. Ostrand, S. J. Cooke, D. P. Philipp, and D. H. Wahl. 2007. A review of the effects of catch-and-release angling on black bass, *Micropterus* spp.: implications for conservation and management of populations. Fisheries Management and Ecology 14:91–101.

Steinhart, G. B., N. J. Leonard, R. A. Stein, and E. A. Marschall. 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., S. J. Cooke, S. S. Killen, D. H. Wahl, D. P. Philipp, and B. L. Tufts. 2005. Behavior of walleye, *Sander vitreus*, and largemouth bass, *Micropterus salmoides*, exposed to different wave intensities and boat operating conditions during livewell confinement. Fisheries Management and Ecology 12:19–26.

Suski, C. D., S. S. Killen, J. D. Kieffer, and B. L. Tufts. 2006. The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live-release angling tournaments. Journal of Fish Biology 68:120–136.

Suski, C. D., and D. P. Philipp. 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., J. H. Svec, J. B. Ludden, F. J. S. Phelan, and D. P. Philipp. 2003. 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.

Venn Beecham, R., B. C. Small, and C. D. Minchew. 2006. Using portable lactate and glucose meters for catfish research: acceptable alternatives to established laboratory methods? North American Journal of Aquaculture 68:291–295.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, and M. Ramenofsky. 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage." American Zoologist 38:191–206.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Englewood Cliffs, New Jersey.