Available online at www.sciencedirect.com

ScienceDirect

Fisheries Research 89 (2008) 9–16

FISHERIES RESEARCH

www.elsevier.com/locate/fishres

Behavioral and physiological responses of the congeneric largemouth (*Micropterus salmoides*) and smallmouth bass (*M. dolomieu*) to various exercise and air exposure durations

Alaina J. White[a], Jason F. Schreer[a,*], Steven J. Cooke[b]

[a] *Department of Biology, State University of New York at Potsdam, 44 Pierrepont Avenue, Potsdam, New York 13676, USA*
[b] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada*

Received 24 December 2006; received in revised form 9 August 2007; accepted 17 August 2007

Abstract

Two of the major stressors associated with the catch-and-release of recreationally angled fish are exercise and air exposure. This study investigated the combined effects of exercise and air exposure duration on the congeneric largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu*, two of the most popular sportfish in North America. We simulated angling by exercising the fish (i.e., chasing by hand) for either 20 or 180 s and then immediately exposed fish to air for random durations ranging from 0 to 10 min. To assess the combined effects of increased exercise and air exposure durations, and the time needed to recover, we monitored several behavioral responses for both species. For largemouth bass, we also measured hematological variables (i.e., lactate, glucose, and hematocrit). Never did exercise and air exposure have a significant effect on the same response measured in the same species, suggesting that there are two separate responses occurring: likely an exercise response and a stress response associated with hypoxia. Our results also indicate that largemouth bass recover from combined exercise and air exposure faster than smallmouth bass. Smallmouth bass took longer to regain equilibrium, to stop leaning, and to return to very shallow (i.e., normal) ventilation depth, as a result of the treatments of exercise and air exposure, than the largemouth bass. This is likely due in part to behavioral and habitat differences between the two species as well as their different aerobic capacities and sensitivities to hypoxia. Interestingly, no mortality was observed despite air exposure durations of up to 10 min. It is still unclear how air exposure interacts with environmental stressors, such as water temperature. We conclude, based on these findings and as suggested from other studies, that air exposure is a significant stressor, and that species-specific guidelines are needed for catch-and-release practices to be most effective, and to best insure the sustainability of fisheries.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Largemouth bass; Smallmouth bass; Air exposure; Exercise; Catch-and-release

1. Introduction

Recreational angling is one of the most popular outdoor activities in North America and indeed around the globe. In the United States alone, recreational fishing generates more than $116 billion in economic output with participation of more than 40 million anglers (American Sportfishing Association, 2006). In 2004, it was estimated that total annual recreational catch worldwide may be in the order of 47 billion fish per year, of which roughly 2/3rd are released (Cooke and Cowx, 2004), and the use of catch-and-release practices continues to increase (Quinn, 1996; Arlinghaus et al., 2007). Many anglers voluntarily practicing catch-and-release view the process as a conservation technique, and assume that the released fish will survive to be caught again in the future (Cooke and Suski, 2005). In response to the over harvest of fisheries, catch-and-release practices are also being mandated by many fisheries management agencies in an attempt to ensure that fisheries are sustainable (Quinn, 1996; Arlinghaus et al., 2007).

Implicit in catch-and-release angling strategies (both voluntary and mandated) is the assumption that the majority of released fish survive. Although high survival rates are fundamental to the goals and success of catch-and-release (Muoneke and Childress, 1994), it is also important to determine the sublethal effects on fish that survive, when considering the success of this practice (Cooke et al., 2002b). Sublethal effects

---

[*] Corresponding author. Tel.: +1 315 267 2290; fax: +1 315 267 3170.
E-mail address: schreejf@potsdam.edu (J.F. Schreer).

0165-7836/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2007.08.008

include physical injury, physiological disturbance, and behavioral alterations, which may lead to increased vulnerability to predation and disease, or reduced foraging or reproductive impairments, which could impair fitness (Cooke et al., 2002b; Cooke and Suski, 2005). To develop angling guidelines that attempt to minimize mortality and the sublethal consequences of catch-and-release, it is necessary to determine and understand the components or stressors associated with catch-and-release (Cooke and Schramm, 2007).

Two of the major stressors associated with catch-and-release angling are exercise and air exposure (Cooke and Suski, 2005). Angling is a combination of aerobic and anaerobic exercise for fish that requires maximum power output from locomotory muscles and the anaerobic metabolism of glycogen (Kieffer, 2000; Schreer et al., 2001). Exercise results in physiological changes, such as depletion of tissue energy stores, accumulation of lactate, acid/base imbalances and osmoregulatory disturbances (Cooke and Suski, 2005). The general consensus among the current body of catch-and-release studies is that the duration of exercise experienced by the fish correlates positively with the magnitude of physiological disturbance and the time required for recovery (Schreer et al., 2001; Suski et al., 2004; Cooke and Suski, 2005). Air exposure occurs upon capture (and after exercise) when anglers are handling the fish in an attempt to remove hooks, weigh and measure fish, and/or admire and photograph fish (Ferguson and Tufts, 1992; Cooke and Suski, 2005). Air exposure is known to cause profound metabolic and anatomical changes associated with collapse of the gill lamellae and adhesion of the gill filaments (Ferguson and Tufts, 1992). Physiological disturbances, that can occur even from short durations of air exposure, include extracellular acidosis (Ferguson and Tufts, 1992; Hopkins and Cech, 1992), accumulation of metabolites (Suski et al., 2004; Hopkins and Cech, 1992), cardiovascular alterations (Cooke et al., 2001), venous hypercapnia (Hopkins and Cech, 1992), and reductions in gas exchange (Ferguson and Tufts, 1992). The consensus is that the effects of air exposure are additive with other stressors and lengthier air exposure tends to result in longer recovery periods (Cooke et al., 2001; Suski et al., 2004; Schreer et al., 2005). While the physiological response of fish to the independent stressors of exhaustive exercise and air exposure are relatively well understood (Tufts et al., 1991; Ferguson and Tufts, 1992), little is known about the interaction of these sublethal stressors (Gingerich et al., 2007).

In this study we assessed the combined effects of various air exposure and exercise durations on both behavioral and physiological variables of two congeneric black bass species, largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu*. Largemouth bass and smallmouth bass are the most highly angled and released species in North America (tens of millions per year) (U.S. Fish and Wildlife Service, 1999), and are fairly well studied (Cooke et al., 2002a; Cooke and Suski, 2005; Siepker et al., 2007). Although several studies have looked at the effects of exercise and air exposure, none have investigated the interaction of these stressors. We predicted that the combined effect on the fish would be greater than just either stressor alone. Further, we predicted that smallmouth bass would be more negatively impacted than largemouth bass because they have reduced hypoxia tolerance (Furimsky et al., 2003) and tend to have higher mortality rates in competitive angling events (Bennett et al., 1989; Hartley and Moring, 1995).

2. Methods

2.1. Study site and animals

This study was conducted in June of 2006 at the Queen's University Biological Station on Lake Opinicon, in Elgin, Ontario (44°31′N, 76°20′W). All fish were collected from Lake Opinicon by anglers using rod and reels and landed within 20 s to minimize physiological disturbance (Kieffer, 2000). Following capture, fish were held in coolers filled with lake water which was changed frequently (at least every 10 min) and all fish were delivered to an indoor wet lab facility within 1 h. Fish were held for at least 24 h prior to experimentation in flow-through tanks (approximately 200 L) provided with lake water. For experiments done using behavioral sampling, largemouth bass ($n = 56$) ranged in size (total length) from 231 to 445 mm (mean total length ± standard error, 331 ± 7.5 mm) and smallmouth bass ($n = 21$) ranged from 238 to 432 mm (307 ± 12.9 mm). During behavioral assessments for largemouth bass, water temperatures ranged from 18 to 23 °C and water temperatures ranged from 19 to 22 °C for smallmouth bass. These temperatures are considered moderate for both species (Armour, 1993). Hematological experiments were restricted to largemouth bass ($n = 46$), which ranged in size (total length) from 266 to 443 mm (345 ± 7.1 mm) at water temperatures of 20–21 °C.

2.2. Behavioral sampling

Daily, eight largemouth and/or smallmouth bass were moved from common holding tanks to individual tanks (200 L flow-though tanks divided into four sections with porous foam dividers) and held overnight (at least 12 h). Laboratory access was restricted to prevent external disturbance during all experimentation. During the move, each fish was placed in a padded V-shaped holder filled with lake water, where total length was measured and a dorsal spine was clipped for identification. The next morning, resting ventilation rates (per minute) for each fish were measured, by counting operculum movements over 30 s and multiplying by 2, as was depth of ventilation or operculum movements (very shallow, shallow, medium, or deep). Also recorded was whether or not each fish had equilibrium, was leaning/unsteady, and was parallel to the bottom, meaning that the fish was level in the water column, rather than tail lower or higher than head. All eight fish were then simultaneously exposed to different treatments of exercise followed by various air exposures. To simulate brief or exhaustive exercise, fish, while in their individual flow-through tanks, were chased by hand for either 20 or 180 s, an approach frequently used for catch-and-release research, especially to assess the effects of exercise (Kieffer, 2000; Cooke et al., 2001, 2003; Suski et al., 2004; Schreer et al., 2005). Following exercise, each fish was immediately held out of the water, by inserting a thumb into their mouth and gripping the lower jaw, for a randomly generated time (generated in SPSS 12.0 (September 2003)) from 0 to 10 min (to the nearest second). Although the 10 min period might seem excessive, it was intended to account for lengthy hook removal followed by measuring, weighing, pictures, etc. After treatment, the fish were replaced into their individual flow-through tanks and monitored for 9 h. All responses were measured immediately and again every 10 min for 3 h, and again at 5 and 9 h. During the first 10 min, the fish were observed continuously and the time of any changes in the responses, besides ventilation rate, were recorded. After 9 h the fish were moved to an outdoor flow-through holding tank (approximately 500 L) until the next morning (24 h post-treatment), to assess delayed mortality, and were then released back into Lake Opinicon.

2.3. Blood sampling

The procedure for the experiments in which blood sampling was done was the same as that for the experiments in which behavioral responses were measured until post-treatment, but was only conducted on largemouth bass. As with the behavioral experiments, each fish was exposed to a treatment of either 20 or 180 s exercise followed by a randomly generated air exposure from 0 to 10 min. After treatment, each fish was returned to its individual flow-through tank and allowed to recover for 2 h. The 2 h recovery period was chosen because in a previous study, largemouth bass exercised for 1 min, by hand chasing, had begun, but were not fully recovered by 2 h (physiological variables, such as glycogen and lactate concentrations, were near but not at resting values) (Suski et al., 2006). At 2 h post-treatment, fish, one at a time, were taken from their tank and placed supine in a padded V-shaped holder filled with water. Therefore their gills were under water for the blood sampling. One person held the fish while another took the blood sample. The whole procedure took less than one minute. Blood samples were taken by inserting a 21 gauge 1.5 in. needle (21G½ Precision Glide Vacutainer Brand Blood Sampling Needles, Becton Dickinson and Company, Franklin Lakes NJ 07417-1885) into the caudal vessel(s) midline in between the anal and caudal fin. A 3 mL vacutainer (Kendall Monoject Blood Collection Tubes with Lithium Heparin 143U.S.P. Units, Tyco Healthcare Group LP, Mansfield, MA 02048) was used to take less than 1 mL of blood. Following this, the vacutainer and then the needle was removed and pressure was applied to the insertion point to stop any bleeding. The fish was then replaced in its tank and released back to the lake within an hour. Blood samples were immediately labeled and placed into a water-ice slurry. Lactate (Lactate Pro Blood Lactate Test Meter, Arkray, Inc., 57 Nishi Aketa-Cho, Higashi-Kujo, Minami-Ku, Kyoto, Japan) and glucose (ACCU-CHEKCompact Plus, Roche Diagnostics, 201, Boul. Armand-Frapper, Laval, Quebec, Canada H7V 4A2) values were determined within 5 min of sample collection on whole blood. These field devices produce results that are comparable to those generated using standard laboratory assays (Beecham et al., 2006). Hematocrit values were then determined by centrifuging the blood for 6 min at 10,000 rpm.

2.4. Data analysis

Prior to analysis, we performed normality tests ($\alpha = 0.01$; Systat version 11, SYSTAT Software Inc., Richmond, California, USA) and transformations were done when necessary. All zeros for response times were converted to 0.01 min. Times were then Ln transformed (time to return to equilibrium, no lean/wobble, parallel to bottom, very shallow ventilation) and proportions (ventilation rate changes: percent change from resting, which was measured pre-treatment) were arcsine square root transformed. Normality was assessed using a Shapiro–Wilk test ($\alpha = 0.01$) (Shapiro and Wilk, 1965; Systat version 11) and homogeneity of variance was tested for the categorical variable (exercise) with a Bartlett's test (Snedecor and Cochran, 1967). For largemouth bass behavioral sampling, total length was Ln transformed. We assessed the effects of air exposure and exercise, while controlling for water temperature and total length, using an analysis of co-variance, ANCOVA (with stepwise linear regression with backward loading) (JMPIN 4.0) (SAS Institute Inc.). We used a level of significance (α) of 0.05 for the hematological responses, and a more conservative level of significance ($\alpha = 0.01$) for the behavioral responses because there were many (12) variables. To compare the largemouth and smallmouth bass, we performed *t*-tests to compare the means of response variables to exercise and air exposure ($\alpha = 0.05$) (Systat version 11). To visualize the data, we performed simple linear regressions where warranted statistically from stepwise linear regressions.

3. Results

No mortality, immediate or delayed (within 24 h post-treatment) occurred during this study. On average, largemouth bass recovered faster or returned to resting levels more quickly than smallmouth bass (Table 1). Note that, as assessed with a *t*-test ($\alpha = 0.05$), largemouth bass regained equilibrium and stopped leaning significantly sooner than smallmouth bass post-treatment of exercise and air exposure. Although not significant, the mean time for ventilation depth to return to very shallow (i.e.,

Table 1
Mean (±S.E.) recovery times of behavioral variables and percent change in ventilation rate due to exposure to 20 or 180 s of exercise and 0–10 min of air exposure in largemouth bass ($n = 56$) vs. smallmouth bass ($n = 21$)

Species	Time to regain equilibrium (min)[a]	Time to stop leaning (min)[a]	Time to become parallel to bottom (min)	Time to return to very shallow ventilation (min)	% change in ventilation rate just after treatment[a]
Largemouth bass	0.54 ± 0.16	36.79 ± 11.39	3.69 ± 1.51	90.36 ± 7.13	30.89 ± 2.09
Smallmouth bass	34.70 ± 26.89	154.34 ± 47.03	3.48 ± 1.69	136.19 ± 25.88	22.07 ± 2.55

[a] Significant difference between species.

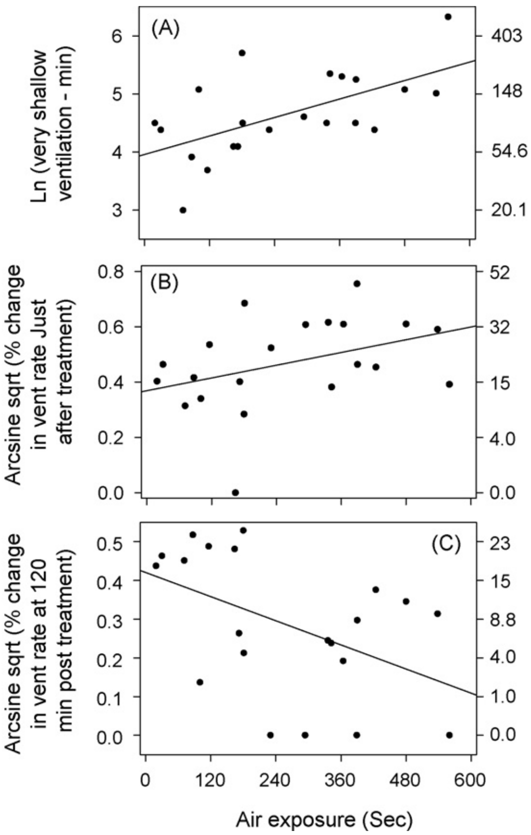

Fig. 1. The significant effects of air exposure on transformed behavioral variables in smallmouth bass ($n = 21$). (A) Time to return to very shallow ventilation depth, (B) % change in ventilation rate just after treatment, (C) % change in ventilation rate at 120 min post-treatment. The y-axis on the right is non-transformed data to show real values. Statistical parameters are shown in Table 2.

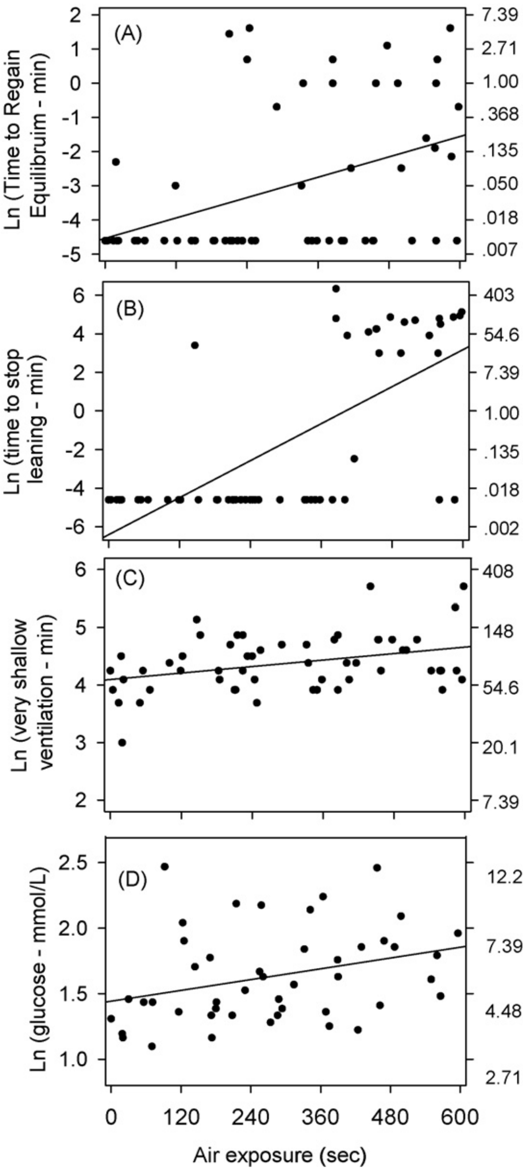

Fig. 2. The significant effects of air exposure on transformed behavioral and physiological variables in largemouth bass ($n = 56$). (A) Time to regain equilibrium, (B) time to stop leaning, (C) time to return to very shallow ventilation depth, (D) glucose concentration in mmol/L. The y-axis on the right is non-transformed data to show real values. Statistical parameters are shown in Table 3.

normal) was quicker in the largemouth bass, and the mean time to become parallel to the bottom was similar for both species. The largemouth bass showed a greater percent change in ventilation rate immediately post-treatment than the smallmouth bass. The only significant percent change in ventilation rate due to increased duration of air exposure, besides initially post-treatment, was at 120 min post-treatment in the smallmouth bass ($F = 11.285$, $P = 0.0047$) (Fig. 1C, Table 2). Increased exercise duration did not result in increased percent change in ventilation rate in either species.

For largemouth bass, as air exposure increased, the time it took fish to regain equilibrium increased ($F = 10.727$, $P = 0.0019$), as did the time to stop leaning ($F = 50.372$, $P < 0.001$), and the time for ventilation depth to return to very shallow ($F = 10.711$, $P = 0.0019$) (Fig. 2A–C, Table 3). For smallmouth bass, as air exposure increased, the time for ventilation depth to return to very shallow ($F = 8.917$, $P = 0.0083$) increased, as did percent change in ventilation rate just after treatment ($F = 9.344$,

Table 2
Statistical parameters from stepwise regression corresponding to each graph in Fig. 1 (smallmouth bass)

Factor	n	Regression equation	r^2	P
Very shallow ventilation[a]	21	$y = 0.003x + 3.958$	0.361	0.004
% change in ventilation rate just after treatment[b]	21	$y = 0.000x + 0.369$	0.148	0.085
% change in ventilation rate at 120 min post-treatment[b]	21	$y = -0.001x + 0.421$	0.229	0.0047

Results are shown for each factor that was significantly affected by air exposure duration. Note that superscripts correspond to the transformation performed.

[a] Ln.

[b] Arcsine sqrt.

Table 3
Statistical parameters from stepwise regression corresponding to each graph in Fig. 2 (largemouth bass)

Factor	n	Regression equation	r^2	P
Time to regain equilibrium[a]	56	$y = 0.005x - 4.531$	0.173	0.001
Time to stop leaning[a]	56	$y = 0.016x - 6.412$	0.480	<0.0001
Very shallow ventilation[a]	56	$y = 0.001x + 4.095$	0.128	0.007
Glucose Concentration[a]	56	$y = 0.001x + 1.443$	0.101	0.031

Results are shown for each factor that was significantly affected by air exposure duration. Note that superscripts correspond to the transformation performed.

[a] Ln.

$P = 0.0071$) (Fig. 1A and B, Table 2). Smallmouth bass exercised for 180 s took significantly longer to regain equilibrium ($F = 20.208$, $P = 0.0003$) than did those exercised for 20 s. For largemouth bass blood sampled, as air exposure increased, glucose concentrations increased ($F = 6.232$, $P = 0.0166$) (Fig. 2D, Table 3). Blood lactate concentrations in largemouth bass exercised for 180 s (mean ± S.E.: 3.69 ± 0.48 mmol/L) were significantly higher than lactate concentrations in those exercised for 20 s (1.35 ± 0.14 mmol/L) ($F = 21.519$, $P < 0.001$). Hematocrit levels were also significantly higher in largemouth bass exercised for 180 s (0.27 ± 0.01) than those exercised for 20 s (0.24 ± 0.01) ($F = 5.617$, $P = 0.0225$). However, there were no significant differences in glucose concentrations between largemouth bass exercised for 180 s (6.11 ± 0.55 mmol/L) and 20 s (4.82 ± 0.28 mmol/L).

4. Discussion

As expected, longer durations of exercise and air exposure had a greater effect on both the largemouth and smallmouth bass. Specifically, more time was required for recovery, or return to pre-treatment conditions, as measured with behavioral and hematological response variables in the largemouth bass and behavioral response variables in the smallmouth. Also consistent with our hypothesis, smallmouth bass were more impacted by the combination of exercise and air exposure, than largemouth bass, as they took longer to recover in three of the four behavioral responses measured. However, we found that prolonged air exposure affected the largemouth bass in more ways, or responses measured, than exercise, whereas the duration of exercise and air exposure affected the smallmouth bass similarly. This suggests that responses are species specific. Exercise and air exposure never had a significant effect on the same response measured in the same species, which suggests that there are also two separate responses occurring; these are likely an exercise response and a stress (hypoxia) response.

For the largemouth bass, as air exposure duration increased, the time for most behavioral response variables to return to pretreatment levels, and blood glucose concentrations, increased. This was expected as studies have shown that increased durations of air exposure usually lead to longer recovery times and other negative effects (Cooke et al., 2001; Suski et al., 2004; Schreer et al., 2005). Rock bass *Ambloplites rupestris* exposed to simulated angling for 30 s and air for 180 s required 4 h to recover while those exposed to simulated angling for 30 s and air for 30 s required 2 h to recover (Cooke et al., 2001). Air exposure of 120 s, rather than 30 or 60 s, resulted in poorer swimming performance of brook trout *Salvelinus fontinalis* (Schreer et al., 2005). Negative effects due to air exposure occur because it results in an almost complete loss of gas transfer and increased oxygen debt, and causes significant accumulation of metabolites and significant reduction in tissue energy stores in the white muscle (Suski et al., 2004).

Although exercise had no significant effect on the behavioral responses observed in largemouth bass, it did cause physiological disturbances. As a result of increased exercise, from brief (20 s) to exhaustive (180 s), both blood lactate concentrations and hematocrit levels increased. Another study on largemouth bass, which measured hematological responses to length of time they were angled/exercised, from 1 to 5 min, also found that as exercise duration increased, blood lactate concentrations rose (Gustaveson et al., 1991). High intensity anaerobic exercise, for which white muscle is used extensively, is experienced during exhaustive angling, and induces a variety of physiological disturbances that are intimately related to metabolism. These include accumulation of lactate, which is an anaerobic metabolic end product (Suski et al., 2004, 2006). Hematocrit, or the percent of erythrocytes in the blood, increased with exercise duration likely in response to the active muscles' increased need for oxygen. An increase in erythrocyte volume of the blood would increase the circulating oxygen transport capacity (Fudenberg et al., 1961). Such a rapid increase in hematocrit is likely due in part to splenic contractions, as the spleen sequesters densely packed erythrocytes, and can expel them into the systemic circulation during strenuous exercise (Bakovic et al., 2005). Exhaustive exercise in rainbow trout led to splenic contraction and an increase in hematocrit values (Mendiola et al., 1997). Other possible explanations for the increase in hematocrit during exercise could be water transport across the capillary wall due to increased interstitial osmotic pressure in the exercising muscles, an extravasation of plasma water caused by a rise in hydrostatic pressure, or an increased vascular permeability (Kanstrup and Exblom, 1984; Senay et al., 1980).

During anaerobic exercise, the fish's white muscles produced lactic acid (and more of it for exhaustive than for brief exercise). However, when fish were held out of the water, they did not produce more lactic acid in response to longer durations of air exposure. This could be due to the fact that they were held in such a way that they moved little, not stimulating white muscle to produce lactic acid as much as if they had been swimming or flailing (amount of movement was similar for all durations of air exposure, mainly only during the first few seconds). The fish could have also withheld from producing significantly higher concentrations of lactate while going without oxygen for increased durations by lowering their metabolic rate, or likely, a combination of both. An alternative explanation is that lactate levels were already maximal for these individual fish. However, glucose concentrations did increase with prolonged air exposure, which suggests that air exposure elicits a stress response that is separate from the exercise response. Glucose is accepted as a physiological indicator of acute stress in fish (Barton and Iwama, 1991). Glucose would be expected to be produced in response to stress, because fish respond to stress with a series of defense mechanisms that are energetically demanding, and therefore costly in terms of metabolic resources (Barton and Iwama, 1991). It would then also be expected that as the stress continues, more glucose is produced, as was the case in this study.

As in the largemouth bass, some of the behavioral responses measured in the smallmouth bass were significantly affected by duration of air exposure, but unlike the largemouth, some were also affected by exercise (note that we had a smaller sample size for smallmouth bass and no blood sampling). That percent change in ventilation frequency, besides immediately post-treatment, was only significantly affected by air exposure at 120 min post-treatment in the smallmouth bass (and never in the largemouth bass) is consistent with past research. Ventilatory frequency has been found to be a factor that does not reflect the severity of a stressor, so its usefulness is limited (Barreto and Volpato, 2004). Both a sudden stimulus (the introduction of a partition for less than 4 s) and an extended stressor (15 and 30 min confinements) evoked similar ventilatory frequency increases in Nile tilapia *Oreochromis niloticus* (Barreto and Volpato, 2004). The smallmouth bass were more impacted by the treatments of exercise and air exposure, than the largemouth bass, as they took longer to recover, or to regain equilibrium, to stop leaning, and to return to very shallow ventilation depth.

It is not surprising that the smallmouth bass' response to exercise and air exposure would differ from the largemouth bass'. Although they are two closely related species, they are different in many ways. They have different behaviors (Miller, 1975), metabolic rates (Cooke and Schreer, unpublished data), thermal preferences and tolerances (Armour, 1993; Wismer and Christie, 1987), different hooking mortality rates from the same water body (Hartley and Moring, 1995), and different physiological adaptations that may result in different responses to such disturbances. Largemouth bass are generally "sit and wait" predators that inhabit shallower, warmer, weedy areas (Heidinger, 1975), whereas smallmouth bass are more "active" predators, and prefer deeper and colder open waters (Coble, 1975). This difference in habitat and selective pressures, such as on their oxygen transport systems, may be a major reason why largemouth bass can cope with exhaustive exercise and air exposure better than smallmouth bass. Largemouth bass, living in warmer water, which is generally more hypoxic, are more tolerant to hypoxia, and have a greater blood oxygen affinity (Furimsky et al., 2003). They would also be expected to have better ways of dealing with lactic acid than smallmouth bass. Smallmouth bass likely have more trouble recovering from exhaustive exercise, or clearing metabolic wastes (lactate), replenishing energy stores, and correcting osmotic and acid/base imbalances, and other physiological disturbances brought on by exhaustive exercise. In a study in which both largemouth and smallmouth bass were exposed to hypoxic conditions simulating catch-and-release tournaments, only the smallmouth bass's arterial blood pH decreased significantly (Furimsky et al., 2003). Further, the blood oxygen content did not change from normoxic values in the largemouth bass, but did in the smallmouth; largemouth bass had an oxygen tension at which Hb was 50% saturated with oxygen that was 8.6 torr lower than that of smallmouth bass (Furimsky et al., 2003). Also, plasma adrenaline concentrations, which did not increase in the largemouth bass, increased in the smallmouth bass by about two orders of magnitude, and cardiac output dropped by about 20% in smallmouth bass, while largemouth bass did not exhibit any significant changes in cardiac output relative to their normoxic control values (Furimsky et al., 2003). The differences in the responses of the largemouth and smallmouth bass to the exercise and air exposure durations, such as the largemouth bass being less affected by the exhaustive exercise, and generally needing less time to recover from both the exercise and air exposure, is likely a combination of all these factors. This also may be why the smallmouth bass, unlike the largemouth, were affected by even small stressors. Although no fish died during this study, it generally took smallmouth bass much longer to recover from even short durations of exercise and air exposure than the largemouth bass.

That no fish died suggests that the durations of exercise and air exposure used are not severe enough to cause death. However, in our study, fish were held in a laboratory setting rather than displaced into regions with potentially suboptimal environmental conditions. An immediate return to the wild could easily have resulted in delayed mortality. Because fish respond to stress with a series of defense mechanisms that are energetically demanding and impair various physiological processes, they are consequently more susceptible to predation, diseases, and induced hyperactivity causing an unnecessary expenditure of energy (Barton and Iwama, 1991; Cooke et al., 2002a). Had these fish been released, they may have been unable to perform various functions, such as maintaining position in a current, and avoiding predators. Hence, there is still a need for additional research focused on evaluating the consequences of combined exercise and air exposure on bass following release in the wild.

From a management perspective, our findings support the general consensus of previous studies, that durations of exercise and air exposure should be minimized, as they lead to sublethal effects, if not mortality. These sublethal effects and physiological disturbances may result in decreases in individual survival (e.g., predator avoidance, foraging success) and in reproductive success (e.g., mate acquisition, parental care/nest guarding) and should be minimized and considered when evaluating management strategies. Although most fisheries managers are concerned with population, community, and ecosystem level implications of catch-and-release angling, it is the effects of this practice on the individual organism that will culminate in changes at these higher levels of organization (Cooke et al., 2002b; Cooke and Schramm, 2007). Although general guidelines are useful, our findings, that largemouth bass and smallmouth bass respond differently to exercise and air exposure, strongly support previous recommendations that species-specific guidelines are needed (Cooke and Suski, 2005), to best insure the sustainability of fisheries and this ever growing activity on which many local economies and communities depend.

Acknowledgments

Support for this study was provided by a SUNY Potsdam Faculty-Undergraduate Summer Research Grant to AJW and JFS, an individual Development Grant, State of New York/United University Professions Joint Labor – Management Committees to JFS and The Rainy Lake Fisheries Charity Trust, the Canadian Foundation for Innovation, the Ontario Research Fund, and Carleton University to SJC. The authors express their appreciation for the field assistance provided by Andrew Gingerich, Kyle Hanson, Mike Donaldson, and Caleb Hasler. Thanks also to the staff at the Queens University Biological Station, and in particular, Frank Phelan, Station Manager. This work was approved by the SUNY Potsdam I.A.C.U.C. and the Carleton Animal Care Committee. We thank two anonymous reviewers for providing comments on the manuscript.

References

American Sportfishing Association, 28 June 2006. Fishing statistics – sales and economic trends. <http://www.asafishing.org/asa/statistics/saleco_trends/>.

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, philosophical, social, and biological perspectives. Rev. Fish. Sci. 15, pp. 175–167.

Armour, C.L., 1993. Evaluating Temperature Regimes for Protection of Smallmouth Bass. United States Department of the Interior Fish and Wildlife Service, Resource Publication 191, Washington, D.C.

Bakovic, D., Eterovic, D., Saratlija-Novakovic, Z., Palada, I., Valic, Z., Bilopavlovic, N., Dujic, Z., 2005. Effect of human splenic contraction on variation in circulating blood cell counts. Clin. Exp. Pharmacol. Physiol. 32, 944–951.

Barreto, R.E., Volpato, G.L., 2004. Caution for using ventilatory frequency as an indicator of stress in fish. Behav. Process. 66, 43–51.

Barton, B.A., Iwama, G.K., 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Ann. Rev. Fish Dis. 1, 3–26.

Beecham, R.V., Small, B.C., Minchew, C.D., 2006. Using portable lactate and glucose meters for catfish research: acceptable alternatives to established laboratory methods? North Am. J. Aquacult. 68, 291–295.

Bennett, D.H., Dunsmoor, L.K., Rohrer, R.L., Rieman, B.E., 1989. Mortality of tournament-caught largemouth and smallmouth in Idaho lakes and reservoirs. Calif. Fish Game 75, 20–26.

Coble, D.W., 1975. Smallmouth bass. In: Stroud, R.H., Clepper, H. (Eds.), Black Bass Biology and Management. Sport Fishing Institute, Washington, D.C., pp. 21–33.

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

Cooke, S.J., Ostrand, K.G., Bunt, C.M., Schreer, J.F., Wahl, D.H., Philipp, D.P., 2003. Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of water temperatures. Trans. Am. Fish. Soc. 132, 1154–1165.

Cooke, S.J., Philipp, D.P., Dunmall, K.M., Schreer, J.F., 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. Fish. Manage. Ecol. 7, 73–79.

Cooke, S.J., Schreer, J.F., Wahl, D.H., Philipp, D.P., 2002a. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Am. Fish. Soc. Symp. 31, 489–512.

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. Am. Fish. Soc. Symp. 30, 121–134.

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.

Ferguson, R.A., Tufts, B.L., 1992. Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for “catch and release” fisheries. Can. J. Fish. Aquat. Sci. 49, 1157–1162.

Fudenberg, H., Baldini, M., Mahoney, J.P., Dameshek, W., 1961. The body hematocrit/venous hematocrit ratio and the “splenic reservoir”. Blood 17, 71–82.

Furimsky, M., Cooke, S.J., Suski, C.D., Wang, Y., Tufts, B.L., 2003. Respiratory and circulatory effects of hypoxia in largemouth bass and smallmouth bass: an application to “live-release” angling tournaments. Trans. Am. Fish. Soc. 132, 1065–1075.

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.

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.

Hartley, R.A., Moring, J.R., 1995. Differences in mortality between largemouth and smallmouth bass caught in tournaments. North Am. J. Fish. Manage. 15, 666–670.

Heidinger, R.C., 1975. Life history and biology of the largemouth bass. In: Stroud, R.H., Clepper, H. (Eds.), Black Bass Biology and Management. Sport Fishing Institute, Washington, D.C., pp. 11–20.

Hopkins, T.E., Cech Jr., J.J., 1992. Physiological effects of capturing striped bass in gill nets and fyke traps. Trans. Am. fish. Soc. 121, 819–822.

Kanstrup, I.L., Exblom, B., 1984. Blood volume and hemoglobin concentration as determinants of maximal aerobic power. Med. Sci. Sports Exerc. 16, 256–262.

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

Mendiola, P., Hernandez, M.D., De Costa, J., Zamora, S., 1997. Trout plasma metabolites, blood factors and spleen contraction: responses to exercise. Revista Española De Fisiologia 53, 217–223.

Miller, R.J., 1975. Comparative behavior of centrarchid basses. In: Clepper, H. (Ed.), Black bass biology and management. Sport Fishing Institute, Washington, D.C., pp. 85–94.

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

Quinn, S., 1996. Trends in regulatory and voluntary catch-and-release fishing. Am. Fish. Soc. Symp. 16, 152–162.

Schreer, J.F., Cooke, S.J., McKinley, R.S., 2001. Cardiac response to variable forced exercise at different temperatures: an angling simulation for smallmouth bass. Trans. Am. Fish. Soc. 130, 783–795.

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

Senay, L.C., Rogers, G., Jooste, P., 1980. Changes in blood plasma during progressive treadmill and cycle exercise. J. Appl. Physiol. 49, 59–65.

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.

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

Snedecor, G.W., Cochran, W.G., 1967. Statistical Methods. Iowa State University Press, Ames, Iowa.

Suski, C.D., Killen, S.S., Cooke, S.J., Kieffer, J.D., Phillip, 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.

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

SYSTAT 11, 2004. Version No. 11.00.01. SYSTAT Software, Inc. Richmond, California, USA.

Tufts, B.L., Tang, Y., Tufts, K., Boutilier, R.G., 1991. Exhaustive exercise in “wild” Atlantic salmon (*Salmo salar*): acid-base regulation and blood gas transport. Can. J. Fish. Aquat. Sci. 48, 868–874.

U.S. Fish & Wildlife Service, 1999. Black Bass Fishing in the U.S., Washington, D.C.

Wismer, D.A., Christie, A.E., 1987. Temperature Relationships of Great Lakes Fishes: A Data Compilation. Great Lakes Fisheries Commission Special Publication 87-3, p. 165.