*Journal of Fish Biology* (2006) **68,** 120–136
doi:10.1111/j.1095-8649.2005.00882.x, available online at http://www.blackwell-synergy.com

# The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live–release angling tournaments

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*(Received 21 September 2004, Accepted 20 June 2005)*

The impact of variation in water temperature and dissolved oxygen on recovery of largemouth bass *Micropterus salmoides* from exercise was examined. For this, largemouth bass were first exercised and recovered for either 1, 2 or 4 h at ambient water temperatures (25° C) in fully oxygenated water. Results showed that exercise forced fish to utilize anaerobic metabolism to meet energy demands, and resulted in reductions in anaerobic energy stores adenosine triphosphate (ATP), Phosphocreatine (PCr) and glycogen. Exercise also resulted in a seven-fold increase in lactate within white muscle. After 2 h of recovery in oxygenated water at acclimation temperature, physiological recovery from exercise was under way, and by 4 h most variables examined had returned to control levels. Next, largemouth bass were exercised at ambient temperatures and recovered for 2 h in environments with either elevated temperature (32° C), reduced temperature (14 and 20° C), hypoxia or hyperoxia. Both elevated and reduced temperature impaired recovery of tissue lactate and tissue ATP relative to fish recovered in water at acclimation temperature, while hyperoxic water impaired recovery of tissue ATP. Moderately hypoxic waters impaired the recovery of plasma glucose, plasma lactate and tissue PCr relative to fish recovered in fully oxygenated water. Results from this study are discussed in the context of critical oxygen and temperature guidelines for largemouth bass. In addition, several recommendations are made concerning remedial treatments used in livewells (tanks) during angling tournaments when fish are recovering from exercise associated with angling.
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Key words: angling tournament; exercise; largemouth bass; oxygen; recovery; temperature.

## INTRODUCTION

To combat declines in freshwater fish abundance (Post *et al.*, 2002) and still allow angling groups to utilize fisheries resources, managers have encouraged anglers to return caught fishes to the water rather than harvest them. This

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practice, commonly known as catch-and-release angling, has been shown to reduce the impact of angling on some fish populations and allow fishes to be caught again (Burkett *et al.*, 1986; Quinn, 1989; Muoneke & Childress, 1994). Over time, this management technique has also grown into a conservation ethic among numerous angling groups (Quinn, 1996), and has helped lead to the growth of the live-release angling tournament industry.

Currently it is believed that there are over 25 000 of these events annually across North America, and largemouth bass *Micropterus salmoides*, (Lacepède) are the most popular species targeted by these events (Shupp, 1979; Duttweiler, 1985; Schramm *et al.*, 1991; Kerr & Kamke, 2003). While angling tournaments have direct economic benefits for host communities, concerns have been expressed that high mortality rates observed following some events can negatively impact fish populations (Schramm *et al.*, 1991). Furthermore, anglers involved in these tournaments target the largest fishes within a system. These large fishes may be the most reproductively valuable members of the population (Suski & Philipp, 2004), and may also be more susceptible to tournament-induced mortality than smaller individuals (Meals & Miranda, 1994). While the reasons for mortality following these events have not been clearly defined, some researchers believe mortality may be caused by the cumulative effects of numerous stressors incurred by fishes throughout the tournament day (Schramm *et al.*, 1987; Kwak & Henry, 1995). Efforts to minimize the multiple stressors experienced by tournament-caught fishes may therefore have the potential to reduce mortality and minimize the impact of tournaments on fish populations.

During a typical angling tournament, fishes that have been caught are held in a livewell until the end of the tournament day, and the period of livewell confinement can range from $<1$ h up to 8 h (Hartley & Moring, 1993). Livewells are essentially tanks in a boat that are filled with water by a pump and allow anglers to keep fishes alive. Livewells are standard equipment on most specialized fishing boats, and are mandatory in most upper-level angling tournaments. Previous research, however, has suggested that livewell confinement may subject tournament-caught fishes to stressors such as low dissolved oxygen (Hartley & Moring, 1993), elevated metabolic wastes (Kwak & Henry, 1995), crowding (Cooke *et al.*, 2002), elevated activity rates (Suski *et al.*, 2005) and elevated temperature. These sub lethal stressors have the potential to accumulate and may negatively impact survival rates (Schramm *et al.*, 1987; Kwak & Henry, 1995).

To minimize the potential negative influences of livewells on fishes, a number of remedial treatments have been prescribed. For example, numerous angling groups advocate the addition of ice to livewells during angling tournaments (Gilliland, 2002). Addition of ice will increase the amount of dissolved oxygen in water, and cooler water will also reduce the metabolic rate of fishes, thereby lowering activity levels and reducing their production of metabolic wastes (Beamish, 1970; Diana, 1983). Similarly, to prevent hypoxia, anglers will infuse oxygen into their livewell (Gilliland, 2002). To date, however, very little is known about the recovery profile of largemouth bass from exercise, and almost nothing about the physiological impacts of different environmental conditions on the post-exercise recovery process in this species. Thus, it is not known if the various proposed treatments intended to minimize the impact of livewell confinement are appropriate.

Based on this background, there were two main objectives for this study. The first was to determine the time required for physiological recovery in largemouth bass exercised in a manner that replicated angling and allowed to recover in fully oxygenated water without the imposition of temperature change. The second was to determine the impacts of temperature or dissolved oxygen concentration on the recovery of largemouth bass from exercise. By examining the recovery of largemouth bass from exercise under different temperature and oxygen conditions, it was hoped to gain insight into the ideal environment that will expedite the recovery of largemouth bass from angling-induced exercise.

## MATERIALS AND METHODS

Largemouth bass were collected by angling from lakes in south-eastern Ontario in July and August of 2002 and 2003. Following angling, fish were transported to the aquatic holding facility of the Queen's University Biological Station (QUBS), located on Lake Opinicon, Ontario, Canada (44° 31′ N; 76° 20′ W). Once at QUBS, fish were kept in holding tanks continuously supplied with fresh, fully oxygenated Lake Opinicon water for at least 48 h prior to experimentation. For all experiments, ambient water temperature averaged 25° C and ranged from 24 to 27° C. The total length ($L_T$) of fish used in the time course recovery experiments ranged from 290 to 460 mm (mean ± S.E. 331 ± 7 mm, $n = 30$), and the $L_T$ of fish used in the recovery media experiment ranged from 275 to 460 mm (335 ± 4 mm, $n = 85$).

### TIME COURSE RECOVERY EXPERIMENT

Control largemouth bass used in the time course recovery experiment were netted from a holding tank and transferred to darkened perspex boxes continuously supplied with fresh, aerated, Lake Opinicon water. After 24–48 h in the boxes, the flow of water to the fish was terminated and a lethal dose of anaesthetic [250 mg $l^{-1}$ 3-aminobenzoic acid ethyl ester methanesulphonate (MS222) buffered with 500 mg $NaCO_3$ $l^{-1}$] was added. Following the cessation of ventilation, fish were sampled for blood and white muscle according to the methods of Suski *et al.* (2003). To induce a physiological disturbance that replicated angling, individual largemouth bass were netted from a holding tank and transferred to an oval tank containing Lake Opinicon water at ambient temperature. Fish were then chased around the tank by tail pinching for 1 min, after which they were transferred to a container of water with a lethal dose of anaesthetic and sampled for blood and white muscle (Suski *et al.*, 2003). To determine the time required for recovery from the physiological disturbances induced by exercise, largemouth bass were exercised for 1 min as described above, and then transferred to darkened perspex boxes continuously supplied with fresh, aerated Lake Opinicon water. After either 1, 2 or 4 h of recovery time, largemouth bass were anaesthetized and sampled for blood and white muscle as noted above.

### RECOVERY MEDIA EXPERIMENT

Results from the first series of experiments revealed that, 2 h after fish were returned to the perspex boxes, the recovery process had begun for most of the monitored physiological variables, but was not complete. As a result, a recovery time of 2 h was chosen for the recovery media experiment. By allowing largemouth bass to recover in different environments for 2 h, it would be possible to see if certain environments accelerated recovery relative to ambient water, or if recovery was impaired.

For the recovery media experiment, largemouth bass were netted from a holding tank and exercised in ambient Lake Opinicon water by tail pinching for 1 min as described above. Following exercise, fish were transferred to darkened perspex boxes and left to

recover for 2 h in environments with altered temperature or dissolved oxygen conditions described below. After 2 h of recovery time, fish were anaesthetized and sampled for blood and white muscle as noted above.

## ENVIRONMENTAL TEMPERATURE VARIATION

The objective of the temperature variation experiment was to examine the impacts of both increases and decreases in ambient temperature on recovery from exercise. Largemouth bass were therefore recovered at 14, 20 and 32° C, a deviation from ambient temperatures of *c.* −11, −5 and +7° C respectively. To achieve these different temperatures, a chiller or an electric heater was used to alter the temperature of aerated Lake Opinicon water held in a central basin. Once the temperature in the central basin reached the desired level, a submersible pump was used to supply aerated perspex boxes with water. Water temperature was continuously monitored during the 2 h recovery period to ensure that it did not deviate > than 1° C from the desired setting.

## ENVIRONMENTAL OXYGEN VARIATION

The oxygen variation experiment examined how dissolved oxygen concentrations that were 50% below full saturation (moderate hypoxia), as well as a supersaturation of dissolved oxygen (hyperoxia), would impact recovery from exercise in largemouth bass. For this, water in a central basin was gassed with either 1) 90% nitrogen +10% oxygen or 2) pure oxygen. During the recovery period, the oxygen content of water in the central basin was continuously monitored using a dissolved oxygen meter (Yellow Springs Instruments, Model 55, Yellow Springs, OH, U.S.A.). For the moderate hypoxia treatment, the mean ± S.E. oxygen content of the water being pumped to the Perspex boxes was 4·00 ± 0·04 mg $l^{-1}$ ($n = 50$ measurements), which represented 49% of full saturation. For the supersaturation treatment, the dissolved oxygen content of this water averaged 222 ± 4% ($n = 10$ measurements) or *c.* 20 mg $l^{-1}$.

## ANALYSES

Analyses for plasma and white muscle variables are described in detail in Suski *et al.* (2003). Briefly, plasma osmolality was quantified with a freezing-point depression osmometer (Advanced Instruments Incorporated, Model 3M0) and plasma chloride using a chloride titrator (Radiometer Incorporated, Model CMT 10). Plasma lactate concentration was measured using a commercially available lactate assay (Sigma-Aldrich Co., Product # 826-A) that followed the methods of Lowry & Passonneau (1972). The plasma concentration of cortisol was measured by competitive protein binding using a commercially available kit (Coat-a-Count, Diagnostic Products Corporation, Los Angeles, CA, U.S.A.). Tissue lactate, phosphocreatine (PCr), and adenosine triphosphate (ATP) concentrations were measured following the enzymatic methods of Lowry & Passonneau (1972) after processing the muscle according to the procedure described in Booth *et al.* (1995). An additional portion of muscle tissue was used to measure glycogen following the methods of Hassid & Abraham (1957). Water content in white muscle was determined by drying pre-weighed frozen tissue in an 80° C oven for several days until a constant mass was obtained.

## STATISTICAL ANALYSES

Comparisons across treatment groups were performed using a one-way ANOVA, followed by a Dunnett's *post hoc* test to compare treatment means to a control group (Zar, 1999). For the time course recovery experiment, physiological variables quantified at the different sampling times were all compared to the control treatment. For the recovery media experiment, physiological variables quantified following recovery in

different environments were compared to two control groups: 2 h recovery in ambient water (ambient) and the control treatment. Statistical analyses were performed using Statview Version 5·0 (SAS, 1998), and the level of significance ($\alpha$) for all tests was 0·05. All results are shown as means ± S.E.

## RESULTS

Following exercise, plasma cortisol concentrations did not differ significantly from control values until 4 h, at which time they doubled [Fig. 1 (a)]. Plasma chloride concentrations did not change from control values at any point following exercise [Fig. 1 (b)], while plasma glucose concentrations increased by 25%

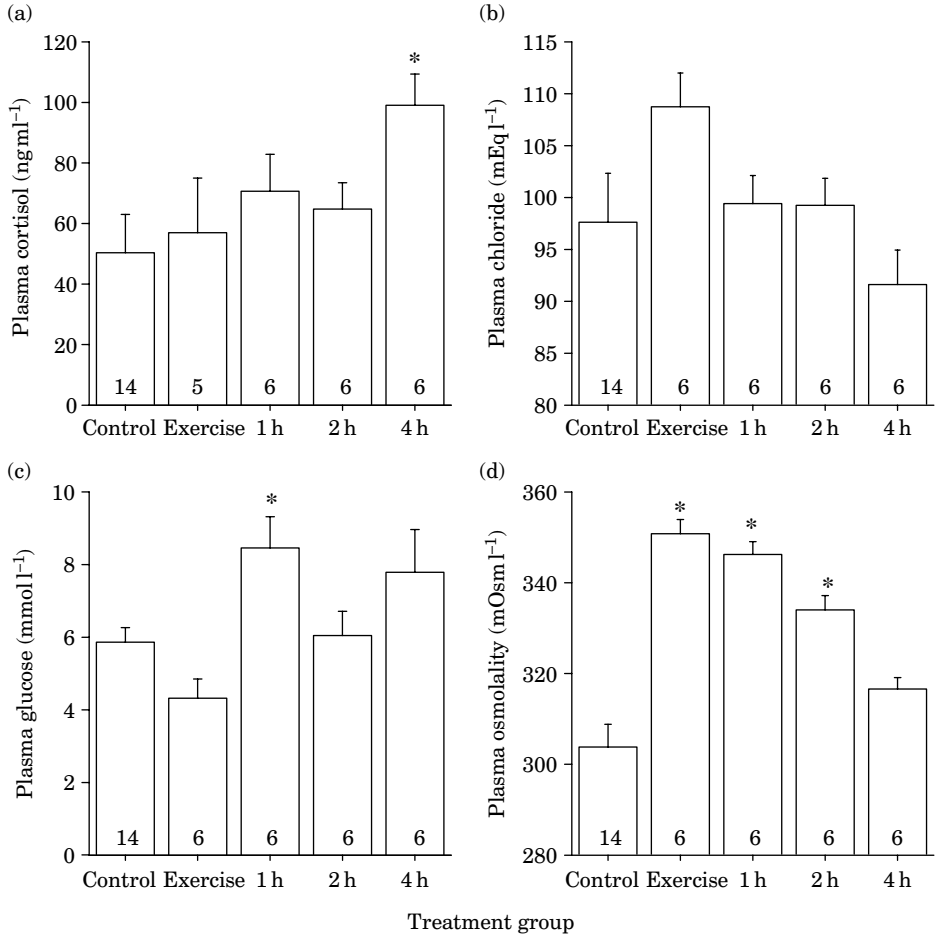


FIG. 1. Plasma (a) cortisol, (b) chloride and (c) glucose concentrations, and (d) osmolality of largemouth bass exercised for 1 min and then recovered up to 4 h in fully oxygenated water at ambient temperature (24° C). Control, undisturbed fish; exercise, fish sampled immediately after 1 min of exercise; 1 h, 2 h and 4 h, sampling times following 1 min of exercise. Values are means + S.E. The sample sizes ($n$) for the different sampling times are given on each bar. *, significant difference from the control group at a sampling time (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

1 h following exercise, but then returned to control values by 2 h [Fig. 1 (c)]. Plasma osmolality increased significantly following 1 min of exercise, and remained significantly above control levels until 4 h [Fig. 1 (d)].

After exercise, plasma lactate concentrations increased approximately four-fold relative to control values, and were approximately seven times greater than control values by 1 h following exercise [Fig. 2 (a)]. This disturbance was corrected, however, following 4 h of recovery. Similarly, exercise resulted in a seven-fold increase in muscle lactate but this variable had returned to control values 2 h after exercise [Fig. 2 (b)]. Muscle PCr, ATP and glycogen concentrations all fell by 75, 40 and 65% respectively after exercise, but returned to control values after 2–4 h of recovery [Fig. 3 (a), (b), (c)]. There was no significant difference in the water content of white muscle at any point during the time course experiment (ANOVA, d.f. = 4, 30; $P = 0{\cdot}66$).

Recovery from exercise in water that was 14° C, above ambient temperature or moderately hypoxic resulted in plasma cortisol concentrations that were significantly elevated relative to control largemouth bass [Fig. 4 (a)]. Similarly, recovery in water that was 14° C or above ambient temperature resulted in plasma cortisol concentrations that were significantly higher than largemouth bass recovered in water at ambient temperature [Fig. 4 (a)]. The plasma chloride concentrations of largemouth bass in the five recovery environments did not differ significantly from either the control or ambient recovery group [Fig. 4 (b)]. Following exercise, largemouth bass recovered in the warm water treatment and in both oxygen treatments showed plasma glucose concentrations that were approximately two and a half times above either control fish or fish recovered in ambient water [Fig. 4 (c)]. The plasma osmolality of largemouth bass from all five recovery treatments did not differ significantly from fish recovered in ambient lake water, but remained significantly elevated relative to the control group [Fig. 4 (d)].

The plasma lactate concentrations of largemouth bass recovered in warm or moderately hypoxic water was approximately twice as high as fish recovered in ambient water [Fig. 5 (a)]. Similarly, following recovery in all of the recovery treatments, plasma lactate concentrations did not return to control levels [Fig. 5 (a)]. All of the temperature variation treatments, as well as the moderate hypoxia treatment, resulted in tissue lactate concentrations that were approximately six times greater than control largemouth bass, and approximately two and a half times greater than fish recovered in ambient water [Fig. 5 (b)]. Following 2 h of recovery in hyperoxygenated water, however, tissue lactate concentrations returned to control levels [Fig. 5 (b)].

Both an increase in water temperature and moderate hypoxia significantly impaired the recovery of tissue PCr relative to fish in ambient water conditions by *c.* 75 and 50% respectively [Fig. 6 (a)]. Following recovery in any of the temperature or oxygen variations, tissue ATP concentrations were *c.* 70% lower than largemouth bass recovered in ambient water, and *c.* 80% below control levels [Fig. 6 (b)]. During recovery, all of the temperature variations used impaired the ability of largemouth bass to restore tissue glycogen to control values, and glycogen values were at least 50% lower than fish recovering at ambient temperatures [Fig. 6 (c)]. The water content of white muscle ranged from 78 to 84% for all individuals sampled as part of the recovery media

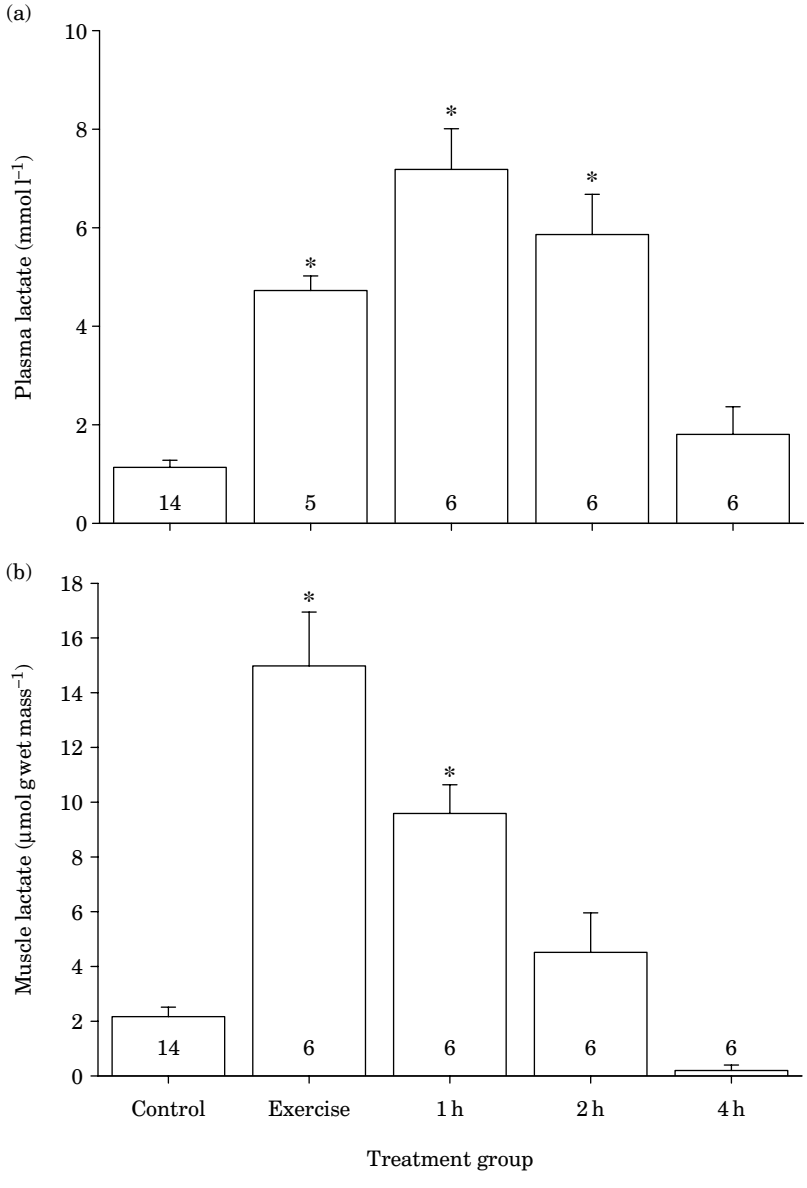


FIG. 2. (a) Plasma lactate and (b) white muscle lactate concentrations (means + S.E., *n* given on each bar) of largemouth bass exercised for 1 min and then recovered up to 4 h in fully oxygenated water at acclimation temperature (24° C). Treatment groups as in Fig. 1. *, significant difference from the control group at sampling time (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

experiment (mean ± S.E. = 79·0 ± 0·1%, $n = 47$,). Although there were significant differences in mean water content across the different treatment groups sampled (ANOVA, d.f. = 6, 40, $P = 0{\cdot}01$), the Dunnett's *post hoc* test did not detect any significant differences between the treatment groups and either the control treatment or the 2 h recovery in ambient water treatment ($P > 0{\cdot}05$).

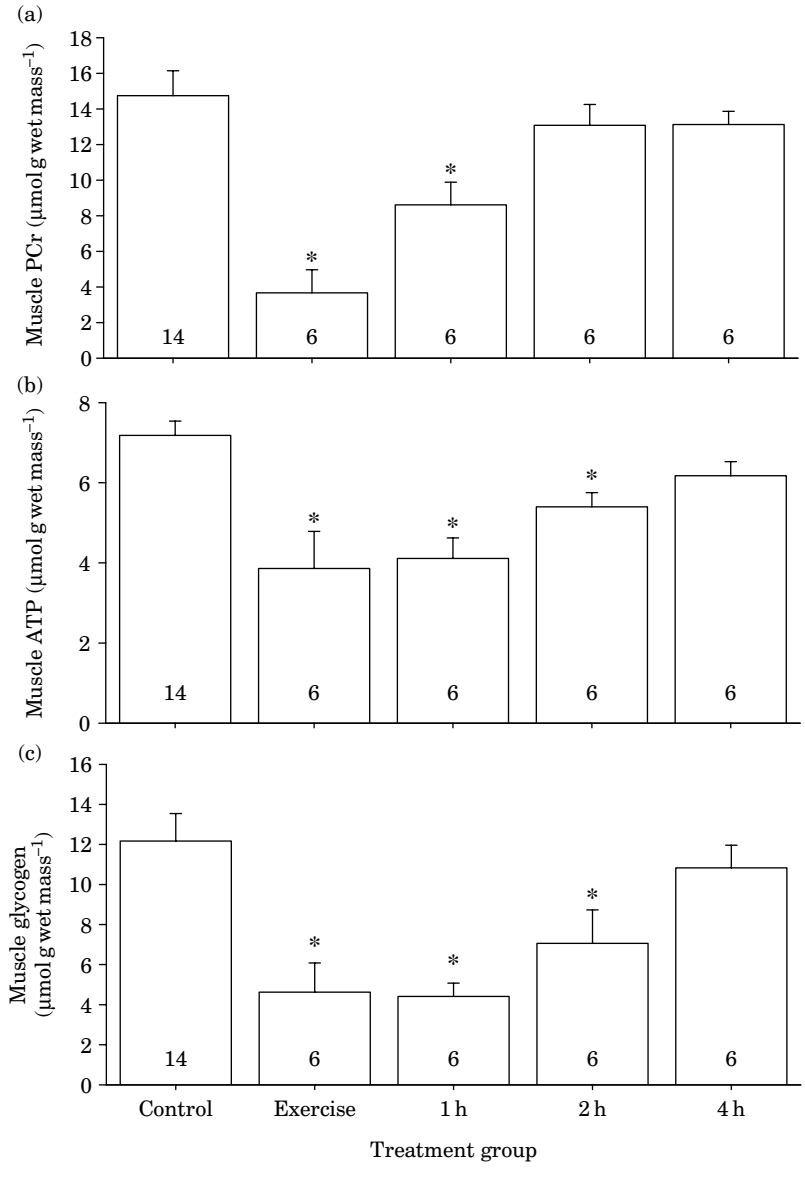


FIG. 3. White muscle (a) phosphocreatine (PCr), (b) adenosine triphosphate (ATP) and (c) glycogen concentrations (means + S.E., *n* given on each bar) of largemouth bass exercised for 1 min and then recovered for up to 4 in fully oxygenated water at acclimation temperature (24° C). Treatment groups as in Fig. 1. *, significant difference from the control group at sampling time (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

## DISCUSSION

The results of numerous studies have shown that the physiological response of fishes to angling is virtually identical to that of burst exercise (Gustaveson *et al.*, 1991; Kieffer *et al.*, 1995, 2002; Wilkie *et al.*, 1996; Suski *et al.*, 2003). In the

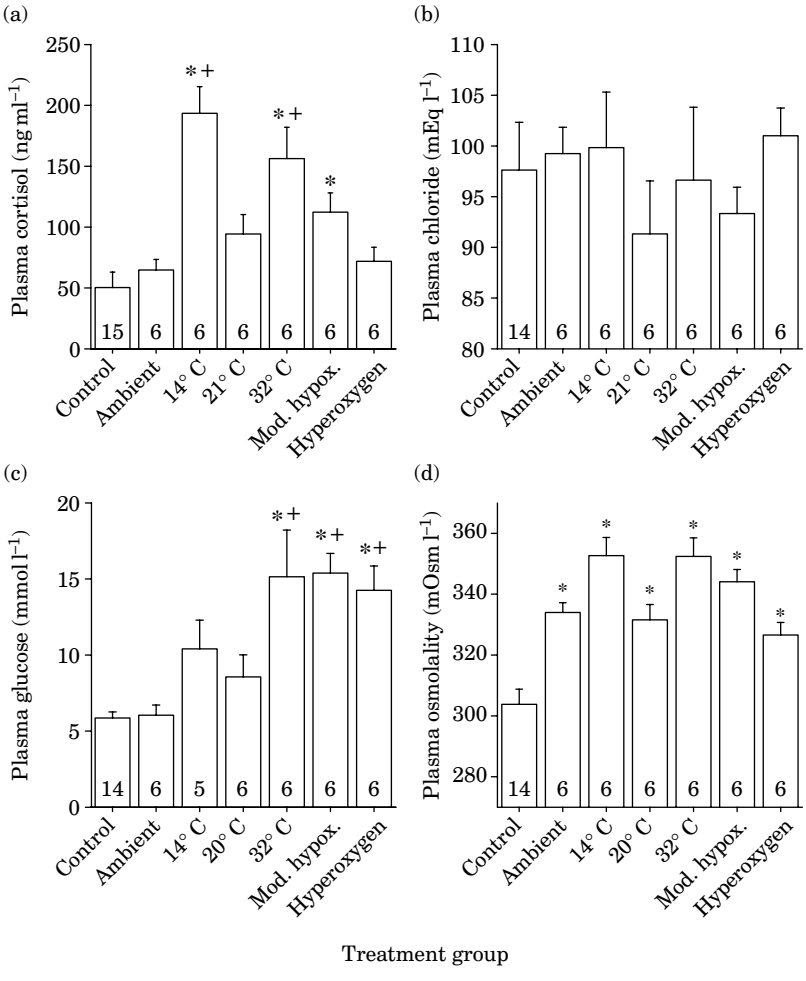


FIG. 4. Plasma (a) cortisol, (b) chloride and (c) glucose concentrations, and (d) osmolality of largemouth bass exercised for 1 min and then recovered for 2 h in an environment with either altered temperature or dissolved oxygen concentration. Control, undisturbed fish; ambient, fish exercised and recovered for 2 h in fully oxygenated water at acclimation temperature; 14°, 21° and 32°, fish exercised and recovered for 2 h at altered water temperatures; Mod. hypox., fish exercised and recovered for 2 h in moderately hypoxic water; hyperoxygen, fish exercised and recovered for 2 h in water supersaturated with dissolved oxygen. Values are means + S.E. The sample sizes ($n$) for the different sampling times are given on each bar. *, significant difference from the control group at a sampling time; +, significant difference from fish recovered at ambient temperature (24° C) and dissolved oxygen (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

current study, the response of largemouth bass to exhaustive exercise was also typical of other species examined. Specifically, exercise resulted in significant decreases in the white muscle energy stores, PCr, ATP and glycogen, and significant increases in lactate concentrations in both white muscle and plasma. Changes in metabolites of this magnitude have previously been shown in largemouth bass caught during actual live-release angling tournaments (Suski *et al.*,

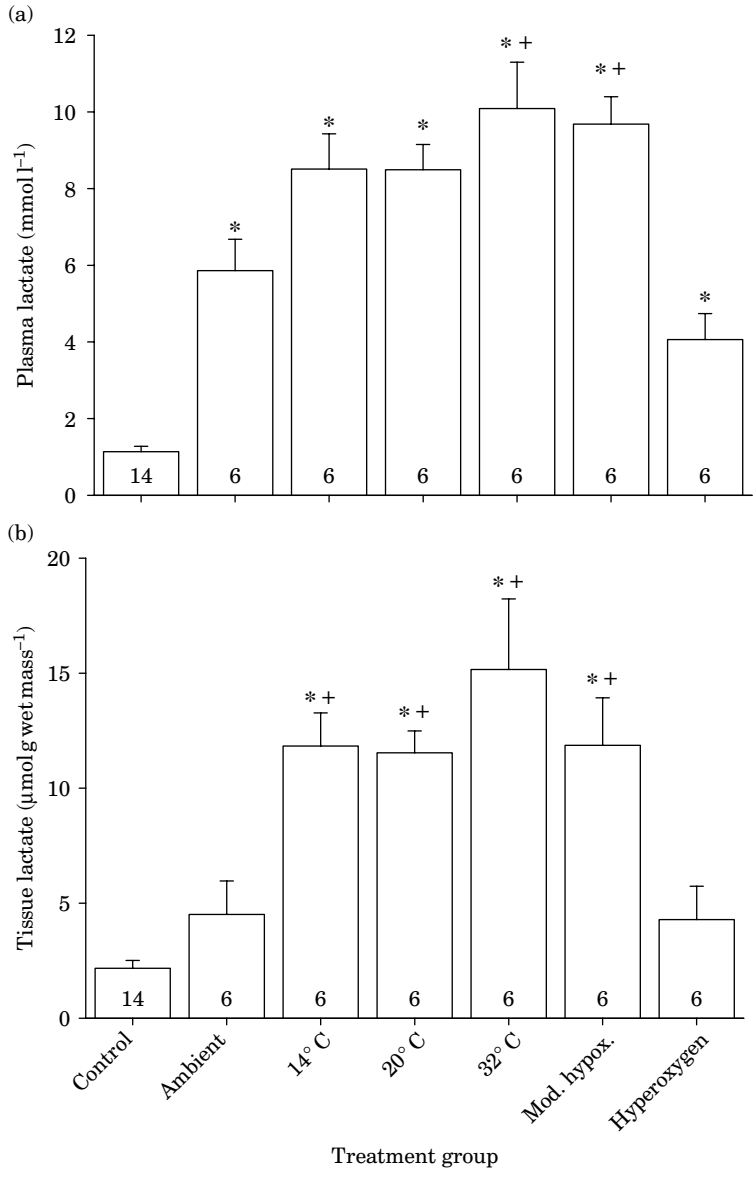


FIG. 5. (a) Plasma lactate and (b) white muscle lactate concentrations (means + S.E., *n* given on each bar) of largemouth bass exercised for 1 min and then recovered for 2 h in an environment with either altered dissolved oxygen concentration or temperature. Treatment groups as in Fig. 4. *, significant difference from control group at sampling time; +, significant difference from fish recovered at ambient temperature (24° C) and dissolved oxygen (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

2003) and following exhaustive exercise (Suski *et al.*, 2004). Exercise also resulted in changes in plasma osmolality but no changes in muscle water content or plasma chloride concentration. The observed increases in plasma osmolality in the current study therefore probably resulted from the addition of osmotically

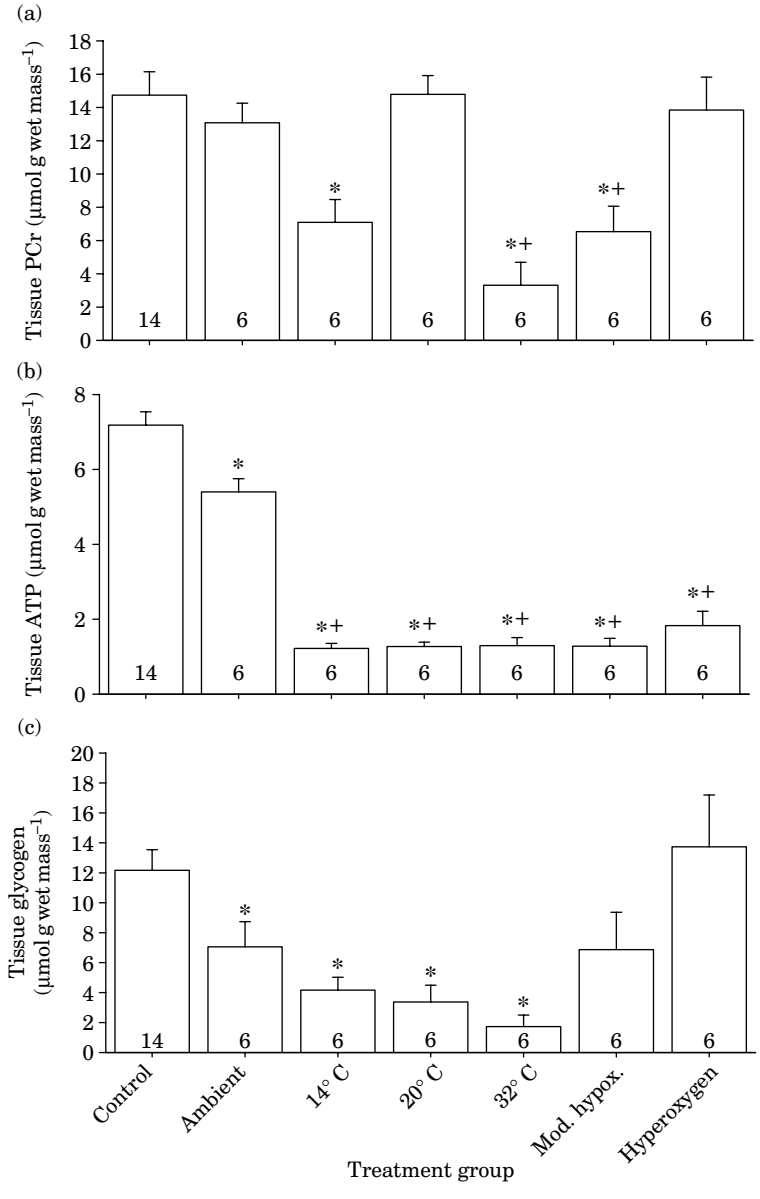


FIG. 6. White muscle (a) PCr, (b) ATP and (c) glycogen concentrations (means + S.E., *n* given on each bar) of largemouth bass exercised for 1 min and then recovered for 2 h in an environment with either altered dissolved oxygen concentration or temperature. Treatment groups as in Fig. 4. *, significant differences from control group at sampling time; +, significant differences from fish recovered at ambient temperature (24° C) and dissolved oxygen (ANOVA, Dunnett's test, $P < 0{\cdot}05$).

active particles to plasma (e.g. glucose, plasma proteins, lactate, $Na^+$, $K^+$ and $Hco_3^-$) (Wood 1991; Suski *et al.*, 2003) because no differences in the water content of white muscle was observed. While the current study used oven drying

to quantify the movement of water into white muscle and found no change following exercise, future studies should corroborate this finding with alternative methods such as [$^3$H]-labelled PEG-4000 (polyethelyne glycol), and also assess if haemo-concentration could have resulted from fluid shifts from plasma into red blood cells (Wang *et al*., 1994). Ion losses have been shown to occur in largemouth bass during prolonged stressors such as hauling (Carmichael *et al*., 1984*a*, *b*). Suski *et al*. (2003), however, showed that live-release angling tournaments did not cause chloride losses in largemouth bass. Previous studies have also shown that the gills of the genus *Micropterus* are relatively less permeable to ion losses as compared to other freshwater species (McDonald *et al*., 1991).

The time required for fishes to recover from exhaustive exercise varies by species, but studies involving rainbow trout *Oncorhynchus mykiss*, (Walbaum) suggest that post-exercise recovery of most the variables measured in this study takes between 2 and 4 h, while tissue glycogen may require in excess of 8 h to return to pre-exercise levels (Milligan, 1996; Richards *et al*., 2002). In largemouth bass, the metabolic and ionic disturbances associated with exhaustive exercise appeared to be corrected by 4 h when fish were held in well-aerated water at acclimation temperature. The series of experiments also demonstrated that 2 h of recovery was an appropriate time to evaluate factors that might facilitate or impede physiological recovery in this species, but future work should examine the impact of extended exposure to these various conditions.

In most fish species, changes in ambient water temperature affect numerous physiological processes (Beamish, 1970; Reeves, 1977; Hochachka, 1988; Hazel, 1993, 1995; Somero, 1995; Jensen *et al*., 2001). In largemouth bass, a decrease in the temperature of the recovery environment elevated lactate concentrations, impaired replenishment of white muscle energy stores and elevated in plasma cortisol concentrations relative to fish recovered at ambient water temperatures. Even though colder water holds greater quantities of dissolved oxygen and reduces the metabolic rate of fishes (Diana, 1983), transferring recovering fishes to cooler water probably reduced the activity rate of channels, pumps and enzymes responsible for the clearance of lactate and replenishment of energy stores (Hochachka, 1988; Moyes *et al*., 1992; Milligan & Girard, 1993; Richards *et al*., 2002). Similar conclusions were reached by both Galloway & Kieffer (2003) and Hyvärinen *et al*. (2004) who observed that acute exposure to cold water slowed the recovery of exercised Atlantic salmon *Salmo salar*, L. and brown trout *Salmo trutta*, L. relative to fishes at warmer temperatures.

Interestingly, warmer water also impaired physiological recovery in largemouth bass. This result contrasts recent work by Galloway & Kieffer (2003) who reported that acute increases in ambient water temperatures significantly accelerated the recovery of juvenile Atlantic salmon from exercise. A possible explanation for these different results may be the fact that the temperatures in the present warm water recovery experiment approached the upper lethal temperature for largemouth bass. Fields *et al*. (1987) showed that the critical thermal maximum of northern largemouth bass acclimated to 24° C was 36·6° C ± 0·51° C (mean ± S.E.) In the current study, largemouth bass were acclimated to *c*. 26° C prior to the experiment, and then recovered at 32° C. Although 32° C is not lethal for largemouth bass, the biochemical or respiratory processes responsible for recovery from exercise may not function optimally at

this temperature (i.e. 'pejus' temperatures), cardiac scope may be reduced (Farrell, 2002) or aerobic scope may be reduced (Pörtner, 2002) and tissues may be required to rely upon anaerobic metabolism for energy thus accumulating anaerobic end products (Hochachka, 1991; Somero, 1995). In this regard, it is noteworthy that numerous studies on heat shock proteins have shown that significant protein damage occurs in most organisms several degrees below their upper lethal temperature (Iwama *et al.*, 1998). While no mortality was observed, there clearly were sublethal impairments arising from this elevated temperature. Wilkie *et al.*, (1996) also found that warm temperatures disrupted post-exercise recovery and increased post-exercise mortality in Atlantic salmon.

The recovery of largemouth bass from exercise was also significantly affected by changes in environmental oxygen levels. While a 50% reduction in environmental oxygen does not appear to initiate anaerobic metabolism in resting largemouth bass (Furimsky *et al.*, 2003), this level of hypoxia does impede recovery of the metabolic disturbance in this species following exhaustive exercise. This is probably due to the fact that the oxygen requirements of fishes are greatly elevated following the cessation of exercise (Scarabello *et al.*, 1991; Wakefield *et al.*, 2004). It has also been shown that the energy required to fuel recovery of the post-exercise metabolic disturbance must be derived aerobically (Moyes *et al.*, 1992; Richards *et al.*, 2002).

In comparison to the other recovery environments used in this study, hyperoxic water had much less of an impact on the physiological variables examined. For example, hyperoxia did not impair the recovery of muscle lactate and glycogen. It is noteworthy, however, that hyperoxia was found to significantly reduce the rate of recovery of muscle ATP. Although acid-base status was not monitored in this study, hyperoxia has also been shown to cause a significant acidosis in fishes due to its effect on ventilation rate (Dejours, 1973; Gilmour & Perry, 1994; Gilmour, 2001). Because ATP plays such an important role as an energy source for numerous physiological processes, and the potential for additional physiological disturbances associated with hyperoxic waters (Dejours, 1973; Gilmour & Perry, 1994; Gilmour, 2001), hyperoxic conditions should probably be avoided in tournament livewells.

Previous work focusing on the physiological impacts of changes in environmental oxygen or temperature for fishes has mainly used quietly resting individuals as subjects (Coutant, 1977; Carmichael *et al.*, 1988; Furimsky *et al.*, 2003). In the wild, fishes commonly encounter environments that differ substantially in both temperature and dissolved oxygen levels (Wetzel, 1983). It is also reasonable to assume that wild fishes may have to cope with additional physiological challenges such as avoiding predators or capturing prey while in these environments. In view of the present results, it may be important to consider that the oxygen thresholds and temperature sensitivity of fishes exposed to additional physiological challenges such as exercise may be very different from those of resting fishes. The oxygen and temperature requirements of fishes should therefore be interpreted cautiously, and possibly even re-evaluated, should fishes be presented with additive sub lethal challenges such as exercise and pollution.

The results of this study also have important implications for individuals associated with live-release angling tournaments. Tournament anglers that add ice to their livewells in an attempt to calm fishes and keep oxygen levels elevated

will probably reduce the rate of post-exercise recovery in their fishes. In view of the present results, it is recommended that tournament anglers attempt to maintain livewell water temperatures as close as possible to the temperature from which fishes were caught to minimize recovery time. Although hyperoxygenated water caused only moderate physiological impairment relative to other treatments, it is also recommended that anglers refrain from using supplemental oxygen, but constantly aerate their livewell to avoid hypoxia.

The authors would like to thank M. Morrissey and M. Fortner for technical assistance and the staff at the Queen's University Biological Station for logistical support. Collection permits were provided by Ontario Ministry of Natural Resources staff. Financial support for this study was provided by grants from Shimano Canada Ltd and the Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Development Program to B.L.T. NSERC also provided graduate support to C.D.S. J.D.K thanks NSERC and the University of New Brunswick for funds.

## References

Beamish, F. W. H. (1970). Oxygen consumption of largemouth bass, Micropterus salmoides, in relation to swimming speed and temperature. *Canadian Journal of Zoology* **48,** 1221–1228.

Booth, R. K., Kieffer, J. D., Davidson, K., Bielak, A. T. & Tufts, B. L. (1995). Effects of late-season catch and release angling on anaerobic metabolism, acid base status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 283–290.

Burkett, D. P., Mankin, P. C., Lewis, G. W., Childers, W. F. & Philipp, D. P. (1986). Hook-and-line vulnerability and multiple recapture of largemouth bass under a minimum total-length limit of 457 mm. *North American Journal of Fisheries Management* **6,** 109–112.

Carmichael, G. J., Tomasso, J. R., Simco, B. A. & Davis, K. B. (1984*a*). Characterization and alleviation of stress associated with hauling largemouth bass. *Transactions of the American Fisheries Society* **113,** 778–785.

Carmichael, G. J., Tomasso, J. R., Simco, B. A. & Davis, K. B. (1984*b*). Confinement and water-quality induced stress in largemouth bass. *Transactions of the American Fisheries Society* **113,** 767–777.

Carmichael, G. J., Williamson, J. H., Caldwell Woodward, C. A. & Tomasso, J. R. (1988). Responses of northern, Florida, and hybrid largemouth bass to low temperature and low dissolved oxygen. *The Progressive Fish-Culturist* **50,** 225–231.

Cooke, S. J., Schreer, J. F., Wahl, D. H. & Philipp, D. P. (2002). Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. *American Fisheries Society Symposium* **31,** 489–512.

Coutant, C. C. (1977). Compilation of temperature preference data. *Journal of the Fisheries Research Board of Canada* **34,** 739–745.

Dejours, P. (1973). Problems of control of breathing in fishes. In *Comparative Physiology* (Bolis, L., Schmidt-Nielsen, K. & Maddrell, S. H. P., eds), pp. 117–133. Amsterdam: North-Holland Publishing Company.

Diana, J. S. (1983). Oxygen consumption by largemouth bass under constant and fluctuating thermal regimes. *Canadian Journal of Zoology* **6,** 1892–1895.

Duttweiler, M. W. (1985). Status of competitive fishing in the United States: trends and state fisheries policies. *Fisheries* **10,** 5–7.

Farrell, A. P. (2002). Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fishes. *Comparative Biochemistry and Physiology A* **132,** 797–810.

Fields, R. S., Lowe, S., Kaminski, C., Whitt, G. S. & Philipp, D. P. (1987). Critical and chronic thermal maxima of northern and Florida largemouth bass and their reciprocal $F_1$ and $F_2$ Hybrids. *Transactions of the American Fisheries Society* **116,** 856–863.

Furimsky, M., Cooke, S. J., Suski, C. D., Wang, Y. & Tufts, B. L. (2003). Respiratory and circulatory responses to hypoxia in largemouth bass and smallmouth bass: implications for "live-release" angling tournaments. *Transactions of the American Fisheries Society* **132,** 1065–1075.

Galloway, B. J. & Kieffer, J. D. (2003). The effects of an acute temperature change on the metabolic recovery from exhaustive exercise in juvenile Atlantic salmon (*Salmo salar*). *Physiological and Biochemical Zoology* **76,** 652–662.

Gilliland, E. R. (2002). Livewell operating procedures to reduce mortality of black bass during summer tournaments. *American Fisheries Society Symposium* **31,** 477–487.

Gilmour, K. M. (2001). The $CO_2$/pH ventilatory drive in fish. *Comparative Biochemistry and Physiology A* **130,** 219–240.

Gilmour, K. M. & Perry, S. F. (1994). The effects of hypoxia, hyperoxia or hypercapnia on the acid-base disequilibrium in the arterial blood of rainbow trout. *The Journal of Experimental Biology* **192,** 269–284.

Gustaveson, A. W., Wydoski, R. S. & Wedemeyer, G. A. (1991). Physiological response of largemouth bass to angling stress. *Transactions of the American Fisheries Society* **120,** 629–636.

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

Hassid, W. Z. & Abraham, S. (1957). Chemical procedures for analysis of polysaccharides. In *Methods in Enzymology*, Vol. **III** (Colowick, S. P. & Kaplan, N. O., eds), pp. 34–50. New York: Academic Press Inc.

Hazel, J. R. (1993). Thermal biology. In *The Physiology of Fishes* (Evans, D. H., ed.), pp. 427–467 Boca Raton, FL: CRC Press, Inc.

Hazel, J. R. (1995). Thermal adaptation in biological membranes: is homeoviscous adaptation the explanation? *Annual Review of Physiology* **57,** 19–42.

Hochachka, P. W. (1988). Channels and pumps – determinants of metabolic cold adaptation strategies. *Comparative Biochemistry and Physiology* **90B,** 515–519.

Hochachka, P. W. (1991). Design of energy metabolism. In *Environmental and Metabolic Animal Physiology* (Prosser, C. L., ed.), pp. 325–351. New York: John Wiley & Sons Inc.

Hyvärinen, P., Heinmaa, S. & Rita, H. (2004). Effects of abrupt cold shock on stress responses and recovery in brown trout exhausted by swimming. *Journal of Fish Biology* **64,** 1015–1026. doi: 10.1111/j.1095-8649.2004.00367.x

Iwama, G. K., Thomas, P. T., Forsyth, R. B. & Vijayan, M. M. (1998). Heat shock protein expression in fish. *Reviews in Fish Biology and Fisheries* **8,** 35–56.

Jensen, F. B., Wang, T. & Brahm, J. (2001). Acute and chronic influence of temperature on red blood cell anion exchange. *The Journal of Experimental Biology* **204,** 39–45.

Kerr, S. J. & Kamke, K. K. (2003). Competitive fishing in freshwaters of North America: a survey of Canadian and U. S. jurisdictions. *Fisheries* **28,** 26–31.

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.

Kieffer, J. D., Rossiter, A. M., Kieffer, C. A., Davidson, K. & Tufts, B. L. (2002). Physiology and survival of Atlantic salmon following exhaustive exercise in hard and softer water: implications for the catch-and-release sport fishery. *North American Journal of Fisheries Management* **22,** 132–144.

Kwak, T. J. & Henry, M. G. (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.

Lowry O. H. & Passonneau, J. V. (1972). *A Flexible System of Enzymatic Analysis*. New York: Academic Press, Inc.

McDonald, G. G., Cavdek, V. & Ellis, R. (1991). Gill design in freshwater fishes: interrelationships among gas exchange, ion regulation, and acid-base regulation. *Physiological Zoology* **64,** 103–123

Meals, K. O. & Miranda, L. E. (1994). Size-related mortality of tournament-caught largemouth bass. *North American Journal of Fisheries Management* **14,** 460–463.

Milligan, C. L. (1996). Metabolic recovery from exhaustive exercise in rainbow trout. *Comparative Biochemistry and Physiology* **113A,** 51–60.

Milligan, C. L. & Girard, S. S. (1993). Lactate metabolism in rainbow trout. *The Journal of Experimental Biology* **180,** 175–193.

Moyes, C. D., Schulte, P. M. & Hochachka, P. W. (1992). Recovery metabolism of trout white muscle: role of mitochondria. *American Journal of Physiology* **262,** R295–R304.

Muoneke, M. I. & Childress, W. M. (1994). Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* **2,** 123–156.

Pörtner, H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology A* **132,** 739–761.

Post, J. R., Sullivan, M., Cox, S., Lester, N., Walters, C. J., Parkinson, E. A., Paul, A. J., Jackson, L. & Shuter, B. J. (2002). Canada's recreational fisheries: the invisible collapse? *Fisheries* **27,** 6–17.

Quinn, S. P. (1989). Recapture of voluntarily released largemouth bass. *North American Journal of Fisheries Management* **9,** 86–91.

Quinn, S. P. (1996). Trends in regulatory and voluntary catch-and-release fishing. *American Fisheries Society Symposium* **16,** 152–163.

Reeves, R. B. (1977). The interaction of body temperature and acid-base balance in ectothermic vertebrates. *Annual Review of Physiology* **39,** 559–586.

Richards, J. G., Heigenhauser, G. J. F. & Wood, C. M. (2002). Lipid oxidation fuels recovery from exhaustive exercise in white muscle of rainbow trout. *American Journal of Physiology* **282,** R89–R99.

SAS (1998). *Statview Version 5.0*. Cary, NC: SAS Institute Inc

Scarabello, M., Heigenhauser, G. J. F. & Wood, C. M. (1991). The oxygen debt hypothesis in juvenile rainbow trout after exhaustive exercise. *Respiration Physiology* **84,** 245–259.

Schramm, H. L. Jr., Haydt, P. J. & Portier, K. M. (1987). Evaluation of prerelease, postrelease, and total mortality of largemouth bass caught during tournaments in two Florida lakes. *North American Journal of Fisheries Management* **7,** 394–402.

Schramm, H. L. Jr., Armstrong, M. L., Funicelli, N. A., Green, D. M., Lee, D. P., Manns, R. E. Jr., Taubert, B. D. & Waters, S. J. (1991). The status of competitive sport fishing in North America. *Fisheries* **16,** 4–12.

Shupp, B. D. (1979). 1978 status of bass fishing tournaments in the United States. *Fisheries* **4,** 11–19.

Somero, G. N. (1995). Proteins and temperature. *Annual Review of Physiology* **57,** 43–68.

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., Killen, S. S., Morrissey, M. B., Lund, S. G. & Tufts, B. L. (2003). Physiological changes in largemouth bass caused by live-release angling tournaments in southeastern Ontario. *North American Journal of Fisheries Management* **23,** 760–769.

Suski, C. D., Killen, S. S., Cooke, S. J., Kieffer, J. D., Philipp, D. P. & Tufts, B. L. (2004). Physiological significance of the weigh-in during live-release angling tournaments for largemouth bass. *Transactions of the American Fisheries Society* **133,** 1291–1303.

Suski, C. D., Cooke, S. J., Killen, S. S., Wahl, D. H., Philipp, D. P. & Tufts, B. L. (2005). Behaviour of walleye (*Sander vitreus* L.) and largemouth bass (*Micropterus salmoides* L.) exposed to different wave intensities and boat operating conditions during livewell confinement – insights from videography. *Fisheries Management and Ecology* **12,** 19–26.

Wakefield, A. M., Cunjak, R. A. & Kieffer, J. D. (2004). Metabolic recovery in Atlantic salmon fry and parr following forced activity. *Journal of Fish Biology* **65,** 920–932. doi: 10.1111/j.1095-8649.2004.00492.x

Wang, Y., Heigenhauser, G. J. F. & Wood, C. M. (1994). Integrated responses to exhaustive exercise and recovery in rainbow trout white muscle: acid-base, phosphogen, carbohydrate, lipid, ammonia, fluid volume and electrolyte metabolism. *Journal of Experimental Biology* **195,** 227–258.

Wetzel, R. G. (1983). *Limnology*, 2nd edn. Philadelphia, PA: Saunders College Publishing.

Wilkie, M. P., Davidson, K., Brobbel, M. A., Kieffer, J. D., Booth, R. K., Bielak, A. T. & Tufts, B. L. (1996). Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Transactions of the American Fisheries Society* **125,** 572–580.

Wood, C. M. (1991). Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. *The Journal of Experimental Biology* **160,** 285–308.

Zar, J. H. (1999). *Biostatistical Analysis*, 4th edn. New Jersey: Prentice Hall Inc.