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Cardiovascular Responses of Largemouth Bass to Exhaustive Exercise and Brief Air Exposure over a Range of Water Temperatures

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Abstract.—In this study we examined the effects of exhaustive exercise and brief air exposure on the cardiovascular function of largemouth bass *Micropterus salmoides* at four water temperatures (13, 17, 21, and 25°C). We used Doppler flow probes to monitor cardiac output and its components (i.e., stroke volume and heart rate) while we manually chased fish to exhaustion to simulate angling, exposed them to air for 30 s, and then recorded patterns of recovery. Resting cardiac variables generally increased with increasing water temperature except for stroke volume, which was temperature independent. Fish heart rate became erratic during exercise, and during air exposure fish exhibited severe bradycardia before becoming tachycardic when returned to the water. Maximal change occurred most rapidly for cardiac output (about 5 min). Several minutes later, changes in heart rate (increase) and stroke volume (decrease) simultaneously reached maximal deviations from resting values. Cardiac output and heart rate increased 150–200% relative to resting values despite 50% reductions in stroke volume, suggesting that largemouth bass are primarily frequency modulators. Maximal changes generally increased with water temperature for cardiac output and heart rate but not for stroke volume, resulting in heightened scope for cardiac output and heart rate with increasing water temperature. Recovery patterns were not influenced by water temperature. Cardiac output and heart rate generally returned to predisturbance levels in approximately 135 min, whereas stroke volume recovered more rapidly (about 110 min). Based on these findings, we suggest that largemouth bass exposed to exhaustive exercise and brief air exposure are capable

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of recovering from handling disturbances in several hours across the range of water temperatures that we examined (13–25°C).

Studies quantifying the biological effects of angling on fish have become more numerous, reflecting the increased interest in voluntary and mandatory catch-and-release angling (Quinn 1996) and the importance in understanding the fate of released fish (Cooke et al. 2002b). To this end, studies have quantified the levels of injury and hooking mortality for many recreationally important fish species to provide managers with estimates of survival for population models (Wydoski 1977; Hayes et al. 1995) and to determine the factors that lead to elevated mortality (Muoneke and Childress 1994). More recently, efforts have focused on understanding the sublethal effects of catch-and-release angling at the level of the individual. This change in focus represents the recognition that although a fish may survive a catch-and-release angling event, there may be sublethal effects that could suppress growth rate or alter fitness (Cooke et al. 2002b). Knowledge of sublethal effects would permit the dissemination of information needed to change angling practices. Reduced sublethal effects of angling would be relevant to animal welfare (Balon 2000) and fisheries management (Wydoski 1977).

Sublethal effects of catch-and-release angling are most commonly examined through basic physiological studies of blood and white muscle biochemistry in the laboratory. There are multitudes of studies, although largely restricted to salmonids, that investigate sublethal effects produced by exercise during angling (e.g., Booth et al. 1995; Wilkie et al. 1997; Kieffer 2000) and air exposure following capture (Ferguson and Tufts 1992). Using indicators of acid–base and metabolic disturbance, these studies have examined the magnitudes of the sublethal effects, the time required for these altered variables to recover, and biological or environmental factors that magnify the effects (Kieffer 2000). However, blood and muscle biochemistry studies can have limited resolution and require either the sequential terminal sampling of different individuals or the cannulation, confinement, and repeated collection of blood from the same individual (Wydoski and Wedemeyer 1976; Gamperl et al. 1994; Iwama et al. 1995). An alternative approach is to use real time measurements of cardiac output (CO), heart rate (HR), and stroke volume (SV) as response variables (Cooke et al. 2001a; Schreer et al. 2001). These cardiovascular variables are intimately linked to metabolic rates in fish and can serve as sensitive indicators of stress (Webber et al. 1998; Brodeur et al. 2001). Specifically, cardiovascular monitoring can provide robust information on predisturbance status, magnitude of disturbance, and duration for recovery. By using this technique, conventionally restricted to basic studies of cardiovascular function, researchers can examine applied questions associated with catch-and-release angling while still contributing to our basic understanding of cardiovascular physiology.

The purpose of this study was to assess the cardiac response and recovery of adult largemouth bass *Micropterus salmoides* to catch-and-release angling, including exhaustive exercise and brief air exposure, across a range of water temperatures. Although largemouth bass are a common and well-studied recreational fish species in North America, there is comparatively little information on the sublethal effects of catch-and-release angling on this species (Cooke et al. 2002b). From hooking mortality assessments, however, it is evident that higher water temperature is one of the factors that may contribute to mortality (Muoneke and Childress 1994; Wilde 1998). Our work differs from previous cardiac studies on smallmouth bass *M. dolomieu* (i.e., Schreer et al. 2001) in that here we exposed fish to air to increase the realism of angling simulations. In addition to examining the applied issue of catch-and-release angling, we also interpret our findings in the context of environmental physiology and cardiovascular performance, presenting some of the most extensive data on in vivo cardiac function for a freshwater non-salmonid teleost fish over a wide range of water temperatures. Interestingly, Schreer et al. (2001) determined that smallmouth bass modulate cardiac output primarily through changes in heart rate, unlike most other teleost fishes (Farrell 1991b). Research on cardiovascular performance of another centrarchid fish, the largemouth bass, may provide additional insight into the frequency modulation anomaly observed in smallmouth bass.

Methods

Study animals.—Fish used for this study were captured from two geographical areas. Those used for experiments at 13°C and 17°C were collected

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during March 2001 from reservoirs in central Illinois with a pulsed-DC electrofishing boat. These fish were held at the Illinois Natural History Survey Aquatic Research Laboratory in Champaign. Fish used for experiments at 21°C and 25°C were collected in June 2001 from Lake Opinicon, Ontario, by anglers using heavy-duty rod and reels that minimized physiological disturbance (i.e., fish were landed within 20 s). Fish were held for at least 48 h before surgery in water-flow-through tanks (about 200 L) provided with lake water in Ontario and pond water in Illinois. Water temperatures at time of capture were within 2°C of the experimental temperature. Minor natural variation in temperature was consistent with ambient conditions. Water temperatures during surgery and data collection were within 0.3°C of desired experimental temperatures.

Surgical procedure and instrumentation.—Surgical procedures and the equipment used to measure cardiac output are described in detail in Cooke et al. (2001a) and Schreer et al. (2001). Briefly, each fish was anesthetized with 60 mg/L clove oil (emulsified with ethanol in a 9:1 ratio of ethanol to clove oil) until the fish lost equilibrium and was nonresponsive. Water containing a maintenance concentration of anesthetic (30 mg/L clove oil) was pumped over the gills during surgery. A flexible silicone cuff-type Doppler flow probe (subminiature 20 MHz piezoelectric transducer: Iowa Doppler Products, Iowa City, Iowa), sized to match the diameter of the vessel, was placed around the aorta and secured with a single suture. The lead wire from the probe was then sutured to the side of the fish in six locations to prevent shifting of the cuff. We used a flowmeter (545C–4 Directional Pulsed Doppler Flowmeter: Bioengineering, The University of Iowa, Iowa City, Iowa) and a digital strip-chart recorder (LabVIEW, version 4.0.1, National Instruments Corporation, Austin, Texas) to monitor cardiac variables.

The Doppler probe transducer emits a pulsed sonic signal that, when reflected by a moving object, results in a shift in signal frequency. This shift in frequency is related to velocity and is recorded as a change in voltage. Peaks in voltage (velocity) represent a heart beat. We used a peak counting algorithm in LabVIEW to determine heart rate over 1-min intervals. The mean voltage per unit time represents flow (or CO); flow can also be calculated in mL per unit time (explained in the subsection on postmortem calibrations). Dividing CO by HR yields SV.

Exhaustive exercise protocol.—Following surgery, individual fish were placed immediately into a 70-L tank (50 cm × 50 cm) and monitored until they had regained equilibrium. Fish were allowed to recover from surgery and to acclimate to the tank for at least 18 h. The experimental tanks were continuously supplied with water (about 35 L/h) at temperatures within 0.3°C of desired experimental temperatures. To simulate exhaustive exercise, fish were chased around the tank by hand until they would no longer respond to caudal stimulation (Cooke et al. 2001a). At this point they would no longer swim and began to lose equilibrium. Cardiac variables were recorded continuously for at least 1 h before the exercise simulation (the resting period), during the exercise simulation, and for at least 5 h postexercise (the recovery period). Access to the laboratory was restricted during resting and recovery to prevent external disturbance.

Postmortem calibrations.—Following experimentation, fish were euthanatized with an overdose of anesthetic (180 mg/L clove oil), and a postmortem calibration was conducted to convert Doppler shift (V) to actual blood flow (mL/min; Schreer et al. 2001). Using a constant infusion pump (Harvard Apparatus, South Natick, Massachusetts), anticoagulated pig's blood was perfused through the aorta to calibrate the probes over a range of flow rates encompassing those recorded during the trials. The hematocrit was not measured for the pig's blood used in this specific study, but previous comparisons yielded strong similarities between pig's blood and largemouth bass blood. Reference flow rates were analyzed with linear least-squares regression.

To determine cardiac morphology, the ventricles were patted dry and weighed to the nearest 0.001 g and expressed as weight-corrected relative ventricular mass (RVM, defined as (ventricular mass/body mass)·100). Ventral aorta diameter was determined from the Doppler cuff lumen (to the nearest 0.1 mm) that was used for each fish. Summary information for total length, mass, aorta diameter, and RVM are presented in Table 1.

Temperature effects on cardiac performance were quantified by calculating Q_{10} rates (Schmidt-Nielsen 1997), using the formula

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2-T_1)},$$

where R_1 and R_2 are the rates of physiological processes at temperatures 1 (T_1) and 2 (T_2). Mean Q_{10} values were calculated across the range of tem-

TABLE 1.—Means (SE) for body characteristics and cardiac variables of largemouth bass affixed with Doppler flow probes in the laboratory and exposed to simulated angling across four water temperatures. Dissimilar letters indicate that character values differed significantly ($P < 0.05$) between temperatures. Statistical tests for resting cardiac variables and time until exhaustion are presented in the text.

Temperature (°C)	N	Total length (mm)	Mass (g)	Cuff size (mm)	Relative ventricular mass	Resting cardiac output ($mL \cdot min^{-1} \cdot kg^{-1}$)	Resting heart rate (beats/min)	Resting stroke volume (mL/kg)	Time until exhaustion (s)
13	11	390 z	918 z	2.3 z	0.067 z	23.51 x	32.0 x	0.710 z	179 z
		(6)	(29)	(0.1)	(0.009)	(0.76)	(0.98)	(0.023)	(10)
17	10	397 z	953 z	2.4 z	0.069 z	29.19 y	40.8 y	0.721 z	187 z
		(6)	(52)	(0.1)	(0.009)	(0.82)	(1.14)	(0.014)	(7)
21	8	348 y	592 y	1.7 y	0.085 z	33.34 y	42.8 y	0.785 z	158 z
		(11)	(67)	(0.1)	(0.007)	(0.91)	(1.39)	(0.017)	(8)
25	8	370 y	748 y	1.8 y	0.079 z	39.1 z	49.0 z	0.801 z	167 z
		(4)	(24)	(0.01)	(0.013)	(1.44)	(1.15)	(0.033)	(9)

peratures that we examined for each resting cardiovascular variable.

Data analysis.—To determine recovery times, traces for CO, HR, and SV (adjusted to resting [100%]), were plotted for each fish as 60-s means and evaluated visually (Schreer et al. 2001). A fish was considered to have recovered when values became stable and returned to within 10% of resting values (Schreer et al. 2001). The maximal disturbance was determined as the greatest observed change in a cardiac variable, either positive (>100% resting) or negative (<100% resting), during the recovery period. The time at which each cardiac variable reached its maximum or minimum value was recorded to the nearest minute.

We first tested normality using normal probability plots and the Shapiro–Wilk *W*-test. Homogeneity of variance was assessed using the Levene's test. Because data were normally distributed and variances were homogeneous, we did not transform the data and we used parametric analyses. Simple one-way analysis of variance (ANOVA) was used to evaluate differences in fish characteristics (i.e., total length, mass, and RVM). We adjusted the dependent variable to account for variation in the site and to facilitate our primary goal of evaluating the influence of temperature on cardiovascular performance (Wildt and Ahtola 1979). We then examined temperature-specific trends in cardiac function using analysis of covariance (ANCOVA) to evaluate differences in baseline and maximal cardiac variables, scope for CO and HR, and time until exhaustion. For time postexhaustion for maximum change in cardiac variables and cardiac recovery time, two-way ANCOVA was used to assess differences among temperatures and cardiac variables, with site as a covariate. Where appropriate, linear least-squares regression analysis was used to examine the relationship between water temperature and the variable of interest, with site as a covariate. Fisher's least significant difference was used to identify least significant differences and mean separation. All statistical assessments were conducted using JMP IN 4.0 (SAS Institute 2001) and SAS 7.0 (SAS Institute 2000). Values reported are means ± SEs and significance was set at $\alpha = 0.05$.

Results

Although total length ($F = 9.51$, $P < 0.001$), mass ($F = 13.34$, $P < 0.001$), and aorta size ($F = 12.02$, $P < 0.001$) of fish used in this study varied significantly among water temperature treatments, RVM did not ($F = 2.19$, $P = 0.110$; Table 1). Resting CO values for largemouth bass increased with water temperature (temp) ($CO_{rest} = 7.10 + 1.27$ temp; $r^2 = 0.80$, $P < 0.001$; $Q_{10} = 1.51 \pm 0.05$) and differed significantly among temperature treatments ($F = 34.04$, $P < 0.001$; Figure 1; Table 1) but not sites. Resting HR values of largemouth bass also increased with water temperature ($HR_{rest} = 4.74 + 1.91$ temp; $r^2 = 0.77$, $P < 0.001$; $Q_{10} = 1.42 \pm 0.10$). Significant differences in resting HR were observed not only for water temperature ($F = 43.69$, $P < 0.001$), but also for study site ($F = 4.87$, $P = 0.034$). Resting SV values did not vary significantly with water temperature or site. However, there was a positive relationship between resting SV and water temperature ($SV_{rest} = 0.59 + 0.0084$ temp; $r^2 = 0.25$, $P = 0.002$; $Q_{10} = 1.11 \pm 0.03$; Figure 1).

The time required for fish to become exhausted from manual chasing did not vary significantly by water temperature or study site (Table 1). In general, fish became exhausted after 140 to 200 s of chasing. There was a weak but nonsignificant trend

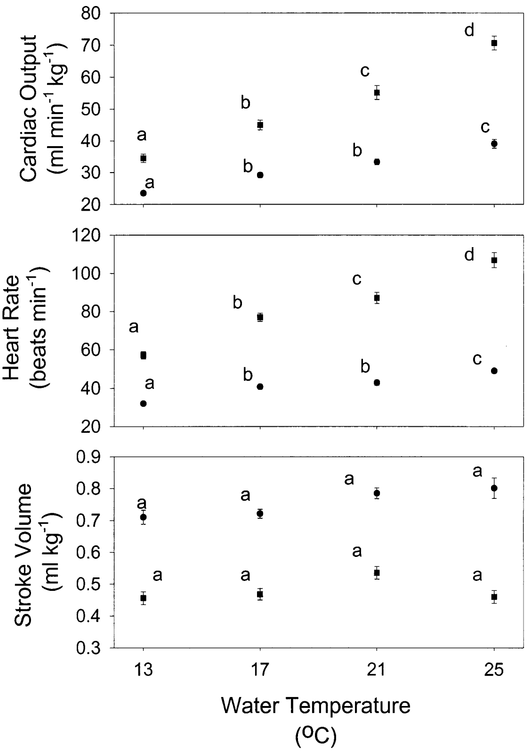

FIGURE 1.—Mean ± SE cardiac values for resting and maximal change (i.e., the cardiac value representing the greatest change from the resting value) in largemouth bass subjected to simulated angling in the laboratory. Data were collected at 13 (N = 11), 17 (N = 10), 21 (N = 8), and 25°C (N = 8) with Doppler flow probes. Dissimilar letters indicate significantly different ($P < 0.05$) values between temperatures for that cardiac variable. Resting rates (circles) were determined from the 60-min period before exercise; maximal values (squares) were determined from the 300-min recovery period following exhaustive exercise and air exposure. Note that for stroke volume, the maximal changes were actually decreases from resting levels.

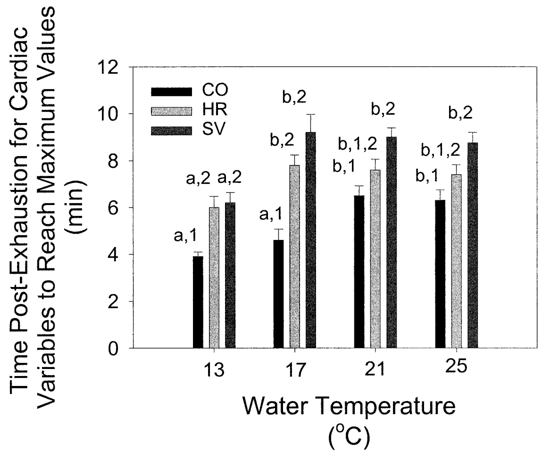

FIGURE 2.—Effects of water temperature on the time postexhaustion when the cardiac variables reached a maximal change from resting values during the recovery period for largemouth bass subjected to simulated angling in the laboratory. Data are means and standard errors. Dissimilar letters indicate significantly different ($P < 0.05$) values between temperatures for each of the cardiac variables: cardiac output (CO), heart rate (HR), and stroke volume (SV). Dissimilar numbers indicate significantly different ($P < 0.05$) values among cardiac variables within a specific temperature. Sample sizes are as in Figure 1.

of decreasing time to exhaustion with increasing water temperature ($r^2 = 0.07$, $P = 0.113$). During the exhaustive exercise largemouth bass HRs became more erratic, reflecting the inherent start–stop action associated with burst exercise. Once exhausted, fish were generally easy to handle although they typically thrashed for several seconds when first grasped by the lower lip. Severe bradycardia was induced when the fish were exposed to air and little movement took place during that 30-s period. The bradycardia was typified by reductions in HR of 50–70%. Upon return to the water, HRs were again variable as they accelerated and became tachycardic within 15 s.

Cardiac variables achieved their maximal change from resting levels within 10 min after being returned to the water. However, variation was observed among water temperatures ($F = 9.88$, $P = 0.002$) and the cardiac variables ($F = 35.27$, $P < 0.001$; Figure 2) but not for study site. For all water temperatures the maximal change in cardiac variables from resting levels generally occurred first in CO (~5 min), second in HR (~7 min), and last in SV (~8 min). Statistically, however, the time when HR and SV reached maximal change from resting did not differ. The time postexhaustion at which maximum CO occurred was significantly higher at 21°C and 25°C than at 13°C and 17°C (by ~2 min). This pattern was different from that observed for HR and SV. For both of these variables, the time at which SV and HR reached the maximal change from resting increased (by 2–3 min) between 13°C and 17°C but was constant thereafter (Figure 2).

The data visualized in Figure 3 are representative of the typical responses of cardiac parameters to exhaustive exercise and air exposure across the range of water temperatures that we examined. Although maximum changes in CO and HR varied with water temperature, SV did not (Figure 1). In

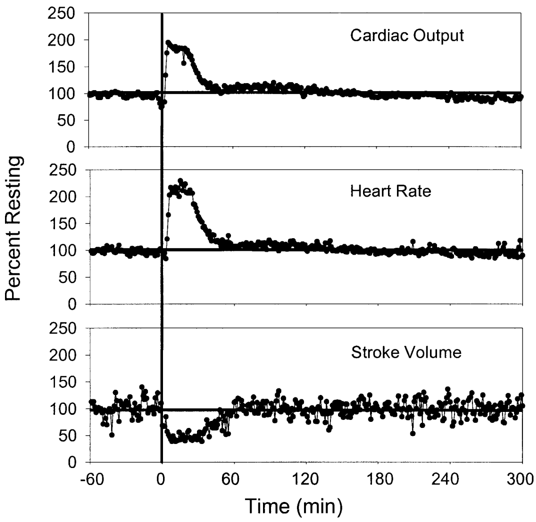

FIGURE 3.—Cardiac response to 150 s of exhaustive exercise and 30 s of air exposure in an individual largemouth bass tested at 25°C. Values plotted represent 1-min means; resting values equal 100%. The vertical shaded line represents the beginning of the simulated angling event that occurred at time 0.

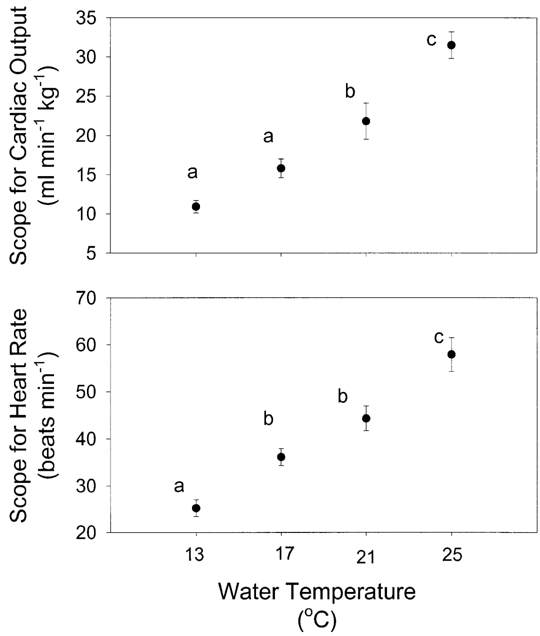

FIGURE 4.—Scope for cardiac output and heart rate for largemouth bass exposed to simulated angling; data are means and standard errors. Dissimilar letters indicate significant differences ($P < 0.05$) between temperatures. Sample sizes are as in Figure 1.

addition, no significant differences in study site were observed for maximum CO, HR, or SV (ANOVA, P's > 0.05). Maximum CO increased with water temperature ($CO_{max} = -4.59 + 2.95$ temp; $r^2 = 0.87$ and $P < 0.001$) and was significantly different across all water temperatures ($F = 76.44$, $P < 0.001$). Maximum change in HR also increased with water temperature ($HR_{max} = 6.15 + 4.00$ temp; $r^2 = 0.84$ and $P < 0.001$) and was significantly different across all water temperatures ($F = 61.47$, $P < 0.001$). Stroke volume differed from both CO and HR in that the maximal change in SV was a decrease, not an increase, in response to exercise. Stroke volume also differed from CO and HR in that differences in maximal change in SV among water temperatures were marginally or nearly significant ($F = 2.84$, $P = 0.056$, Figure 1). In addition, no relationship between water temperature and maximal change in SV was observed (temp; $r^2 = 0.002$, $P = 0.380$).

Scope for CO varied significantly with water temperature ($F = 35.85$, $P < 0.001$) but not study site (Figure 4). There was a significant trend between increasing water temperature and increasing cardiac scope ($CO_{scope} = -11.69 + 1.67$ temp; $r^2 = 0.75$ and $P < 0.001$. Scope for HR also generally differed among water temperatures ($F = 33.06$, $P < 0.001$) and there was a positive relationship among scope for HR and water temperature ($HR_{scope} = -9.52 + 2.65$ temp; $r^2 = 0.74$ and $P < 0.001$; Figure 4). Similar to scope for CO, scope for HR did not differ by study site ($P > 0.05$).

Cardiac recovery times did not vary with water temperature or site for any cardiac variables that we examined (Figure 5); however, significant differences were observed in the recovery times for the different cardiac variables ($F = 18.36$, $P < 0.001$). Cardiac output and HR returned to resting values generally within 130 min across all temperatures. Stroke volume consistently recovered more quickly (~110 min) than did CO and HR.

Discussion

Catch-and-release angling for largemouth bass and other fish species is a common activity in North America and elsewhere. Information on the sublethal effects of catch-and-release angling is limited for largemouth bass. Our study used measurements of cardiac activity to examine the effects of simulated exhaustive angling and short duration air exposure on largemouth bass across four water temperatures. The results have implications for understanding catch-and-release angling effects in this and other species and con-

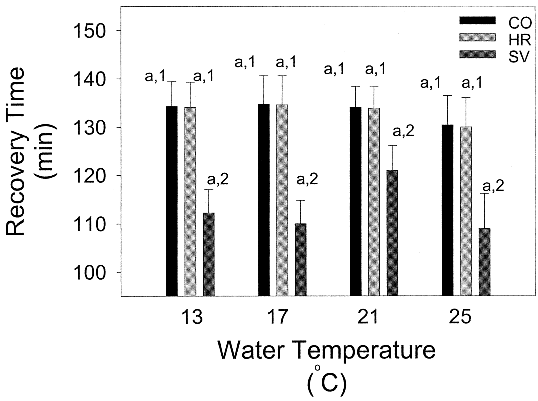

FIGURE 5.—Time required for largemouth bass cardiac variables—cardiac output (CO), heart rate (HR), and stroke volume (SV)—to return to resting levels following 150 s of exhaustive exercise and 30 s of air exposure; data are means and standard errors. Dissimilar numberss indicate significantly different ($P < 0.05$) values among cardiac variables within a specific temperature; the values for each of the cardiac variables were not significantly different between temperatures. Sample sizes are as in Figure 1.

tribute to our understanding of the basic cardiovascular performance of largemouth bass across a range of water temperatures.

Our data add to the scant information on resting cardiac values of largemouth bass across a wide range of water temperatures. Reynolds and Casterlin (1978) used the thermodilution technique to quantify cardiac output in largemouth bass; an approach that typically overestimates cardiac output (Farrell and Jones 1992). Their data collected at 12°C provided estimates of 44 $mL \cdot min^{-1} \cdot kg^{-1}$ for CO, 30 beats/min for HR, and 1.46 mL/kg for SV (Reynolds and Casterlin 1978). At 13°C our HR values were similar (~32 beats/min) to those of Reynolds and Casterlin (1978), but our CO and SV values at 13°C were about 50% lower than their values at 12°C. The first published study in which Doppler flow probes were used on largemouth bass examined the cardiac response of a single fish that was exposed to various tournament stressors in a live well at 26°C (Cooke et al. 2002c). However, due to interference from the boats motor and other electronic equipment, baseline shifts in voltage were observed (Cooke, personal observation), making the actual values presented unreliable and, thus, useful only for relative comparisons. More recently, Cooke et al. (2003) provided data on resting values at 3°C collected using Doppler flow probes in the laboratory. Resting values were 9.0 $mL \cdot min^{-1} \cdot kg^{-1}$ for CO, 7.6 beats/min for HR, and 1.22 mL/kg for SV. Values in our study (all at temperatures higher than 3°C) were consistently higher for CO and HR but lower for SV, probably because of ventricular hypertrophy at 3°C (Driedzic et al. 1996). Indeed, in our study RVMs were similar across a range of temperatures (RVMs about 0.07–0.08), but Cooke et al. (2003) observed RVMs at 3°C that were about 20% heavier than those in our study.

The resting cardiac variables we measured for largemouth bass generally fell within the same range as those for other temperate freshwater teleost fishes, such as rainbow trout *Oncorhynchus mykiss* (Brodeur et al. 2001), northern pikeminnow *Ptychocheilus oregonensis* (Kolok and Farrell 1994), and the largescale sucker *Catostomus macrocheilus* (Kolok et al. 1993). In addition, resting cardiac values for the congeneric smallmouth bass (Schreer et al. 2001) and, to a lesser degree, for the confamilial rock bass *Ambloplites rupestris* (Cooke et al. 2001) were similar to the values we obtained for largemouth bass. For example, at 16°C, resting cardiac output values of smallmouth bass (29.8 $mL \cdot min^{-1} \cdot kg^{-1}$) were similar to resting values for largemouth bass at 17°C (29.2 $mL \cdot min^{-1} \cdot kg^{-1}$). At 16°C, rock bass had lower cardiac output values (10.4 $mL \cdot min^{-1} \cdot kg^{-1}$) than both largemouth and smallmouth bass. At the same temperatures, rock bass HR exhibited values that were higher (48.7 beats/min) than largemouth bass (40.8 beats/min) and smallmouth bass (34.5 beats/min). Stroke volume differed the most among the three centrarchids, rock bass (0.18 mL/kg) exhibiting values that were about four times lower than largemouth bass (0.72 mL/kg) and smallmouth bass (0.87 mL/kg).

Resting values for HR in our study increased with temperature, similar to patterns observed across different taxa (see Farrell 1991b; Farrell and Jones 1992). There was a weak trend of increasing resting SV with temperature, but this trend was somewhat anomalous, considering that the increase in HR with temperature should have affected cardiac filling time and, thus, decreased end-diastolic volume (Farrell et al. 1996). This limit on cardiac filling time may be more apparent following exercise and at higher heart rates, as discussed below. There is clearly substantial interspecific variation in resting cardiovascular variables at a specific temperature, even within families, but in general, largemouth bass seem to display resting values that are within the range of the other temperate teleost fishes previously examined.

In our study, scope for cardiac output increased threefold between 13°C and 25°C, and scope for heart rate also followed a similar pattern, more than doubling between 13°C and 25°C. Cardiac scope is thought to be maintained or even increase with increasing water temperature until maximum cardiac output plateaus. At this point, resting cardiac output continues to rise, reducing available scope (Farrell and Jones 1992; Farrell et al. 1996; Schreer et al. 2001). In salmonids, maximal cardiac scope is consistent with maximal aerobic scope and swimming performance, and generally occurs at an optimum temperature (i.e., ~15°C in rainbow trout; Farrell 2002). In largemouth bass, this optimal temperature is much higher than observed in salmonids. Indeed, in our study, the highest temperature that we examined (25°C) actually had the largest cardiac scope. Similarly, pioneering research by Beamish (1970), suggested that swimming performance and aerobic scope for largemouth bass peaked at about 30°C and decreased substantially by 34°C.

Maximum heart rates for most teleost fishes appear to be about 120 beats/min (Farrell 1991a; Lillywhite et al. 1999). In our study, values approached but did not exceed this value at our highest temperature (25°C). Based upon these results and those of Beamish (1970), we predict that at temperatures slightly higher than 25°C, the cardiac scope would decrease as resting heart rates continued to increase with temperature and as the maximum heart rate plateaued (probably at ~120 beats per min). The same trend has also been observed in smallmouth bass at temperatures several degrees lower, reflecting the lower thermal optima of smallmouth bass (Schreer and Cooke 2002) relative to largemouth bass.

Maximal changes in cardiovascular variables for largemouth bass were generally similar to maximal values observed in other temperate freshwater fishes. For example, in our study, largemouth bass typically increased heart rate by 100–200% and cardiac output by 50–100%. Interestingly, however, largemouth bass stroke volume decreased about 50% across the range of temperatures that we examined. This level of increase in cardiac output is consistent with values observed in other temperate freshwater fishes (see Farrell 1991b). However, the findings of our study are somewhat anomalous, in that the increase is attributable to an increase in HR and the SV actually decreased. To date, the only clear example of reductions in SV following exercise in fish can be found in the congeneric smallmouth bass. In that species, SV generally decreased about 20% immediately following exercise but then increased to 150% of resting levels (Schreer et al. 2001). In our study of largemouth bass exposed to exercise and air, SV did not ever increase substantially above resting levels. Only decreases in SV in response to exercise and air were observed (Figure 3). The reduction in SV following exercise was probably due to limitations on cardiac filling time associated with high HR, and the negative subsequent effects on end-diastolic volume. It is somewhat anomalous, however, that across the range of temperatures, the maximal change in SV was similar. At 25°C, maximal change in SV was about 10% greater (i.e., lower SV) than the other temperatures suggesting that, at temperatures higher than 25°C, the increased maximal HR would further affect cardiac filling time and thus reduce SV. Threshold temperatures that negatively affect cardiac performance in largemouth bass have apparently not been reached in research conducted to date.

Disturbance through burst exercise results in an increased metabolic rate and consequently an increase in CO and one or both of its components, HR and SV (Farrell and Jones 1992). In our study, almost all of the change in cardiac output may be accounted for by alterations in heart rate (i.e., stroke volume always decreased and heart rate increased). Farrell (1991b) suggested that there is an evolutionary trend from volume-modulated to frequency-modulated cardiac output. This study is not the first account of frequency modulation among the centrarchid fishes (see Schreer et al. 2001; Schreer and Cooke 2002; Cooke et al. 2002a). Our data provide additional strong evidence of frequency modulation for some fish in the centrarchid family. Because some centrarchids tend to increase CO through changes in HR, opportunities may exist for using HR telemetry to study catch-and-release issues in free-swimming centrarchids, as has been done on Atlantic salmon *Salmo salar* (Anderson et al. 1998). Thorarensen et al. (1996) has criticized heart rate telemetry for estimating the metabolic rate of free-swimming fish. This criticism arises largely because of the use of heart rate telemetry to estimate the metabolic rate of volume modulators. Our data suggest that the use of heart rate transmitters to assess the metabolic rates of largemouth bass may be possible (see Cooke et al. 2002a) and would add a new dimension to research on the effects of catch-and-release angling on bass.

In our study, CO always reached maximal value before HR and SV, while HR was increasing and

SV was decreasing. This result, which is anomalous because CO is the product of those two components, was due to the fact that stroke volume changes were generally negative and heart rate values were generally positive. Stroke volume was generally lowest when heart rate was highest, probably reflecting the reduced time for cardiac filling (Farrell and Jones 1992). The thermal trends we observed in the time until maximum cardiac values were reached (i.e., generally reaching peak values more rapidly at 13°C than at other temperatures) did not coincide with the time required for cardiac variables to return to resting levels.

The time required for cardiac variables to return to preexercise levels was approximately 135 min. These results are consistent with the recovery of cardiac variables in other studies. For example, Schreer et al. (2001) exercised smallmouth bass briefly (~20 s) or exhaustively (~120–180 s) in a respirometer at 12, 16, and 20°C. They reported that cardiac variables for briefly exercised fish returned to preangling levels within 0–85 min, whereas exhaustively angled fish generally took longer to recover (20–210 min). The exhaustively angled fish were exercised for similar durations to fish in our study but were not exposed to air. Several recent studies by our group indicate that cardiac recovery duration is influenced greatly by air exposure; longer exposures lead to longer recovery periods in both rock bass (Cooke et al. 2001a) and smallmouth bass (Cooke et al. 2002c). In our study, air exposure duration was standardized to 30 s. Smallmouth bass exercised by manual chasing and then exposed to air for 30 s at 14°C, took about 120 min to recover (Cooke et al. 2002c). Similarly, rock bass exercised until exhaustion by manual chasing in 16°C water and then exposed to air for 30 s required between 70 and 130 min for all cardiac variables to recover (Cooke et al. 2001a). Thus, based on these collective data, centrarchid fish that are exercised to exhaustion in 12–25°C water and then exposed to air for 30 s, will generally exhibit full cardiac recovery by about 130 min postdisturbance. A study on a different family, Salmonidae, determined that free swimming Atlantic salmon equipped with HR transmitters required as much as 16 h for HR to recover from exhaustive exercise at both 8°C and 16°C (Anderson et al. 1998). In our study and other studies on centrarchid fish, SV typically returned to predisturbance levels more rapidly than HR and CO (Schreer et al. 2001). Heart rate and CO generally return to predisturbance levels at the same time, indicating again that these species are frequency modulators.

Across the range of water temperatures that we examined (13–25°C), no obvious temperature effects on recovery time were noted. Schreer et al. (2001) also reported that cardiac recovery time following burst exercise by smallmouth bass was not strongly influenced by water temperatures between 12°C and 20°C. Interestingly, however, Schreer et al. (2001) observed a trend towards expedited recovery at 16°C, suggesting an optimal recovery temperature. Recovery optima have also been documented for recovery of white muscle metabolites and energy stores (see Kieffer 2000). At extremely low water temperatures (3°C) largemouth bass may require longer to recover than at higher temperatures. Recovery times for largemouth bass at 3°C ranged from about 140–150 min (Cooke et al. 2003), approximately 20% longer than fish in our study. Furthermore, fish in that study were not exposed to air, an additional disturbance that probably would have prolonged recovery, as has been observed in smallmouth bass (Cooke et al. 2002c). Based upon these studies, it seems apparent that for centrarchid fishes temperature does influence cardiac recovery following exercise, although it may at extremely low (<13°C) or extremely high (>25°C) temperatures. Indeed, the range of temperatures that we examined (13–25°C) are within the tolerable range for largemouth bass.

Only one published study documents the physiological responses of largemouth bass to angling. In that study Gustaveson et al. (1991) noted blood chemistry changes that became more extreme with increasing water temperature. Their first blood samples were taken 1 h following release into a net pen. Most of these values had peaked by this time, but some values were higher at the next sampling interval (8 h). Our results are not directly comparable because Gustaveson et al. (1991) used different angling durations, protocols (e.g., unknown air exposure duration), and water temperatures. In a study of smallmouth bass catch and release, Kieffer et al. (1995) determined that white muscle disturbances were substantial following prolonged angling, but most variables recovered within 2–4 h. Air exposure has been identified as an additional source of disturbance to the physiology of fish. A blood chemistry study using cannulated rainbow trout revealed that the additive effects of exercise and air exposure created high levels of blood lactate and substantial acid–base disturbance (Ferguson and Tufts 1992). Additionally, air exposure caused collapse and adhesion of gill filaments and was correlated with increased levels of mortality (Ferguson and Tufts 1992). Cooke et al. (2000) angled nesting male largemouth bass from their nests and nonnesting males and exposed them to air for 30 s; locomotory activity levels remained depressed from preangling activity levels for about 1 h for nonnesting males and for more than 24 h for nesting males. Collectively, our research, combined with the growing body of other studies, suggests that largemouth bass angled to exhaustion between 13°C and 25°C and briefly exposed to air are capable of surviving and recovering from these types of stressors. However, higher (or possibly lower) water temperatures, extended air exposure durations, or other cofactors (e.g., disease) could magnify the disturbances, retard recovery, and possibly result in death.

A potential cause for variation in our study that is worth noting is the source of the test fish. Although fish were collected from similar habitats and with similar physiochemical characteristics, fish were collected from different latitudes and different watersheds, so local adaptations may be present. Indeed, largemouth bass have been shown to exhibit local adaptation at much smaller distances than those used here (Philipp and Claussen 1995; Cooke et al. 2001b). Fish were collected and experimented upon in central Illinois at 13°C and 17°C and in eastern Ontario at 21°C and 25°C, but all fish used in this study were the northern subspecies of largemouth bass. Interestingly, in our statistical analyses we determined that study site rarely contributed to the variation we observed in cardiovascular physiology. Only for resting HR did study site significantly contribute to the variation observed. Because we did not study fish in different latitudes at the same water temperature and during the same season, we are unable to quantitatively examine intraspecific cardiovascular performance, although we did consider site as a covariate in statistical analyses. Physiological characteristics may vary among populations and environments (Nelson et al. 1994), but the plasticity of cardiac output and other cardiac variables is unknown. Although differences in cardiac variables may exist among these populations, our study was not designed to explicitly test that hypothesis. Additional research on intraspecific variation in cardiovascular physiology would be useful to further explore this issue.

The results of our research on largemouth bass provide several conclusions for management. Recovery of cardiac variables were not influenced by water temperature, suggesting that, within the range of temperatures that we examined (13–25°C), largemouth bass are capable of reasonably rapid cardiac recovery (approximately 135 min). At slightly higher water temperatures, however, there may be severe limitations on cardiovascular performance and recovery that may result in magnified disturbance, protracted recovery, or possibly mortality (Schreer and Cooke 2002). Another management implication deals with air exposure. In our study, a short air exposure (approximately 30 s) following exercise was not lethal but probably delayed recovery, based upon comparisons with other published data (e.g., Cooke et al. 2002c). We suggest that air exposure duration for largemouth bass should be limited to 30 s and, if possible, avoided completely.

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