Low temperature cardiac response to exhaustive exercise in fish with different levels of winter quiescence

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Abstract

We examined the cardiac responses of different fish species to anaerobic exercise at low temperatures (3 °C). Three species of sympatric warmwater fish with perceived differences in winter activity were used for this comparative study: the winter-quiescent largemouth bass (*Micropterus salmoides*); the winter-active white bass (*Morone chrysops*); and the intermediately winter-active black crappie (*Pomoxis nigromaculatus*). Perceived differences in winter activity were reflected in cardiac responses; e.g. basal cardiac values were lowest for largemouth bass, highest for white bass, and intermediate for black crappie. In addition, cardiac recovery was most rapid for white bass, slowest for largemouth bass and intermediate for black crappie. When disturbed at low temperatures, largemouth bass and black crappie elevated cardiac output principally through increases in heart rate despite substantial decreases in stroke volume. Conversely, white bass principally used stroke volume modulation to change cardiac output. The results of this study indicate that different species respond differently to exercise at low temperatures. Management strategies should recognize that such variation exists and ensure that management decisions are based upon an understanding of the low temperature exercise physiology and winter biology of the species of interest.
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1. Introduction

The severity and longevity of winter in North America varies among regions, with different populations of a given species often being exposed to very different winter conditions depending upon their latitude. In the mid-latitude regions of sub-arctic North America, fish frequently experience water temperatures in lakes and rivers below 4 °C for several months during the winter (Power, 1997). For most fish species, water temperature is an important determinant of many behavioral attributes and physiological processes (Fry, 1971; Ultsch, 1989). Low water temperatures experienced during winter by fish generally lead to restricted food consumption (Hathaway, 1927), slow digestion rates (Fänge and Grove, 1979),

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reduced swimming abilities (Beamish, 1978), limited mobility and activity (Fry, 1971), and a general reduction in metabolism (Fry, 1971; Brett and Groves, 1979) and other physiological processes. Despite general patterns of reduced activity in the winter, substantial interspecific variation does exist (i.e. degree of activity or quiescence) (Crawshaw, 1984). Although studies have documented various aspects of the winter ecology of some temperate freshwater fish (e.g. salmonids; Cunjak and Power, 1986; Cunjak, 1996), the winter ecology of most fishes is generally poorly understood.

One of the most robust indicators of metabolic rate in fish is cardiac output and its components, heart rate and stroke volume (Farrell and Jones, 1992). As with most physiological processes, these cardiac parameters are intimately linked to water temperature, usually being lower at cold temperatures and higher at warmer temperatures (Farrell, 1984, 1996a, 2002). Departures from this pattern are rare but stroke volume may be higher at lower temperatures in some fish species (Driedzic et al., 1996). Investigations of cardiac parameters at temperatures below 5 °C in fish have been restricted to species that occupy Antarctic regions (e.g. Axelsson et al., 1992; Macdonald, 1997). Temperate investigations have examined cardiac activity at cool water temperatures but these are generally in the 5–12 °C temperature range (see Kolok and Farrell, 1994; Webber et al., 1998), several degrees warmer than the water temperatures occupied by many fish in the winter.

Additionally, there is also little known about the response of fish to anaerobic exercise at winter water temperatures (Kieffer, 2000). Sustained swimming and recovery from burst swimming at low temperatures require support from the cardiovascular system to deliver oxygen and transport nutrients and waste products to and from skeletal muscle (Driedzic et al., 1996). The ability of fish to perform anaerobically in the winter is important for several biological activities such as predator avoidance and food acquisition, as well as to survive environmental disturbances (e.g. adjustment to ice dynamics including frazil ice and hanging dams, and variable water flows). Ability to respond to exercise in the winter is also important for coping with human induced disturbance in the form of recreational catch-and-release angling.

Three species of closely related sympatric warmwater fish common in sub-arctic North America are largemouth bass (*Micropterus salmoides*), white bass (*Morone chrysops*), and black crappie (*Pomoxis nigromaculatus*). Each of these species, has different levels of winter activity as reflected in feeding, movement rates, catchability, and metabolism. Largemouth bass are sluggish at water temperatures below 8 °C (Johnson and Charlton, 1960), leading to the notion that they are dormant in the winter (Crawshaw, 1984; Lemons and Crawshaw, 1985). Furthermore, during the winter largemouth bass are rarely captured by anglers (Scott and Crossman, 1973), cease feeding in both laboratory (Johnson and Charlton, 1960) and field conditions (Keast, 1968a; Sullivan, 1985), exhibit substantial reductions in swimming performance (Beamish, 1970; Cooke et al., 2001a), and undertake very little movement (Demers et al., 1996; Raibley et al., 1997). In contrast, white bass remain much more active in the winter. Evidence supporting that supposition consists of their relative ease of capture by anglers (Scott and Crossman, 1973; Jenkins and Burkhead, 1994), their continued food consumption (Willis et al., 2002), and their mobility (Beck and Willis, 2000). Black crappie are intermediate to these two species in activity during the winter. Despite reducing food consumption substantially during the winter, black crappie continue to forage (Pearse, 1919; Keast, 1968b) and are frequently targeted and occasionally captured by anglers (Keast, 1968b; Scott and Crossman, 1973).

The objective of this study was to compare the low temperature cardiac response to exhaustive exercise in three species of fish with different winter activity levels; largemouth bass which are dormant in the winter, white bass, which are relatively active during the winter, and black crappie which exhibit intermediate winter activity levels. We hypothesized that winter activity levels of the fish would correspond to patterns in cardiac response to exercise. Specifically, we hypothesized that more winter active fish (i.e. white bass) would have higher basal cardiac values, take longer to exhaust, and recover most rapidly relative to species with intermediate winter activity (black crappie) and winter quiescent species (largemouth bass).

2. Materials and methods

2.1. Study animals

All fish used for this study were captured from Coal Dock Cove, an off-channel area of the La

Table 1
Meristics and basal cardiac parameters for white bass, black crappie, and largemouth bass at 3 °C

Parameter	White bass	Black crappie	Largemouth bass
N	10	9	12
Total length (mm)	311 ± 7[a]	234 ± 13[b]	333 ± 4[a]
Mass (g)	388 ± 30[a]	222 ± 46[b]	611 ± 38[c]
AVM (g)	0.368 ± 0.029[a]	0.198 ± 0.030[b]	0.488 ± 0.017[c]
RVM	0.095 ± 0.003[a]	0.097 ± 0.006[a]	0.082 ± 0.004[a]
Diameter of ventral aorta (mm)	1.46 ± 0.05[a]	1.22 ± 0.05[b]	1.82 ± 0.06[c]

All values are means ± 1 S.E. Dissimilar letters indicate significantly different ($P < 0.05$) values among species.

Grange Reach, a 125.6-km segment of the Illinois River, near Havana, Illinois. Coal Dock Cove is a constructed body of water, contiguous with the main river channel at some time during most years, but is subject to dewatering or isolation from the main channel at low river levels. The cove has abundant populations of largemouth bass, black crappie, and white bass and provides a secure site that is monitored continuously for temperature. Average temperatures at the site range from approximately 1–6 °C during the month of December when the fish were captured. Additional site descriptions are included in Raibley et al., (1997).

Individuals ($N = 9$–12) of each species (Table 1) were captured using a pulsed DC electrofishing boat and held at the Illinois Natural History Survey Aquatic Research Laboratory for a minimum of five days prior to experimentation. Water temperatures at time of capture were 3 ± 1 °C. Fish were held under natural photoperiod conditions in a 3000 l flow-through tank continuously supplied with pond water, also at 3 ± 1 °C. Fish were thus acclimated to natural winter conditions including slight diel variation.

2.2. Surgical procedure and cardiac output apparatus

Each fish was anaesthetized prior to surgery with 60 mg clove oil l^{-1} (emulsified with ethanol, 9:1 ethanol/clove oil) for approximately 8 min, until the fish had lost equilibrium and was non-responsive. An anaesthetized fish was placed on its side on a wetted sponge. The anaesthetized state was maintained during surgery by irrigating the gills with water containing a maintenance concentration of anaesthetic (30 mg clove oil l^{-1}). Surgical procedure was identical to that described by Schreer et al. (2001). Briefly, a flexible silicone cuff-type Doppler flow probe (subminiature 20

MHz piezoelectric transducer: Iowa Doppler Products, Iowa City, Iowa, USA), sized to match the diameter of the vessel, was placed around the aorta. The cuff was secured with a single suture and additional sutures were used to secure the wire to the body wall. The entire procedure took 15–30 min for each fish and due to the frigid water temperatures and subsequent loss of finger dexterity usually required two surgeons.

A flowmeter (545C-4 Directional Pulsed Doppler Flowmeter: Bioengineering, The University of Iowa, Iowa City, Iowa, USA) and a digital strip-chart recorder (LabVIEW, Version 4.0.1, National Instruments Corporation, Austin, Texas, USA) were used to monitor cardiac function. The Doppler transducer emits a pulsed sonic signal and due to Doppler shift, when the signal is reflected from a moving object in the blood (e.g. a red blood cell), a shift in the signal frequency is observed. This shift in frequency represents a velocity and is measured as a change in voltage. Peaks in voltage (velocity) indicate individual heart beats, and counting peaks per unit time yields heart rate. The mean voltage per unit time is an index of flow or cardiac output. Flow can also be calculated directly in ml time^{-1} (see post-mortem calibration section). Cardiac output divided by heart rate yields stroke volume.

2.3. Exhaustive exercise protocol

Following surgery, individual fish were placed into a 70 l tank (50×50 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. A darkened area covering approximately 30% of the tank provided cover and ensured that the fish were not disturbed by general laboratory activity. The experimental tanks were continuously supplied with pond water at 3 ± 1 °C.

To simulate exercise, fish were chased in the tank by hand (Cooke et al., 2001b) until they reached exhaustion (the fish would no longer swim and would lose equilibrium). Cardiac parameters were recorded continuously for at least 1 h prior to the exercise simulation (the resting period), during the exercise simulation, and for at least 6 h post-exercise (the recovery period).

2.4. Postmortem calibrations

Following experimentation, fish were euthanized with an overdose of anaesthetic (180 ppm clove oil), and a post-mortem calibration was conducted to convert Doppler shift (in Volts) to actual blood flow (ml min^{-1}) (Cooke et al., 2001b). For this calibration, the head, including the pericardial cavity, was separated from the rest of the fish. The sinus venosus, atrium, and ventricle were removed and the bulbus arteriosus was catheterized with tubing (PE 120) for perfusion of the ventral aorta. Using a constant infusion pump (Harvard Apparatus, South Natick, Mass, USA), anticoagulated pig blood was perfused through the aorta to calibrate the probes over a range of flow rates encompassing those recorded during the trials. Reference flow rates were analyzed with linear least squares regression. The ventricles were patted dry and weighed to the nearest 0.001 gram with weights reported as absolute (AVM) and relative (RVM) ventricular mass. Ventral aorta diameter was determined from the Doppler cuff lumen (to the nearest 0.1 mm) that was used for each fish.

2.5. Data analysis

To determine recovery times, cardiac traces for each fish were adjusted to resting (100%) and evaluated visually. A fish was considered to be recovered when values returned to resting and became stable (within 10% of resting values; Schreer et al., 2001). Maximal disturbance was determined as the greatest change in a cardiac parameter (either positive or negative) during the recovery period. One-way analysis of variance (ANOVA) and the conservative Tukey post-hoc test were used to test for differences among species. All tests were conducted using Systat V 7.0 and significance was evaluated at $\alpha = 0.05$. All values presented represent means $\pm$ S.E.

3. Results

Meristics data for fish used in this study are presented in Table 1. The AVM varied significantly among species (ANOVA, $P < 0.05$) (Table 1), with largemouth bass hearts weighing the most, black crappie hearts the least, and white bass hearts an intermediate amount. When mass corrected, the RVM did not vary among species (ANOVA, $P > 0.05$) (Table 1). The diameter of the ventral aorta varied significantly among species (ANOVA, $P < 0.05$) (Table 1) and was largest for largemouth bass, smallest for black crappie, and intermediate for white bass. As expected, basal cardiac parameters (cardiac output, heart rate, and stroke volume) at 3 °C were low for all three species. The basal cardiac output values for white bass (16.7 ± 3.4 ml/min/kg) were significantly higher than largemouth bass (9.0 ± 0.7 ml/min/kg) (ANOVA, $P < 0.05$, Fig. 1). Cardiac output of black crappie (12.3 ± 2.0 ml/min/kg) was intermediate and not significantly different from the other two species. Basal heart rate values were similar between white bass (15.1 ± 0.9 beats/min) and black crappie (13.3 ± 0.7 beats/min) (ANOVA, $P > 0.05$), but significantly lower (by approximately 50%) for largemouth bass (7.6 ± 0.3 beats/min) (ANOVA, $P < 0.05$, Fig. 1). Basal stroke volume values were not significantly different among all three species (ANOVA, $P > 0.05$). Stroke volume of white bass was 0.98 ± 0.23 (ml/kg), black crappie was 0.95 ± 0.15 (ml/kg), and largemouth bass was 1.22 ± 0.07 (ml/kg) (Fig. 1).

The length of time each species took to become exhausted varied somewhat among species. White bass exhausted in similar durations (160 ± 8.51 s) to both of the other species (ANOVA, $P > 0.05$). Black crappie exhausted significantly more rapidly (149.89 ± 8.89 s) than did largemouth bass (179.25 ± 6.47 s) (ANOVA, $P < 0.05$). Because the fish were exercised to exhaustion, recovery times were protracted and ranged from approximately 80–140 min for each of the cardiac parameters (Fig. 2). Recovery times were significantly different among all species for each of the cardiac parameters (ANOVA, $P < 0.05$, Fig. 2). White bass cardiac parameters recovered most rapidly (usually by 80 min); largemouth bass recovered most slowly (usually by approximately 140 min); and black crappie recovery took intermediate periods of time (usually by 100 min).
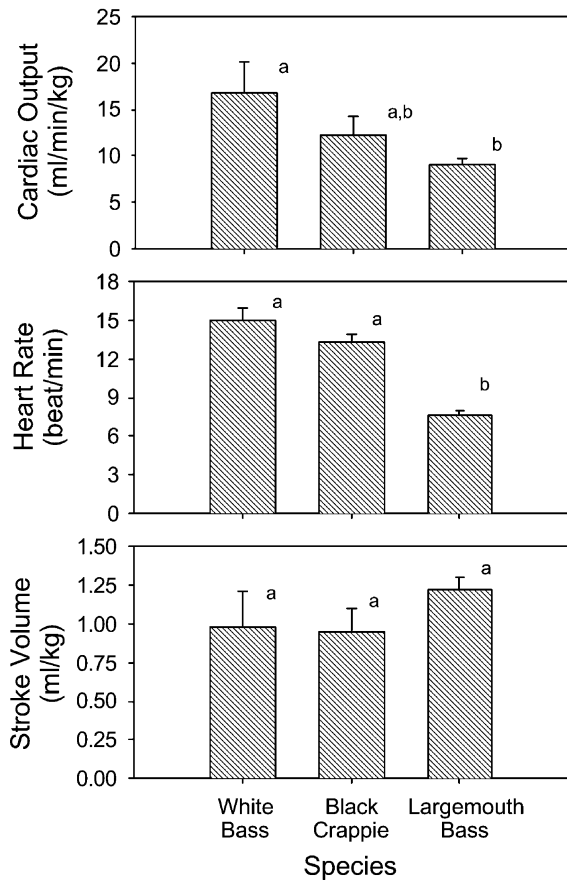
Fig. 1. Panel graph of basal cardiac values for white bass, black crappie and largemouth bass at 3 °C. All values are means±S.E. Dissimilar letters indicate significant differences ($P < 0.05$).

The maximum cardiac disturbances (% change from basal) during recovery varied among species for heart rate and stroke volume, but not cardiac output. Mean maximal disturbance of cardiac output was generally 150% for all species (ANOVA, $P > 0.05$) (Fig. 3). Heart rate increases were proportionally the lowest for white bass ($\sim 140\%$), intermediate for black crappie ($\sim 225\%$), and highest for largemouth bass ($\sim 425\%$), values that were significantly different among species (ANOVA, $P < 0.05$, Fig. 3). Maximal stroke volume disturbance was similarly low for black crappie and largemouth bass ($\sim 75\%$) (ANOVA, $P > 0.05$), whereas white bass were significantly higher than both of the other species ($\sim 150\%$) (ANOVA, $P < 0.05$, Fig. 3). The relative contributions of heart rate and stroke volume to the factorial exercise induced change in cardiac output varied
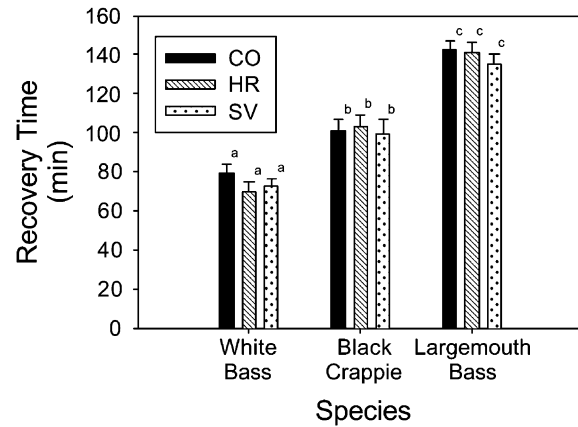

Fig. 2. Cardiac recovery times following exhaustive anaerobic exercise of white bass, black crappie and largemouth bass at 3 °C. All values are means±S.E. Dissimilar letters indicate significant differences ($P < 0.05$).

among species (see Fig. 4 for equation). For largemouth bass the relative contributions to the change in cardiac output was 124% for heart rate and -24% for stroke volume. Black crappie values were more extreme, 156% of the increase in cardiac output being attributed to heart rate and -56% to stroke volume. White bass exhibited a more typical pattern with heart rate contributing less (45%) to the change in cardiac output than stroke volume (55%). The scope for cardiac output varied among species, but was marginally non-
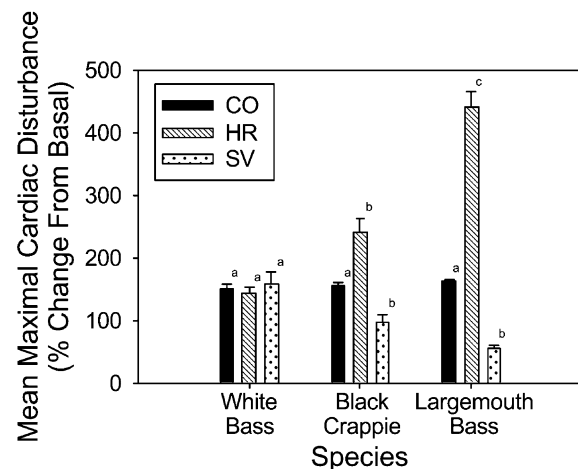

Fig. 3. Mean maximal change in cardiac parameters over resting values (100%) during recovery from exhaustive anaerobic exercise. Values are presented for white bass, black crappie and largemouth bass at 3 °C. All values are means±S.E. Dissimilar letters indicate significant differences ($P < 0.05$).
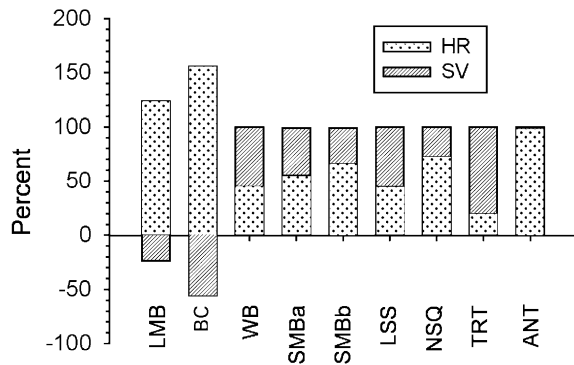
Fig. 4. The percentage contribution of heart rate (HR) and stroke volume (SV) to the exercise induced change in cardiac output in eight fish species. Data for largemouth bass (LMB), black crappie (BC), and white bass (WB), are for 3 °C and are from this study. Other data are from the literature; smallmouth bass (SMB) are for 12 °C for briefly (SMBa) and exhaustively (SMBb) exercised fish from Schreer et al. (2001); largescale sucker (LSS) exercised at 5°C from Kolok et al. (1993); northern squawfish (NSQ) exercised at 5 °C from Kolok and Farrell (1994); rainbow trout (*Oncorhynchus mykiss*) (TRT) exercised at 9–10.5 °C from Kiceniuk and Jones (1977); general pattern of several Antarctic (ANT) fish below 1 °C from Axelsson et al. (1992). Relative contributions calculated using a modified version of the formula outlined in Thorarensen et al. (1996) (e.g.%contribution = 100. log $(HR_{max}/HR_{rest})/(\log(HR_{max}/HR_{rest}) + \log(SV_{max}/SV_{rest}))$. Maximum change substituted for maximum increase when stroke volume decreased.

significant (ANOVA, $P > 0.05$). Mean scope for cardiac output was 5.4 ± 1.5 ml/min/kg for largemouth bass, 7.0 ± 1.9 ml/min/kg for black crappie, and 9.1 ± 1.6 ml/min/kg for white bass.

4. Discussion

The basal cardiac measurements indicate that, at winter temperatures, white bass are the most metabolically active of the three species examined, largemouth bass are the least active, and black crappie are intermediate. The findings of this study are in general agreement with the perceived levels of winter activity and with the hypothesis that more active fish at a given temperature have higher basal cardiac values than less active ones. The basal cardiac values that we report here are novel in several respects. First, these data represent some of the lowest cardiac output and heart rate levels reported, due in large part to the very low water temperatures. Secondly, these data are also the first reliable cardiac performance data for these species of fish. Only largemouth bass had been previously

examined, and those authors (Reynolds and Casterlin, 1978) used the thermodilution technique, an approach that typically overestimates cardiac output (Farrell and Jones, 1992). Their data were collected at 12 °C and were much higher than the data we collected at 3 °C.

Recovery from anaerobic exercise is severely limited at low temperatures, however, substantial interspecific variation may exist (Kieffer, 2000). In our study, there were significant interspecific differences in the recovery times. In general, each of the cardiac parameters for the fish examined followed the graded trend of expected winter activity. White bass recovered more quickly than black crappie and largemouth bass, respectively. Although temperature influences the storage, utilization, and recovery of metabolic fuels, the largest effects are on the production and removal of metabolic end-products (Kieffer, 2000). Indeed, with the exception of PCr, low water temperature retards the recovery rates of energy stores (ATP and glycogen) (Kieffer et al., 1994; Wilkie et al., 1997; Kieffer, 2000) as well as the clearance of lactate (Wilkie et al., 1997). It is important to note, however, that the cardiac parameters we examined are not direct indicators of trends in metabolic recovery. Indirectly, increased cardiac performance (i.e. the movement of more blood per unit time) will deliver oxygen to deal with the oxygen debt (Gaesser and Brooks, 1984) and will facilitate the removal of the byproducts (Satchell, 1991). Based on this strong interrelationship among cardiac performance and the clearing of byproducts, we suggest that white bass appear to be better adapted to low temperature anaerobic exercise as evidenced by the more rapid cardiac recovery than both black crappie and largemouth bass.

Many, but not all fish species exhibit increases in relative ventricular mass when exposed to low temperatures (Driedzic et al., 1996). In our study, relative ventricular mass was similar across species ($\sim 0.1\%$ of total body mass). Cold adaptation in the winter quiescent largemouth bass (Kolok, 1992) results in increased relative ventricular mass, perhaps to maintain performance. Although there is sufficient evidence that largemouth bass exhibit increases in relative ventricular mass, empirical evidence for the anticipated increase in stroke volume to maintain cardiac output is still somewhat rare. Forthcoming data that include resting stroke volumes of largemouth bass at 13, 17, 21

and 25 °C that are all between ~ 0.7 and 0.8 ml/ kg (Cooke Unpublished Data), provide additional evidence that stroke volume is increased at low temperatures likely due to the increase in relative ventricular size. Interestingly, this increase in stroke volume appears to be most relevant in maintaining cardiac output at the resting levels when largemouth bass heart rates are extremely low (~ 9 BPM). Indeed, we observed decreases in stroke volume and substantial increases in heart rate in response to exercise to affect an increase in cardiac output and subsequent delivery of oxygen to tissues when exercised at 3 °C.

Recovery from 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). Farrell (1991) suggested that there is an evolutionary trend from volume-modulated to frequency-modulated cardiac output. This phenomenon can be observed in the comparison of white bass, black crappie, and largemouth bass; largemouth bass increased cardiac output through a massive increase in heart rate ($\sim 425\%$) despite a reduction in stroke volume; black crappie increased heart rate ($\sim 225\%$), although stroke volume did not change; white bass increased heart rate to a lesser extent ($\sim 140\%$), but stroke volume increased more ($\sim 150\%$). The magnitude of the reduction in stroke volume found in largemouth bass and black crappie in response to anaerobic exercise is unique. This study is not the first account of frequency modulation among the centrarchid fishes (the family in which largemouth bass and black crappie are taxonomically classified; See Cooke et al., 2001b; Schreer et al., 2001; Schreer and Cooke, in press). Until these recent studies, frequency modulation was thought to be restricted to the very high performance tuna and some Antarctic fishes (Farrell, 1991, 1996b). The majority of fish have a 40 to 60% contribution from SV (Farrell and Jones, 1992). Our study provides evidence that frequency modulation may be ubiquitous within the Centrarchidae family (Sunfish family). Interestingly, the white bass which are classified taxonomically in the Percichthyidae (temperate bass family), are also members of the same order as the Centrarchidae [i.e. Order Perciformes (Percomorphi)], yet do not appear to be frequency modulators. Additional studies exploring the presence of this trait in the Perciformes and the ubiquity and plasticity of the response to different

stressors (e.g. thermal change, air exposure, exhaustive exercise, forced swimming) are required.

Several studies by Kolok and associates have provided the first evidence for variation in physiological performance at low water temperatures relative to the winter activity levels of the fish species. Kolok et al. (1993) and Kolok and Farrell (1994) and suggest that in winter quiescent fish species, the relationship between water temperature and scope for cardiac output (in addition to other cardiac parameters) may differ from that of winter active species. Specifically, in winter quiescent fish, scope for cardiac output may decrease with temperature, whereas in winter active species, it may not change. Our values varied by up to 40% among species with largemouth bass, the least active species having the lowest scope for cardiac output. The highest values were obtained from the active white bass. From these examples, there appears to be a trend with increasing scope at a lower water temperature for species that are more active in the winter, consistent with previous findings.

Understanding the behavioral and physiological effects of exposure to low water temperatures for extended periods of time such as those encountered during winters in North America also have implications for conservation and management. Indeed, while the conservation of energy is essential for most fish in the winter (Ultsch, 1989), reduced activity/mobility can also be detrimental because predator avoidance and food acquisition are important aspects of life during any season. Environmental variation and habitat structure also greatly influence survival and activity throughout the winter season. Winter habitat choice is based on minimizing energy expenditure (Carlson, 1992) and protection from adverse physiochemical conditions (e.g. ice, low oxygen, winter freshets) and access to refugia (Cunjak, 1996). Ice (surface, frazil, and anchor ice) is common in many rivers and can reduce winter habitat space and suitability (Power et al., 1993). Habitats that encompass a variety of microhabitats are required to conserve both winter active and winter quiescent fish. We presume that fish exhibiting different winter activity levels will face different threats during the winter period. For example, winter active fish (e.g. white bass) must acquire sufficient food resources and be able to move freely among different habitats. Winter quiescent fish such as largemouth bass

require refugia that are consistent with minimizing energy expenditure and protection from adverse conditions. In addition to avoiding predators and capturing food, low temperatures also have the potential to place limits on a fish's ability to perform and recover from catch-and-release angling induced anaerobic exercise (Kieffer, 2000). Among all species, optimal temperatures for performance and recovery likely exist, with both extremes (i.e. high temperature vs. low temperature) resulting in performance impairments and delayed recovery (Schreer et al., 2001; Farrell, 2002). Our results indicate that different species respond differently to exercise at low temperatures and that management strategies should recognize that such variation exists and ensure that management decisions are based upon an understanding of the low temperature exercise physiology and winter biology of the species of interest.

Acknowledgments

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