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Effects of incremental increases in silt load on the cardiovascular performance of riverine and lacustrine rock bass, *Ambloplites rupestris*

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"Capsule": *Cardiovascular compensation in fish exposed to elevated levels of silt.*

Abstract

Rock bass (*Ambloplites rupestris*) are a widespread centrarchid species with both riverine and lacustrine populations. After precipitation events, rivers often carry elevated silt loads, where as lakes generally remain free from suspended silt and sediment. To examine the physiological effects of silt on rock bass, we conducted a series of experiments using fish from Lake Opinicon and the Grand River in Ontario. Ultrasonic Doppler flow probes were surgically affixed around the ventral aorta to monitor cardiovascular performance. After recovery from surgery replicated treatment groups were exposed to incremental increases in silt load (made from bentonite slurry), while cardiac output and its two components, heart rate and stroke volume, were measured simultaneously. Although both groups of rock bass responded significantly to low concentrations of silt (10 NTU), the response by riverine rock bass was rapidly extinguished by acclimation or physiological adjustment. Compensatory mechanisms to minimize cardiac (and respiratory) disruption attributable to increases in suspended silt appear to be inherent in rock bass of riverine origin. These fish appear to fully compensate for interference in gas exchange at the gill surfaces 60 min after initial exposure. In contrast, individual lacustrine rock bass were highly variable in their response to elevated silt concentrations. Changes in stroke volume and cardiac output suggested no clear compensatory mechanism or strategy to cope with increased silt levels.

Keywords: Silt; Sediment; Cardiac output; Respiratory impairment; Acclimation; Rock bass

1. Introduction

Suspended sediment, or silt, is an ubiquitous feature in many aquatic environments and heavy silt loads have undoubtedly been a major selective pressure during the evolution of many fish species (e.g., Hubbs, 1940; Horkel and Pearson, 1976). Several recent reviews (i.e., Kerr, 1995; Anderson et al., 1996; Henley et al., 2000) have examined the role of silt on fish and have concluded that the majority of the research has focused on the ecological consequences of increased silt load (e.g., elimination of suitable spawning habitat, disruptions in feeding, reduced growth), with few studies examining the physiological consequences of silt on fish. Physiological effects of silt include loss of respiratory capacity of gill surfaces (Waters, 1995), interference with excretory function of the gills, and excessive mucus secretion (Ellis, 1944). Elevated silt loads do not generally result in direct mortality except during early life history stages (Cordone and Kelley, 1961). Other than respiratory impairment, sublethal effects of elevated turbidity include avoidance, reduced feeding and growth, reduced tolerance to disease and toxicants, and physiological stress (Lloyd, 1987).

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Since cardiovascular variables are inextricably linked to the metabolic rates of fish, they can be used to monitor how fish respond to different stressors (Webber et al., 1998; Brodeur et al., 2001). Researchers have used cardiovascular performance as an indicator of how fish respond to variations in environmental conditions including water temperature (Farrell et al., 1996; Schreer and Cooke, 2002), pH (Brodeur et al., 1999), salinity (Claireaux et al., 1995), and hypoxia (Farrell, 1982). No studies to date, however, have examined the cardiovascular response of fish to variations in silt, despite previous research that suggests the respiratory system can be compromised by elevated silt loads (Ellis, 1944; Waters, 1995).

Most research on the effects of silt has focused on salmonids. Wallen (1951), however, described effects of elevated turbidity on warmwater fishes and suggested that because warmwater streams are often muddy, fish that inhabit these areas may have evolved behaviourial or physiological mechanisms that allow them to tolerate periodically high concentrations of suspended sediment. Rock bass (*Ambloplites rupestris*) are a common warmwater species with populations that occur in both lacustrine and riverine environments. Recent research suggests that there is a large degree of phenotypic plasticity and/or genetic differentiation among populations of rock bass that inhabit different environments, and these two characteristics produce morphological variation in response to disparate selection pressures associated with different environmental conditions (Brinsmead and Fox, 2002).

Riverine environments are inherently more heterogeneous than lacustrine environments with regard to habitat types and environmental conditions. They are also subject to a large number of unpredictable and potentially catastrophic events (Baltz and Moyle, 1982; Ryder and Pesendorfer, 1982). In strong contrast to the generally stable, homogenous conditions in lakes, riverine environments are more hydrodynamically challenging (Baltz and Moyle, 1982; McLaughlin and Grant, 1994). Suspended silt is one environmental factor that varies strongly between riverine and lacustrine environments. Silt pulses can be quite common in streams and rivers, especially in regions where land use practices lead to erosion, runoff, and variable flow regimes (Kerr, 1995). Considering major differences in silt loading between riverine and lacustrine environments, we predict that riverine rock bass will exhibit demonstrable cardiovascular adaptations that allow them to cope with variable silt loads. Specifically, we expect the cardiac performance of riverine rock bass to be less affected by increases in silt load than lacustrine fish which are coping with an unfamiliar stressor. We also predict that the cardiac response among individual riverine fish will be less variable than among individual lacustrine fish.

The objectives of this study were to (1) examine cardiovascular responses of rock bass to increasing and excessive silt loads and (2) compare cardiovascular responses among riverine and lacustrine rock bass. To accomplish this, we monitored the cardiovascular performance of rock bass from a lake and a river in Southern Ontario after exposing them to increasing silt loads over a 2 h period. Our overall goal was to define the implications of excessive silt in aquatic environments in relation to environmental management and conservation of fish species.

2. Materials and methods

2.1. Study site and animals

Rock bass for these experiments were angled from Lake Opinicon in Eastern Ontario (44° 34′ N, 76° 20′ W, $n=10$, TL (mean ± SE) = 196 ± 8 mm, mass = 136 ± 9 g) and the Grand River near Cambridge in Southwestern Ontario (43° 25′ N, 80° 25′ W, $n=11$, TL = 170 ± 4 mm, mass = 89 ± 6 g) in June and July 2000. We were not concerned that differences in body size between riverine and lacustrine rock bass would affect the results of these experiments because, (1) the size range of fish used in this study was reasonably small, (2) unpublished research from our group indicates that heart rate of rock bass does not vary across this size range, and (3) unpublished data from our group examining the cardiac output of rock bass across a gradient of water temperature indicated that size was not required as a covariate and did not alter the performance of the ANOVA model.

Typical habitat occupied by rock bass in Lake Opinicon included shallow littoral areas with cobble and boulder substrate and large patches of aquatic macrophytes. In the Grand River, rock bass generally occupied areas near the shoreline with rock and cobble substrate, and were particularly abundant immediately downstream from a low-head weir within the study area (Bunt et al., 2001). Prior to experimentation, fish were held without food in flow-through tanks containing either lake or river water for at least 24 h and no more than 3 days.

3. Surgery and instrumentation

Surgical procedures and the equipment used to measure cardiac output are described in detail elsewhere (Cooke et al., 2001; Schreer et al., 2001). Briefly, at least 24 h post-angling, each rock bass was anaesthetized with 60 ppm clove oil (9:1 ethanol emulsifier:clove oil) until fish lost equilibrium and was non-responsive. Water containing a maintenance concentration of anesthetic (30 ppm 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, USA), 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, USA) and a digital strip-chart recorder (LabVIEW, Version 4.0.1, National Instruments Corporation, Austin, Texas, USA) 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 particle velocity and is recorded as a change in voltage. Peaks in voltage (velocity) represent individual heart beats. 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 cardiac output (CO). Dividing CO by heart rate (HR) yields stroke volume (SV). Difficulties with some postmortem calibrations led us to focus on heart rate rather than including SV and CO for baseline comparisons. Shifts in voltage, however, can still be used to provide an index of relative change in SV and CO, without information on actual SV or CO.

4. Experimental protocol

Following surgery, each fish was allowed to recover for 24 h in one of four plastic tanks (0.3×0.5×0.5 m) with 20 l of lake or river water, aeration, a line for introducing silt and a second line for drawing water samples (Fig. 1). The post-surgical recovery period was sufficient in duration based on previous work that resulted in no post-surgical changes in cardiac output of smallmouth bass (*Micropterus dolomieu*) over a one week period (Schreer et al., 2001). We have similar results for largemouth bass (*Micropterus salmoides*) that has yet to be published where four fish were monitored for up to 10 days after surgery. One of the main factors contributing to our ability to use short recovery times with bass is the relative ease with which we can conduct the surgeries on these fish. The surgery requires less than 15 min and most of this time is spent suturing the cuff leads to the body wall of the fish. Unlike other species, we have almost 100% survival with this surgery and there is no blood loss. Blood loss may be one of the main factors that determines the duration of the recovery period. Furthermore, in a recent study conducted in our lab, we exposed bass to multiple extended doses of clove oil anesthetic for up to 3 h. Cardiac recovery was complete within 2 h despite the fact that this duration of anethesia was several times longer than that used for these experiments. Therefore, we are confident that fish responded the same way in our experiments as they would have if we had waited 48 h or 1 week prior to experimentation.

Due to the sensitive nature of wild fish, experiments were conducted with researchers and fish in separate rooms, and care was taken to minimize sound production and vibration. We chose bentonite as a surrogate for naturally occurring silt because it is non-toxic, relatively pure (i.e., no contamination that could confound results), and readily available. Furthermore, comparable experiments have been conducted using bentonite to investigate effects of turbidity on the respiratory efficiency of other centrarchid species (e.g., Horkel and Pearson, 1976). The aerator was used to ensure that oxygen levels were sufficient to support rock bass for the duration of the experiment, and to keep the bentonite in suspension. Each experiment was conducted at 18–21 °C and began with the collection of 10 min of baseline data prior to the initial introduction of 100 ml of bentonite slurry (particle size = 2.5–4 μm, concentration 3000 mg/l) into each of four replicate tanks (concentration 3000 mg/l into 20 l = 150 mg/l). At subsequent 10 min intervals, a 100 ml water sample was withdrawn for turbidity estimates, and 100 ml of bentonite slurry was added to each tank (i.e. 150 mg/L incremental increases). Turbidity was measured with a Hach Turbidimeter, and reported in NTU.[1] At 110 min and each 10 min interval thereafter, 100 ml of concentrated bentonite slurry was added to each tank to significantly increase turbidity (692 mg/l incremental increases). Collection of data continued for 140 min after the initial bentonite introduction.

4.1. Analysis

For analysis, SV, HR and CO were averaged over each minute for every 10 min interval. Data were transformed to represent percentage change from baseline levels to illustrate relative differences in the magnitude and timing of response to silt for each group of fish. We first compared the resting cardiovascular variables for lacustrine and riverine fish using *t*-tests for central tendency and Levene's test to assess differences in variance. Next, we used repeated measures ANOVA to test the hypothesis that the mean change in cardiovascular variables differed among lacustrine and riverine fishes across the entire experimental period. We then examined variation within fish and compared this variation between lacustrine and riverine fish. This involved

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[1] NTU = Nephelometric Turbidity Units. FTU = Formazin Turbidity Units. When a formazin standard is used for calibration FTU = NTU.

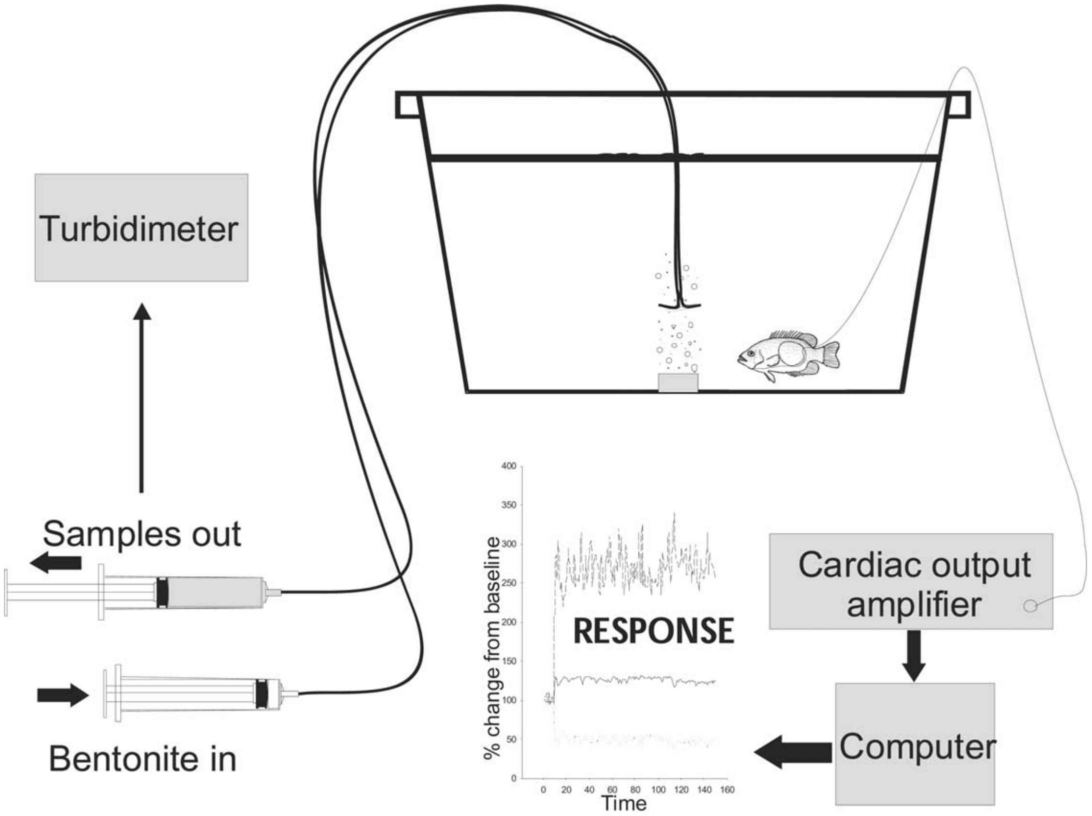

Fig. 1. Schematic representation of experimental set-up for delivery of bentonite and monitoring of cardiac response.

obtaining the $\log_{10}$ variance for individual fish and then comparing the $\log_{10}$ variance for fish in the two different groups using a *t*-test. To assess among/across fish variation, we computed the mean values for each cardiac variable for both lake and riverine fish and used a Levene's test to compare the residual variation. All statistical analyses were conducted using JMPIN (SAS Inc.). Values reported are means (±1 S.E.) and statistical tests were considered significant at alpha = 0.05.

5. Results

Actual resting mean heart rate of lacustrine rock bass was significantly lower (42.9 ± 5.5 beats/min) than mean resting heart rate of riverine rock bass (63.2 ± 6.5 beats/min; *t*-test, $t = -3.21$, $P = 0.005$). Relative resting values for both stroke volume and heart rate were also both significantly higher for riverine fish compared to lacustrine fish (*t*-test, CO, $t = -6.71$, $P < 0.001$; SV, $t = 7.41$, $P = 0.012$). Interestingly, although mean resting values differed between lacustrine and riverine rock bass, the amount of variation was similar among the sites for all cardiac variables. During experimentation, silt concentration, as measured by changes in turbidity, increased exponentially in both the lake and riverine treatments (Fig. 2). During the experiment, high turbidity obscured detailed observations of fish, and care was taken to avoid disturbing them. However, we were able to observe the lead wires for the Doppler flow probe and this allowed us to observe fish movement throughout the tank. During early stages of the experiment, rock bass did not avoid suspended bentonite nor did they appear to be in any form of distress at any time during the study. There was no direct mortality attributable to elevated silt loads over the duration of the experiment for either lacustrine or riverine rock bass.

In general, both riverine and lacustrine fish responded after the second pulse of silt (turbidity approximately 5 NTU) with changes in both stroke volume and heart rate, which therefore affected cardiac output. There was, however, no consistent direction in the change of cardiovascular variables for fish from either location. The repeated measures ANOVA indicated that only stroke volume differed in response to silt between lake and riverine fish (repeated measures ANOVA, $F = 1.81$, $P = 0.048$). Although the change in stroke volume was more extreme for lacustrine fish than riverine fish, there was substantial individual and temporal variability.

Based upon these visually detectable patterns of variation, we undertook additional analyses that focused on the patterns of variation both within fish (over time) and among fish during the addition of silt. Over the exposure period, lacustrine fish exhibited a much more varied response, with some fish increasing CO and SV, others decreasing CO and SV, and some fish keeping them constant. HR, SV, and particularly, CO were relatively stable for riverine fish throughout the entire period that silt was introduced (Fig. 3). Cardiac output and stroke volume for lacustrine fish varied significantly more than for riverine fish across the range of silt concentrations (*t*-test CO, $t = 6.08$, $P < 0.001$; SV, $t = 3.00$, $P = 0.013$). No differences in individual variation were observed for heart rate. Similar patterns were observed when we examined variation in cardiovascular response among individual fish. This analysis was based on our assumption that there were minimal trends across time as detected by the repeated measures ANOVAs, so we could evaluate the degree of variation among fish from the river and the lake. Cardiac output and stroke volume for lacustrine fish varied significantly more across the range of silt concentrations (Levene's test, CO, $F = 9.32$, $P = 0.008$; SV, $F = 11.35$, $P = 0.004$). No differences in individual variation were observed for heart rate. Cardiovascular variables for lacustrine fish tended to stabilize after maximum silt concentration was reached relative to the variation that was observed during the graded increase period. Although riverine fish exhibited increased stability in cardiovascular variables after maximum silt concentrations were reached, riverine fish were already reasonably stable during the period of increased silt loading.

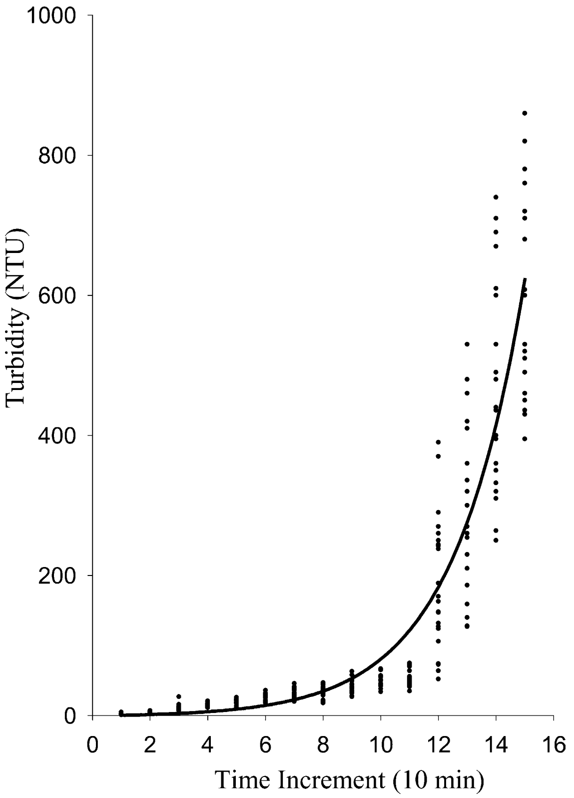

Fig. 2. Incremental increases in silt loading as indicated by changes in turbidity during the experimental procedure ($r^2 = 0.85$, $P < 0.001$).

6. Discussion

Consistent with our predictions, the findings from this experiment indicate that the cardiovascular response of lacustrine rock bass to silt was more extreme than that of riverine rock bass. Although the mean responses were

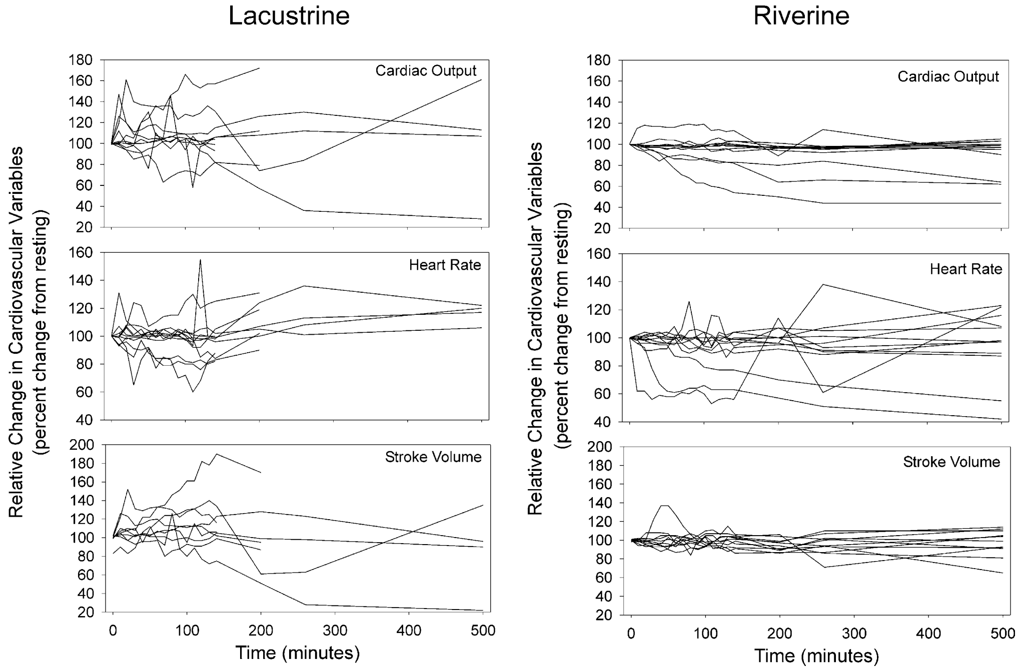

Fig. 3. Cardiac response by lacustrine and riverine rockbass to incremental increases in silt load.

similar, cardiovascular adjustments by lacustrine fish were extremely variable, resulting in significantly more variation than we observed with riverine fish. Prior to disturbance, the level of variation was uniform between sites. Following the introduction of silt, however, lacustrine fish exhibited highly variable and inconsistent patterns of cardiovascular activity. Our results suggest that the compensatory mechanisms that can minimize cardio-respiratory disruption caused by increases in the concentration of suspended silt are more prevalent in rock bass that live in rivers than in rock bass that live in lakes.

Horkel and Pearson (1976) measured ventilation rates of green sunfish (*Lepomis cyanellus*) exposed to bentonite suspensions. They noted that an increase in ventilation rate during highly turbid conditions was a likely mechanism designed to compensate for reduced respiratory efficiency in an attempt to maintain constant rates of oxygen uptake. At 25 °C, ventilation rates for green sunfish increased by 70% at turbidity levels exceeding 898 FTU[2] (Horkel and Pearson, 1976). Similar to our results with rock bass, green sunfish also exhibited rapid acclimation or physiological adjustment to high turbidity, and in many cases, ventilation rates rapidly returned to pre-treatment levels (Horkel and Pearson, 1976). Although sockeye salmon (*Oncorhynchus nerka*) respond to sublethal exposure to bleached kraft mill effluent by increasing volume of flow over the gills, this response is rapidly extinguished through acclimation or physiological adjustment (Davis, 1973). We cannot discount the possibility that visual stimulation associated with the appearance of silt elicited the observed responses; however, we did not observe the typical bradycardia induced by fright, as has been observed for other stressors (Cooke et al., 2003). The possibility of a "fright" response during experimentation has also been suggested by Davis (1973) and Horkel and Pearson (1976). In future studies, researchers may consider running these types of experiments in darkness to eliminate this possibility.

Long-term exposure to high turbidity may cause thickening of the gill epithelium and loss of respiratory function (Bell, 1973). During short-term exposure to silt, Berg and Northcote (1985) reported increases in the frequency of gill flaring by salmonids during periods of elevated turbidity, which they interpreted as a behavioural mechanism to facilitate clearing of suspended sediment on the gill surfaces. In a similar study, Servizi and Martens (1992) reported an eightfold increase in "cough" behaviour among salmonids exposed to suspended sediment concentrations of 230 mg/l. Although in the present study, concentrations of suspended sediment exceeded levels that elicited behavioural responses by salmonids in prior studies, behavioural mechanisms to clear silt from gill surfaces were not detected among rock bass. Furthermore, in the present study, maximum turbidity was below that produced by Horkel and Pearson (1976), which may explain why HR, SV and CO were not affected after the initial response when silt increased from nearly undetectable levels to approximately 5 NTU. It should be noted that turbidity in the Grand River rarely exceeds 95 NTU, even during high flows, suggesting that short-term effects of elevated turbidity on adult rock bass are negligible. Long-term effects may include reduced foraging efficiency, reduced growth, and chronic physiological stress that may induce disease and parasites (Trautman, 1933; Wallen, 1951; European Inland Fisheries Advisory Commission, 1964). Furthermore, elevated levels of suspended silt negatively affect fish habitat by filling pools, decreasing water depth, and reducing availability of critical habitat. For example, a major construction project that mobilized large amounts of silt in Michigan was proposed by King and Bell (1964) as an explanation for the extirpation of smallmouth bass from some reaches of the Red Cedar River. In addition, Richardson and Jowett (2002) described negative correlations between silt loads in New Zealand streams and fish habitat, fish abundance and species diversity.

Despite the fact that many early studies report that fish were generally able to withstand silt concentrations up to 100,000 mg/l (Waters, 1995), the present study demonstrated that rock bass respond to silt concentrations several orders of magnitude less than this. Disparate physiological responses to silt among lacustrine and riverine rock bass suggest that lacustrine rock bass may be more sensitive to suspended silt, especially during long-term exposures. In addition, the actual composition of silt varies widely among natural systems and in experimental research. Further research may be necessary to clarify how size and angularity of silt particles may affect how fish respond (Servizi and Martens, 1992; Birtwell, 1999; Lake and Hinch, 1999). Bentonite particles are flat, rectangular and highly angular under a high power microscope; however, short-term mortality of rock bass was negligible. In contrast, Martin et al. (1984) proposed that the high angularity of volcanic ash was responsible for the loss of salmonid fisheries in affected areas. Fish generally avoid areas with elevated concentrations of suspended silt, resulting in environments devoid of fish (Waters, 1995). Warmwater species vary in their tolerance to elevated silt loads at different stages in their life histories (e.g., Smit et al., 1998), and at different water temperatures. The responses also vary with duration of exposure. Future studies should

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[2] Comparisons between mg/l and NTU are confounded by the chemical composition and physical properties of the suspended sediment. In this study, 300 mg/l of bentonite produced a mean turbidity of 11.4 NTU. According to The European Inland Fisheries Advisory Commission (1964), freshwater systems with concentrations of suspended solids that exceed 400 mg/ L are rarely able to support viable fisheries.

address these issues, as well as physiological effects of silt with differing chemical (e.g., Strmac et al., 2002) and physical characteristics. There is now sufficient evidence to confirm that both lacustrine and riverine fishes respond physiologically to suspended silt. In response, activities and practices that minimize anthropogenic and natural inputs of suspended sediment into aquatic environments have the potential to benefit fish communities worldwide.

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