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The effects of noise disturbance from various recreational boating activities common to inland waters on the cardiac physiology of a freshwater fish, the largemouth bass (Micropterus salmoides)

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ABSTRACT

1. Recreational boating continues to grow in popularity, yet little is known about the effects of noise disturbance from boating on fish. Therefore, this study evaluated the organism-level cardiovascular disturbance associated with different recreational boating activities using largemouth bass (*Micropterus salmoides*) as a model.
2. Cardiac output and its components (heart rate and stroke volume) were monitored in real time, allowing for the determination of the magnitude of disturbance and the time required for recovery. Fish responses to three noise disturbances (canoe paddling, trolling motor, and combustion engine (9.9 hp)) for 60 s were contrasted using a Latin squares design.
3. Exposure to each of the treatments resulted in an increase in cardiac output in all fish, associated with a dramatic increase in heart rate and a slight decrease in stroke volume. The level of change in cardiac output and its components increased in magnitude from the canoe treatment to the trolling motor treatment with the most extreme response being to that of the combustion engine treatment. Furthermore, time required for cardiovascular variables to recover varied across treatments with shortest periods for the canoe paddling disturbance ($\sim$15 min), the longest periods for the combustion engine ($\sim$40 min), and intermediate recovery periods for the trolling motor ($\sim$25 min).
4. Collectively, these results demonstrate that fish experienced sublethal physiological disturbances in response to the noise propagated from recreational boating activities. This work contributes to a growing body of research that has revealed that boating activities can have a number of ecological and environmental consequences such that their use may not be compatible with aquatic protected areas. Future research should evaluate how free-swimming fish in the wild respond to such stressors relative to frequency of exposure and proximity to noise as most research to date has occurred in the laboratory.

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KEY WORDS: fish; stress response; conservation physiology; disturbance; boating

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INTRODUCTION

Power boating began early in the 20th century and has increased in popularity in the last few decades. A survey conducted in 1996 suggested that 9.3% of Canadians participate in power boating activities annually (Environment Canada, 2002). In the USA, there were over 12 million registered recreational power boats in 2002 (NMMA, 2004). There are several documented and potential negative ecological and environmental consequences associated with the high participation rates of recreational boaters (reviewed in Mosisch and Arthington, 1998; Asplund, 2000). These consequences include, but are not limited to, erosion (Nanson *et al.*, 1994) and turbidity from wakes (Moss, 1977; Yousef *et al.*, 1980), mixing or suspension/mobilization of nutrients (Moss, 1977; Yousef *et al.*, 1980), disturbance (from noise, presence of boat, or wake) or injury of aquatic organisms including plants (e.g. scarring and uprooting of macrophytes; Zieman, 1976; Vermaat and de Bruyne, 1993; Asplund and Cook, 1997; Bell *et al.*, 2001), birds (Kahl, 1991; Mikola *et al.*, 1994; Burger, 1998), marine mammals (Richardson *et al.*, 1995; Nowacek *et al.*, 2004; Wartzok *et al.*, 2004; Rommel *et al.*, 2007), and fish (Lagler *et al.*, 1950; Mueller, 1980; Boussard, 1981; Wolter and Arlinghaus, 2003), release of hydrocarbons and other substances from combustion and fuel spills (Jackivicz and Kuzminski, 1973; Schenk *et al.*, 1975; Mastran *et al.*, 1994; Kempinger *et al.*, 1998), as well as the creation of noise pollution (Mosisch and Arthington, 1998). It is also important to note that non-motorized boating disturbances (e.g. sailing boats, rowing boats, kayaks, canoes) can also disturb wildlife, although this topic has been explored in detail only for waterfowl (York, 1994). In terms of boating disturbance on vertebrates, most studies have focused on marine mammals (see review in Richardson *et al.*, 1995; with an emphasis on understanding the frequency of collisions, consequences of noise interference with animal communication, behavioural alterations, or physical damage to the hearing apparatus) or birds (see review in York, 1994; with an emphasis on documenting flush distances). Far fewer studies have focused on fish (but see Popper *et al.*, 2004 for a summary of fish hearing and noise impacts) despite the fact that many populations of marine and freshwater fish are imperilled (Richter *et al.*, 1997; Leidy and Moyle, 1998; Musick *et al.*, 2000). Given the recent increases in a number of human activities such as underwater drilling, shipping, seismic exploration, and in particular recreational boating, there is growing awareness of the need to study anthropogenic noise and its effects on aquatic ecosystems (Myrberg, 1990). Furthermore, there is a need to determine which recreational boating activities are compatible with aquatic protected areas (Agardy, 1994; Suski and Cooke, 2007) and to determine the utility and need for other restriction such as no wake zones (Asplund and Cook, 1999).

Many fish species rely on their hearing for sensing activity in their surroundings (Popper *et al.*, 2004), so that noise from boats has the potential to cause disturbance. Anthropogenic noises will often create frequencies less than 1.0 kHz, which is in the hearing range of many fish (Scholik and Yan, 2002). There are many sources of anthropogenic noise in aquatic ecosystems, including noise propagated from boats. All boats, no matter their size, create noise that contributes to ambient underwater noise through propeller singing, propeller cavitation, propulsion or the use of other machinery (Richardson *et al.*, 1995). Vessel noise is composed of narrowband sounds that are tonal (i.e. sound that is composed of discrete frequency components) and broadband sounds at specific frequencies. The frequencies and levels of these two sounds are dependent upon vessel size, speed and design. However, it is believed that in coastal and inland areas, where there is an abundance of recreational boats with higher speed propellers and engines, the sound is actually louder than from larger vessels (Richardson *et al.*, 1995).

As noted earlier, little work has evaluated the response of fish to noise disturbance from boats, and most work that has been done has focused on behavioural endpoints or injury. For example, Vabø *et al.* (2002) studied the vessel avoidance behaviour of Norwegian spring spawning herring (*Clupea harengus*) using acoustic surveys. The authors found that the most common behavioural reactions to a passing vessel in the form of avoidance was body tilting as well as vertical and horizontal swimming which is reflective of predator avoidance reactions. A freshwater fish (longear sunfish; *Lepomis megalotis*) exhibited altered nesting behaviour in the presence of boating activity (Mueller, 1980). In addition, excessive noise has been found to temporarily alter hearing thresholds in fish or to annihilate hair cells of auditory maculae (Scholik and Yan, 2002; Popper *et al.*, 2004). Scholik and Yan (2002) exposed the fathead minnow (*Pimephales promelas*) to the noise created by a 55 hp outboard engine for 2 h. Exposure to this type of noise resulted in temporary hearing loss in the fish. Smith *et al.* (2004) suggested that noise-induced damage to the fish ear may occur quickly. Popper *et al.* (2004) suggested that underwater noise may cause physiological disturbance alongside behavioural changes and physical damage in fish, although this has only recently been studied. Wysocki *et al.* (2006) considered physiological disturbance (i.e. stress response) in fish as a response to noise propagated from a ship. The study demonstrated that ship noise elicited elevation of stress hormone titres (as measured by cortisol expression in the water) in several species of freshwater fish regardless of their hearing sensitivities. However, in general there is little information available on the physiological response of fish to noise, particularly in the context of recreational boating.

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Recently, there has been an interest in using physiological tools to assess conservation problems (i.e. conservation physiology; Wikelski and Cooke, 2006) and this approach has relevance to recreational boating disturbance. Hence, the focus of this study was to characterize the sublethal physiological consequences of boating activity (i.e. magnitude and extent of these disturbances) on a teleost fish.

For the purpose of this study, the cardiovascular response of fish to different boating noise disturbances was monitored because the cardiovascular system serves as an excellent indicator of the stress response in fish (Cooke *et al.*, 2003a) as it is linked to whole organism metabolic rates (Webber *et al.*, 1998; Farrell, 2002). Furthermore, by monitoring cardiac output in real time, it is possible to determine the time required to recover from disturbance with very fine resolution (to the nearest minute; Schreer *et al.*, 2001; Cooke *et al.*, 2003a). The freshwater teleost fish, the largemouth bass (*Micropterus salmoides*), was used as a model because it is the most popular sportfish in North America and occurs in systems that receive immense pressure from a diverse array of recreational boat types and propulsion devices including paddles, electric trolling motors, and combustion engines. Furthermore, the cardiovascular response of largemouth bass to a number of stressors (e.g. exercise, air exposure, simulated avian predation) have previously been studied, providing an opportunity to assess the relative magnitude of the various boating disturbances compared with other stressors. The specific objectives were (1) to characterize the cardiac disturbance from the noise stimuli of three different sonic intensities associated with recreational boating (canoe paddle, electric trolling motor, and combustion engine), and (2) to quantify the cardiac recovery time following each stressor. It was predicted that the level of disturbance and recovery time would be greatest for the combustion engine, least for the paddle, and intermediate for the electric trolling motor. The ultimate goal of this research was to provide information to managers and regulatory bodies to enable them to respond better to recreational boating concerns with the expectation that conflict (e.g. with aquatic protected areas) will become more common in the coming years.

METHODS

Experimental animals

Nine largemouth bass were used for this study (Table 1). These fish were caught in May 2006 at Lake Opinicon in Elgin, Ontario, Canada (N 44° 33′ 56.0″ W 76° 19′ 23.6″). Lake Opinicon is a shallow (mean depth = 4.5 m) mesotrophic natural lake of moderate size (787 ha) on the Rideau Canal system and is regarded as a popular fishing destination.

Table 1. Descriptive statistics for the fish ($n = 9$) utilized in the study including size and baseline cardiac values

Variables	Mean ± SEM	Minimum	Maximum
Total length (mm)	270.44 ± 41.89	226	338
Mass (g)	270.89 ± 131.84	116	508
Resting cardiac output ($mL\,min^{-1}\,kg^{-1}$)	29.22 ± 2.74	24.2	33.1
Resting heart rate (BPM)	39.63 ± 4.63	29.5	45.1
Resting stroke volume ($mL\,kg^{-1}$)	0.75 ± 0.01	0.73	0.77

Almost all boating traffic is recreational in nature and includes pleasure boating, canoeing, water skiing, and fishing. A wide range of boat types are used on the lake including canoes, small fishing boats (powered by both electric trolling motors and combustion engines), and larger pleasure craft. Fish were captured using standard angling gear and techniques. Once captured, the fish were held (for a minimum of 12 h before experimentation) in a water-flow-through holding tank (150 cm × 62 cm × 55 cm) that was continuously supplied with fresh lake water, at the Queen's University Biological Station. All of the methods used in this study were approved by Carleton University's Animal Care Committee (Protocol B06-02).

Surgical procedure

The surgical procedure used in this study follows that described by Cooke *et al.* (2003a), and is briefly outlined below. Using three fish per treatment day, each fish was individually introduced to a bath containing a solution of water and $60\,mg\,L^{-1}$ of clove oil (emulsified with ethanol in a 9:1 ratio of ethanol to clove oil). This solution was used to anaesthetize the animal to a point where equilibrium was lost (approximately 5 min). The fish was then placed on a wet sponge on the operating table where a solution containing $30\,mg\,L^{-1}$ of clove oil (maintenance dose) was pumped over the gills to ensure that the fish remained anaesthetized. The gills and operculum of the fish were held back using a plastic oval shaped cover which was placed behind the first gill arch to provide unimpaired access to the aorta.

Using a pair of blunt forceps, the connective tissue surrounding the ventral aorta was carefully removed. A Doppler flow probe (sub-miniature 20 MHz piezoelectric transducer: Iowa Doppler Products, Iowa City, Iowa) was selected for each fish based on the diameter of the aorta. The sizes of the flow probes varied from 1.2 to 1.6 mm. The cuff-like silicon probe, once checked for sufficient signal strength, was placed onto the aorta and held in position by a single suture. The lead wire attached to the probe was sutured three

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times to the exterior of the fish to ensure that the cuff remained in position during any fish movement.

To monitor cardiac output, a flow meter (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) were used. The procedure took approximately 30 min for each fish and was repeated for two more fish on each treatment day to give a total of three fish per trial. Following surgery, the three fish were given approximately 12 h to recover in individual chambers located in an undisturbed experimental tank (150 cm × 62 cm × 55 cm). The experimental tank was continuously supplied with fresh lake water. The fish were considered to have 'recovered' from surgery once they displayed normal cardiac output, a period of at least 6 h (Cooke *et al*., 2003a). Cardiac parameters of the fish were recorded for several hours before treatment and for several hours post-treatment.

Experimental apparatus and treatments

Experimentation occurred in a water-flow-through tank (approximately 200 L; 150 cm × 62 cm × 55 cm) at the Queen's University Biological Station in Elgin, ON. Fish were held in individual chambers (36 cm × 12.5 cm × 30 cm) that were essentially partitions within a plastic storage bin (50 cm × 36 cm × 30 cm). Fish were separated such that they could not see each other (Figure 1). Each chamber was screened on the side facing the disturbance arena with the front of their head oriented towards the disturbance. The bottom and back of the chambers were perforated to enable constant oxygenation. The chambers were covered so that the presence or movement of researchers would not be visible to the fish. Access to the room where the experimental tank was housed was limited to research staff during experimental manipulations. A wave baffle was positioned between the fish-holding chambers and the experimental area (where the motors were mounted and where the paddle was used) to prevent hydrodynamic disturbance. The effectiveness of the baffle was tested with a digital flow meter before experimentation.

Following recovery, the fish were exposed to each of the three separate treatments; the operation of a 9.9 hp combustion engine, an electric motor and a canoe paddle. Both motors were mounted in the chamber before fish were introduced to the chambers. The operation of the combustion engine consisted of starting the mounted engine using the pull cord and allowing it to operate in neutral. Similarly, the mounted trolling motor was turned on manually and operated at low speed. Finally, the canoe paddle was stroked in back and forth motions in the water in front of the wave baffle in the tank at a rate of 20 strokes min^{-1}. Treatment time was held constant at 60 s for each disturbance type and was always applied in the disturbance arena at the opposite end of the experimental apparatus to where the fish were held. The fish were exposed to the first treatment and were then given a minimum of 3 h to recover; fish were considered to have recovered once they resumed a normal cardiac output (Cooke *et al*., 2003a). Upon recovery, fish were exposed to the second treatment. Again, the fish were given a minimum of 3 h to recover before being exposed to the third and final treatment. This entire procedure was repeated for two more sets of three fish. The order of treatments was randomized for each treatment day (i.e. Latin squares design; Cochran and Cox, 1957). This experimental design enabled efficient use of animals. Furthermore, given the cardiac plasticity of fish,

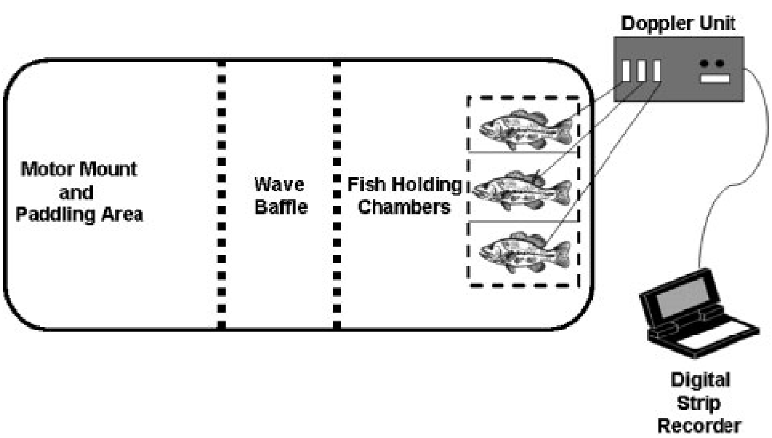

Figure 1. Experimental apparatus consisting of a water-flow-through tank (approx 200 L), a wave baffle and fish-holding chambers (36 cm × 12.5 cm × 30 cm), which were subdivided sections of a larger plastic bin.

DOI: 10.1002/aqc

this approach also allows for each animal to be exposed to each treatment (in different orders). Water temperatures varied between 18 and 20°C during experiments.

Calibration

To calibrate the flow probes, the fish were individually euthanized using a lethal dose of clove oil ($180\,\mathrm{mg\,L^{-1}}$). The probes were calibrated to convert Doppler shift (V) to blood flow measurement ($\mathrm{mL\ min^{-1}}$; Schreer *et al.*, 2001) and to enable the determination of cardiac output (CO) and stroke volume (SV). Heart rate (HR) was determined using a counting algorithm that was interfaced with the digital strip recorder. In order to conduct a postmortem calibration the head and the pericardial cavity of each fish were removed and the heart was exposed. With the use of a constant infusion pump (Harvard Apparatus, South Natick, Massachusetts), an aqueous solution with suspended particular matter water was pumped through the ventral aorta of the fish. This permitted calibration of the probes over a range of flow rates including flow rates that were recorded throughout the treatments. This procedure was completed following each treatment day for all three treatment days.

Data analysis

Resting CO, HR and SV values were recorded, corrected using calibrations, and plotted to evaluate the extent of disturbance and the recovery time. Maximal disturbance was classified as the greatest change in value either positive (from baseline) or negative (from baseline) for each cardiac variable. Recovery times following treatments were determined by plotting CO, HR and SV mean values for each fish. Fish were considered to have recovered when their cardiac parameters reflected their baseline cardiac values (Schreer *et al.*, 2001). In this experiment, treatments were fixed and fish number was random for each of the three trials. A mixed model repeated measures ANOVA was used for analysis after verifying that the data were normal and variances were equal (Levene's Test). Significance was assessed at $P<0.05$ and all analyses were conducted using JMP (V 4.0, SAS Institute, Cary, NC). Unless otherwise noted, all values are means $\pm$ SEM.

RESULTS

Baseline cardiac performance was recorded for each of the nine fish (Table 1) in the study before treatment and following 12 h of surgical recovery. The mean resting CO for fish used in this experiment was $29.22 \pm 2.74\,\mathrm{mL\,min^{-1}\,kg^{-1}}$, the mean resting HR was 39.63 ± 4.63 BPM, and the mean resting SV was $0.75 \pm 0.01\,\mathrm{mL\,kg^{-1}}$. All fish survived the monitoring period and were successfully calibrated, enabling the determination of cardiac output and stroke volume.

During the 60 s treatment periods, all fish responded with an intense bradycardia (data not shown). However, within several minutes following treatment, the fish became tachycardic. Specifically, cardiac output and heart rate were consistently elevated and stroke volume decreased irrespective of treatment. However, the maximum cardiac values varied significantly across treatments (CO, $F=46.5$, $P<0.0001$; HR, $F=39.9$, $P<0.0001$; SV, $F=89.46$, $P<0.0001$; Figure 2). The combustion motor elicited the greatest cardiac disturbance (mean $\pm$ SEM percentage change in variables from baseline; CO, $43.67 \pm 18.13\%$, HR, $67.08 \pm 19.49\%$, and SV, $-23.71 \pm 2.76\%$) and the canoe paddle the least (mean $\pm$ SEM percentage change in variables from baseline; CO, $19.60 \pm 15.60\%$, HR, $28.52 \pm 16.14\%$, and SV, $-15.73 \pm 6.14\%$). The trolling motor elicited intermediate levels of disturbance (mean $\pm$ SEM percentage change in variables from baseline; CO, $31.04 \pm 15.57\%$, HR, $44.09 \pm 14.35\%$, and SV, $-16.75 \pm 4.32\%$).

Recovery rates also varied significantly among treatments (Figure 3). For CO ($F=119.7$, $P<0.001$), HR ($F=129.03$,

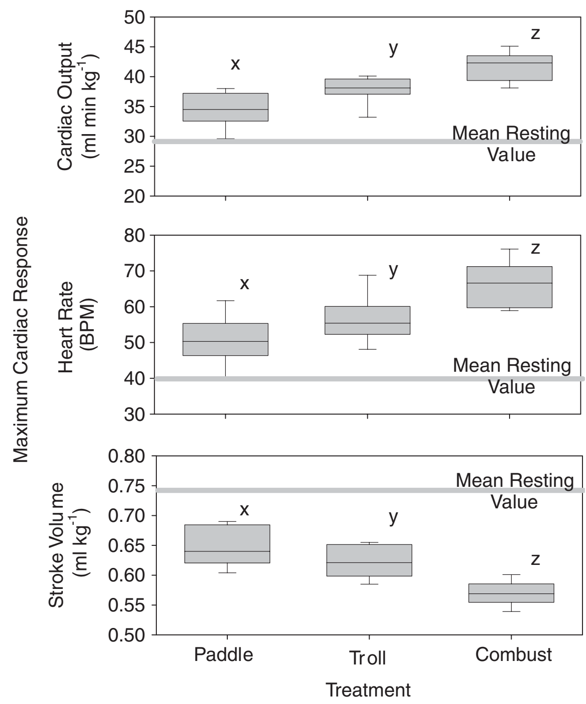

Figure 2. Maximum values achieved for the cardiac parameters of largemouth bass following treatment. The error bars represent the 5th and 95th percentiles and the lines represent the median. Mean resting values for each parameter are also plotted on the panels as a grey line ($n=9$).

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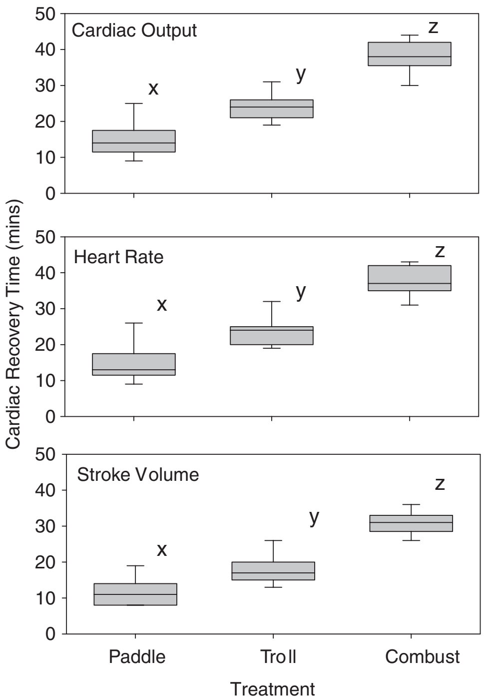

Figure 3. Recovery times of largemouth bass cardiac parameters following treatment. The error bars represent the 5th and 95th percentiles and the lines represent the median ($n = 9$).

$P < 0.001$), and *SV* (F = 138.46, $P < 0.001$) recovery was most rapid for the canoe simulation (mean $\pm$ SEM recovery time; *CO*, 15.00 ± 4.48 min, *HR*, 14.88 ± 5.11 min, *SV*, 11.44 ± 3.71 min) and took the longest for the combustion motor (mean $\pm$ SEM recovery time; *CO*, 38.00 ± 4.39 min, *HR*, 37.89 ± 4.01 min, *SV*, 30.89 ± 3.10 min). Recovery times were intermediate for the trolling motor treatment (mean $\pm$ SEM recovery time; *CO*, 23.78 ± 3.67 min, *HR*, 23.44 ± 4.03 min, and *SV*, 18.00 ± 3.87 min). *SV* tended to recover more rapidly than *CO* or *H*R. There was a significant effect of 'individual' on *HR* for recovery ($P = 0.024$) and *SV* for recovery ($P = 0.028$), indicating that not all individuals recovered at the same rate. No other individual effects were found among other analyses.

DISCUSSION

Previous research has revealed that cardiac output is a sensitive indicator of fish stress and has been used to assess responses to exercise, air exposure, water temperature alterations, handling, and other human activities (Schreer *et al*., 2001; Schreer and Cooke, 2002; Cooke *et al*., 2003a, 2004b). This is the first study to use cardiac output or other cardiac variables to assess fish responses to boating disturbance. In addition, this is the only boating disturbance study to have monitored fish stress in real time. This study revealed that fish do experience cardiovascular alterations in response to different recreational boating activities and that the recovery time varies relative to the magnitude of the disturbance.

The cardiovascular system of fish, similar to that of other vertebrates, consists of a heart, arteries, arterioles, capillaries and veins (Farrell and Jones, 1992). This is a closed system that transports oxygen, via red blood cells, from the gills to tissues throughout the body (Satchell, 1991). Cardiac output is the volume of blood pumped by the cardiovascular system per minute (measured at the point where blood exits the heart (Farrell, 1991b)). Cardiac output typically increases when there is a greater demand for oxygen in the body, such as following exercise or stress (Webber *et al*., 1998). Cardiac output is quantified as the product of the heart rate and the stroke volume in $\mathrm{mL\,min^{-1}\,kg^{-1}}$ (Farrell, 1991b; Satchell, 1991) and can be quantified using Doppler flow probes as in this study (Cooke *et al*., 2003a). An increase in cardiac output of largemouth bass reflects a dramatic increase in heart rate and a decrease in stroke volume (i.e. frequency modulation; Farrell, 1991b; Cooke *et al*., 2003a). Although an increase in cardiac output itself is usually not deleterious, it is indicative of elevation in metabolic requirements and reduces cardiac scope (Farrell, 1991a). Hence, cardiac output is an extremely sensitive measure of whole organism condition.

In this study, exposure to all three treatments caused alteration compared with baseline values. Cardiac output and heart rate increased while stroke volume decreased. The magnitude of change was greatest for the combustion motor. This finding is consistent with the notion that this is the noisiest of the three treatments tested. Although actual frequency and volume were not measured in this study, there is ample evidence to support the notion that the canoe treatment was the least noisy and that the combustion motor was the noisiest (Richardson *et al*., 1995). The trolling motor also caused cardiac disturbance although not to the same extent as the combustion engine. Electric trolling motors are used extensively in inland waters to enable anglers to manoeuvre in shallow waters. In fact, these electric trolling motors are probably most popular on 'bass boats' – a vessel type specifically designed to target black bass. Typically anglers would use their combustion motors to reach their general fishing site and then use the trolling motor to move within the site. Clearly, even trolling motors create noise that elicits a disturbance in bass.

To our knowledge, this is the first study to evaluate fish or wildlife responses to electric motors. The treatment that had

DOI: 10.1002/aqc

the least effect on cardiac disturbance was the canoe paddle which was consistent with our prediction and belief that paddles generate the least amount of noise. Nonetheless, the paddle did cause $\sim$20% increase in cardiac output (which was roughly half the increase noted in cardiac output for the combustion engine ($\sim$40%). Interestingly, there are several other studies that have documented disturbances of fish associated with canoeing. Todd (1987) determined that of the various human activities (e.g. swimming, gigging, canoeing, boating) in small Missouri streams, canoeing during the spawning season was the most deleterious activity for smallmouth bass (*Micropterus dolomieu*). Because smallmouth bass spawn in shallow waters where powerboats cannot go, powerboats were not as detrimental as canoes in this study. However, a study by Mueller (1980) determined that another sunfish species, the longear sunfish, was disturbed by powerboats during spawning. The behavioural disturbance was greater from slow-moving boats than from fast-moving boats. Interestingly, trolling motors are intended to manoeuvre boats in shallow waters and at slow speeds. There is clearly a need for future research to determine the relative impacts of different boating activities in field settings because this laboratory study was unable to vary proximity to the disturbance or speed.

Because bass have been well studied with respect to their cardiac response to different stressors, it is possible to put the disturbance from the various boating activities in context. For purposes of comparison, this discussion focuses on heart rate because it has been studied independent of cardiac output and stroke volume in some cases (Cooke *et al*., 2002). In terms of the magnitude of disturbance, heart rate increases were 29% for canoe, 44% for trolling motor and 67% for the combustion motor. The combustion motor values are at the lower end of ranges of cardiac disturbances that have previously been documented for bass. For example, when largemouth bass were exercised to exhaustion and brief air exposure, heart rate increased by 78 to 108% (Cooke *et al*., 2003a) and by 95% following a tournament weigh-in (Suski *et al*., 2004). Similar disturbances to those observed for the canoe treatment have previously been noted for a bass following a small movement (10 s displacement, 28%; Cooke *et al*., 2002) or when large bass are exposed to a simulated heron attack (20%; Cooke *et al*., 2003b). The magnitude of heart rate disturbance for the trolling motor treatment compares with simulated predator attacks on bass by osprey models (44%; Cooke *et al*., 2003b). Hence, the canoe and trolling motor disturbance are similar to ecologically relevant disturbances such as swimming activity and predation attempts. However, the frequency with which these ecological events occur relative to the frequency of boating disturbance is unknown.

In addition to the magnitude of disturbance, the recovery time for cardiac variables was also quantified. The time required for recovery following the treatments was directly related to the magnitude of response in cardiac activity. This trend was consistent for all three cardiac parameters. Recovery time for cardiac output and heart rate was similar for all three treatments and slightly longer than stroke volume. If cardiac output were to remain elevated for extended periods, there would be conflict with other metabolic processes (e.g. growth, digestion, locomotory activity; Priede, 1985) and fish could succumb to metabolic-rate-dependent mortality (Priede, 1977). Hence, disturbances (such as the combustion motor) that lead to prolonged elevations in cardiac output are costly. Although no studies have previously assessed the energetic consequences of boating disturbances on fish, Batten (1977) found that sailing boats disturbed waterbirds to the level that it was energetically inefficient to forage in that lake. Compared with other studies of cardiac recovery times in centrarchids, disturbance from recreational boating activities range from mild to moderate. For example, the recovery time for heart rate following exposure to the combustion motor ($\sim$48 min) was comparable to moderate exercise (Cooke *et al*., 2003a) whereas the canoe treatment ($\sim$15 min) was similar to ecologically relevant activities such as exposure to simulated predation (Cooke *et al*., 2003b). Only one other study has evaluated the stress response of fish following exposure to boating noise. Wysocki *et al*. (2006) measured cortisol levels secreted into the water after half an hour of boat noise exposure in different freshwater species and found significant elevations compared with no-noise or white-noise controls. However, they were unable to monitor recovery rates. The only study to evaluate recovery from stress was by Smith *et al*. (2004), although the noise that they studied was generated experimentally and was not intended to mimic a boat. They found that goldfish exposed to noise had cortisol levels spike within 10 min and then return to pre-treatment levels within 60 min of exposure to the noise source, although they had only three points in time to assess the physiological dynamics of cortisol (basal, 10 min, 60 min). Indeed, in most fish, cortisol release does not peak until 10 min following application of a stressor and often stays elevated for several hours (e.g. following exercise; Gamperl *et al*., 1994) suggesting that the noise generated by Smith *et al*. (2004) resulted in a minimal stress response. Cardiac variables have been shown to be extremely responsive to stress (Schreer *et al*., 2001) and thus, to our knowledge, this is the first study to quantify the physiological recovery time following exposure to different noise stressors in real time (to the nearest minute).

There are several limitations of this study that are worthy of discussion as it will help to guide future research. Specifically, the study did not consider the effect of proximity to noise, as all fish were an equal distance from the noise sources. Proximity to noise sources may have an effect on the level of cardiovascular disturbance, as it has been determined to

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influence behaviour (Mueller, 1980). Water depth may also have an effect on the frequency and level of noise perceived by fish, because sound transmission varies between deep and shallow water; as water depth increases, sound wave velocity decreases (Richardson *et al.*, 1995). There is also a need to evaluate the extent to which fish are able to compensate for this disturbance. Furthermore, studies should document short-term and long-term physiological responses to noise in fish. This study, documented reasonably rapid recovery (less than an hour). However, it would be of interest to consider if there is potential for long-term effects on fish arising from elevated cortisol (Smith *et al.*, 2004) and/or altered cardiovascular activity (this study). In addition, this study exposed fish to a rather abrupt noise (silence followed by 60 s of noise followed by silence) which may have elicited a startle response. For example, Schwarz and Greer (1984) noted that Pacific herring (*Harengus pallasi*) exhibited alarm responses in reaction to motorboat noise, particularly when abrupt changes in temporal characteristics of the sound occurred. Studies should also be conducted in different seasons as previous research on birds has revealed that effects of boating disturbance were more severe during the reproductive period (Kahl, 1991). Ideally, these studies would include field observations of boat traffic to provide realism to the frequency of boat disturbance for controlled laboratory experiments. There is a need for future research to evaluate how free-swimming fish in the wild respond to such stressors: this would be possible with field physiology techniques such as biotelemetry (Cooke *et al.*, 2004a) and could be replicated in systems of different size (e.g. small lakes to coastal environments).

Little research to date has evaluated the sublethal consequences of boating disturbance on fish. Considering the growing popularity of recreational boating activity, fish will increasingly be exposed to a variety of boating disturbances. Information on fish responses to boating disturbance is needed to manage aquatic protected areas better and to reduce conflict between human activity and aquatic ecosystems. In North America there is increasing use of aquatic protected areas to reduce or eliminate direct fisheries exploitation (Saunders *et al.*, 2002; Suski and Cooke, 2007). However, rarely do aquatic protected areas, particularly in fresh water, include zonation that restricts boat use. In some smaller lakes and reservoirs in North America (usually associated with parks in conservation areas), use of combustion motors is often prohibited in an effort to minimize user conflicts (Suski and Cooke, 2007), shoreline erosion (Mosisch and Arthington, 1998), or disturbance of birds (York, 1994), but electric motors and non-motorized boats are usually permitted. Interestingly, this current work suggests that even non-motorized boats and electric motors can produce physiological disturbance. Hence, when evaluating the type of boating activities allowed within aquatic protected areas, even non-combustion motors or paddling that produce relatively little noise can have an impact on individual fish and may need to be excluded or restricted depending on the goals of a given protected area. At present, we are unaware of any freshwater protected areas in temperate regions where boating is restricted in an effort to reduce noise disturbance impacts on fish. Indeed, it is still unclear whether these individual sublethal effects result in fitness impairments or population level impacts. Such information would be needed to understand the ecological relevance of boating noise on fish and to determine if aquatic protected areas and zonation are a useful tool for reducing it independent of more conventional goals associated with reducing exploitation.

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