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Does motor noise from recreational boats alter parental care behaviour of a nesting freshwater fish?

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Abstract

1. Recreational boating activity has the potential to generate noise pollution that may influence wild fish. Such noise may be particularly relevant to fish engaged in parental care (PC), where alterations in behaviour could influence individual fitness and productivity of fish populations.

2. Here, the PC behaviour of the freshwater largemouth bass (*Micropterus salmoides*) was examined to determine whether disturbance from boat noise altered paternal behaviour. Changes in nest-tending and brood-guarding behaviour were measured following exposure to noise treatments of 1-min duration using underwater play-backs of recorded boat noises.

3. One experiment compared the behaviour of bass tending eggs before, during, and after exposure to high-speed or idling combustion motors, or an electronic bow-mounted trolling motor. No significant differences in the time on nest, number of pectoral fin beats, and number of turns between the pre-treatment, treatment, and post-treatment periods for all three motor types were observed.

4. A second experiment assessed the impacts of noise (high-speed combustion motor only) on the behaviour of nesting bass across the development stages of offspring (i.e. egg, egg-sac fry, and swim-up fry). During the egg-sac fry stage, nest-guarding males turned significantly less on the nest during the noise treatment compared with the long-term post-treatment period, indicating a stage-specific impact of boat noise on parental behaviour. The effect was transient, however, and limited to the period that the noise was present.

5. Given that PC and recreational boating activity tend to co-occur in nearshore areas, prolonged or frequent repeated exposure of nesting fish to boat noise during the egg-sac fry stage could have adverse consequences for fitness and reproductive output. Efforts to restrict recreational boating activity in the vicinity of fish engaged in PC (e.g. through the use of set-backs) would be a risk-averse approach to mitigating the effects of noise pollution on fish.

KEYWORDS

behaviour, fish, largemouth bass, noise, recreational boating

1 | INTRODUCTION

Human interactions with aquatic ecosystems (marine and freshwater) have led to reductions in habitat quality and a loss of biodiversity around the globe (Dudgeon et al., 2006; Worm et al., 2006). Some of the largest and most well-studied human impacts on these ecosystems are those from fisheries exploitation, habitat alteration, climate change, and various forms of pollution. One form of pollution that has recently garnered significant attention from the scientific community is anthropogenic noise (Slabbekoorn et al., 2010). In aquatic systems, anthropogenic noise is produced by various sources, including energy generation from hydroelectric dams (Miyamoto, McConnell, Anderson, & Feist, 1989), hydrokinetic turbines (Cada et al., 2007), resource exploration and extraction (e.g. seismic exploration and drilling; Hildebrand, 2009), commercial shipping (Hildebrand, 2009; Neenan et al., 2016), and recreational boating (Arthington & Mosisch, 1998; Haviland-Howell et al., 2007). These artificial noises can be ecologically problematic in a number of ways. For example, anthropogenic noise can mask the natural aquatic soundscape, thereby interfering with the potential cues animals use for navigation, communication, and survival (Neenan et al., 2016; Popper & Hastings, 2009; Radford, Kerridge, & Simpson, 2014). In addition, noise can itself be a form of disturbance or stress, with associated effects on the neuroendocrine system, reproduction and development, metabolism, cardiovascular health, cognition and sleep, audition and balance, and the immune system (reviewed in Kight & Swaddle, 2011; Kunc, McLaughlin, & Schmidt, 2016; Popper & Hastings, 2009; Popper & Hawkins, 2015). Whereas the majority of research on anthropogenic noise has focused on impacts to marine mammals (e.g. Ellison, Southall, Clark, & Frankel, 2012; Rolland et al., 2012; Southall et al., 2008), there has been growing interest recently in the potential impacts on sea turtles and fish (Popper et al., 2014; Popper & Hastings, 2009; Slabbekoorn et al., 2010). As fish are generally most sensitive to low frequencies (<1000 Hz), they may be particularly vulnerable to impacts from anthropogenic noise (Popper & Fay, 2011).

Of particular concern is noise generated from combustion engines, which are the typical operating systems of commercial and recreational watercrafts. Recreational boating is an extremely common leisure activity worldwide (Clarke Murray, Pakhomov, & Therriault, 2011; Lloret, Zaragoza, Caballero, & Riera, 2008). For example, in North America, recreational boating has been steadily increasing in prevalence since the 1950s (Cooke & Murchie, 2015; Gifford, 2015). Several recent studies have investigated the potential impacts of boat noise on freshwater fishes. Scholik and Yan (2002) showed that 2 hours of exposure to boat noise elevated the hearing thresholds of fathead minnows (*Pimephales promelas*). Wysocki and Ladich (2005) measured the hearing thresholds of three freshwater fish species under elevated (white noise) conditions and saw that increases in background noise significantly elevated the overall hearing thresholds. A follow-up study (Wysocki, Dittami, & Ladich, 2006) with three other freshwater species showed that noise from boats elicited a significant cortisol response, but continuous white noise did not. They also noted that there was no significant difference in response from the hearing 'specialists' versus hearing 'generalists' (i.e. species with unique hearing structures that allow the detection

of acoustic pressure versus species that primarily detect sound through particle motion) (Popper & Fay, 2011). Nichols, Anderson, and Širović (2015) found that giant kelpfish (*Heterostichus rostratus*) exhibited a stress response (an increase in cortisol) to intermittent boat noise, but not to continuous noise or control conditions, suggesting that the temporal nature of noise plays an important role in the animal's response. Taken together, these studies suggest that increased noise can increase hearing thresholds, but whether fish become stressed – and how this may alter their behaviour – remains unclear. Furthermore, despite an overall trend suggesting deleterious effects of noise on fishes (Cox, Brennan, Dudas, & Juanes, 2016), there are still many knowledge gaps, especially in freshwater species that lack hearing specializations. Beyond fish, recreational boating noise and activity can influence the behaviour of turtles (e.g. Jain-Schlaepfer, Blouin-Demers, Cooke, & Bulté, 2017) and waterbirds (Vos, Ryder, & Graul, 1985).

Aquatic noise pollution may be particularly important for fish species that actively provide parental care (PC), as this period can be the most vulnerable life stage for the developing offspring. PC is common among teleost fish, occurring in approximately 22% of all families, with 3000–5000 individual species believed to provide PC (Blumer, 1982; Gross & Sargent, 1985). Notably, 95% of fish that engage in PC include some level of brood guarding (Blumer, 1982; Gross & Sargent, 1985). Most species that engage in parental care live in shallow, nearshore systems (e.g. the littoral zones of lakes or coral reef habitats; see Blumer, 1982), which are the same environments that have been subject to extensive anthropogenic disturbance, and where recreational boating is common. In freshwater systems in temperate North America, most recreational watercraft are operated in the spring and summer (Bulté, Carrière, & Blouin-Demers, 2010; Lorenz, Gabel, Dobra, & Pusch, 2013), when temperate endemic freshwater species such as those in the family Centrarchidae engage in PC (Cooke & Philipp, 2009). If noise disturbance during the PC period disrupts PC ability or behaviour, then impacts on fitness levels can occur at the level of the individual, which could influence the productivity of fish populations. As nearshore fish populations face many threats, noise from recreational boats during the PC period could be particularly detrimental and represent a significant conservation concern. Indeed, the PC period has been regarded as a particularly sensitive period for a variety of organisms (Wong & Candolin, 2015), and fish that provide PC are considered to be at greater risk of imperillment compared with fish that have other reproductive strategies (Parent & Schriml, 1995).

The largemouth bass (*Micropterus salmoides*) is a PC-providing fish species native to lake and river systems throughout much of North America. Although largemouth bass are not imperilled, they do play important roles (often as the top piscivore) in freshwater systems, and serve as a useful model for the 30+ other species of the Centrarchidae that provide PC (some of which are rare or otherwise imperilled; Cooke & Philipp, 2009). Largemouth bass spawn in shallow littoral regions of lake and river systems, often along shorelines in close proximity to human development or activity (e.g. cottages, docks, and beaches; Mesing & Wicker, 1986). Male largemouth bass actively guard the nests containing developing eggs and fry for 3–4 weeks (Cooke, Philipp, Wahl, & Weatherhead, 2006). In fact,

males expend energy equivalent to swimming upwards of 40 km per day engaging with nest predators, without actively leaving the nest site (Cooke, Philipp, & Weatherhead, 2002). In addition to brood defence during the egg stage, the egg-sac fry stage (in which larvae possess basic anatomical development, including differentiated eyes, tail, and a prominent large yolk sac; Cooke et al., 2002; Hubbs & Bailey, 1938; Ridgway, 1988), and the swim-up fry stage (in which small black pigmented larvae navigate up and down within the water column; Cooke et al., 2002; Hubbs & Bailey, 1938), parental males actively 'fan' the nest with their pectoral fins to circulate oxygen and clear away debris during the early phases of care (Cooke et al., 2002). To compound the energetic and physiological challenges during the PC period, nest-guarding males curtail active foraging, and consequently receive little or no nutritional intake for the duration of the PC period (Heidinger, 1975; Miller, 1975). As such, PC is powered largely through endogenous energy stores (Cooke et al., 2006). Indeed, parental males have a limited energy budget during the PC period to successfully rear a brood to independence. This limited energy budget could leave males more susceptible to human disturbance, and ultimately could result in nest abandonment (Zuckerman & Suski, 2013).

This study evaluated changes in parental care behaviour of nest-guarding largemouth bass exposed to disturbance from boat noise. Specifically, three distinct noise disturbances were simulated at the nest site of parental largemouth bass tending eggs to quantify changes in PC behaviour, including: (i) a boat with a combustion motor passing nearby at high speed; (ii) the same boat passing by at idling speed; and (iii) an electric trolling motor passing by. Each of these noise treatments provided a realistic emulation of the acoustic pressure field produced by recreational boating activities (Jackivicz & Kuzminski, 1973). The predicted outcome was that boat noise would decrease the nest-guarding behaviour of largemouth bass during the egg stage, and that these changes would be more pronounced when fish were exposed to higher-intensity boat noises.

A second experiment tested whether the effect of the high-speed boat passing nearby on nest-guarding behaviour of the male bass differed depending on the brood stage (i.e. eggs, egg-sac fry, and swim-up fry). The prediction was that guarding males with a more developed brood would spend more time away from the nest, as PC tends to decrease as the offspring mature towards independence (Cooke et al., 2002). The results of this study are considered in relation to the cryptic impacts of boat noise on fishes during critical life-history phases. Potential implications for conservation managers and recommendations for future work are also discussed.

2 | METHODS

2.1 | Study site and species

Data collection occurred on Lake Opinicon in South Frontenac, Ontario, Canada in May 2016. Lake Opinicon is part of the Rideau Canal system, and contains several littoral regions with plenty of woody debris, providing a highly complex habitat for aquatic life (Figure 1; Crowder, Bristow, King, & Vanderkloet, 1977). Almost all boating activity on Lake Opinicon is recreational, including fishing, pleasure boating, water skiing, and canoeing (Graham & Cooke, 2008). Bulté et al. (2010) reported that ~5000 boats used the Rideau Canal locks at Lake Opinicon, but this number failed to incorporate 'resident' boats or those launched and removed on a transient basis.

2.2 | Acoustic recordings and playbacks

First, recordings of three types of boat sounds were made at Lake Opinicon in an area with a mixed substrate (fines over gravel and rock) and a water depth of 6 m. The sound trap (300 STD hydrophone, 48-kHz sample rate; Ocean Instruments Inc., San Diego, CA, USA)

FIGURE 1 Photograph of a largemouth bass on a nest with the hydrophone mounted in the background. Note the soft, largely organic sediment into which the hydrophone stand was driven, and the thick vegetation around the nest

was anchored 2 m from the surface, and the boat (a 5.4-m aluminium-hulled fishing boat with a 75 HP Evinrude E-Tec outboard motor; Evinrude, Sturtevant, WI, USA) passed by at a distance of 10 m from the sound trap. For the 'high-speed' (HS) treatment, the boat made a single pass at high speed (operating at 5000 rpm); for the 'idle' (ID) treatment, the same boat passed by at an idle speed (600 rpm). For the 'trolling' (TR) treatment, the main engine was turned off and the same boat passed by using only the trolling motor (Minn-Kota 75-lb thrust trolling motor; Minn-Kota, Racine, WI, USA). All sound files were truncated to a 1-min duration to match the duration of the high-speed pass-by. As fishes are most sensitive to sounds below 1 kHz, all sound files were low-pass filtered at 1 kHz; this also helped to remove unnecessary distortions from the underwater speaker at higher frequencies.

Next, playbacks were calibrated in the same part of Lake Opinicon to ensure that the output from the speaker system matched the acoustic stimulus generated by the boat. The sound trap was placed in the same position and same water depth and the underwater speaker system was used to generate sounds. An iPod (7th generation iPod Nano; Apple Inc., Cupertino, CA, USA) and preamplifier (Stealth Bomber; Cerwin Vega, Los Angeles, CA, USA), powered by a boat battery, played the sounds through a single UW-30 speaker (University Sound UW30; Lubell Labs Inc., Whitehall, OH, USA), which was mounted on a pole 2.5 m from the hydrophone. The noise treatment playback files were reproduced from the iPod speaker system at various volumes until the acoustic spectra of the sounds received on the hydrophone emulated the actual boat passes. Audio spectrograms produced using RAVEN PRO and MATLAB were used to make visual comparisons between the boat and motor sound files, and the sound pressure levels (SPLs) received were compared. Once adequate settings for the amplifier were obtained, the same settings were used for the playbacks in Lake Opinicon at the site of the bass nests. Recordings of the three sound stimuli were also made at the site of a largemouth bass nest in Lake Opinicon. Although particle motion is a more salient cue for fishes than acoustic pressure (Popper & Fay, 2011; Radford, Montgomery, Caiger, & Higgs, 2012), a particle motion sensor was not available for this study. Therefore, the results presented here should be used in a comparative nature, and not interpreted as a response to absolute sound levels.

2.3 | Noise disturbance experiments

In total, 58 male nest-guarding largemouth bass (33–48 cm in length) were located using snorkelling surveys of the littoral zones. To assess the effect of boat noise on PC, 36 males guarding the egg stage were selected and further subdivided into noise treatment type: 12 HS, 11 ID, and 13 TR. To assess differences in response to HS noise across different brood stages, a further 13 males guarding the egg-sac fry stage (ESF), and nine males guarding the swim-up fry stage (SUF) were treated with HS noise. Upon identification of an active nest-guarding male, the nest was marked with a PVC identification tile, and a nest-site assessment was conducted. The nest-site assessment included recording the egg stage, water temperature, nest depth, weather, habitat complexity, number of predators, approximate male size, and egg score. Egg stage was recorded as eggs, ESF, or SUF, depending on

the brood development stage. Habitat complexity was given a ranking of low, moderate, or high, where low complexity indicated little vegetation and no wood, moderate complexity indicated some vegetation and small pieces of wood, and high complexity indicated abundant vegetation or lily pads and large logs or stumps (Twardek et al., 2017). The predator score was obtained by counting brood predators of largemouth bass within a 2-m radius from the nest for 1 min (Gravel & Cooke, 2013). Egg score (the relative number of eggs present in the nest) was assessed, ranging from a low score of 1 to a high score of 5 (Suski & Philipp, 2004).

After the initial nest assessment, cameras (Hero 3+; GoPro Inc., San Mateo, CA, USA) were placed approximately 1.0–1.5 m away from the nest, and an underwater speaker was placed approximately 2.5–3.0 m from the nest. Speakers and cameras were placed on metal poles that were gently driven into the soft sediment. The speaker was suspended from the metal pole by a rope to prevent the speaker from vibrating the metal post. Pilot assessments determined that a 5-min acclimation period was a sufficient buffer to remove any effects of the researcher and equipment on PC. This also allowed enough time to let disturbed sediment settle to the bottom, ensuring useable video footage. After the 5-min acclimation period, there was a 5-min pre-treatment period to quantify baseline PC behaviour, followed by a 1-min sound treatment and a 10-min post-treatment period.

Following the same methodology as described above, a second experiment tested the effects of only HS acoustic stimuli on additional nest-guarding males with ESF (n = 13) as well as SUF (n = 9) brood stages. This data collection period occurred from 17 to 22 May 2016, after the egg brood stage. None of the fish used in the first experiment were re-used for the second experiment, apart from the egg-stage data for the combustion motor at HS, which were re-used in this analysis (n = 12).

2.4 | Data analysis

Video analysis involved recording and quantifying the behaviour of the guarding male bass. Each 16-min video (5-min pre-treatment, 1-min treatment, and 10-min post-treatment) was dissected into 1-min intervals. The behaviours analysed included those previously recognized as important to sunfish PC (Gallagher, Lawrence, Jain-Schlaepfer, Wilson, & Cooke, 2016): time on the nest (i.e. residency in seconds); number of 90° turns while on the nest; and the number of pectoral fin beats while on the nest.

Similarly to Liu (2014), the median of the response variables for the pre-treatment and the last 9 min of the post-treatment period was taken for each fish to generate four different time periods: the pre-treatment median (from five 1-min values), the actual treatment (value from 1 min), the actual first minute of post-treatment (value from 1 min), and the post-treatment median (from nine 1-min values). The medians were taken to balance the sample sizes and thus the variance across time periods. The four time periods were further categorized into the HS, ID, or TR treatments (i.e. the experiment on differing noise types at the egg stage), and eggs, ESF, and SUF stages (i.e. the experiment on HS noise at differing brood stages). Therefore, the statistical test performed for each experiment was a two-way analysis of variance (ANOVA) with repeated measures

across time groups (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median). Tukey's honest significant difference (HSD) post-hoc analyses were run to determine whether there were differences between the time periods within the particular noise treatment or brood-stage category. All statistical analyses were performed in JMP 9, and figures were created in R STUDIO and MATLAB.

3 | RESULTS

3.1 | Experiment 1: differing noise types at the egg stage

Sound pressure levels received from the real boat recording, the calibrated sound playbacks, and the sound levels received on bass nests are shown in Table 1, and acoustic spectra from the three motor types are shown in Figure 2. There was no evidence of alterations in parental care behaviour for largemouth bass at the egg stage associated with 1 min of noise emanating from combustion (at idle or cruising speed) or electric trolling motor noise during the 10 min in which behaviour was monitored after treatment. Residency under pre-treatment conditions across the treatments was consistently high (with a global pre-treatment mean of 58.1 ± 7.6 s), and did not vary among the four treatment periods within the three noise treatment types (ANOVA; $F = 0.259$, $P = 0.954$; Figure 3). Similarly, the numbers of turns in the nest were similar under pre-treatment conditions, and were not significantly influenced by any of the three noise types across the four stages (ANOVA; $F = 1.202$, $P = 0.311$; global pre-treatment mean of 6.0 ± 2.5 turns per min; Figure 4). The number of fin beats while on the nest neither significantly differed under pre-treatment conditions nor among the three noise treatments across the four treatment periods (ANOVA; $F = 1.229$, $P = 0.299$; global pre-treatment mean of 63.7 ± 8.1 beats per min; Figure 5).

3.2 | Experiment 2: high-speed noise at differing brood stages

For the brood stages treated with the noise of the high-speed boat motor, the results showed a significant reduction in the number of 90° turns (Figure 6). Under the ESF brood stage, nest-guarding males turned significantly fewer times during the treatment period (5.2 turns

TABLE 1 Received sound pressure level at frequencies <1000 Hz for the three boat engine types, from recordings of the real boat pass-bys, the output from the speakers at the calibration site in Lake Opinicon, and from recordings at a real bass nest in Darlings Lake. All recordings were 60 s in duration and all units are in dB re. 1 µPa. The received level (root mean squared (RMS) average sound pressure < 1000 Hz) for a real boat that passed at high speed approximately 20 m from the nest in Darlings Lake was 104.23 dB, and ambient noise at the same location (with no boat) was 84.56 dB

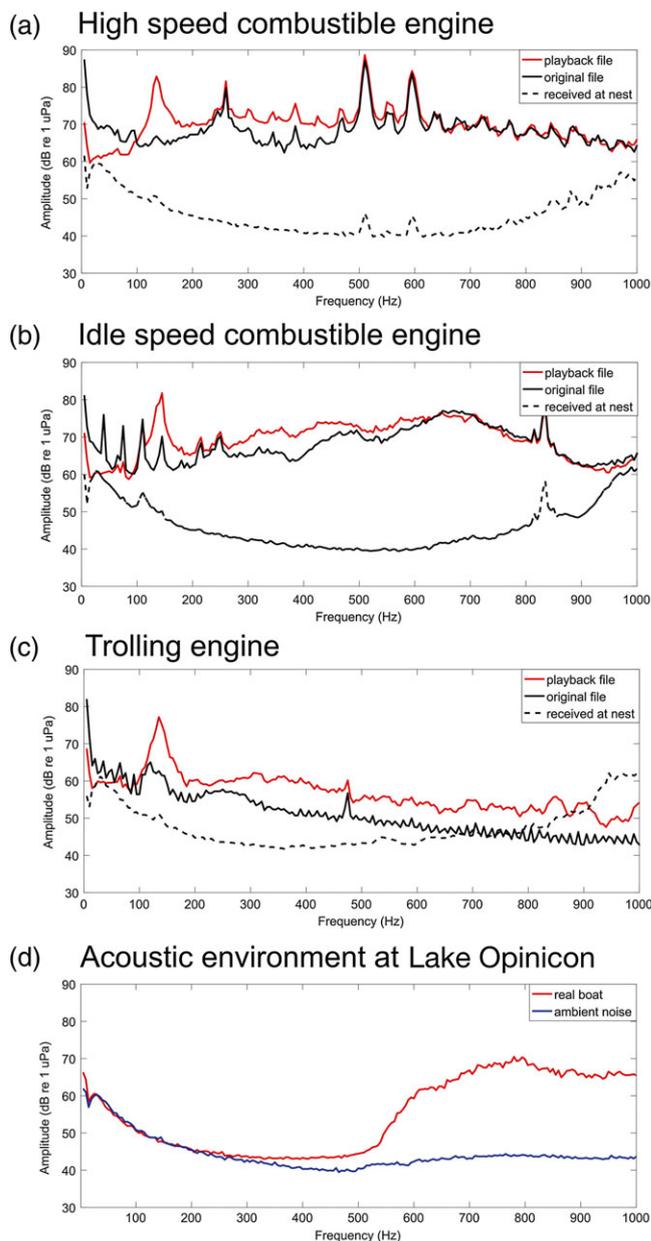|	High-speed boat	Idling boat	Trolling engine
From real boat	115.47 dB	108.66 dB	96.50 dB
From speaker system	115.43 dB	108.54 dB	99.60 dB
At site of nest	105.72 dB	94.90 dB	98.56 dB

FIGURE 2 Acoustic spectra for each of the three sound types as well as acoustic conditions at the experimental site in Lake Opinicon. (a–c) Black lines, sounds recorded from the real boat engine; red lines, boat sounds reproduced by the speaker system at the calibration site; dashed black lines, boat sounds reproduced by the speaker system at nest sites. Although the sounds reproduced by the speaker system (red lines) were well matched to the original recordings from the boat, in the experimental site at Darlings Lake, the shallow water, soft sediment, and thick vegetation layer served as an environmental filter, absorbing much of the low-frequency energy. This is apparent in panel (d), which shows the acoustic spectrum from another boat that passed by the experimental site at a distance of 20 m: the sounds from this boat barely exceeded ambient noise (blue line). This filter helps to explain the relatively minimal response observed in largemouth bass in the present study, and may serve as a natural buffer, mitigating some of the deleterious effects from boat noise

per min) than the long-term post-treatment period (8.2 turns per min; ANOVA; $F = 4.425$, $P = 0.010$; Figure 6). Moreover, the males turned more during the long-term post-treatment period when compared with both the pre-treatment period (7.1 turns per min) and the
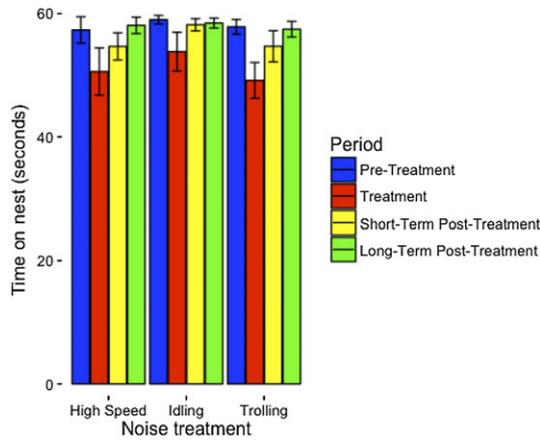
FIGURE 3 Time on the nest for egg-guarding largemouth bass males on Lake Opinicon, Ontario, Canada, in early May. The average time is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median) under each noise treatment type (i.e. high speed, idling, or trolling). Error bars are the standard errors
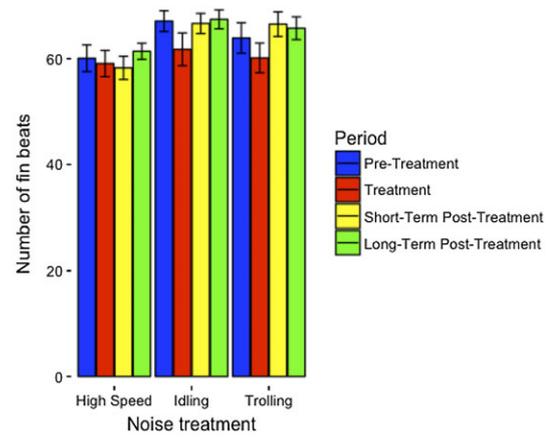

FIGURE 5 Number of pectoral fin beats for egg-guarding largemouth bass males on Lake Opinicon, Ontario, Canada, in early May. The average number of fin beats per minute is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment) under each noise treatment type (i.e. high speed, idling, or trolling). Error bars are the standard errors
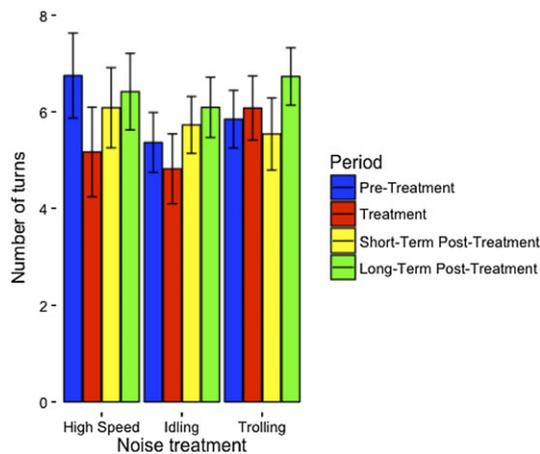

FIGURE 4 Number of 90° turns on the nest for egg-guarding largemouth bass males on Lake Opinicon, Ontario, Canada, in early May. The average number of turns per minute is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median) under each noise treatment type (i.e. high speed, idling, or trolling). Error bars are the standard errors
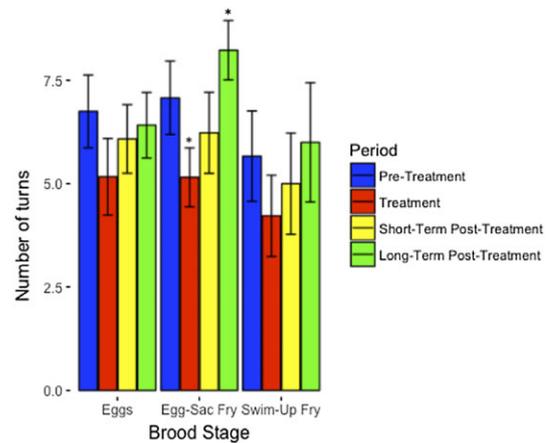

FIGURE 6 Number of 90° turns for nest-guarding largemouth bass males across brood stage (i.e. eggs, egg-sac fry, and swim-up fry) on Lake Opinicon, Ontario, Canada, in mid-May treated with high-speed boat motor noise. The average number of turns per minute is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median). Error bars are the standard errors, and significant differences at the 0.05 level are marked with an asterisk

short-term post-treatment period (6.2 turns per min), although the difference was not significant (Tukey's HSD test; $P = 0.558$ and 0.121, respectively; Figure 6). A similar trend was observed for the egg and SUF stages, although the difference was not significant (ANOVA; $F = 0.470$, $P = 0.829$; Figure 6). Both residency (ANOVA; $F = 0.530$, $P = 0.784$; Figure 7) and the number of fin beats (ANOVA; $F = 0.685$, $P = 0.662$; Figure 8) of nest-guarding largemouth bass under all three brood stages were not significantly affected by the combustion motor at cruising speed during the 10 min in which PC behaviour was monitored after treatment.

4 | DISCUSSION

This study demonstrated the context-dependent influence of boat noise on the behaviour of a widely studied, socio-economically valuable

freshwater fish during a critical life-history phase. Specifically, data showed a reduction in PC behaviour in largemouth bass during the ESF brood stage (Figure 6). The ESF are highly dependent on nest-guarding from the parental male, as they are immobile and do not have anti-predatory capabilities (Cooke et al., 2002; Hubbs & Bailey, 1938; Ridgway, 1988; Zuckerman & Suski, 2013). Therefore, any time when the male is off the nest renders the brood highly susceptible to nest predation by other species, thereby resulting in implications for potential fitness. Cooke et al. (2002) found that relative electromyography (EMG) activity, burst swimming activity, and relative range of largemouth bass were elevated during the ESF stage compared with all other brood stages, suggesting that males invest most heavily in PC duties during the ESF stage. As such, the reduction in turning observed during the noise treatment could have consequences for the offspring, as turning is a measure of vigilance, where the male
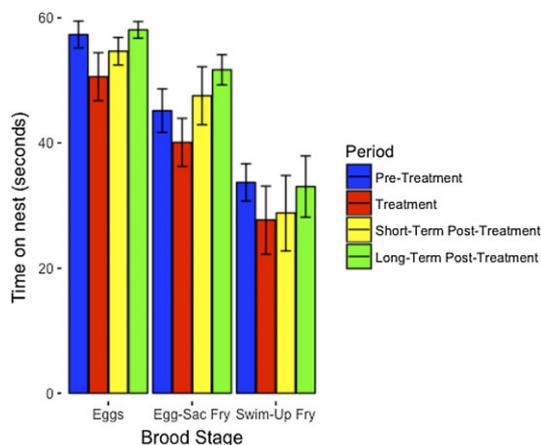
FIGURE 7 Time on the nest for nest-guarding largemouth bass males across brood stage (i.e. eggs, egg-sac fry, and swim-up fry) on Lake Opinicon, Ontario, Canada, in mid-May treated with high-speed boat motor noise. The average time is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median). Error bars are the standard errors
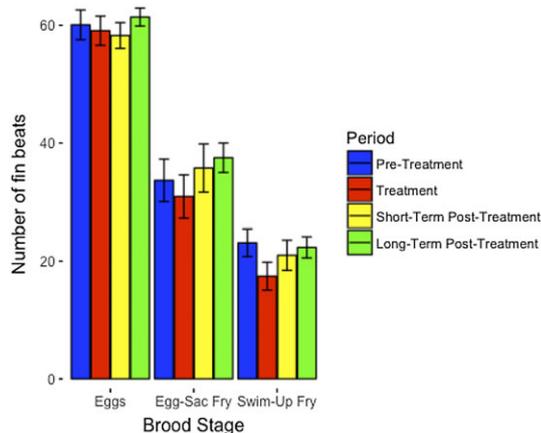

FIGURE 8 Number of pectoral fin beats for nest-guarding largemouth bass males across brood stage (i.e. eggs, egg-sac fry, and swim-up fry) on Lake Opinicon, Ontario, Canada, in mid-May treated with high-speed boat motor noise. The average number of fin beats per minute is given for each treatment period (i.e. pre-treatment median, treatment, short-term post-treatment, and long-term post-treatment median). Error bars are the standard errors

monitors the nest from all directions: more vigilant males will turn more often (Hinch & Collins, 1991). If males are turning less because of human disturbance, the brood could be vulnerable to predation attempts. Nonetheless, this impact was transient and limited to the 1-min period during which the noise treatment was applied. Nest predators are omnipresent in most systems where bass nest, however, and even a temporary reduction in nest vigilance may enable predators to devalue the nest, which can result in reductions in reproductive output and even trigger premature nest abandonment (Stein & Philipp, 2015).

Three different types of boat noise (i.e. HS, ID, and TR) were used in this study, but there were no significant effects on the behaviour of egg-guarding male largemouth bass (Figures 3–5). This result was at first somewhat surprising, considering that Graham and Cooke

(2008) found that largemouth bass exhibited an increase in cardiac output when exposed to the sounds of a combustion engine, a trolling motor, and a canoe in the laboratory. The hard edges of a tank, however, will inevitably distort the acoustic field and can increase particle motion in certain areas (Akamatsu, Okumura, Novarini, & Yan, 2002; Okumura, Akamatsu, & Yan, 2002). Graham and Cooke (2008) used a wave baffle to minimize mechanical disturbance in the experiments, but without a particle motion sensor inside the tank it is impossible to know the stimulus that the fish received during the treatments. Furthermore, when very close to a sound source (e.g. tens of centimetres), as the fish were in the 2008 study, particle motion is the dominant acoustic cue, rather than acoustic pressure. The present study was conducted in the field to understand whether largemouth bass would be disturbed by boats passing their nests at realistic distances (e.g. in the order of tens of metres). The shallow, soft-bottom and macrophyte-rich environment in which the bass live appeared to serve as a de facto acoustic filter, effectively absorbing sounds below ~600 Hz (Figure 2D). It is expected that in extremely shallow water, the lowest frequencies will not propagate (i.e. 'low-frequency cutoff'; Urick, 1975), but the ~2-m layer of soft vegetation and silt/organic matter probably enhanced this effect. The sounds from the high-speed engine, for example, decreased by 10 dB when they were played in the shallow waters of the lake (Table 1). Although a distance of 2 m from a boat may be more realistic than in the previous laboratory study, the degree of dampening caused by the highly absorptive acoustic environment meant that the fish in this study received rather low levels of acoustic stimuli.

Several factors could explain the null results, such as the minute direct risk of boat noise to largemouth bass, habituation, and the auditory capacities of the fish. First, boat noise alone does not impose a large risk directly to nesting adult largemouth bass, so bass could ignore the noise if it has not caused harm in the past. Second, largemouth bass may become habituated to noise after long-term frequent (even if transient) exposure; however, this is unlikely with the constantly changing nature of the sound produced from a high-speed boat passing by (Neo et al., 2014). Third, although there are limited data on hearing sensitivity in largemouth bass, it is generally understood that they hear best at frequencies of 300 Hz and below, and do not hear as well as most other fishes (Holt & Johnston, 2011; Jones & Johnson, 2005). The relatively strong response observed in the laboratory (Graham & Cooke, 2008), where particle motion levels were high, compared with the minimal response in the present study, where both pressure and particle motion levels were low, sheds light on the context-dependent nature of noise impacts on fishes, and opens the door for additional study. Future studies should include in situ particle motion measurements at different distances from noise sources, aiming to understand the distance at which a boat pass-by becomes detectable and stressful. In addition, the environmental influence on sound propagation in different freshwater environments should be considered.

Overall, this study found weak evidence for the effects of boat noise on PC of largemouth bass, except during one stage of offspring development. Although boat noise does not impose an acute survival risk to the nesting adult largemouth bass, this study suggests that changes in PC behaviour are a potential consequence, which could

lead to offspring mortality (e.g. predation, as has been observed in a PC-providing coral reef fish; Nedelec et al., 2017), and thus loss of parental fitness. Summed over areas with heavy boating activity and high densities of nest predators, these sublethal impacts could be appreciable to the fitness and stock status of this socio-economically and ecologically valuable species. Owing to the potential noise-filtering of shallow littoral zones with submerged aquatic vegetation, freshwater fishes living in ephemeral lakes may be less susceptible to anthropogenic noise. Moreover, it is possible that fish such as smallmouth bass, which engage in PC on firmer substrates, may be more susceptible to noise pollution.

The fact that much PC activity in marine and freshwater fish occurs in nearshore areas subject to intense recreational boating activity makes the findings from this study more broadly important. These are the same habitats that are subject to other stressors (e.g. habitat alteration, light pollution, eutrophication; Arthington, Dulvy, Gladstone, & Winfield, 2016), such that noise could make a challenging life-history activity (i.e. PC) even more difficult for fish (sensu Algera, Gutowsky, Zolderdo, & Cooke, 2017). To mitigate the effects of noise on fish engaged in PC, it may be possible to restrict boating activity from key PC habitats (e.g. nesting sites in the case of largemouth bass) during periods where priority species (e.g. imperiled species) are engaged in that activity. This might be in the form of outright closures or simply implementing set-backs that restrict boating within a given distance from nesting areas. Such restrictions on boating already exist in some nearshore areas to protect waterbirds engaged in PC (Rodgers & Smith, 1995), demonstrating the proof of concept for such a management strategy. Future research should consider other fish species in aquatic systems with differing complexities and acoustic dynamics, and explore the extent to which effects vary among species, habitat, season, life stage, life-history events, and additional stressors (such as nest predators). Moreover, to refine potential mitigation strategies (e.g. set-backs), and guide management strategies, it will be necessary to identify the distances between the noise source and the fish engaged in PC at which the effects are negligible.

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