Journal of Comparative Physiology A (2020) 206:1–14
https://doi.org/10.1007/s00359-019-01381-x

ORIGINAL PAPER

The effect of biological and anthropogenic sound on the auditory sensitivity of oyster toadfish, *Opsanus tau*

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Received: 24 July 2019 / Revised: 8 November 2019 / Accepted: 11 November 2019 / Published online: 10 December 2019

Abstract

Many aquatic organisms use vocalizations for reproductive behavior; therefore, disruption of their soundscape could adversely affect their life history. Male oyster toadfish (*Opsanus tau*) establish nests in shallow waters during spring and attract female fish with boatwhistle vocalizations. Males exhibit high nest fidelity, making them susceptible to anthropogenic sound in coastal waters, which could mask their vocalizations and/or reduce auditory sensitivity levels. Additionally, the effect of self-generated boatwhistles on toadfish auditory sensitivity has yet to be addressed. To investigate the effect of sound exposure on toadfish auditory sensitivity, sound pressure and particle acceleration sensitivity curves were determined using auditory evoked potentials before and after (0-, 1-, 3-, 6- and 9-day) exposure to 1- or 12-h of continuous playbacks to ship engine sound or conspecific vocalization. Exposure to boatwhistles had no effect on auditory sensitivity. However, exposure to anthropogenic sound caused significant decreases in auditory sensitivity for at least 3 days, with shifts up to 8 dB SPL and 20 dB SPL immediately following 1- and 12-h anthropogenic exposure, respectively. Understanding the effect of self-generated and anthropogenic sound exposure on auditory sensitivity provides an insight into how soundscapes affect acoustic communication.

Keywords AEP · Sound pressure level · Particle acceleration level · Anthropogenic · TTS

Introduction

Aquatic organisms are exposed to various abiotic (e.g., waves, wind and rain), biotic (e.g., invertebrates, fishes and marine mammal vocalizations) and anthropogenic (e.g., nearshore and offshore construction, ship traffic, seismic exploration and sonar) sounds. These various sound sources have the potential to interfere with, or mask, acoustic communication in the underwater soundscape (Popper and Hawkins 2016, 2019; Putland et al. 2019). It has previously been shown that exposure to anthropogenic sound may negatively affect the behavior (e.g., foraging, movements, predator/prey interactions and mating) and physiology (e.g., hearing, oxygen consumption and heart rate) of aquatic organisms (for review see Slabbekoorn et al. 2010; Radford et al. 2014; Williams et al. 2015; Shannon et al. 2016; Popper and Hawkins 2019). While research on the effects of exposure to anthropogenic sound has been conducted on marine mammals (e.g., Holt et al. 2008; Sivle et al. 2012; Pirotta et al. 2015), less is known regarding the effect of anthropogenic sound on fishes (Hawkins et al. 2015). Additionally, the effect of self-generated sounds on the signaler's auditory sensitivity remains largely unexplored.

In fishes, sound detection is mediated by the displacement of mechanoreceptive sensory hair cells in the lateral line and inner ear (Flock and Wersäll 1962; Flock 1965; Wersäll et al. 1965; Hudspeth and Corey 1977; Hudspeth 1985). However, similar to the auditory systems of terrestrial organisms (Hamernik et al. 1974; Saunders and Dooling 1974), high intensity and/or prolonged sound exposure may result in hair cell damage, which leads to decreases in auditory sensitivity or temporary threshold shifts (TTS). For example, TTS following exposure to white noise (0.2–4.0 kHz; 158 dB re. 1 μPa) was observed for up to 3 days in goldfish (*Carassius auratus*) and 14 days in catfish (*Pimelodus pictus*) (Amoser and Ladich 2003). Moving forward, it is critical to characterize and understand the acoustical stimulus that induces auditory sensitivity shifts and recovery due to the vital role sound detection serves in underwater communication.

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The oyster toadfish (*Opsanus tau*) is a vocal fish species found along the eastern coast of the United States. In late spring to early summer, male toadfish establish nests in shallow waters and acoustically attract females to their nest via an advertisement vocalization, termed a boatwhistle (Gray and Winn 1961; Fine 1978). Male toadfish produce boatwhistles throughout the day with peak calling usually between 1900 and 0200, with some individuals producing boatwhistles every 4 s for almost the entire night (Van Wert and Mensinger 2019). Conspecifics can detect these vocalizations via both the lateral line (Radford and Mensinger 2014; Cardinal et al. 2018; Mensinger et al. 2019) and inner ear otoliths (Fay and Edds-Walton 1997a, b; Maruska and Mensinger 2015), with sound intensities reaching up to 150 dB re. 1 µPa within the nest (Mensinger 2014). However, the effect of long-duration exposure to boatwhistle vocalizations on auditory sensitivity is unclear.

Toadfish require hard substrates for their nests and are often found under docks or piers, placing them in close proximity to anthropogenic sound sources. Additionally, male toadfish exhibit high nest fidelity (Maruska and Mensinger 2009; Mensinger 2014; Putland et al. 2018), which may make them more susceptible to the negative effects of anthropogenic sound than mobile species that can swim away from the source (Faulkner et al. 2018). Therefore, the toadfish is an excellent model to investigate the effects of anthropogenic sound. Previously, Vasconcelos et al. (2007) have shown that Lusitanian toadfish (*Halobatrachus didactylus*) auditory detection is masked during anthropogenic sound playbacks; however, the effect of prolonged exposure on auditory sensitivity has yet to be investigated. The goals of the present study were to determine toadfish baseline auditory sensitivity and the effect of anthropogenic sound or male boatwhistle vocalizations on toadfish auditory sensitivity.

Materials and methods

Animal husbandry

Adult toadfish ($n = 15$; 12 males and 3 females, standard length: 26.0 ± 3.4 cm; mean ± SD) were obtained from the Marine Biological Laboratory in Woods Hole, MA and housed at the University of Minnesota Duluth. All toadfish were collected from Buzzards Bay near New Bedford, MA between May and July 2018. At the University of Minnesota Duluth, toadfish were maintained in 515 L polypropylene recirculating tanks (120 cm length × 95 cm width × 40 cm water depth, 1.55 cm thick; Miller Manufacturing, Eagan, MN) filled with artificial saltwater (35 PSU, Instant Ocean, Blacksburg, VA) that was mechanically, chemically, and biologically filtered (1500 Penn-Plax Cascade™ filters) and maintained at 18.0 ± 0.5 ℃.

Auditory evoked potential (AEP) recordings

Auditory evoked potential (AEP) recordings were conducted between November 2018 and February 2019. AEPs were performed in a 375 L cylindrical fiberglass experimental tank (90 cm diameter × 60 cm water depth) placed on a 1 cm thick rubber mat to dampen vibrations. The experimental tank was enclosed within a galvanized angle iron frame (110 × 125 × 180 cm) covered on three sides and the top with FOAMULAR Insulation Sheathing (2.54 cm thick; Owens Corning, Toledo, OH) to reduce background sound.

Toadfish were anesthetized by immersion in a buffered 0.005% tricaine artificial seawater solution and immobilized with an intramuscular injection of 0.01% pancuronium bromide (600 µg/kg^1). Toadfish were suspended in a mesh sling above the experimental tank using an adjustable arm boom stand (Omano Microscopes, China). Two insulated stainless-steel electrodes (Rochester Electro-Medical Inc., Tampa, FL) were subcutaneously inserted into the midline of the toadfish head. The reference electrode was positioned 5 mm from the rostrum and centered between the nares, while the recording electrode was inserted along the dorsal midline directly above the brainstem approximately 6 mm anterior to the posterior end of the cranium. For serial testing, a small bolus of cyanoacrylate gel was placed on the epidermis of the toadfish immediately posterior to the recording electrode to ensure that the electrode was inserted in the same position in subsequent testing. Toadfish were submerged with their dorsal surface 5 cm below the surface and their ventral surface 40 cm above the monopole underwater speaker (Clark Synthesis AQ-339; Littleton, CO; Frequency range: 30–17,000 Hz). Electrodes were connected to a headstage (gain = 10 ×) that attached to an extracellular differential amplifier (gain = 100 ×; Dagan, Minneapolis, MN). The signal was filtered (band pass: 0.03–3 kHz) and recorded with Spike2 software (Cambridge Electronic Design Ltd, Version 8) using a custom Spike2 script (Cambridge Electronic Design; Cambridge, UK) and monitored on a portable computer.

Initial AEP testing revealed that toadfish ($n = 5$) did not respond to pure tones > 500 Hz; therefore, subsequent AEP recordings were conducted in response to 100, 120, 140, 160, 180, 200, 220, 240, 260, 280, 300, 350, 400 and 500 Hz pure tone bursts (50 ms, 500 repetitions, 3 ms delay). AEP waveforms were verified subjectively by AEP visual inspection and objectively by fast Fourier transform power spectrum analysis (FFT, Hamming Window = 1024), with the presence of a significant peak (FFT level ≥ 0.001 µV) at two times the stimulus frequency (Higgs et al. 2002; Egner and Mann 2005; Sisneros 2007; Bhandiwad et al. 2017).

After baseline AEP sensitivity curves were determined, individual toadfish were placed in a 375 L trough (50 cm water depth; top: 125 cm × 75 cm maximum width, bottom: 100 cm × 50 cm; Rubbermaid Commercial Products, Winchester, VA) sound exposure tank. An underwater speaker (Clark Synthesis AQ-339; Littleton, CO; frequency range: 30–17,000 Hz) was submerged at one end of the tank and was connected to an amplifier (Bosch Plena; Farmington Hills, MI) and Roland 4-channel portable recorder (R-44; Roland Corporation; Hamamatsu, Japan). A mesh barrier was placed at the opposite end to restrict toadfish to 50–80 cm from the speaker (Fig. 1a). Toadfish ($n = 5$ fish/treatment) received one of three treatments: a 12-h playback of an underwater sound recording from an individual male toadfish boatwhistle vocalization (fundamental frequency: 180 Hz) that was 425 ms in duration followed by 3.575 s of silence (playback frequency: 0.25 Hz), which reflects the timing of toadfish vocalizations in a natural setting (Putland et al. 2018; Van Wert and Mensinger 2019), or a continuously looped 1- or 12-h playback of a broadband anthropogenic sound recorded underwater from an idling 15 m research vessel (Detroit Diesel 12 V-71 engine; power output: 7–1193 kW; single screw; broadband frequency range: 30–12,000 Hz; 2-min duration) (Fig. 1b–e). Following sound exposure, toadfish were tested immediately (0 day), and then 1, 3, 6 and 9 days after exposure.

Sound exposure

Sound pressure (SPL; dB_{rms} re. 1 µPa) and particle acceleration levels (PAL; dB_{rms} re. 1 ms^{-2}) were determined in the experimental tank during playbacks at 18 locations within the enclosed area containing the toadfish. The benthic toadfish spent almost their entire time on the substrate; therefore, measurements were made approximately 7.5 cm from the bottom to correlate with inner ear position. Sound pressure levels were determined using a suspended calibrated hydrophone (HTI-96-MIN; High Tech Inc., Long Beach, MS; open circuit voltage (OCV) with preamp battery = −165 dB re. 1 V/µPa), while particle acceleration levels were calculated using a neutrally buoyant waterproofed triaxial accelerometer (Model: W356A12/NC; PCB Piezotronics, Depew, NY; Sensitivity: $X = 10.47$ mV ms^{-2}; $Y = 10.35$ mV ms^{-2}; $Z = 10.29$ mV ms^{-2}) connected to a signal conditioner (Model: 482C; PCB Piezotronics, Depew, NY). All data were recorded using PowerLab data acquisition system and analyzed offline as the voltage root mean square (rms) using LabChart software (Version 8). V_{rms} values measured with the hydrophone were converted into dB and then corrected for the open circuit voltage (Eq. 1). Sound pressure level for boatwhistles and anthropogenic sound was maintained at approximately 150 dB_{rms} re 1 µPa between 80 and 550 Hz within the toadfish area.

$$\text{dB}_{\text{rms}}\ \text{re.}1\ \mu\text{Pa} = 20\,\text{Log}_{10}\left(V_{\text{rms}}\right) - \text{OCV}. \tag{1}$$

V_{rms} values for each axis (X, Y and Z) of the particle accelerometer were calibrated to the sensitivity of the accelerometer and used to calculate the magnitude of particle acceleration in dB scale (Eq. 2) (Vetter et al. 2018, 2019; Nissen et al. 2019).

$$\text{dB}_{\text{rms}}\ \text{re.}1\ \text{ms}^{-2} = 20\,\text{Log}_{10}\left(\sqrt{X^2 + Y^2 + Z^2}\right). \tag{2}$$

All calculations for sound pressure and particle acceleration levels were performed within a custom Matlab software (Version2017a) script.

Particle acceleration thresholds

Particle acceleration sensitivity was determined via a waterproofed triaxial accelerometer that was placed within the AEP experimental tank at the position of the toadfish head during testing. For a given frequency, particle acceleration measurements were made across the corresponding sound intensity range. Using a custom Matlab (Version 2017a) script, particle acceleration measurements (V_{rms}) for each axis (X, Y and Z) were corrected for the sensitivity of the accelerometer (Fig. 2) and particle acceleration level sensitivity curves were determined (Eq. 2).

Statistical analysis

To determine the effects of sound exposure and recovery period on the auditory sensitivity of toadfish, a two-way repeated measure analysis of variance (ANOVA) with frequency (Hz) and time (baseline, 0, 1, 3, 6 or 9 days post-exposure) as factors and sensitivity measurements as the dependent variable was performed. A Holm–Sidak post hoc test determined significant sensitivity shifts from baseline for each frequency ($\alpha = 0.05$). All statistical analyses were performed using SigmaPlot software (Version 13).

Results

Sound exposure

The mean background PAL and SPL measured 7.5 cm from the bottom within the toadfish area of the exposure tank was -48.4 ± 1.7 dB_{rms} re. 1 ms^{-2} PAL and 102.5 ± 0.9 dB_{rms} re. 1 µPa SPL, respectively (Fig. 3a). PAL and SPL increased during boatwhistle playbacks, to -3.8 ± 1.5 dB_{rms} re. 1 ms^{-2} PAL and 151.9 ± 0.9 dB_{rms} re. 1 µPa SPL (Fig. 3b), while anthropogenic playbacks attained levels up to -4.1 ± 2.9 dB_{rms} re. 1 ms^{-2} PAL and 152.1 ± 1.2 dB_{rms} re. 1 µPa SPL (Fig. 3c).

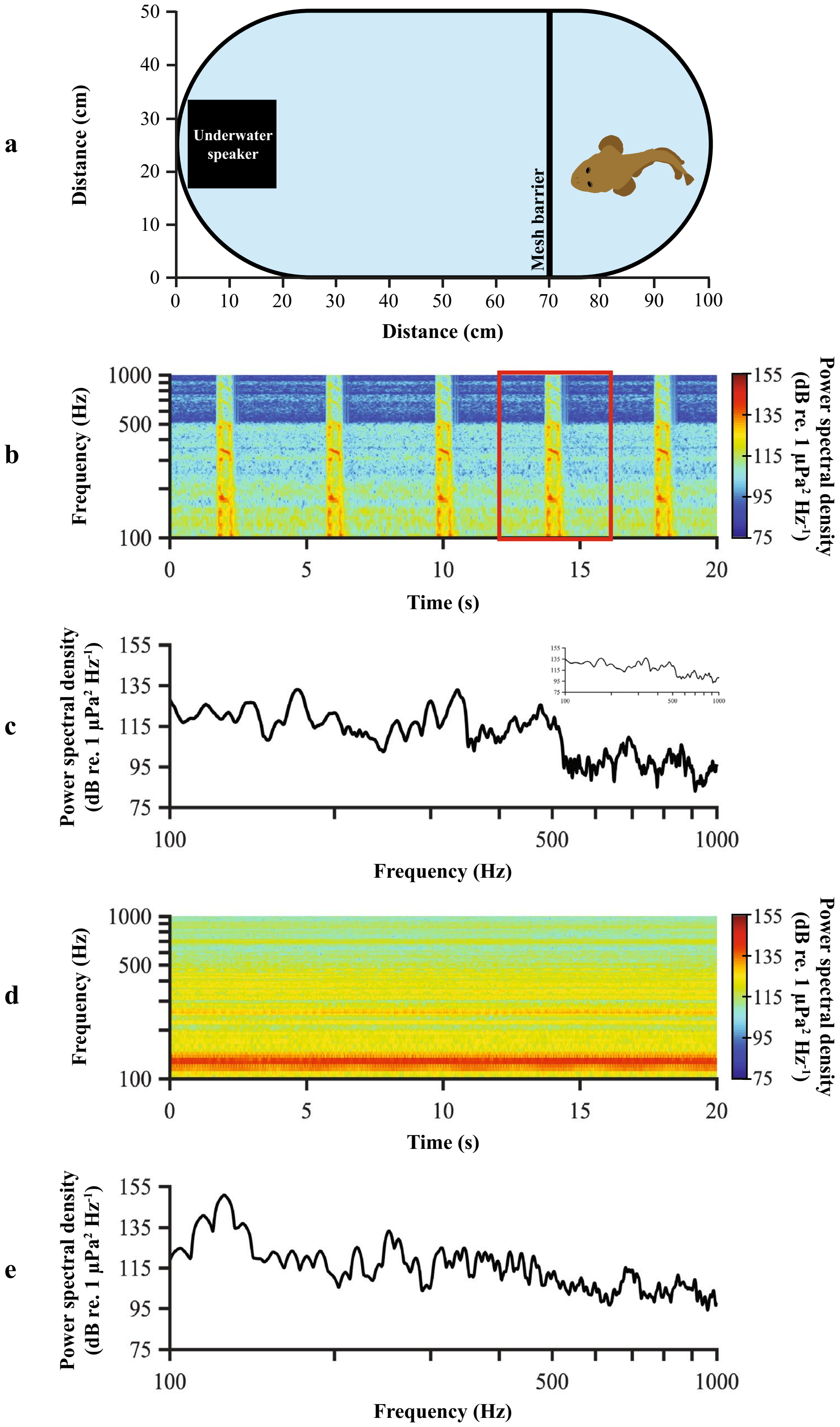


Fig. 1 Sound exposure. **a** Top view schematic of sound exposure tank showing the underwater speaker and toadfish position. The mesh barrier maintained toadfish a minimum distance of 50 cm from the speaker. **b** Spectrogram of the boatwhistle vocalization playback (180-Hz fundamental frequency; 425-ms duration; 0.25-Hz playback frequency; 150 dB re. 1 µPa). Red box indicates the time region over which the (**c**) power spectral density curve was generated. Inset represents the power spectrum of a single boatwhistle vocalization. Anthropogenic sound playback (150 dB re. 1 µPa) **d** spectrogram and **e** power spectral density curve

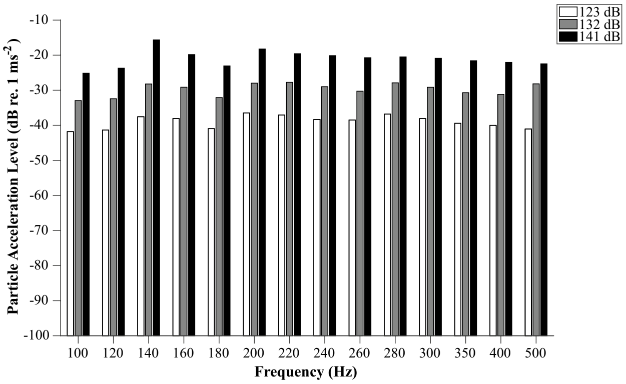


Fig. 2 Particle acceleration levels (dB re. 1 ms^{-2}) across all frequencies used during AEP testing for three representative sound pressure levels (123 (white), 132 (gray) and 141 (black) dB re. 1 µPa). Particle acceleration was measured using a triaxial accelerometer positioned at the level of the fish head

Auditory evoked potentials

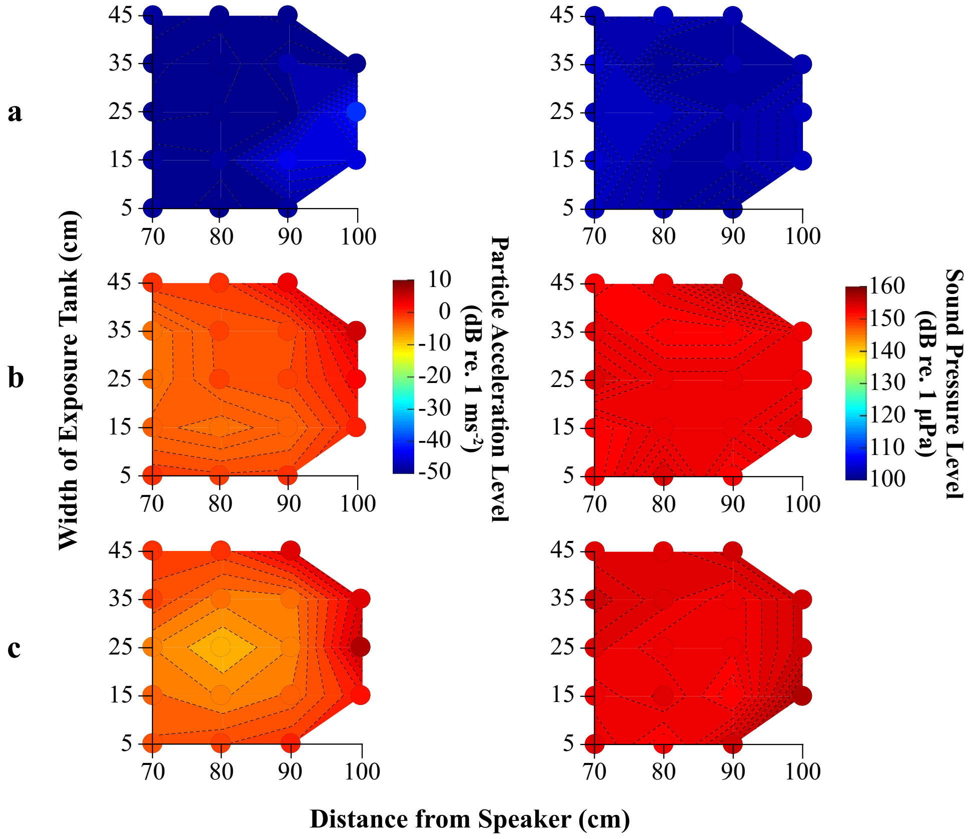
Toadfish ($n = 15$, 12 males and 3 females) responded to all tested frequencies between 100 and 500 Hz. Figure 4 displays two representative AEP waveforms and FFT analyses in response to 220 and 400 Hz, respectively. Baseline SPL (dB_{rms} re. 1 µPa) and PAL (dB_{rms} re. 1 ms^{-2}) AEP responses were observed at all frequencies tested (Fig. 5). Fish displayed greatest auditory sensitivity at 100 Hz (SPL: 116.2 ± 6.1 dB_{rms} re. 1 µPa; PAL: − 49.1 ± 6.6 dB_{rms} re. 1 ms^{-2}) and 120 Hz (SPL: 116.3 ± 6.4 dB_{rms} re. 1 µPa; PAL: − 47.2 ± 6.2 dB_{rms} re. 1 ms^{-2}), with sensitivity decreasing up to 500 Hz (SPL: 145.1 ± 3.6 dB_{rms} re. 1 µPa; PAL: − 17.9 ± 3.9 dB_{rms} re. 1 ms^{-2}) (Fig. 5). AEPs above 500 Hz were not detectable at the maximum sound pressure levels presented (150 dB re. 1 µPa).

Anthropogenic playbacks

Following 1-h anthropogenic sound exposure ($n = 5$, 4 males and 1 female), temporary SPL and PAL auditory sensitivity shifts were observed in all fish between 100 and 400 Hz (Fig. 6) with two fish showing no response to 500 Hz. To determine if auditory sensitivity significantly shifted from baseline measurements, a two-way repeated measures ANOVA was conducted between 100 and 400 Hz. Significant threshold shifts at 500 Hz were determined by removing day 0 from analysis and only post hoc values at 500 Hz were used to determine significant sensitivity shifts across 1, 3, 6 and 9 days post-exposure.

Significant auditory sensitivity shifts from baseline (two-way repeated measures ANOVA, $d.f. = 5$, $F = 8.58$, $P < 0.001$) were observed only across PAL auditory

Fig. 3 Sound maps in the toadfish end of the tank for particle acceleration (dB re. 1 ms^{-2}; left) and sound pressure level (dB re. 1 µPa; right) for **a** background, **b** boatwhistle playbacks and **c** anthropogenic sound playbacks. The maps were constructed from the average measurements ($n = 5$) at 18 locations 7.5 cm from the bottom within the toadfish area



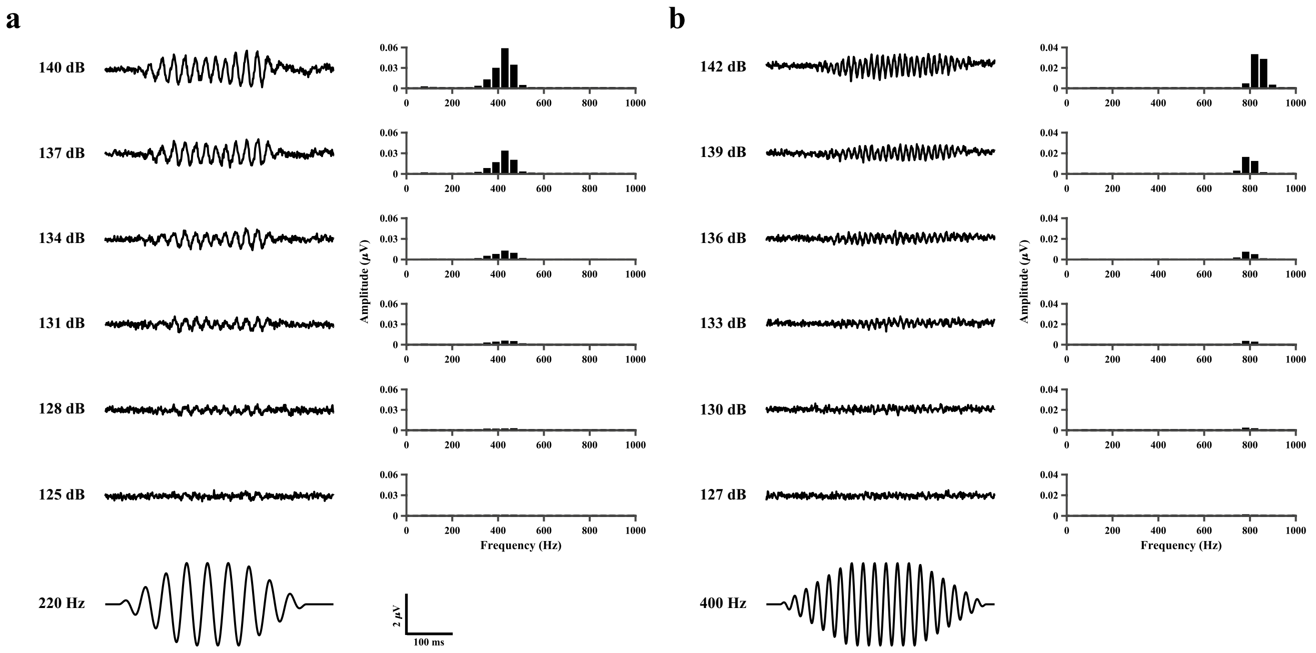


Fig. 4 Auditory evoked potential (AEP) response to **a** 220 Hz and **b** 400 Hz. Each panel displays the average AEP trace (500 repetitions) for the indicated sound pressure level (dB re. 1 µPa) on the left and the fast Fourier transformation (FFT) analysis on the right. AEP thresholds were determined to be 128 and 130 dB re. 1 µPa for 220 and 400 Hz, respectively

sensitivity curves (Table 1). Significant PAL auditory sensitivity shifts were observed at 100, 160, 180, 200 and 300 Hz (Holm–Sidak, $P<0.05$) immediately following (0 day) anthropogenic sound exposure with significant shifts at 100, 120, 160, 180, 200, 300, and 350 Hz persisting at day one. By day three, significant shifts from baseline were observed at 160, 180, and 300 Hz; however, by day six, there was no significant difference between pre- and post-exposure PAL measurements (Table 1; Fig. 6).

Following 12-h anthropogenic sound exposure, temporary SPL and PAL sensitivity shifts were observed across all frequencies (0–400 Hz), with four fish exhibiting no response at 500 Hz ($n=5$, four males and one female; Fig. 7). Significant auditory sensitivity shifts across all frequencies (100–400 Hz) were observed for both 12-h anthropogenic SPL (two-way repeated measures ANOVA, $d.f.=5$, $F=12.34$, $P<0.001$) and PAL sensitivity curves (two-way repeated measures ANOVA, $d.f.=5$, $F=12.51$, $P<0.001$). Recovery of auditory sensitivity was observed as soon as day one; however, significant shifts (Holm–Sidak, $P<0.05$) were sustained for SPL sensitivity curves at 140, 160, 200 and 260 Hz and for PAL sensitivity curves at 100, 140, 160, 200 and 260 Hz. At day three, significant shifts (Holm–Sidak, $P<0.05$) persisted at 100, 140, 160, 200, and 240 Hz for both SPL and PAL auditory sensitivity curves; however, by day six significant SPL and PAL sensitivity shifts were no longer observed (Holm–Sidak, SPL: $P=0.26$; PAL: $P=0.26$, Tables 2, 3; Fig. 7).

Boatwhistle playbacks

Following exposure to 12-h of boatwhistle playbacks (180-Hz fundamental frequency; 425-ms duration; 0.25-Hz playback frequency), toadfish ($n=5$; four males and one female) displayed an increased auditory sensitivity (8 dB SPL or 6 dB PAL) to frequencies between 300 and 500 Hz compared to baseline auditory sensitivity curves (Fig. 8). However, no significant auditory sensitivity (SPL and PAL) shifts were observed when compared to baseline levels (two-way repeated measures ANOVA, $d.f.=5$, SPL: $F=2.684$, $P=0.052$, PAL: $F=1.393$, $P=0.27$) (Fig. 8).

Discussion

Toadfish auditory responses were observed in response to frequencies ranging from 100 to 500 Hz, with greatest sensitivity observed in response to frequencies within the fundamental frequency range (100–225 Hz) of toadfish vocalizations. Additionally, toadfish were capable of retaining auditory sensitivity when exposed to playbacks of conspecific vocalizations; however, significant sensitivity shifts were observed following exposure to anthropogenic sound playbacks.

Previous studies had indicated a slightly extended toadfish auditory range up to 800 Hz (Yan et al. 2000), while a classical conditioning study observed a range up to 700 Hz in

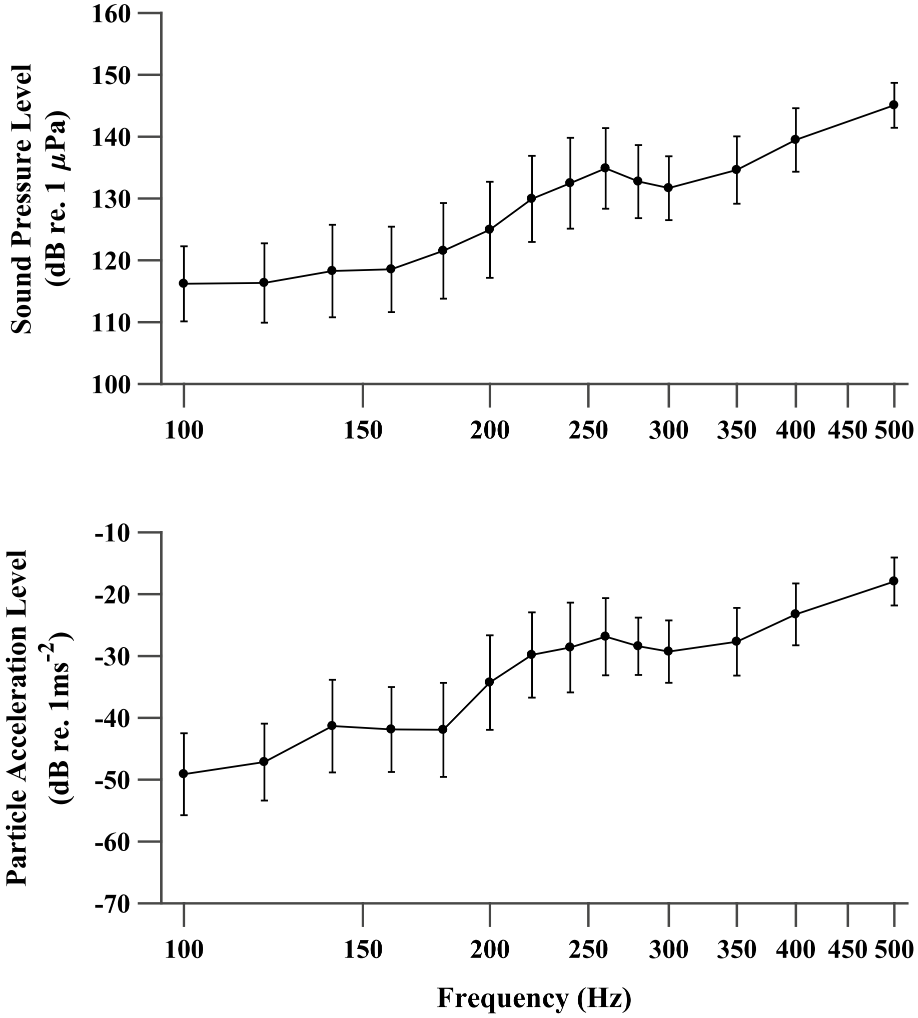


Fig. 5 Baseline sound pressure level (dB re. 1 µPa; top) and particle acceleration level (dB re. 1 ms^{-2}; bottom) sensitivity curves needed to evoke an AEP response is plotted versus sound frequency (Hz). Data are plotted as mean ± 1 SD ($n = 15$)

the laboratory and up to 400 Hz in the natural environment (Fish and Offutt 1972). While previous field experiments allowed for characterizing toadfish auditory sensitivity in their natural environment, the physiological experiments conducted in the laboratory likely had a complex acoustic field that was not accurately characterized relative to both sound pressure and particle motion. Therefore, these studies are complicated by only measuring auditory sensitivity relative to sound pressure components of the stimulus (Fish and Offutt 1972; Yan et al. 2000). Additionally, while it has been hypothesized that toadfish may be capable of detecting sound pressure via indirect secondary pathways (Edds-Walton et al. 2015) similar to the plainfin midshipman (*Porichthys notatus*) (Colleye et al. 2019), previous experiments (Fish and Offutt 1972; Yan et al. 2000) were not adequately designed to explicitly test sound pressure detection. The underwater sound presentation used here, which included measuring the particle motion as it is the component of underwater sound that all fish are capable of detecting (Popper and Fay 2011), may provide a more accurate analysis of the toadfish auditory capabilities and sensitivity. The differences between SPL and PAL auditory sensitivity curves show the necessity of measuring both acoustical parameters as SPL analysis alone would have underestimated the impacts of anthropogenic sound exposure.

The effects of anthropogenic sound exposure on fishes are just beginning to be understood, and it is important to measure baseline auditory sensitivity to determine if anthropogenic exposure has a negative effect on the auditory system. For example, behavioral experiments have shown that anthropogenic sound may impact reproductive behaviors (Ladich 2013; Bruintjes and Radford 2013), predator/prey interactions (Voellmy et al. 2014a, b; Simpson et al. 2015), larval fish orientation and settlement (Radford et al. 2011; Holles et al. 2013) and schooling (Sarà et al. 2007; Herbert-Read et al. 2017). Physiological experiments have determined that anthropogenic sound may increase stress (Santulli et al. 1999; Wysocki et al. 2006; Sierra-Flores et al. 2015), damage auditory structures (McCauley et al. 2003; Smith et al. 2006), mask auditory signals (Ramcharitar and Popper 2004; Wysocki and Ladich 2005; Codarin et al. 2009) and induce temporary

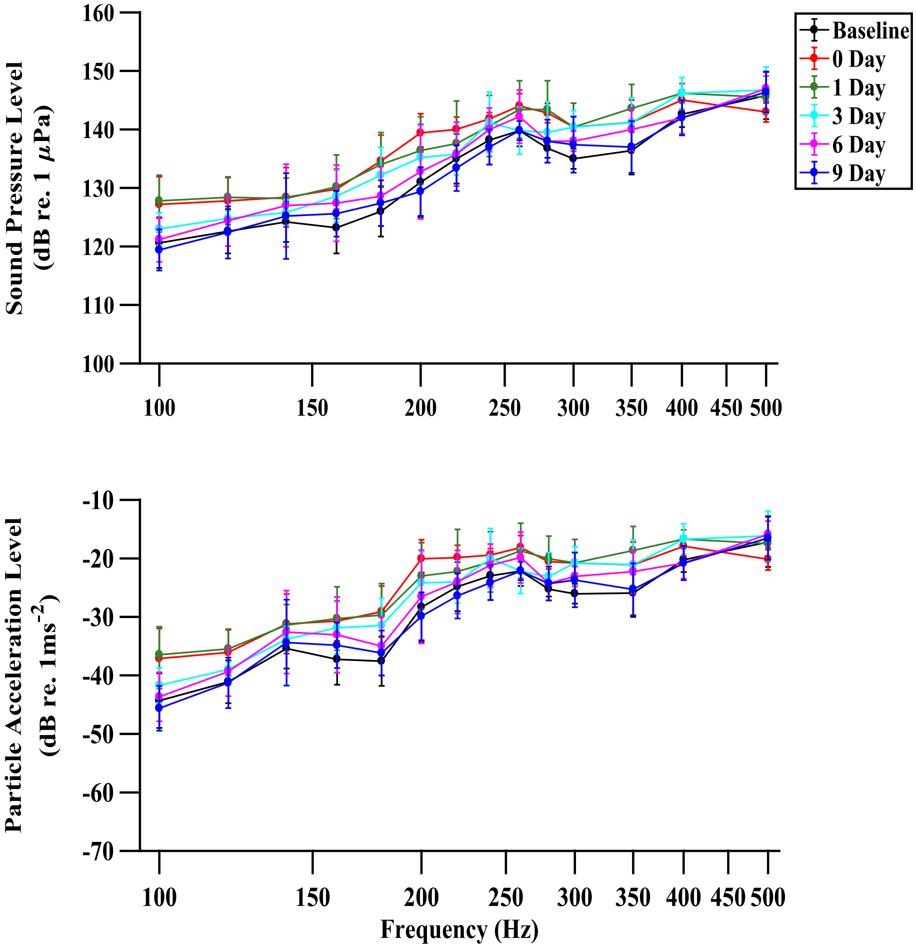


Fig. 6 Auditory sensitivity curves for data related to exposure to 1-h of continuous broadband anthropogenic sound [Frequency range: 30–12,000 Hz; sound pressure ~ 150 dB re. 1 μPa (80–550 Hz)]. The minimum sound pressure (dB re. 1 μPa; top) and particle acceleration (dB re. 1 ms^{-2}; bottom) levels needed to evoke an AEP response is plotted versus frequency (Hz). Colors represent the pre-exposure (baseline, black) and post-exposure (day 0, red; day 1, green; day 3, light blue; day 6, pink; day 9, blue) to 1-h of continuous broadband anthropogenic sound. Data are plotted as mean ± 1 SD ($n = 5$)

Table 1 Particle acceleration level (dB re. 1 ms^{-2}) sensitivity shifts during serial testing after exposure to 1-h anthropogenic sound

	Frequency (Hz)													
	100	120	140	160	180	200	220	240	260	280	300	350	400	500
0 day	$P < 0.001$	ns	ns	$P = 0.004$	$P < 0.001$	$P < 0.001$	ns	ns	ns	ns	$P = 0.045$	ns	ns	ns
1 day	$P < 0.001$	$P = 0.025$	ns	$P = 0.002$	$P < 0.001$	$P = 0.03$	ns	ns	ns	ns	$P = 0.041$	$P = 0.001$	ns	ns
3 day	ns	ns	ns	P = 0.035	$P = 0.008$	ns	ns	ns	ns	ns	$P = 0.048$	ns	ns	ns
6 and 9 day	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table values show significance levels in comparison to baseline (Holm–Sidak, $P < 0.05$)

ns not significant

auditory threshold shifts (Smith et al. 2004, 2006; Popper et al. 2005; Vasconcelos et al. 2007; Nissen et al. 2019). However, it is crucial to acknowledge that effects upon fish behavior and physiology will vary depending upon many factors, including differing environmental conditions, sound sources, perceived sound characteristics and species (Parvulescu 1964; Rogers et al. 2016; Popper and Hawkins 2019; Popper et al. 2019). Additionally, given that research has been performed on a limited number of fish species, the results from the present experiments should not be used to generalize across species.

Within coastal recreational waterways, passive acoustic monitoring studies have observed that anthropogenic sound pressure levels produced by recreational vessels do not often surpass 120 dB re. 1 μPa (Haviland-Howell et al. 2007; Erbe 2013; Marley et al. 2017). However, many toadfish reside in areas frequented by commercial vessels, and in the coastal waters of Massachusetts, anthropogenic sound pressure levels produced by research vessels, tug boats and private yachts may exceed 160 dB re. 1 μPa (71–224 Hz) (Hatch et al. 2012), and have the potential to mask boatwhistle vocalizations. To simulate anthropogenic sound that

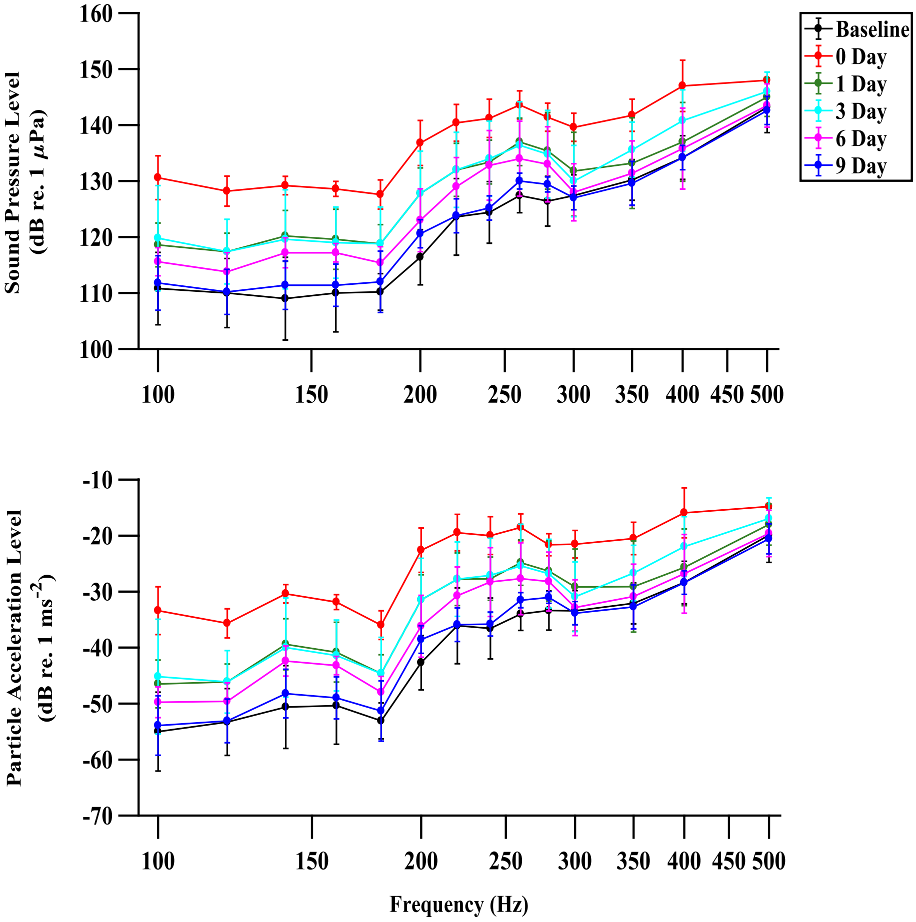


Fig. 7 Auditory sensitivity curves for data related to exposure to 12-h of continuous broadband anthropogenic sound [Frequency range: 30–12,000 Hz; sound pressure ~ 150 dB re. 1 µPa (80–550 Hz)]. The minimum sound pressure (dB re. 1 µPa; top) and particle acceleration (dB re. 1 ms^{-2}; bottom) levels needed to evoke an AEP response is plotted versus frequency (Hz). Colors represent the pre-exposure (baseline, black) and post-exposure (day 0, red; day 1, green; day 3, light blue; day 6, pink; day 9, blue) to 12-h of continuous broadband anthropogenic sound. Data are plotted as mean ± 1 SD (*n* = 5)

toadfish may encounter, source level underwater recordings were taken from the Marine Biological Laboratory's RV Gemma (15 m) while it idled at its dock in Eel Pond, Woods Hole, MA, where a reproducing toadfish population resides (Putland et al. 2018; Van Wert and Mensinger 2019). In this study, even short-duration (1-h) anthropogenic exposure led to significant auditory sensitivity shifts up to 8 dB SPL or 9 dB PAL immediately after sound exposure, with sustained exposure (12-h) resulting in greater shifts up to 20 dB SPL or 22 dB PAL and frequency shifts persisting for at least 3 days. Fish in both treatments recovered by day six, indicating the impact was transient; however, repeated exposure may lead to permanent sensitivity shifts.

The behavioral impacts that decreased auditory sensitivity may have on toadfish have yet to be determined; however, reproductive success relies on females detecting male vocalizations (Fish 1972). The proclivity of toadfish for hard substrates often places them near docks and pilings with high boat traffic and human activity that may impact toadfish auditory sensitivity. Additionally, male toadfish exhibit high nest fidelity (Maruska and Mensinger 2009; Mensinger 2014; Putland et al. 2018), which may make them susceptible to anthropogenic sounds as they are unlikely to leave the area. Therefore, the decreased auditory sensitivity following anthropogenic sound exposure could negatively impact toadfish reproductive success.

Toadfish populations are also exposed to natural ambient sound including the vocalizations of conspecifics. Field recordings of toadfish vocalizations highlight that individuals can produce sound intensities ranging from 130 to 140 dB re. 1 µPa at 1 m (Tavolga 1971) with individuals vocalizing up to 15 times per minute during the night (Ricci et al. 2017; Putland et al. 2018; Van Wert and Mensinger 2019). At close proximity (< 20 cm), within the nest, boatwhistle vocalizations also reverberate and approach source level sound intensities up to 150 dB re. 1 µPa (Mensinger 2014). Additionally, boatwhistle vocalizations can be interspersed by grunts, which target conspecifics vocalizations, resulting in sustained frequent and high intensity sound throughout the night (Maruska and Mensinger 2009; Mensinger 2014). However, significant shifts in auditory sensitivity were not observed following boatwhistle playbacks. Since toadfish were tested outside their mating season, it is possible toadfish were not as sensitive to sound and were not affected by the conspecific playbacks. For example, *P. notatus* display seasonal auditory plasticity, with increased auditory

Table 2 Sound pressure level (dB re. 1 μPa) sensitivity shifts during serial testing after exposure to 12-h anthropogenic sound

	Frequency (Hz)													
	100	120	140	160	180	200	220	240	260	280	300	350	400	500
0 day	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P=0.003$	$P=0.001$	$P<0.001$	N/A
1 day	ns	ns	$P=0.007$	$P=0.033$	ns	$P=0.01$	ns	ns	$P=0.036$	ns	ns	ns	ns	ns
3 day	$P=0.048$	ns	$P=0.012$	$P=0.043$	ns	$P=0.006$	ns	$P=0.036$	ns	ns	ns	ns	ns	ns
6 and 9 day	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table values show significance levels in comparison to baseline (Holm–Sidak, $P<0.05$)

ns not significant

Table 3 Particle acceleration level (dB re. 1 ms^{-2}) sensitivity shifts during serial testing after exposure to 12-h anthropogenic sound

	Frequency (Hz)													
	100	120	140	160	180	200	220	240	260	280	300	350	400	500
0 day	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	$P=0.004$	$P=0.003$	$P<0.001$	$P<0.001$	N/A
1 day	$P=0.049$	ns	$P=0.005$	$P=0.028$	ns	$P=0.005$	ns	ns	$P=0.043$	ns	ns	ns	ns	ns
3 day	$P=0.018$	ns	$P=0.009$	$P=0.041$	ns	$P=0.005$	ns	$P=0.033$	ns	ns	ns	ns	ns	ns
6 and 9 day	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table values show significance levels in comparison to baseline (Holm–Sidak, $P<0.05$)

ns not significant

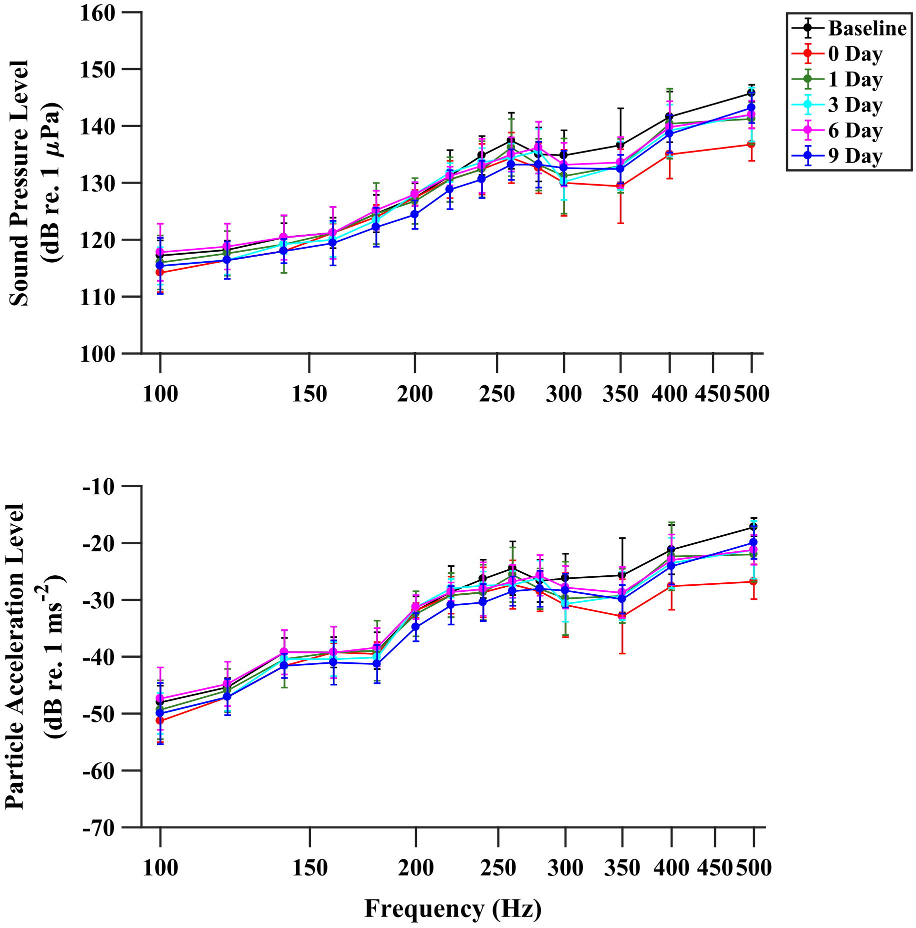


Fig. 8 Auditory sensitivity curves for data related to exposure to 12-h of boatwhistle playbacks (425 ms duration; 180 Hz fundamental frequency, 0.25 Hz playback frequency, sound pressure ~ 150 dB re. 1 μPa (80–550 Hz)). The minimum sound pressure (dB re. 1 μPa; top) and particle acceleration (dB re. 1 ms^{-2}; bottom) levels needed to evoke an AEP response is plotted versus frequency (Hz). Colors represent the pre-exposure (baseline, black) and post-exposure (day 0, red; day 1, green; day 3, light blue; day 6, pink; day 9, blue) to 12-h of boatwhistle playbacks. Data are plotted as mean ± 1SD ($n = 5$)

sensitivity occurring during the summer mating season, due to changes in both circulating hormone levels (Sisneros et al. 2004; Rohmann and Andrew 2011; Perelmuter et al. 2019) and hair cell density (Coffin et al. 2012; Lozier and Sisneros 2019). The boatwhistle vocalizations also have a narrow frequency range compared to the anthropogenic sound and the AEPs may have missed finer scale sensitivity changes. Additionally, it has been postulated that toadfish have an adaptive filter or a mechanism to cancel out self-generated noise and allow for sustained auditory sensitivity similar to *P. notatus* (Weeg et al. 2005). However, if this mechanism exists, it is more likely utilized during the production of self-generated sounds as the adaptive filter needs to be activated prior to vocalizing and would not become activated from sounds produced by conspecifics or speakers. Yet, it remains possible that the consistent inter-call interval (4 s) allowed the toadfish to anticipate the next call and activate the adaptive filter mechanisms.

The AEP technique allowed for minimally invasive monitoring and sequential testing of fish auditory sensitivity following exposure to varying sound treatments. While this technique has previously been used to investigate hearing loss, caution should be used in interpreting the data. Although the AEP tank (375 L) is larger than many other AEPs set-ups (Vasconcelos et al. 2007; Ladich and Schulz-Mirbach 2013), it is still a relatively small tank, which results in a complex sound environment with sound reverberations or echoes that may influence results (Parvulescu 1964; Rogers et al. 2016). The sound exposure experiments tried to alleviate some of the complications of small tanks by limiting the toadfish to a specific area allowing for relatively uniform sound pressure and particle acceleration levels. Additionally, it must be noted that AEPs represent a gross sensitivity response and behavioral experiments or single unit recordings could potentially reveal greater auditory sensitivity.

In conclusion, exposure to even short durations (1-h) of high intensity (~ 150 dB re. 1 μPa) anthropogenic sound is capable of causing significant temporary sensitivity shifts that are sustained for at least 3 days post-exposure. These significant sensitivity shifts may be enough to impact female sound source localization and the reproductive success of these fish.

Acknowledgements The authors would like to acknowledge the Marine Resources Center staff at the Marine Biological Laboratory for providing toadfish. Funding was provided by National Science Foundation Grants IOS 1354745 and DBI 1359230 and 1659604 to AFM, and by the National Science Foundation Graduate Research Fellowship Program under grant DGE 1804377 to LSR. All experimental procedures conformed to NIH guidelines for animal care and use of animals, and were approved by the University of Minnesota Institutional Animal Care and Use Committee under Protocol ID: 1903-36856A.

Compliance with ethical standards

Conflict of interest The authors declare no competing financial interests.

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