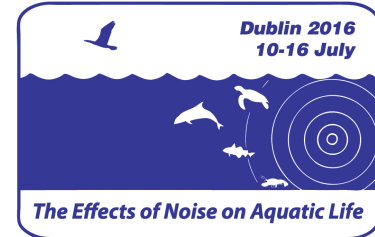




## Fourth International Conference on the Effects of Noise on Aquatic Life

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## The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments

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The Lombard effect (an involuntary increase in vocal levels in noisy environments) has been shown for humans, birds, and mammals. Here, we use experimental playbacks of vessel noise and other natural sounds in the normal soundscape of the oyster toadfish *Opsanus tau* to test if the Lombard effect occurred. Experiments were conducted at a noisy site adjacent to a port with high vessel traffic and in a quiet embayment. We played back vessel noise (inboard and outboard motor noise), predator sounds (bottlenose dolphins) and snapping shrimp sounds for 600 s and recorded the vocalizations made by toadfish in experimental dens during 600 s periods before, during, and after the playback period. Average call power of vocalizations increased by 6.8 dB during and 8.7 dB re  $1 \mu\text{Pa}^2$  after playbacks of noise relative to pre-period levels, demonstrating the Lombard effect in toadfish. Fish at the noisy site had higher average call power relative to the quiet site. There was no change in the fundamental frequency of calls in after noise playback (average frequency was 224-233 Hz). Communication signals by oyster toadfish males may be masked by very loud vessels, and the Lombard effect is an attempt to overcome masking.



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## 1. INTRODUCTION

The Lombard effect was discovered by Etienne Lombard over 100 years ago (Lombard, 1911). Human speakers will increase their voices in noise, raising both the sound intensity and changing the frequency of their speech to overcome background noises (Zollinger and Brumm, 2011). The Lombard effect has also been documented in animals, including monkeys, whales, birds, and frogs (Brumm and Zollinger, 2011; Hotchkiss and Parks, 2013; Kaiser and Hammers, 2009). Although the Lombard effect has been demonstrated in a species of freshwater fish in a laboratory study (Holt and Johnston, 2014), it has not been documented in free-ranging fishes subjected to increased levels of ambient or anthropogenic noise. In these previous studies on animals, the Lombard effect concept has been expanded to include more than amplitude changes alone, because background noises can cause shifts in call frequency spectra, call duration, and rate of calling. For example, North Atlantic right whales *Eubalaena glacialis* and South Atlantic right whales *E. australis* produce higher fundamental frequencies and call at a lower rate in the presence of vessel activity than without vessels (Parks et al., 2007).

Ecologically, an increase in vocalization amplitude due to the Lombard effect can maintain an animal's "active space" – the region around the animal where its communication signal is detectable by other conspecifics (like potential mates and competitors). The active space of an animal's vocalizations is dependent upon the acoustic properties of the environment, the frequency and amplitude of the emitted call, the hearing sensitivity of the intended receiver, and the ambient noise level (Miksis-Olds and Tyack, 2009). Increasing masking noise leads to a decrease in the active space in which animals are able to detect a conspecific signal (Jensen et al., 2009; Van Parijs and Corkeron, 2001). For example, a finback whale's (*Balaenoptera physalus*) 20 Hz call may be audible at over 1000 km in ideal conditions but moderate shipping noise can reduce this range to 90 km (Payne and Webb, 1971). As shipping noise has continued to increase, the active space of this same call has been reduced to 32 km (Tyack, 2008), which amounts to a 97% total reduction in active space, with a 65% reduction in just the past 30 years.

Evolutionarily, the Lombard effect has been hypothesized to be the result of positive selection for animals with louder mating calls in noise-filled soundscapes, which have resulted in increased reproductive fitness (Brumm and Slabbekoorn, 2005). Animals that exhibit the Lombard effect have a higher chance of attracting mates and communicating to others in the presence of increased noise levels in the environment than those animals that do not exhibit this effect (Brumm and Slabbekoorn, 2005). Without the Lombard effect, the conspecific signal becomes masked (Jensen et al., 2009; Vasconcelos et al., 2007), which could result in decreased fitness. For example, female American treefrogs (*Hyla cinerea*) needed a higher amplitude of a synthetic call stimulus to exhibit behavioral responses to male courtship calls in the presence of noise compared with females exposed to the same stimulus without noise (Ehret and Gerhardt, 1980). In another study, brown tree frogs (*Litoria ewingii*), increased the average pitch of their calls by 4.1 Hz/dB of traffic noise, increasing the active space of the signal by 24% (Parris et al., 2009). The Lombard effect ultimately increases the chances of a male attracting a mate. Animals that have the ability to increase the amplitude of their vocalizations can compensate for increased background noise levels, thus communicating effectively with mates and conspecifics (Brumm and Slabbekoorn, 2005).

Given the relative benefits and costs of the Lombard effect in other species and the increasing noise levels in the sea, several questions arise: Do marine fishes exhibit the Lombard

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effect in a natural environment with vessel noise? Do fishes have the ability to increase their vocal amplitude or shift vocalization frequencies in order to increase their active space and communicate with others in noisy shipping areas? How does vessel noise affect a fish's ability to communicate? In this paper and two others presented at this meeting (Krahforst et al., 2016; Sprague et al., 2016), we attempt to answer these questions.

Here we demonstrate the Lombard effect using field playback experiments in oyster toadfish *Opsanus tau* living at a site near an active navigation channel in a coastal port (noisy site) and a site far from the port in a secluded estuarine embayment with few passing vessels (quiet site) in North Carolina (USA). Oyster toadfish make advertisement boatwhistle calls from oyster reefs or other shelter sites during summer (May – September) along the Western Atlantic Ocean (Gray and Winn, 1961). These boatwhistle calls are made by males to attract females to the calling sites (nests in a hard substrate) for mating. The females deposit clutches of eggs that adhere to the hard substrate, which are fertilized and then guarded by the males. Mating success and attraction of females depend on the males being heard by females that are passing near the calling sites. Vessel noise has been shown to interfere with the reception of the mating calls by females (masking) in a related species of toadfish (Vasconcelos et al., 2007).

Finally, it has been shown that other types of sounds, besides vessel noise, are able to influence males calling rates, specifically sounds from a predator on oyster toadfish, the bottlenose dolphin *Tursiops truncatus* (Dunsha et al., 2013; Gannon et al., 2005; McCabe et al., 2010). Bottlenose dolphins are sound producers that can produce stress responses and suppress calling rates in Gulf toadfish (Remage-Healey et al., 2006). In a related study in this volume (Krahforst et al., 2016), we report the suppression of oyster toadfish mating calls due to bottlenose dolphin sound playbacks. Below, we present the results of experimental vessel noise and bottlenose dolphin playbacks on the oyster toadfish vocalization amplitude and call frequency to examine the Lombard effect in a natural environment with and without vessel noise.

## 2. METHODS

### A. STUDY SITES

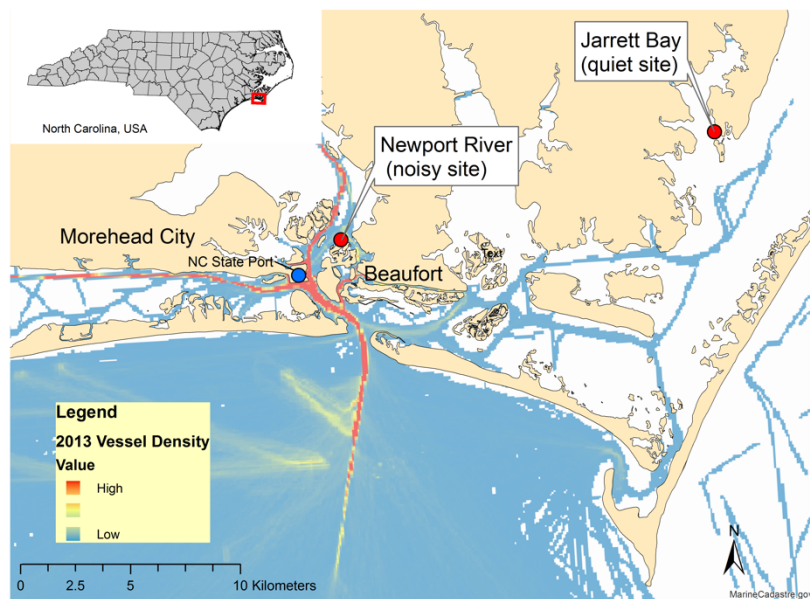
Playback studies were conducted in natural environments in North Carolina, USA. We established experimental shelters at two sites, one a noisy site (Newport River, NPR) and at a quiet site (Jarret Bay, JBS; Fig. 1). Our characterization of these sites as “noisy” and “quiet” are based on three lines of evidence. First, the noisy site had high levels of observed boat activity (>100 vessels per day) and the quiet site had low levels of boat activity (<25 vessels per day). Second, noise levels at the NPR site were measured to establish background noise baselines (Sprague et al., 2016). Finally, the noisy site (NPR) was near a busy State of North Carolina cargo port and the Intracoastal Waterway, which is the main route for commercial and pleasure vessels heading north and south along the USA's eastern seaboard. The North Carolina State Port area and Intracoastal Waterway have very high vessel densities, as measured by the AIS (Automatic Information System) signals broadcast from passing vessels in 2013 (Fig. 1). Our noise measurements, vessel counts conducted by us at each site, plus the annual AIS estimates of vessel density led us to characterize NPR as a noisy site. The quiet (JBS) had very few AIS targets passed by in 2013, and our visual counts and noise measurements confirmed this site was quiet.

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## B. PLAYBACK EXPERIMENTS

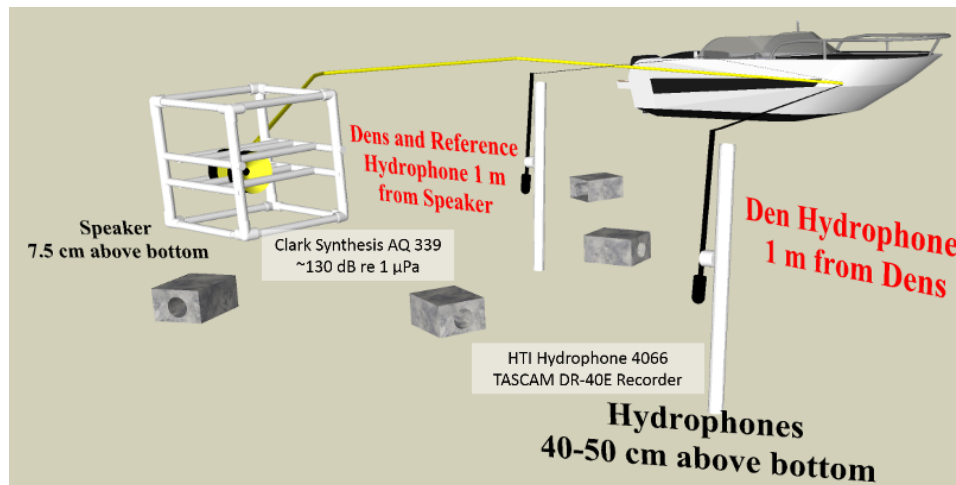
Cement block shelters (cube with 20 cm sides, and with an internal opening containing 7.6 cm PVC tube), or oyster toadfish “dens”, were deployed in 1-m water depth in May and June 2013 (Fig. 2). Forty-eight dens were placed at each site, in replicated experimental units (four dens per experimental unit, 12 experimental units per site) with 96 total dens at both sites. Experimental oyster toadfish dens were colonized rapidly after deployment (within one month), prior to playback experiments. Visual inspection of toadfish in the dens was completed by a snorkeler during daylight prior to the playbacks. Experimental playbacks were done at night in July and August 2013 beginning after sunset (2000-2015 local time) and continuing until all replicates had been exposed to sound playbacks (~0600 local time on the next morning). Occupancy was roughly 25-50% of dens based on the visual inspection (at least one fish per four dens). Animal protocols were approved by East Carolina University’s Institutional Animal Care and Use Committee under Animal Use Protocol (#D292).



**Figure 1.** Study sites (red dot symbols) for playback experiments near Morehead City, North Carolina, USA. The noisy site was at Newport River (NPR), which is near the North Carolina State Port (blue dot) and the US Intracoastal Waterway (high vessel density shown in red shading, source: BOEM and NOAA, [marinecadastre.gov](http://marinecadastre.gov)). The quiet site was located at Jarrett Bay (JBS) an area with no AIS-equipped vessels.

Playback experiments were conducted in July and August 2013. The following playback experimental design was replicated twenty times at noisy site (NPR) and twenty-four times at the quiet site (JBS). There were forty-four total playback trials, each trial with a randomly assigned sound type played through a single speaker to a set of four oyster toadfish dens. Playbacks treatments were done using six recordings of sound types (snapping shrimp, six playbacks; inboard vessel motor, ten playbacks; outboard vessel motor, six playbacks; low-frequency bottlenose dolphin sounds, six playbacks; high-frequency dolphin sounds, eight playbacks; and simultaneous playback of both inboard vessel motor and low-frequency dolphin sound, eight playbacks). Details of these sounds’ spectra and source levels are given elsewhere in this volume (Krahforst et al., 2016).

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**Figure 2.** Experimental playback setup, with an underwater speaker, oyster toadfish dens, the amplifier on an anchored boat with the motor off, and two hydrophones (Reference hydrophone at 1 m and recording hydrophone at 2 m).

We played back these sound types from an anchored vessel (motor shut off) via a computer (Panasonic Toughbook CF-30), through a 400 W amplifier (Pyle PLMRA400), and an underwater speaker (Clark AQ 339). Two hydrophones were deployed to measure received levels and fish responses: (1) a reference hydrophone (InterOcean Model 902 calibrated listening system) positioned 1 m from the speaker in the center of the dens was used to get received sound pressure levels ( $SPL_{rms}$  in dB re 1  $\mu\text{Pa}$ ), measured within the frequency range of the system (20 to 20,000 Hz); (2) a den hydrophone (HiTech, model HTI 96-min), which was positioned 2 m from the speaker, behind the shelters to make recordings of fish responses. Recordings (600 s prior to playback, 600 s during playback, and 600 s after playback) of male oyster toadfish boatwhistle calls were made from the latter hydrophone on a TASCAM DR-40 digital recorder at 44.1 kHz sampling rate to 16-bit sample size wav files. These files were later processed for received levels and call power measurements after correcting for differences in record level. See our companion paper (Krahforst et al., 2016) for a summary of received sound levels and representative spectra at the latter hydrophone.

### C. Data Analysis

Recorded wav files were imported into Raven Pro (<http://www.birds.cornell.edu/raven>), oyster toadfish boatwhistle calls were identified by a listener, and a selection box was drawn around each audible call on the spectrogram interface of the software. The selection box defined the spectral and temporal extent of each call. Oyster toadfish call start times, ends times, minimum and maximum frequencies as defined by that box were exported as a selections table from Raven. The selection table and the “native” wav file was next imported to Matlab (<http://www.mathworks.com>). A calibration correction was applied to adjust for the HTI 96-min hydrophone sensitivity and sound recordings were corrected for record-level differences after computing call power in Matlab.

We determined the oyster toadfish call power using the Welch power spectral density algorithm (Welch, 1967), which computed the time-averaged power spectral density for the measured sound pressures for each call. All fish call power measurements were computed as mean squared sound pressure levels in dB re 1  $\mu\text{Pa}^2$ , which are proportional to average sound power. We obtained these mean squared sound pressure levels by summing the time-averaged

power spectral density samples from the Welch algorithm from the minimum call frequency to the maximum call frequency and multiplying the sum by the frequency sample interval between each of the samples (i.e., the frequency sample interval from the FFT used in the Welch algorithm).

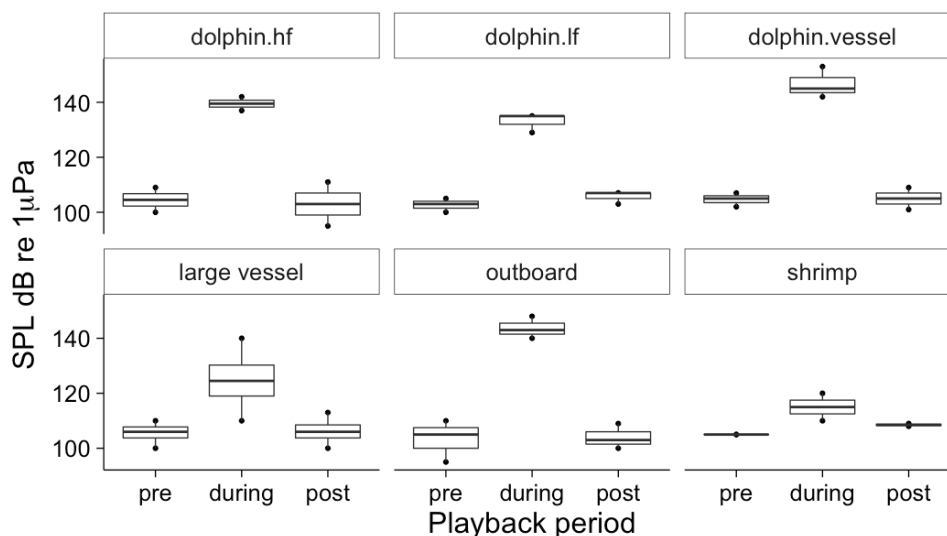
We compared average call power of the calls in the pre-, during-, and post-playback periods using a repeated measures Analysis of Variance (ANOVA). The Lombard effect was computed by subtraction of the average call power in the pre-playback period from the post-playback average call power, for replicates in which calls occurred in both periods. A one-sample t-test was used to compare the differences  $D$  computed for each replicate with detectable calls within sound-playback treatments using formula:

$$D = CP_{post} - CP_{pre}$$

where  $CP_{post}$  is the average call power post-playback and  $CP_{pre}$  is the pre-playback average call power. Measurements of sound pressure levels and oyster toadfish call power are displayed graphically as box plots. Box plots show the 50% range around the median (horizontal line) with upper and lower bounds of the box defined by the interquartile range (between the 25th and 75th percentiles). Vertical lines (upper and lower “whiskers”) are defined by 1.5 x interquartile range, and points falling within this region are shown. Points shown outside of the range indicated by the vertical lines are extreme measurements.

### 3. RESULTS

Ambient sound pressure levels  $SPL_{rms}$ , measured at the reference hydrophone, were increased during playback by 15 dB to 40 dB re 1  $\mu$ Pa relative to pre-playback and post-playback levels (Fig. 3). The smallest increase in  $SPL_{rms}$  occurred during the snapping shrimp playback, and the greatest increase occurred during the simultaneous playback of high-frequency dolphin and large vessel sounds, and of the outboard motor sound playbacks.



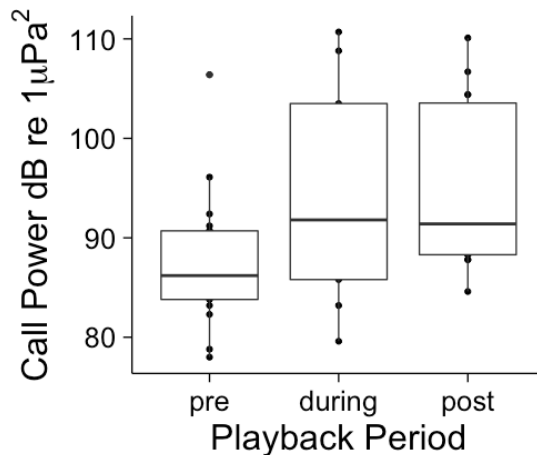
**Figure 3.** Ambient sound pressure levels ( $SPL_{rms}$  dB re 1  $\mu$ Pa) before, during, and after playbacks measured 1 m from source speaker at reference hydrophone, for playbacks of various types. SPLs were read directly off an InterOcean 902 calibrated listening system VU meter and represent the energy over entire spectrum (20-20,000 Hz).

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Oyster toadfish were regularly detected on recordings from the recording hydrophone while making boatwhistle reproductive advertisement calls. Agonistic oyster toadfish grunt calls were also detected, and although these were uncommon, they are included in this analysis. The rate of advertisement calling by males fell during playbacks; in the case of simultaneous dolphin and vessel sound playbacks, no calls were detected during playback. Please see further results on call rate changes from these experiments elsewhere in this volume (Krahforst, et al., 2016).

The average call power increased during and after playbacks, from 95.2 dB re 1  $\mu\text{Pa}^2$  in the pre-playback period, to 102.0 dB re 1  $\mu\text{Pa}^2$  during playbacks, and to 103.9 dB re 1  $\mu\text{Pa}^2$  after the playbacks (Fig. 4). A repeated-measures ANOVA was used to compare the average power of the calls among playback periods, allowing us to reject the hypothesis of equality of mean call power among playback periods ( $P = 0.036$ ). The subtraction of the pre-period average call power for these data yielded a Lombard effect of between 6.8 dB (during playback) and 8.7 dB (after playback).

The call power generally followed the same pattern of increased power during and after playback when compared to the pre-playback period (Fig. 5). This pattern was true for natural sounds of snapping shrimp (shrimp), high-frequency dolphin (dolphin.hf), and low-frequency dolphin (dolphin.lf) sound playbacks. The average call power of the oyster toadfish varied by playback type.



**Figure 4.** Oyster toadfish average call power (dB re 1  $\mu\text{Pa}^2$ ) of boatwhistle and grunt calls during 600 s periods pre-playback, during playback, and post-playback, for all playback types combined. For interpretation, see box plot description in the Data Analysis section.

Oyster toadfish exposed to snapping shrimp, predator, and vessel sound playbacks increased their call power in all treatments, significantly increasing the post-playback average call power after the pre-playback average call power was subtracted (Table 1; one-sample  $t$ -test of the post-pre difference  $D$ , with expected  $\mu = 0$ ,  $t = 4.301$ ,  $df = 14$ ,  $P = 0.001$ ). The Lombard effect occurred for all sound type playbacks. The inboard motor (large vessel) sounds caused the greatest increase in average call power in the post-playback period when compared with the pre-playback period ( $\bar{D} = 15.7$  dB), and the outboard motor sound the least ( $\bar{D} = 4.7$  dB), although there were no significant differences among means of the playback sound types (pairwise  $t$ -tests among treatments,  $P = 1.0$  for all treatment comparisons; Fig. 6).

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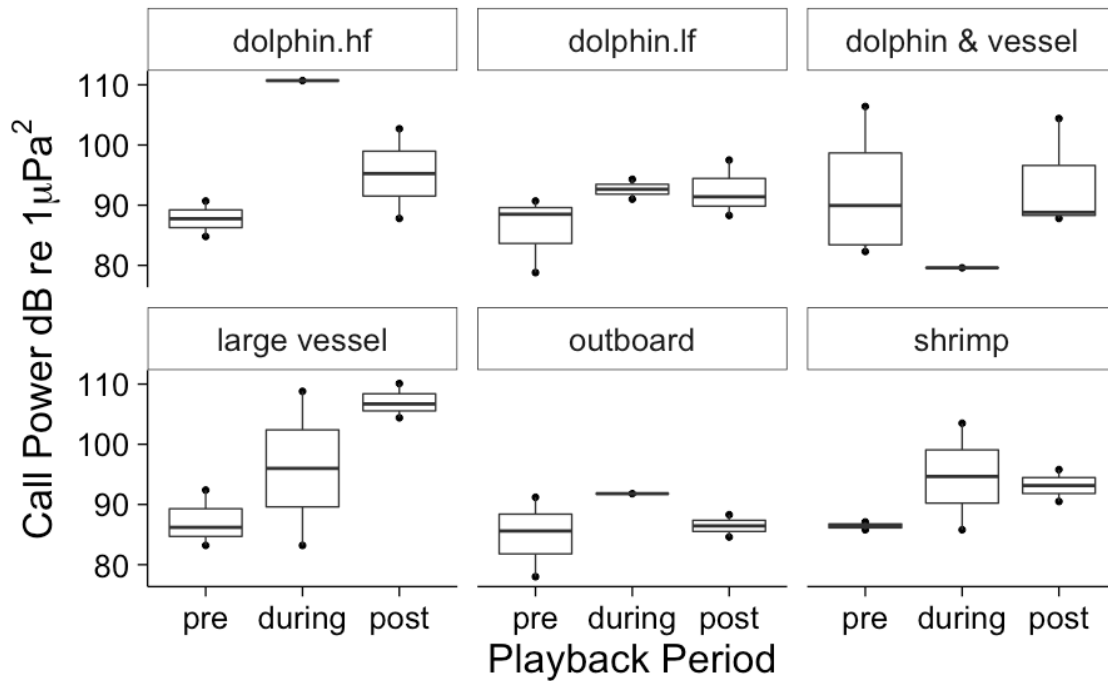
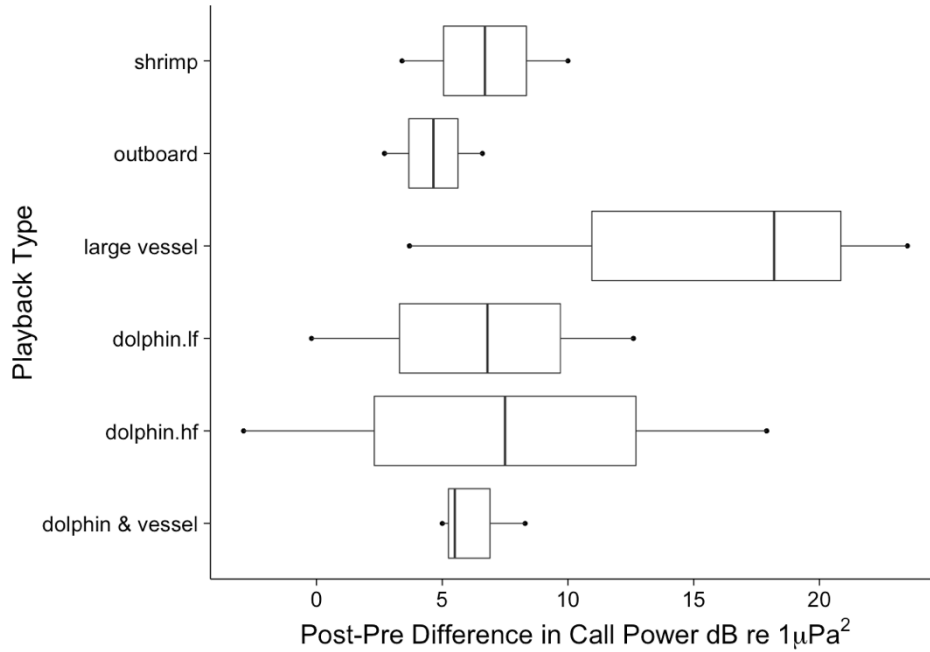


Figure 5. The call power (dB re  $1 \mu\text{Pa}^2$ ) of oyster toadfish boatwhistle and grunt calls during 600 s periods pre-playback, during playback, and post-playback, for each of the playback types. The sound spectra for each of the playback types are given in Krahforst et al. (2016). Playback sound type names are given above each plot: *dolphin.hf* is high-frequency dolphin sound, *dolphin.lf* is low-frequency dolphin sound, *dolphin & vessel* sound is simultaneous playback of low-dolphin and large vessel sound, *large vessel* sound, *outboard* motor sound, and *shrimp* is snapping shrimp, *Alpheus* sp., sound.

Table 1. The average call power in the pre-playback ( $CP_{pre}$ ) and post-playback ( $CP_{post}$ ) periods.  $\bar{D}$  is the mean difference between the  $CP_{post}$  and  $CP_{pre}$  for all replicates within each playback type, s.e.m. is the standard error of the mean for  $D$ , and  $N$  is the number of replicates.

Playback treatment	$CP_{pre}$ dB re $1\mu\text{Pa}^2$	$CP_{post}$ dB re $1\mu\text{Pa}^2$	$\bar{D}$ dB	s.e.m.	N
Shrimp	86.5	93.2	6.7	2.65	2
Outboard	81.8	86.5	4.7	1.85	2
Large Vessel	91.9	107.1	15.1	1.66	3
Dolphin, high-frequency	87.8	95.3	7.5	7.45	2
Dolphin low-frequency	86.0	92.4	6.4	2.70	3
Vessel & Dolphin	87.4	93.7	6.3	5.37	3
Overall means	87.2	95.3	8.1	1.88	15





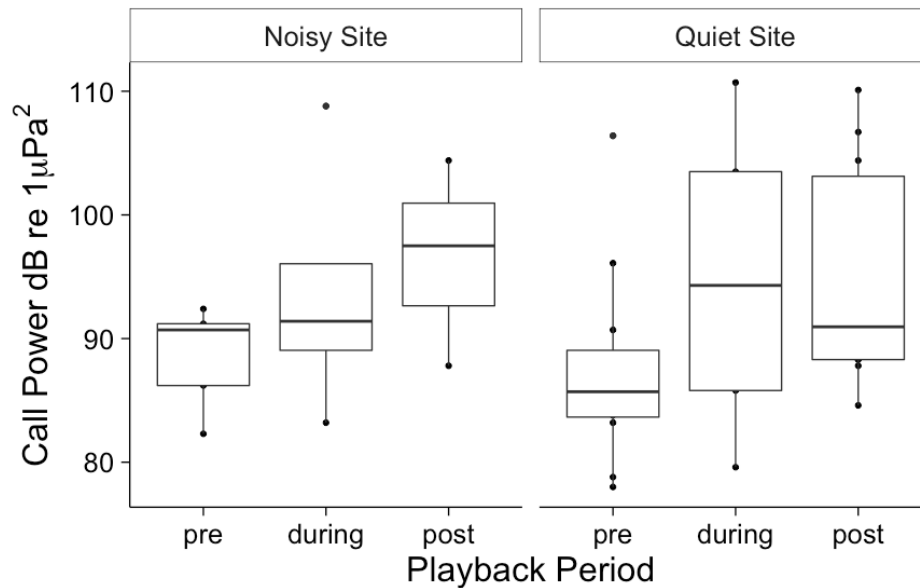
**Figure 6.** The difference in average call power (post-playback minus pre-playback average call power) as a function of playback sound type, with trials at both sites combined.

The average call power differed between the noisy and quiet sites in the pre-playback period. Average call power increased following the same pattern of higher power than the pre-playback period in the during- and after-playback periods when all sound playback types are combined (Fig. 7). Thus, there was evidence of the Lombard effect at both the noisy and quiet sites, but the noisy site also had oyster toadfish that were louder in the pre-playback period than in the quiet site.

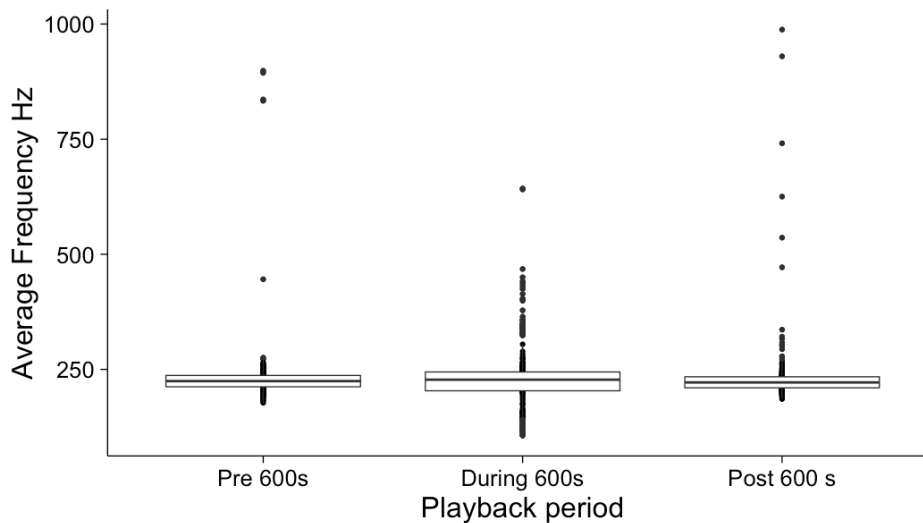
The frequency of the calls did not change relative to the pre-playback frequency which was 228 Hz (Fig. 8). Thus, there was no evidence of a Lombard effect in terms of a change in pitch of the call. There were no significant differences in average call frequency between pre-playback period, during-playback period or post-playback period or in terms of minimum or maximum call frequency (Table 2).

**Table 2.** The average, minimum and maximum frequency (Hz) of oyster toadfish boatwhistle and grunt calls in before, during and after periods of the playback experiments.

Playback Period	Average Frequency (Hz)	Minimum Frequency (Hz)	Maximum Frequency (Hz)
Pre-playback	228.2	177.3	898.6
During Playback	224.2	106.2	643.0
Post-Playback	233.9	185.6	988.0
All periods	228.1	106.2	988.0



**Figure 7.** The median call power of oyster toadfish boatwhistle and grunt calls during 600 s periods pre-playback, during playback, and post-playback, for each of the playback type at noisy (NPR) and quiet (JBS) sites.



**Figure 8.** The average frequency of oyster toadfish boatwhistle and grunt calls during 600-s periods pre-playback, during playback, and post-playback, for all playback types combined.

#### 4. DENS. DISCUSSION

There was an increase in oyster toadfish average call power during and after playbacks of the six sound types. However, no change in call frequency was observed due to the playback of anthropogenic noise or predator sounds.

The Lombard effect was estimated to be between 6.8 dB during the playback period and 8.7 dB re 1  $\mu\text{Pa}^2$  immediately after the playback period for oyster toadfish. Thus, non-predatory noises, whether natural background sounds, like snapping shrimp, or anthropogenic sounds, like inboard and outboard motor sounds, caused the Lombard effect in oyster toadfish. The large

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vessel Lombard effect was estimated to be 15.7 dB re 1  $\mu\text{Pa}^2$  in the post-playback period, while the outboard motor effect was estimated to be 4.7 dB re 1  $\mu\text{Pa}^2$ . Although sound playbacks increased the difference in average call power after playback significantly (rejection of the null hypothesis of no change in average call power), the six sounds types tested did not differ significantly in the terms of the effect of noise on the average call power. There were fifteen replicated dens that met the criterion of having multiple calls detected in both the pre-playback and post-playback periods, consequently there was low statistical power to detect a difference among treatment means.

While all oyster toadfish showed an increase in average call power after playback, some playbacks that included predator sounds also caused a reduction in the calling rate (Krahforst et al., 2016). In the case of the simultaneous playback of vessel noise and the dolphin predator sounds, there were no boatwhistle calls observed during playback (Krahforst et al., 2016), although there was one grunt detected. This shows the context-dependent nature of the Lombard effect that we observed: in the case of a natural predator sound, oyster toadfish decreased their calling rates, and stopped calling altogether when a predator sound was played with vessel noises. Many calls that were observed during playbacks of the dolphin predator sounds were louder than pre-playback calls, but there were very few of them, and some were actually lower in amplitude after playbacks (the post-playback minus pre-playback difference was negative). We cannot say with certainty that the Lombard effect occurred during these predator sound playbacks but appeared to have an effect after playbacks.

There was an overall higher call power in the pre-period at the noisy site (NPR). In a related study published in this volume, we measured the  $SPL_{rms}$  sound pressure levels were measured at the oyster toadfish dens at the noisy site (NPR) and reached an  $SPL_{rms}$  of 110 dB to 130 dB re 1  $\mu\text{Pa}$  during the passage of an inboard motor vessel (Sprague et al., 2016). At the Rachel Carson Estuarine Research Reserve South Middle Marsh site, another nearby quiet site, the  $SPL_{rms}$  was 80 dB to 100 dB re 1  $\mu\text{Pa}$ , yielding up to a 30 dB difference in maximum levels of ambient noise between the noisy and the quiet site (Sprague et al., 2016). At the noisy NPR site, the sound-exposure level (SEL) during various vessel types passing was estimated to be 132 dB to 135 dB re 1  $\mu\text{Pa}^2 \cdot \text{s}$  after being weighted for oyster toadfish hearing (Sprague et al., 2016). Thus, ambient noise at the noisy NPR site is largely due to vessels passing by frequently, thus yielding high sound exposure levels for oyster toadfish in those dens. It appears that at the noisy NPR site, the approximately 30 dB increase in SPL above background ambient noise and 132 dB to 135 dB re 1  $\mu\text{Pa}^2 \cdot \text{s}$  toadfish-weighted sound exposure level due to vessel noise has produced a larger Lombard effect in the fish that were present at the site.

We have demonstrated that both anthropogenic vessel noises and natural background sounds such as snapping shrimp can cause the Lombard effect in oyster toadfish. The Lombard effect has been previously demonstrated in a freshwater fish, the blacktail shiner, *Cyprinella venusta* (Holt and Johnston, 2014). This study extends the Lombard effect in fishes to include oyster toadfish, a marine fish that is subjected to noise occurring in busy ship channels.

Large vessels in the area near our noisy site produced sound pressure levels comparable to those SPLs we produced experimentally with our loudspeakers (Sprague et al., 2016), and the vessel noise was common at that site due to the Intracoastal Waterway nearby. Although sound pressure levels were comparable to those produced by a vessel passing by, particle motion fields will be produced by passing vessels as well. We did not measure particle motion produced by either passing vessels or our loudspeakers during sound playback. Fishes like the oyster toadfish are sensitive to particle motion (Popper and Fay, 2011) and Zeddies et al., 2012 showed that plainfin midshipman fish *Porichthys notatus* uses the particle motion field for phonotaxis. Thus,

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one could ask if the particle motion field produced by our speaker system [(Zeddies et al., 2012)] accurately simulated the particle motion field of a vessel passing by our site. We cannot answer this question at the current time, but particle motion measurements during playback of sounds from our speakers and from passing vessels are planned in the near future.

Vessel noise at levels similar to those used in our playbacks may have ecological consequences such as masking, in which female toadfish cannot hear males' calls (Vasconcelos et al., 2007). Continuous vessel noise can have increased metabolic costs for the males (Amorim et al., 2002), and may cause sonic muscle fatigue (Mitchell et al., 2008) in an attempt to overcome the noise. In addition, in variable vessel noise areas, such as near a navigation channel, there could be an increase the rate of detection by predators if the signal-to-noise ratio increases due to the Lombard effect and remains high after noise stops. We observed increased oyster toadfish amplitudes after the sound playbacks ended, which could expose fish to bottlenose dolphin predators. Thus, there could be an inherent trade-off between the Lombard effect and the risk of predation, as had been suggested for birds (Patricelli and Bickley, 2011).

Finally, bottlenose dolphin predator sounds did produce a small Lombard effect in our study, but this was coupled with a decline in calling rates, producing very few calls on which to measure the effect during bottlenose dolphin sound playback treatments. The few calls that did occur (grunts rather than boatwhistles) were elevated in amplitude. In contrast to the vessel sounds, the predator sound playback resulted in reduced oyster toadfish calling rates (Krahforst et al., 2016), thereby making the Lombard effect absent during playbacks and smaller amplitude increase in the after-playback period. The predator sounds inhibited calling by males, reducing the mating opportunities and likely fitness. The same response has been observed previously in Gulf toadfish *Opsanus beta* (Remage-Healey et al., 2006) and in silver perch *Bairdiella chrysoura* (Luczkovich et al., 2000). When both vessel noise and bottlenose dolphin sounds co-occurred in our playback experiments, the calling rates of oyster toadfish were dramatically lower (Krahforst et al., 2016), suggesting that the involuntary increase amplitude of vocalizations (the Lombard effect) can be suppressed in times of danger, perhaps due to the increase in stress hormone cortisol inhibiting the vocal motor pathway (Remage-Healey et al., 2006). Additional research needs to be completed to assess the ecological, physiological, energetic, and reproductive consequences of the Lombard effect in fishes.

## 5. CONCLUSION

There was an increase in oyster toadfish average call power during and after playbacks of the six sound types. The Lombard effect due to all background noises was estimated to be between 6.8 and 8.7 dB re 1  $\mu\text{Pa}^2$  for oyster toadfish. There was no change in the dominant frequency of the oyster toadfish boatwhistle calls due to background noise.

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