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2025

Original citation:

Woods, M. B., Halliday, W. D., Balshine, S., & Juanes, F. (2025). Boat noise reduces vocalization rate and alters vocal characteristics in wild plainfin midshipman fish. *Marine Pollution Bulletin*, *212*, 117563. https://doi.org/10.1016/j.marpolbul.2025.117563

Marine Pollution Bulletin 212 (2025) 117563

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Boat noise reduces vocalization rate and alters vocal characteristics in wild plainfin midshipman fish

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ARTICLE INFO

Keywords:
Lombard effect
Noise pollution
Acoustic communication
Soniferous fishes
Mate attraction
Porichthys notatus

ABSTRACT

Anthropogenic noise pollution has been accelerating at an alarming rate, greatly altering aquatic soundscapes. Animals use various mechanisms to avoid acoustic masking in noisy environments, including altering calling rates or the frequency (pitch) of their vocalizations or increasing the amplitude (loudness) of their vocalizations (*i.e.,* exhibiting the Lombard effect), but few studies have examined this vocal plasticity in fishes. We tested the effects of *in situ* motorboat noise on the agonistic and mating vocalizations of nesting plainfin midshipman fish (*Porichthys notatus*), and found that midshipman fish reduce and alter their vocalizations in the presence of boat noise. During boat noise, fish produced four times fewer agonistic vocalizations compared to ambient control periods. The fish also increased the frequency of mating hums and the amplitude of grunts and growls during boat noise. This study is the first to experimentally demonstrate the Lombard effect in fishes using real motorboat noise.

1. Introduction

Many aquatic animals rely heavily on sound for communication, to navigate, forage, attract mates, detect predators, and generally assess their environments (Duarte et al. 2021; Myrberg 1997). Sound is a highly effective method of underwater communication and sensory perception because it travels more efficiently in water than in air, and because compared to light, underwater sound can propagate much farther without attenuation (Urick 1983; Duarte et al. 2021; Slabbekoorn et al. 2010). However, over the last few decades, rising levels of anthropogenic noise have greatly altered underwater soundscapes. Human-made noise has been shown to negatively affect aquatic animals in a variety of ways, including reducing the space available for communication, physically damaging hearing organs, altering auditory thresholds, and causing a slew of behavioural and physiological changes (Duarte et al. 2021; Ladich 2019; Popper and Hawkins 2019; Shannon et al. 2016). While there is growing evidence of these negative effects, relatively little research exists on how noise affects underwater vocalizations, especially in temperate environments. In this study, we address this research gap and explore how anthropogenic noise influences the quality and quantity of underwater vocalizations.

Several fish species vocalize to attract mates and to defend territories and young (Ladich et al. 2006). One such species is the plainfin midshipman (*Porichthys notatus*), a soniferous (sound-producing) toadfish that produces a loud, multi-harmonic hum to attract mates. The hum has a fundamental frequency of ~100 Hz, with dominant harmonics between 200 and 400 Hz, and can last for several minutes to upwards of an hour (Halliday et al. 2018; Sisneros 2012). Plainfin midshipman also produce two agonistic vocalizations—short grunts and longer growls—which are employed during nest defence against rival males and egg predators and have a fundamental frequency of ~60–100 Hz (Brantley and Bass 1994; McIver et al. 2014; Woods et al. 2022). Grunts (~0.5 s each) can be produced individually or in a rhythmic series called a grunt train, which can last for several minutes and include hundreds of grunts (McIver et al. 2014). Growls are frequency modulated vocalizations that vary in length, lasting up to several seconds (~0.5–10 s; Brantley and Bass 1994; McIver et al. 2014). Midshipman produce these three vocalizations by rapidly contracting specialized sonic muscles wrapped around their swim bladder; as the muscles vibrate, they drum on the gas-filled bladder, producing low-frequency, multi-harmonic vocalizations (Balebail and Sisneros 2022; Cohen and Winn 1967; Greene 1924).

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https://doi.org/10.1016/j.marpolbul.2025.117563
Received 4 October 2024; Received in revised form 13 December 2024; Accepted 12 January 2025

Plainfin midshipman fish spend most of the year in deep water (> 200 m) but in the late spring migrate to the shallow intertidal zone for their summer breeding season (Arora 1948). In the intertidal zone, males dig nesting cavities under large rocks and hum to attract incoming females to their nests. Females are extremely sensitive to the specific frequencies of the dominant harmonics of male hums, especially during the breeding season (Sisneros and Bass 2003). Hum amplitude also appears to be an honest signal of male quality (size and condition; Balebail and Sisneros 2022), so it is likely that females choose males based on the acoustic qualities of their hums (McKibben and Bass 2001; McKibben and Bass 1998; Sisneros 2012). After spawning, males care for young but also continue humming to attract additional females to their nests (Bose et al. 2016; Brantley and Bass 1994). These shallow nearshore midshipman breeding grounds can be bombarded by motorboat noise, especially during the late spring and summer breeding months (May–August), when recreational boat use is at its peak (Halliday et al. 2018). Because midshipman fish are sensitive to and rely heavily on sound, boat noise in their breeding areas could have strong detrimental effects for communication and mate attraction. Furthermore, given that low-frequency boat noise completely overlaps with the dominant frequencies of plainfin midshipman vocalizations, motorboat noise is likely to mask acoustic communication of the plainfin midshipman (Halliday et al. 2018).

One strategy to overcome masking by loud background noise—such as boat noise—is to alter the rate, duration, frequency (pitch), or loudness of vocalizations (Brumm and Zollinger 2011). By altering the temporal characteristics (rate or duration) of vocalizations by calling more often or for longer, animals can increase the redundancy of their vocal signals, improving the chances of a receiver hearing them in a noisy environment (Shannon et al. 2016). Increasing the amplitude (sound-level, or loudness) of calls in the presence of loud background noise is another strategy, allowing the sender to be heard above the noise source; this phenomenon is referred to as the Lombard effect (Brumm and Zollinger 2011). Individuals may also shift the frequency of vocalizations out of the range of the noise source, which helps to avoid masking and may allow the signal to be received against loud background noise (Brumm and Zollinger 2011). Changes in vocalization frequency and amplitude in response to noise have been observed in many terrestrial and aquatic mammals and birds (Kunc et al. 2022), but have only been investigated in three fish species to date, two of which were toadfishes (Brown et al. 2021a; Holt and Johnston 2014; Luczkovich et al. 2016; Ogurek et al. 2024).

Shifting the frequency of one's vocalizations may not always be a viable strategy, and increasing the amplitude of vocalizations may not be energetically sustainable, especially over the long term. Instead of calling more often or more loudly, signallers may instead reduce their calling rates and wait for the background noise to decrease before resuming normal vocalizations (Ladich 2019). A reduction in calling rate when confronted by noisy environments has been observed in several fish species (Ladich 2019), including the plainfin midshipman (Brown et al. 2021a; Ogurek et al. 2024; Woods et al. 2023), Lusitanian toadfish (Vieira et al. 2019), oyster toadfish (Mackiewicz et al. 2021), meagre (Matos et al. 2024; Vieira et al. 2021), and two goby species (de Jong et al. 2018).

In a previous study using wild plainfin midshipman fish, Brown et al. (2021a) found that nesting males increased their call amplitude, decreased their call frequency, and produced calls less often in response to an artificial low-amplitude tonal stimulus. However, this artificial noise stimulus did not have the broadband frequency typical of boat noise, but instead strongly resembled a midshipman hum in fundamental frequency and accompanying harmonics. It is possible that the males in that study may have changed their calls because the artificial noise mimicked having additional competing, vocalizing males in the area, and may not reveal how these fish respond to anthropogenic noise, such as noise from boat engines. Few studies have used boat noise from a real motorboat to experimentally test the Lombard effect; most have used playbacks or noise already occurring in the area (*e.g.*, near a ferry terminal or marina), the latter of which is not a controlled stimulus. For example, in Ogurek et al. (2024), wild plainfin midshipman nesting near a marina decreased how often they vocalized and increased the frequency (pitch) of grunts and hums when boat noise was present. While these types of studies can provide useful information on how fish respond to noise, we still lack experimental evidence of the Lombard effect in fishes in response to anthropogenic noise.

In the current study, we experimentally manipulated the exposure of wild plainfin midshipman to anthropogenic noise by systematically introducing motorboat noise. We did this by driving a motorboat near experimental nests to assess if and how nesting plainfin midshipman males alter their vocalizations. We predicted that in the presence of motorboat noise, plainfin midshipman fish would 1) decrease their calling rate, in particular their agonistic grunts and growls, as these shorter vocalizations may be easier to temporarily forego during short bouts of boat noise, 2) shift the frequency of their calls away from the dominant boat harmonics to avoid masking, and 3) increase the amplitude (loudness) of their vocalizations (*i.e.*, exhibit the Lombard effect).

2. Methods

2.1. Field site and nest construction

We conducted this study in the intertidal zone of Hood Canal in Brinnon, Washington, USA on a private beach during May–June 2022. We constructed 55 artificial nests out of 30 cm × 30 cm concrete tiles (Fig. 1c), which plainfin midshipman guarder males readily inhabit (Brown et al. 2021b; DeMartini 1988; Woods et al. 2022), and placed them in five groups, each consisting of either eight (single row; though one group only had seven) or 16 (double row) tiles, along the middle and lower intertidal (Fig. 1b), with 1 m between tiles and at least 5 m between groups. Nests were checked for occupancy every few days at low tide, or by snorkelers when the nests were submerged. Once at least six nests in a group were occupied by males guarding eggs, we considered that group ready for testing.

We do not know the exact number of males whose vocalizations were recorded during trials due to the many natural nests found in the area; however, based on the most recent nest checks of our experimental nests, our estimates are as follows: Group 1 – $N = 12$, Group 2 – $N = 9$, Group 3 – $N = 12$, Group 4 – $N = 7$, Group 5 – $N = 8$.

2.2. Noise stimulus

We used a 4-m flat-bottom aluminum hull motorboat equipped with a 9.9 hp Yamaha outboard engine driven near the nests as our noise stimulus. During boat noise periods, the boat was driven in continuous loops at full-throttle for the entirety of each 10-min noise period. The closest point of the loop was approximately 20 m from the nest group being tested (Fig. 1a). At the furthest point, the boat was approximately 60 m from the nest group. We chose this distance because plainfin midshipman nests are typically in shallow water, so the noise they usually experience in the intertidal would not normally come from boats driven directly over the nests. For consistency, the boat was always driven by the same individual (MBW).

2.3. Experimental trials

Each of the five nest groups received one trial, each on a different night, with at least two nights without noise manipulations between groups. At least 24 h before each trial began, a SoundTrap acoustic recorder (ST300 STD or ST300 HF; Ocean Instruments New Zealand) was placed in the centre of the nest group to be tested (AR in Fig. 1) to record the vocalizations of the fish in the focal group, as well as the boat noise we were exposing them to.

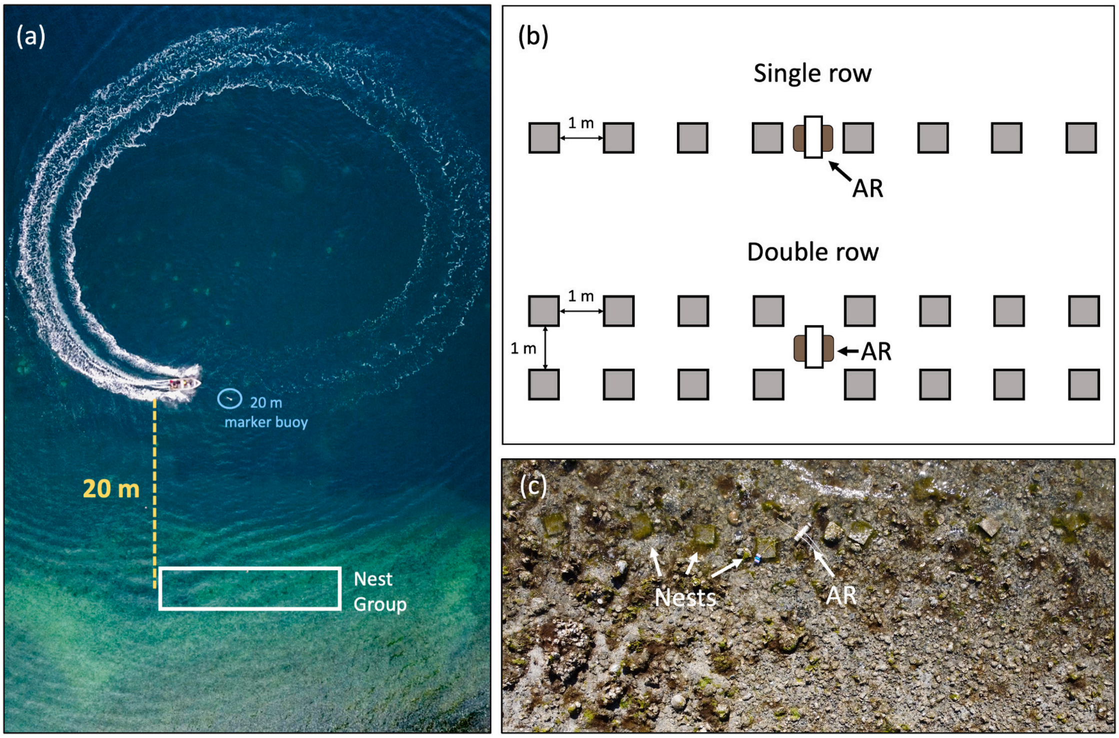

Fig. 1. Experimental setup. (a) Aerial photograph taken during the boat noise period of an experimental trial, showing the path of the boat loop, location of the submerged intertidal nests in the nest group being tested, and the 20 m marker buoy (20 m from the center of the nest group) which was used to steer the boat in consistent loops at the correct distance from the nests. (b) Schematic diagram of the two nest group arrangements for the five groups tested: 8 nests in a single row or 16 nests in a double row, with the acoustic recorder (AR) positioned in the middle of the nest groups. (c) An aerial photograph of a single-row nest group (consisting of 8 nests).

As plainfin midshipman fish are nocturnal and primarily hum at night, we conducted trials at dusk, between 20:20 and 21:30. We did not conduct trials later at night, as recreational boat noise is rare after dusk, and safety protocols favoured driving boats while there was still some daylight. Directly before trials began, the boat was quietly rowed away from the nests (> 150 m) and into deeper water, where the engine was then started and allowed to warm up. The first boat noise treatment began approximately 45 min before sunset.

Each trial night consisted of three 10-min boat noise treatments and four 10-min ambient control treatments, including the ambient baseline and follow-up periods. Trials began with a 10-min baseline period before the boat engine was started. There were then three 10-min intervals of continuous boat noise, interspersed by 10-min quiet periods where the boat engine was off. Finally, a 10-min follow-up period was conducted once the boat engine was turned off. During boat noise periods, the boat was driven continuously at full throttle. During the ambient control periods, the boat engine was turned off, the boat was away from the nests, and no noise was introduced.

2.4. *Acoustic analysis*

All bioacoustic analyses were performed using Raven Pro acoustic software (version 1.6.5; Cornell Lab of Ornithology, Ithaca, New York, USA). Spectrograms were built in Raven Pro with 7000 samples, a Hanning window with 50 % overlap, and time and frequency axes set to 10 s and 1000 Hz, respectively, and vocalizations were annotated manually. We selected three 1–3 s measurements of hum vocalizations present during each of the seven 10-min trial periods: one near the beginning, one in the middle, and one at the end of the trial period, taking care to pick the loudest and clearest hums present. Both the fundamental frequency (F_0) and the first harmonic (F_1) were measured for each hum when these signals were both audible and visible in the spectrograms. Every clear individual grunt (not in a grunt train) and every clear growl during each of the trial periods was enumerated and analyzed. In the case of grunt trains, the clearest grunt in the train was selected for amplitude, frequency, and duration analyses and the rest of the grunts in that train were simply counted. The presence/absence of hums in each trial period was also recorded. For the peak power density (PPD; a measure of amplitude) analysis, we used the first harmonic (F_1) of each vocalization, as F_1 was often the most prominent harmonic. No vocalizations were scored or analyzed if they occurred during the minutes between trial periods when the boat was being started or driven away from the nests. Additionally, we measured the PPD of boat noise segments in a subset of trials so that we could directly compare the PPD of boat noise to that of the vocalizations.

Metrics of underwater sound levels were processed in two ways using the PAMGuide package (Merchant et al. 2015) in Matlab (version 2016b; Mathworks, Natick, Massachusetts, US). First, power spectral densities (PSD), a high-resolution metric of amplitude which quantifies sound levels for every Hz in a frequency range, were computed using a Hanning window with 50 % overlap and 1 s bins in the 20 Hz to 10 kHz range. Second, sound pressure levels (SPL), which measure the sum of power across a broad frequency range, were calculated in third octave bands using a Hanning window with 50 % overlap and 1 s bins. We then summed the power of the three bands centered on 80, 100, and 125 Hz and converted back to decibels, thus calculating SPL in the octave band centered on the midshipman hum fundamental frequency.

2.5. *Statistical analysis*

We conducted all statistical analyses in R (v.4.0.4; R Core Team 2021). Acoustic masking from the boat noise could have made it harder to detect quieter calls during noise trial periods compared to ambient control periods. Thus, to account for this potential masking effect, we set a threshold for the ambient periods such that the lowest amplitude vocalization in the ambient periods could not be lower than the lowest amplitude vocalization in the boat noise periods. Therefore, we used the peak power density of the lowest-amplitude vocalizations during the boat noise treatment (82 dB re 1 μPa) as a cutoff threshold for the vocalizations in the ambient periods. Julian date was not included as a term in any of the models because each group was tested on a different day, which would lead to collinearity if both group and date were included in the models.

For all models, we used ANOVA Wald chi-squared tests (*car* package), with contrasts summed to zero in any models with an interaction term to properly account for the interaction, and we used contrast ratios (*emmeans* package) to calculate the magnitude of any observed effects. The presence/absence of hums was not modelled, as hums were present in every trial period. To account for multiple comparisons, we calculated adjusted p-values for all behavioural variables ($N = 12$) using the Holm method (Holm 1979).

2.5.1. *Agonistic vocalization rates*

We fit a negative binomial generalized linear mixed-effect model (GLMM; *glmmTMB* package) to the counts of agonistic vocalizations (grunts and growls) recorded for each nest group in each trial period to test the effects of noise treatment (ambient control *vs.* boat noise). We included trial period and nest group as random intercepts to account for the repeated-measures design, and noise treatment as the fixed effect. We used ANOVA type II Wald chi-squared tests (*car* package) to test the effect of boat noise on agonistic vocalizations and we used contrast ratios (*emmeans* package) to calculate the magnitude of the observed effect. We fit additional negative binomial GLMMs with the same fixed and random effects to test the effect of boat noise on growls and grunts individually. We also modelled the number of grunts in each grunt train during boat noise *vs.* ambient periods, using an additional negative binomial GLMM with the same fixed and random effects as above.

2.5.2. *Duration of agonistic vocalizations*

We used linear mixed-effects models (LMMs; *lme4* package) to examine the effect of noise treatment on the duration of agonistic vocalizations: grunts and growls. We examined each separately because grunts are typically much shorter than growls. The growl data were log-transformed to achieve normality. Trial period and nest group were included as random intercepts in both models, with noise treatment as the fixed effect. We could not analyze the duration of hums because it is difficult to distinguish when hums of different fish start and stop.

2.5.3. *Peak frequency of vocalizations*

We built LMMs to test the effect of noise treatment on the peak frequency (in Hz) of all three vocalization types. We fit a single LMM for the fundamental frequency (F_0) of all vocalizations. Noise treatment (ambient control or boat noise), vocalization type (grunt, growl, or hum), and their interaction were included as fixed effects in the model. Water temperature (recorded by the SoundTrap acoustic recorders) was averaged over each 10-min trial period and was included as an additional fixed effect (mean-centered), as previous studies have shown a correlation between water temperature and frequency of plainfin midshipman vocalizations (Halliday et al. 2018; McIver et al. 2014). Nest group and trial period were both included as random intercepts to account for the repeated-measures design.

To further examine the effect of noise on hum peak frequency, we fit an additional LMM for the first harmonic (F_1) of hums. Due to the acoustic properties of shallow water, the propagation of the various harmonics differed, and F_1 often propagated more strongly than F_0, especially for hums, giving us a larger sample size for F_1 hums. The F_1 hum model included noise treatment and water temperature (mean-centered) as fixed effects and trial period and nest group as random intercepts.

2.5.4. *Amplitude of vocalizations*

PPD, measured in decibels (dB re 1 μPa), was used as the primary measurement of amplitude to examine the effects of boat noise on amplitude of all three plainfin midshipman vocalizations. Peak power density is defined as the amplitude of the grid cell (grid cell dimensions are defined by the Fast Fourier Transform used to calculate the spectrogram) with the greatest amplitude within an annotation.

We fit a single LMM to examine the effect of noise treatment on the PPD of the first harmonic (F_1) of all vocalizations. Noise treatment (ambient control or boat noise), vocalization type (grunt, growl, or hum), and their interaction were included as fixed effects in the model, and nest group and trial period were included as random intercepts.

Sound pressure levels (SPL), again measured in dB re 1 μPa, were also modelled using an LMM with treatment as the fixed effect and nest group and trial period as random intercepts. This model compared the overall sound levels during ambient control and boat noise periods rather than the amplitude of individual vocalizations.

2.6. *Ethical note*

All procedures in this study complied with guidelines set by the ASAB/ABS (2012) and the Canadian Council on Animal Care (Olfert et al. 1993) and were approved by the University of Victoria Animal Care Committee (AUP: Juanes-2021-012). After experiments concluded, all equipment was removed, and the experimental fish were allowed to continue guarding their brood in their artificial nests at the study site for the remainder of the breeding season.

3. Results

3.1. *Rates of agonistic vocalizations*

We observed a significant decrease in midshipman agonistic vocalizations during boat noise ($\chi^2 = 26.58$, df $= 1$, $p_{adj} < 0.0001$), with an average of 4.4 times fewer vocalizations (95 % CI: 2.4–7.8) in boat noise periods compared to ambient control periods when the boat engine was off (Fig. 2a). There were 4.4 times fewer grunts (95 % CI: 2.2–8.9) during boat noise (Fig. 2b) and 3.6 times fewer growls (95 % CI: 2.4–5.6) during boat noise compared to ambient control periods (Fig. 2c).

Additionally, grunt trains were shorter during boat noise compared to ambient periods ($\chi^2 = 8.76$, df $= 1$, $p_{adj} = 0.02$). On average, grunt trains during boat noise periods contained 2.8 times fewer grunts (95 % CI: 1.4–5.4).

3.2. *Duration of agonistic vocalizations*

The duration of agonistic vocalizations was affected by noise treatment (Fig. 3). Grunts were longer on average during boat noise periods compared to ambient control periods, though not statistically significant ($\chi^2 = 3.90$, df $= 1$, $p_{adj} = 0.1$), while growls were shorter during boat noise periods ($\chi^2 = 5.67$, df $= 1$, $p_{adj} = 0.05$). On average, grunts lasted for 0.164 s and were 0.013 ± 0.007 s longer during boat noise periods compared to ambient periods, where they lasted for an average of 0.149 s. Growls were approximately 1.3 times (95 % CI: 1.0–1.7) shorter during boat noise periods, where they lasted an average of 1.64 s, compared to growls in the ambient periods, which had an average duration of 2.31 s.

3.3. *Peak frequency of vocalizations*

Boat noise had a significant effect on the peak frequency of the hum first harmonic (F_1), which was on average 4.18 ± 1.44 Hz (est. ± SE) higher during the boat noise treatment compared to during the ambient control treatment ($\chi^2 = 8.48$, df $= 1$, $p_{adj} = 0.02$; Fig. 4). Water temperature also had a significant effect on hum F_1 ($\chi^2 = 12.85$, df $= 1$, $p_{adj} = 0.003$), with an average increase of approximately 10.33 ± 2.88 Hz

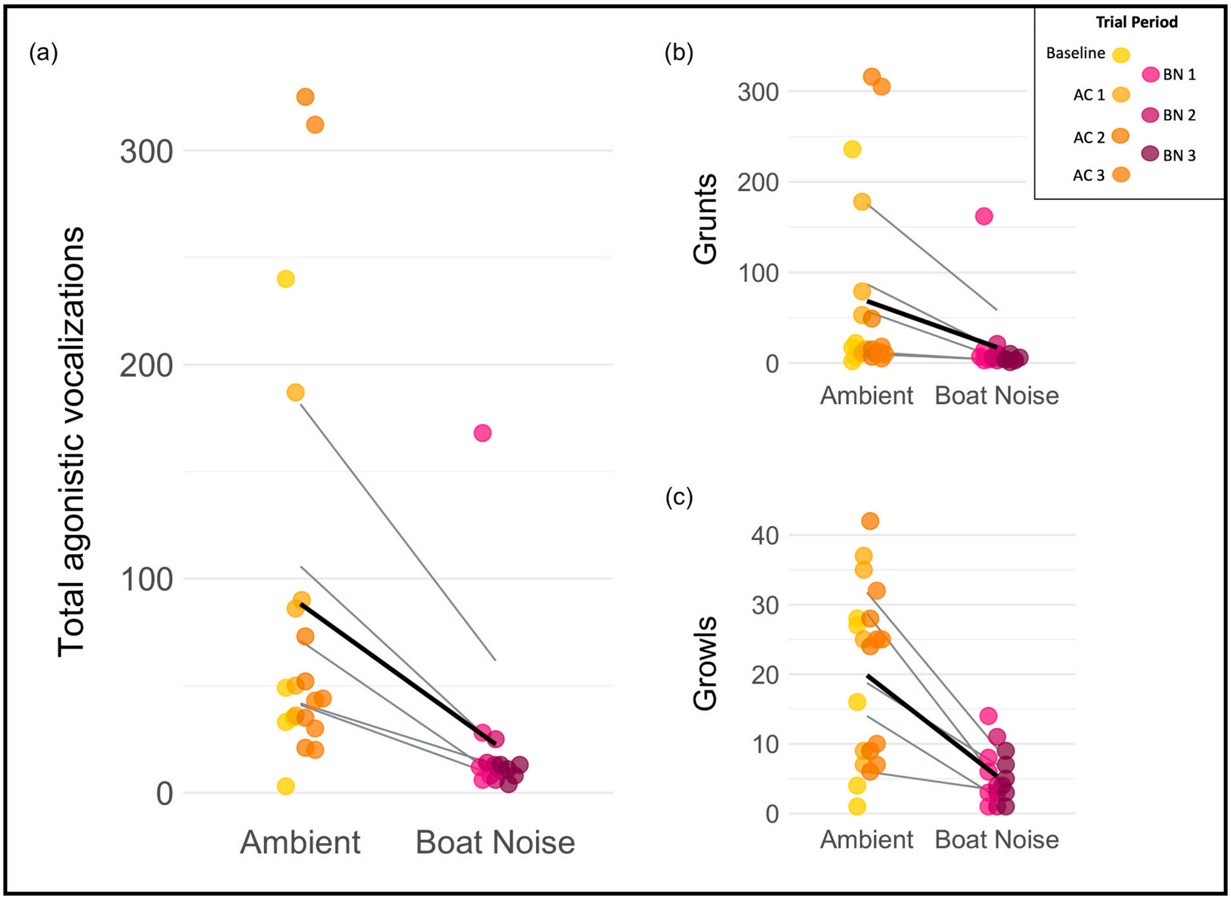

Fig. 2. Sum of agonistic vocalizations produced by groups of guarder male plainfin midshipman during 10-min trial periods of continuous boat noise or ambient control periods when the boat was turned off and away from the nests. (a) Total number of combined grunts and growls (agonistic vocalizations), (b) number of grunts, and (c) number of growls recorded from each of the five nest groups in each trial period. AC = Ambient Control, BN = Boat Noise, with the numbers referring to subsequent 10-min experimental periods within a trial. Colours represent trial periods, with darkening colours representing trials that occurred later into the night. Thin grey lines show the mean number of vocalizations for each group within the ambient and boat noise periods, and the thick black lines show the mean across all five groups.

for every 1 °C increase in water temperature (Fig. A.1).

We did not observe an effect of boat noise on the fundamental (F_0) peak frequency of any of the vocalization types ($\chi^2 = 0.12$, df = 1, $p_{adj} = 0.73$). However, temperature had a significant effect on F_0 peak frequency ($\chi^2 = 6.60$, df = 1, $p_{adj} = 0.04$), and the different vocalization types differed significantly in their peak fundamental frequencies ($\chi^2 = 23.68$, df = 2, $p_{adj} < 0.0001$). For every 1 °C increase in water temperature, there was an increase of approximately 11.28 ± 4.39 Hz (Fig. A.2).

3.4. Amplitude of vocalizations

When examining the effect of boat noise on the peak power density (PPD) of the first harmonic of midshipman vocalizations, we observed a significant effect of noise treatment ($\chi^2 = 14.43$, df = 1, $p_{adj} = 0.001$; Fig. 5), as well as a significant interaction between noise treatment and call type ($\chi^2 = 11.09$, df = 2, $p_{adj} = 0.02$), with grunts and growls both increasing in amplitude in the presence of boat noise. On average, grunts were 6.3 ± 1.4 dB (est. ± SE) louder during boat noise periods compared to ambient periods, while growls were 5.1 ± 1.3 dB louder during boat noise. We did not observe an effect of noise treatment on hum amplitude.

Call type was also a significant term in our model ($\chi^2 = 70.22$, df = 1, $p_{adj} < 0.0001$). Overall, hums were the loudest call, with a mean PPD of 106 dB, followed by growls with a mean PPD of 100 dB, with grunts being the quietest call, with a mean PPD of 97.2 dB (Table 1; Fig. 5).

We measured the PPD of individual boat noise segments (by harmonic) in a subset of trials by taking measurements from the loudest (when the boat was passing closest to the nests) and the quietest (when the boat was at the most distant point of the loop) parts of the boat noise periods. The mean PPD of the boat noise measurements was 103.2 dB (F_0 mean = 104 dB, F_1 mean = 103 dB). The mean PPD of all three call types during boat noise periods (but not ambient periods) was higher or equal to the mean PPD of the boat engine (Table 1).

3.5. Quantification of boat noise and experimental soundscape

Our boat noise trials caused large increases in underwater sound levels, including broadband sound and individual tonal signals (Fig. 6; Fig. 7). Power spectral densities (PSD) for the control period show strong peaks at roughly 100, 200, 300, and 400 Hz, which are caused by midshipman humming, but underwater sound levels otherwise show a 30 dB width from 1st to 99th percentile, with decreasing power as acoustic frequency increases (Fig. 6). Conversely, the boat noise periods show the same peaks from midshipman hums, but also include multiple additional peaks from tonal boat noise, and in frequencies >100 Hz, power has a 50 dB range that does not decrease with increasing frequencies (Fig. 6). Moreover, PSD in the 200 to 1000 Hz range reaches >90 dB in the boat noise period, whereas in the ambient control period, PSD only goes as high as 85 dB in the 200–500 Hz range and down to a maximum of 65 dB in the 800–1000 Hz range (Fig. 6). PSD is therefore as much as 30 dB higher in the 800–1000 Hz range in boat noise periods

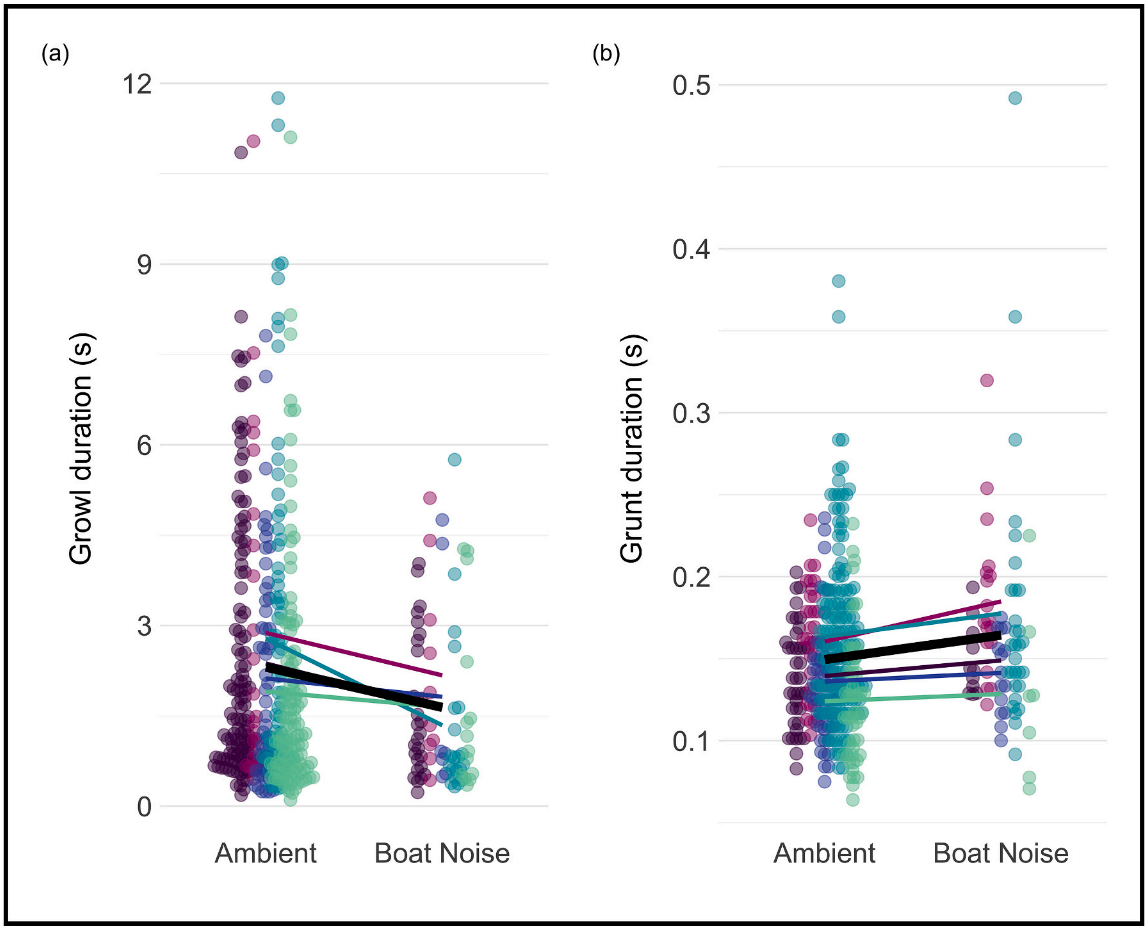

Fig. 3. Duration (in seconds) of agonistic growl (a) and grunt (b) vocalizations produced by guarder male plainfin midshipman fish in each of five nest groups (denoted by the different colours) during boat noise and ambient control periods. Coloured lines show the mean peak frequency for each group within ambient and boat noise periods, and the thick black lines show the mean across all five groups.

compared to ambient control periods. The spectrograms in Fig. 6c–d exemplify the broadband nature of the boat noise, compared to the strong harmonic structure of the midshipman hums, which have the highest amplitude in the lower frequencies (< 500 Hz). The vertical yellow bands spanning the entire frequency range in Fig. 6d represent each boat pass as the boat was at the point of the loop closest to the experimental nests, while the horizontal yellow bands in Fig. 6c–d represent midshipman hums, with the highest amplitude at ~200 Hz (hum F_1).

Sound pressure levels (SPL), which allow us to compare the sum of power across a broad frequency range, were significantly higher during boat noise periods compared to ambient control periods ($\chi^2 = 5.89$, df = 1, $p = 0.015$), with a mean increase of 10.4 ± 4.3 dB (est. ± SE) during boat noise (Fig. 7). The mean SPL in the ambient periods was 95.7 dB, while the mean SPL in the boat noise periods was 106 dB. Within each treatment (ambient and boat noise), the trends in SPL were relatively consistent across trial periods and between groups (Fig. 7b). We did see a trend of increased sound levels later at night (darker coloured boxplots in Fig. 7b), in both the ambient and boat noise treatments, though it was more pronounced in the ambient treatment, where noise levels were lower overall (Fig. 7b). This temporal trend is likely a result of there being more males humming later at night, as the hum chorus at midshipman breeding sites typically peaks around midnight (Halliday et al. 2018).

4. Discussion

When exposed to boat noise, wild nesting plainfin midshipman fish altered their vocalizations, producing four times fewer agonistic vocalizations (grunts and growls), and altering the acoustic properties of all three of their calls. In the presence of boat noise, we observed a 4 Hz increase in the frequency of the mating hum and a 5–6 dB increase in the amplitude of both grunts and growls. Our study bolsters the evidence for the Lombard effect in fishes and is the first *in situ* study using experimentally-introduced real motorboat noise to establish this effect.

Our first prediction was that plainfin midshipman would produce fewer vocalizations during boat noise because by waiting to vocalize until after the noise has stopped, males may avoid wasting energy by having their calls masked by noise. While we found support for this idea, several studies on birds and mammals have reported the opposite pattern. Under noisy conditions, some species increase their vocalization rate, theoretically because increasing signal redundancy increases the likelihood that it will be heard by the intended receivers, even in noisy environments (Brumm and Zollinger 2011; Shannon et al. 2016). One fish species that may adopt such a strategy is the brown meagre, *Sciaena umbra*, in which Picciulin et al. (2012) observed an increase in vocalization pulse rates under noise. However, most previous studies focusing on fish (albeit only a handful have been conducted to date), like our study, have shown a decrease in vocalizations under noisy conditions (Ladich 2019). For example, in a laboratory study, male two-spotted gobies (*Pomatoschistus flavescens*) and painted gobies (*Pomatoschistus pictus*) both decreased their courtship vocalization rates in response to

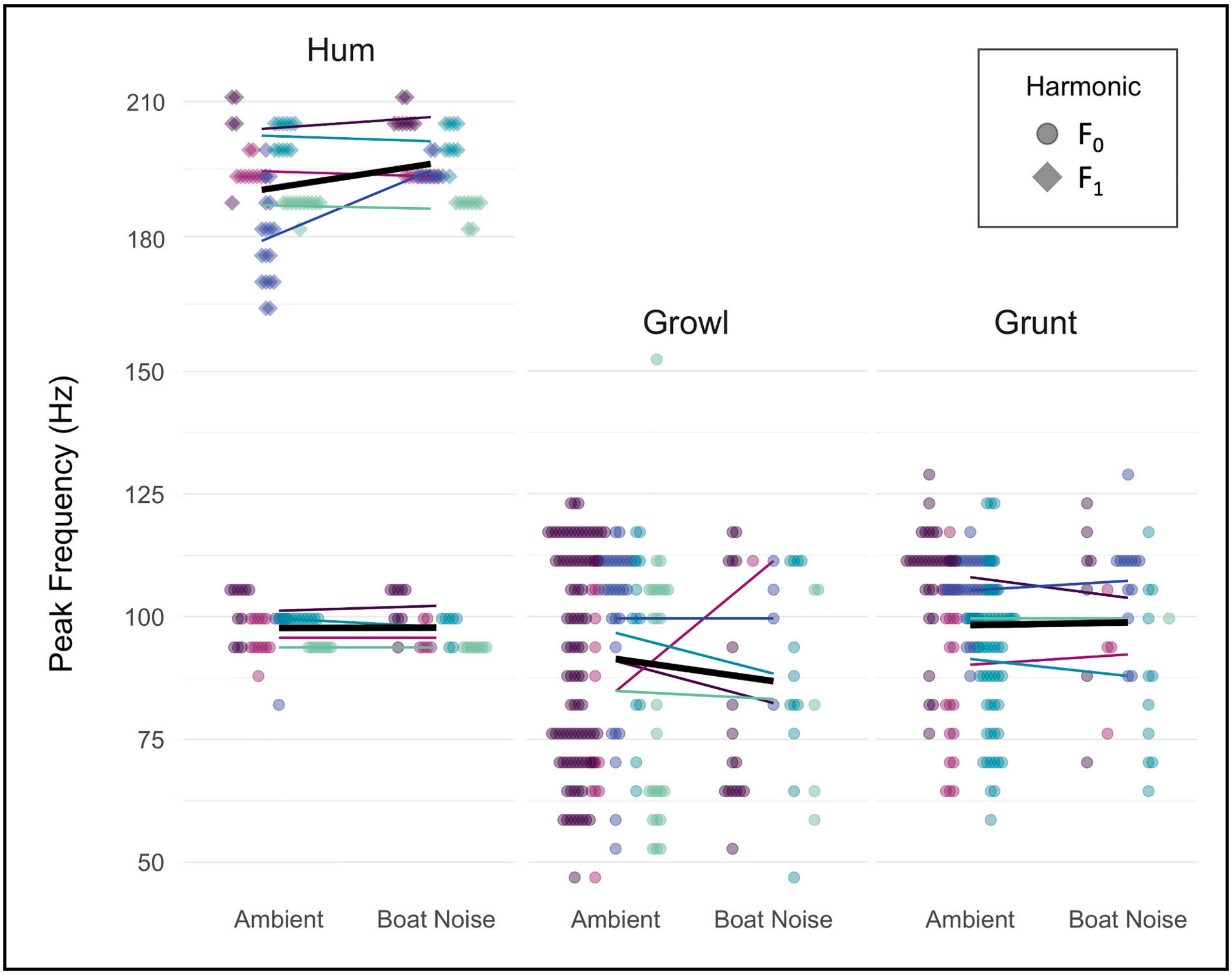

Fig. 4. Peak frequency (in Hz) of the vocalizations produced by guarder male plainfin midshipman in each of five nest groups (represented by the different colours) during boat noise and ambient control trial periods. Both the fundamental frequency (F_0) and first harmonic (F_1) of mating hums are shown, and F_0 is shown for agonistic grunts and growls. Coloured lines show the mean peak frequency for each group within ambient and boat noise periods, and the thick black lines show the mean across all groups.

artificial noise, which may have led to the observed decrease in spawning success in painted gobies under noisy conditions (de Jong et al. 2018). In a field study on the oyster toadfish, *Opsanus tau*, call rates dropped by 32 % following exposure to an idling boat engine, although no changes in amplitude were observed (Mackiewicz et al. 2021). The Lusitanian toadfish has also been shown to decrease its calling rate in response to boat noise playback (Alves et al. 2021; Amorim et al. 2022). This effect has also been documented in our study species, the plainfin midshipman. In the field, Brown et al. (2021a) found that nesting plainfin midshipman males exposed to a chronic artificial tonal noise produced fewer vocalizations, and Woods et al. (2023) observed fewer agonistic vocalizations on trial days with boat noise compared to days without boat noise. Additionally, Ogurek et al. (2024) observed fewer vocalizations when boat noise was present in recordings of plainfin midshipman nesting near a marina.

One remaining question is whether there are fitness consequences associated with such a reduction in agonistic vocalizations. In plainfin midshipman, every spring there is intense nest competition, with frequent territory disputes and many nest-takeovers, and this competition can result in offspring mortality or cannibalism of young (Bose et al. 2016; Bose et al. 2014). Agonistic vocalizations likely play an important role in nest and offspring defence. Cullis-Suzuki (2015) and Woods et al. (2022) observed that plainfin midshipman use their agonistic calls to deter egg predators such as crabs and gunnels. If nest owners produce fewer grunts and growls while boats are around, then noise could lead to more territory intrusion by predators or competitors (other guarder males and/or sneaker males), and ultimately result in lowered reproductive success. However, it is also possible that boat noise also deters predators and/or competitors (Cullis-Suzuki 2015). As our boat noise stimulus only lasted 10 min at a time and ceased completely within an hour, the males in our study could have opted to rely on other methods of territory and offspring defence, such as lunging and biting, during the short periods of boat noise. Nedelec et al. (2017) found that boat noise playbacks in the field increased defensive behaviours, decreased parental care behaviours, and ultimately led to decreased offspring survival in a brooding coral reef fish, *Acanthochromis polyacanthus*. Woods et al. (2022) similarly observed an increase in defensive behaviours during boat noise playbacks in plainfin midshipman guarding empty nests in the lab; however, no changes in agonistic vocalizations were observed. These results suggest that nest-guarding fish may switch to different defence tactics in the presence of noise. The increases in more active (and likely energetically costly) defensive behaviours like biting, lunging, and chasing may lead to less time spent on parental care (as seen in the Nedelec study) and unnecessary energy expenditure. Future field studies that employ the tandem use of both cameras and acoustic recorders would be useful to assess whether a reduction of agonistic vocalizations is accompanied by a compensatory increase of other agonistic defensive behaviours. Similarly, there is a need to

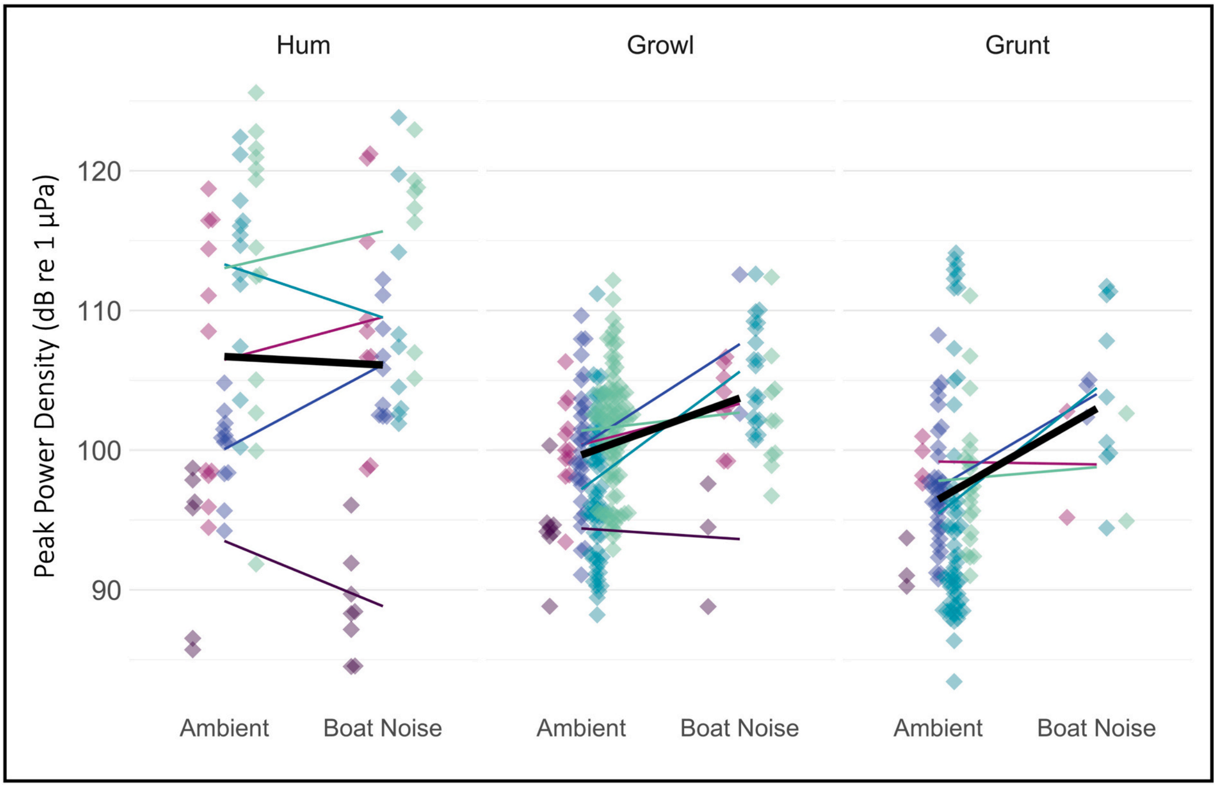

Fig. 5. Peak power density (amplitude) of the first harmonic (F_1) of plainfin midshipman vocalizations during 10-min periods of continuous boat noise and 10-min ambient control periods. Colours denote the five nest groups, each tested on a different night. Coloured lines show the mean peak frequency for each group within ambient and boat noise periods, and the thick black lines show the mean across all groups.

Table 1
Mean peak power density (PPD) for the first harmonic (F_1) of each vocalization type and boat noise measurements from a subset of trials. The overall mean represents the mean across all periods, regardless of noise treatment. All amplitude measurements are in dB re 1 µPa.

Call Type	Overall	Ambient Periods	Boat Noise Periods
Hum	106 dB	107 dB	106 dB
Growl	100 dB	99.7 dB	104 dB
Grunt	97.2 dB	96.5 dB	103 dB
Boat	*103 dB*	–	*103 dB*

explore how body condition, stress hormone levels, and parental care are impacted by both chronic and acute noise exposure in plainfin midshipman fish, as well as in other fishes.

While both the number of individual grunts and grunts per grunt train decreased, we did observe an increase in individual grunt duration, though not statistically significant. Increased duration of short vocalizations (below a few hundred milliseconds; a range encompassing midshipman grunts but not growls) has been identified as a mechanism to increase signal recognition in noisy conditions in other animals, including humans (Brumm and Slabbekoorn 2005). We did not see this effect on growls, which are much longer-duration vocalizations than grunts; in fact, we observed a non-significant decrease in growl duration during boat noise. A decrease in growl duration may be related to a decrease in agonistic call rate; in our study, agonistic vocalizations may not have been as effective during boat noise periods, so it is possible that males conserved energy with fewer vocalizations and shorter growls, and potentially relied upon other methods of nest defence during those noisy periods.

Another way that animals avoid vocal masking from noise is to shift the frequency of their calls away from the dominant frequencies of the noise (Brumm and Slabbekoorn 2005). We observed such a shift with a mean increase of approximately 4 Hz in the first harmonic of the mating hum during boat noise periods. To our knowledge, ours is the third study to date to observe a frequency shift in fish vocalizations in response to noise, and the first to experimentally establish this effect using real boat noise (previous studies: Brown et al. 2021a; Ogurek et al. 2024). It was previously thought that fish were not capable of these sorts of vocal adjustments (Ladich 2019). Consistent with our study, Ogurek et al. (2024) observed an increase in the peak frequency of the mating hum of wild plainfin midshipman exposed to nearby vessel noise. In contrast, Brown et al. (2021a) observed a decrease in the fundamental frequency of the hum in nesting plainfin midshipman exposed to a tonal noise stimulus. The tonal artificial noise stimulus used in Brown et al. (2021a) was a fairly quiet signal and could have been perceived by other vocalizing males in the area as an additional male. In contrast, the real boat noise used in our study was a much louder stimulus and likely masked most hums. By shifting their signal frequency away from the dominant harmonics of the boat noise, the fish may have been trying to avoid masking and produce a signal that could be perceived despite the background noise. We do not know whether a frequency shift of only 4 Hz would increase the detectability by females, rendering further research focused on female plainfin midshipman sound perception and mate choice in the presence of anthropogenic noise necessary. Increases in acoustic frequency are a commonly observed vocal adjustment in noisy environments in other species (Brumm and Slabbekoorn 2005), rendering the findings of our study consistent with expected outcomes in response to noise.

Ambient water temperature also had a significant effect on vocalization frequency in our study. This relationship has been previously described in plainfin midshipman (*e.g.,* Brantley and Bass 1994; McIver et al. 2014), and has also been observed in several fishes and other ectothermic species (Ladich 2018). For every 1 °C increase in water temperature, we observed an 11 Hz increase in fundamental frequency on average for all three vocalization types, and a 10 Hz increase in the

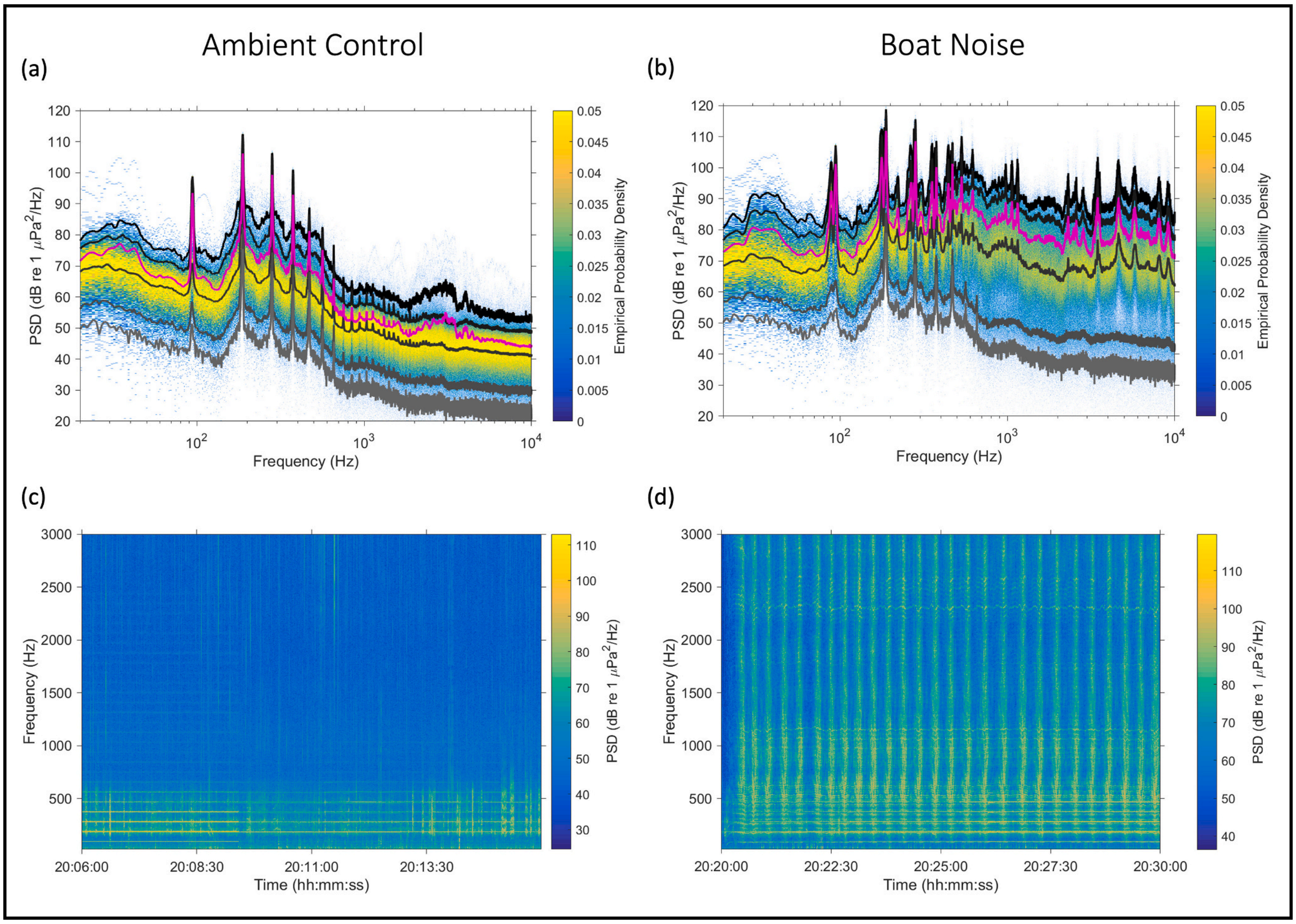

Fig. 6. Power spectral densities (PSD) (a, b) and spectrograms (c, d) for example ambient control (a, c) and boat noise (b, d) trials. PSD plots are displayed as the 1st, 5th, 50th, 95th, and 99th percentiles and the root mean squared (RMS) average amplitudes across frequencies.

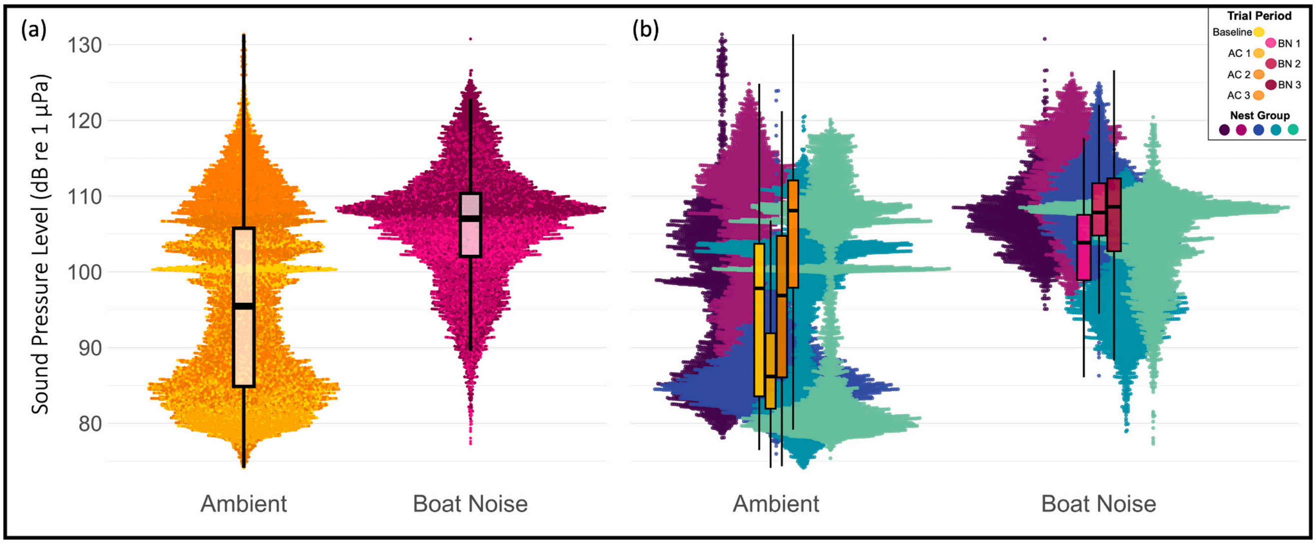

Fig. 7. Sound pressure levels (SPL) in the 80 Hz octave band (71–141 Hz) during the four ambient control (yellow-orange) and three boat noise (pink-purple) periods of experimental trials. Each point represents one second of recording for each 10-min trial period, for each of the five nest groups. (a) Boxplots represent the overall median and interquartile range for all data from each treatment, plotted on top of the raw data, coloured by trial period. (b) Boxplots show the median and interquartile range for each trial period, and are plotted on top of the raw data for each of the five nest groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hum first harmonic. As both noise and temperature continue to rise globally, it is possible that these could have a compounding effect on the frequency of midshipman vocalizations, leading to higher frequency vocalizations over time.

In the presence of boat noise, the fish also produced grunts and growls with significantly increased amplitude (peak power density). Hence plainfin midshipman appear to exhibit the Lombard effect, and this result provides support for our third and final hypothesis. On average, grunts were 6 dB louder and growls were 5 dB louder during periods of boat noise compared to ambient control periods. To date, there have only been three other studies that have found the Lombard effect in fishes (Brown et al. 2021a; Holt and Johnston 2014; Luczkovich et al. 2016). When exposed to white noise playbacks in aquaria, blacktail shiners (*Cyprinella venusta)* increased the amplitude of their burst vocalizations (Holt and Johnston 2014). In the field, oyster toadfish increased the amplitude of their vocalizations during and after noise playbacks (Luczkovich et al. 2016), and plainfin midshipman fish increased their hum amplitude in response to a low-amplitude tonal noise stimulus (Brown et al. 2021a).

Mating hums are typically louder and longer vocalizations than grunts and growls in plainfin midshipman, and hums were the only vocalization for which we did not observe an effect of boat noise on vocalization amplitude. When Brown et al. (2021a) tested the effect of a much quieter, low-amplitude noise stimulus on nesting plainfin midshipman fish, they observed an increase in hum amplitude. However, as argued above, the acoustic similarity of the tonal noise stimulus and midshipman mating hums means that the amplitude adjustment observed in Brown et al. (2021a) may have been an example of how fish adjust vocalizations in response to additional competition. It is also worth noting that in both our study and in Brown et al. (2021a), groups of fish were recorded rather than individual fish, so the changes in amplitude observed could have either been true individual vocal adjustments or the outcome of individual fish joining or leaving the hum chorus.

In a meta-analysis on the Lombard effect, Kunc et al. (2022) argued that signal-to-noise ratio is a key factor in explaining whether the Lombard effect will be observed, with lower signal-to-noise ratios being more likely to elicit the Lombard effect. In reptiles and amphibians, studies that did not observe the Lombard effect had significantly higher signal-to-noise ratios than those that observed an effect (Kunc et al. 2022). In our study, hums had the highest signal-to-noise ratio, which may explain why we observed the Lombard effect in the lower amplitude grunts and growls but not the louder mating hum. We saw the largest effect of boat noise on vocalization amplitude in grunts, which are the quietest midshipman vocalization, meaning that grunts generally had the lowest signal-to-noise ratio during boat noise periods.

Another possibility is that the fish in our study were already producing mating hums at a maximal amplitude, but they were able to increase the amplitude of their quieter grunts and growls. The amplitude of grunts and growls increased during boat noise to close to the amplitude of hums in both noise and ambient treatments. This result suggests that midshipman males may be producing mate advertisement calls, which are intended for long-distance communication, near their physiological limits, while agonistic calls, which are used for short-range interactions, are typically quieter and therefore have more potential to increase in amplitude.

In conclusion, using much needed field-based manipulations of real-world anthropogenic noise, we show that boat noise affects plainfin midshipman vocal behaviour; males decreased the rates of agonistic vocalizations, while increasing the frequency of their mating hums and the loudness of their agonistic vocalizations. This study is one of the few to ever establish the Lombard effect in fishes, and it is the first study to establish this effect using a real motorboat as a noise stimulus. Our study should help to raise awareness about the need for noise reduction strategies, such as vessel quietening and boat slowdown measures. Currently many of these programs are strictly voluntary and not legally mandated, which may be sufficient if compliance and awareness are high. Further field studies using realistic noise stimuli will be instrumental in determining how anthropogenic noise is affecting wild populations of fishes and other aquatic organisms.

CRediT authorship contribution statement

Mackenzie B. Woods: Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **William D. Halliday:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Sigal Balshine:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Francis Juanes:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Madeleine Thomson, Megan Thompson, and Alex Schmill for their assistance with fieldwork and analysis, and Eileen Carr, Alan Lindsay, and their family for use of their property. We also thank Joseph Sisneros and Bridget Maher for assistance with fieldwork preparation and logistics. Joseph Sisneros and David Punzalan are also thanked for their feedback on an earlier version of the manuscript. This research was funded by Mitacs Accelerate, NSERC Discovery grants, and student research grants from the Animal Behaviour Society and Sigma Xi.

Appendix A

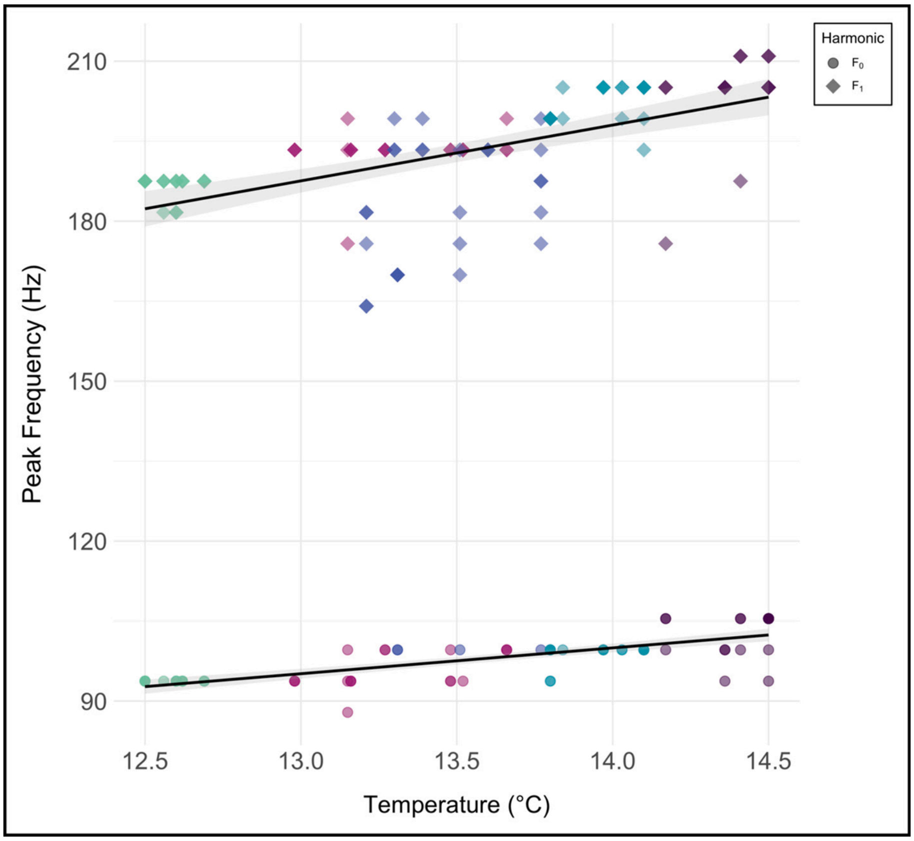

Fig. A.1. Hum peak frequency *vs.* temperature. Relationship between water temperature (average temperature over each 10-min trial period) and the fundamental frequency (F_0) and first harmonic (F_1) of all the mating hum. Colours represent the five nest groups. Black trendlines represent linear models (refer to main text for details) and standard errors for each harmonic.

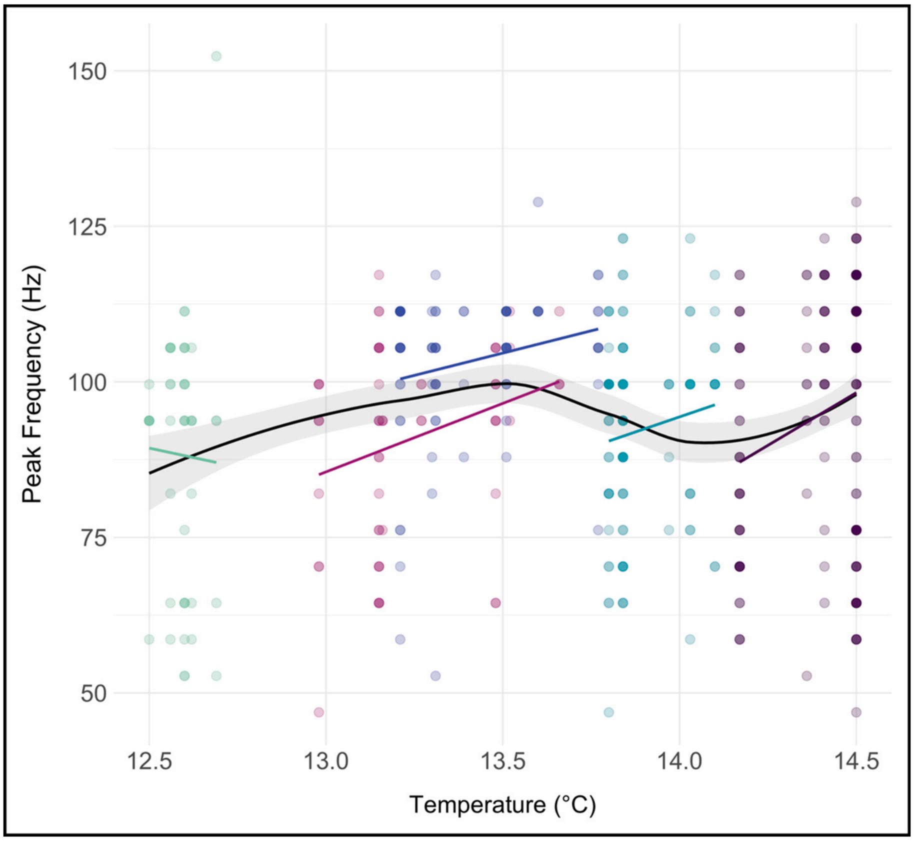

Fig. A.2. Vocalization F_0 peak frequency *vs.* temperature. Relationship between water temperature (average temperature over each 10-min trial period) and the fundamental frequency (F_0) of all three call types combined. Colours represent the five nest groups. Coloured trendlines represent linear models for each nest group and the black overall trendline = geometric smooth with standard error.

Data availability

Data will be made available on request.

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