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Boat noise impedes vocalizations of wild plainfin midshipman fish

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A R T I C L E I N F O

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A B S T R A C T

Marine noise is recognised as a growing threat that can induce maladaptive behavioural changes in many aquatic animals, including fishes. The plainfin midshipman is a soniferous fish with a prolonged breeding period, during which males produce tonal hums that attract females, and grunts and growls during agonistic interactions. In this study, we used acoustic recordings to assess the effects of boat noise on the presence, peak frequencies, and durations of plainfin midshipman calls in the wild. We found that all three call types were less likely to occur, and the peak frequencies of hums and grunts increased in the presence of boat noise. We also show that loud and quiet boat noise affected plainfin midshipman vocalizations similarly. As anthropogenic noise is likely to increase in the ocean, it will be important to understand how such noise can affect communication systems, and consequently population health and resiliency.

1. Introduction

Sound is used by numerous marine organisms, including mammals and fishes, and in many cases acoustic sensation is critical for survival. Anthropogenic noise, prominently from vessel engines, has increased over the past century (Andrew et al., 2002; Andrew et al., 2011; McDonald et al., 2006) and is altering natural soundscapes across many different aquatic habitats (Hildebrand, 2009). Vessel noise is generally a broadband noise dominated by low frequency tones that often overlap with the frequency ranges that most soniferous marine organisms are sensitive to (Vasconcelos et al., 2007). Negative impacts of anthropogenic vessel noise have been well documented across taxa, including cetaceans, marine invertebrates, and fishes (Williams et al., 2015). As the human population and industrial activity increase, ocean noise is likely to continue growing. However, it remains unclear how extensively and severely this rising anthrophony will affect natural soundscapes and the degree that animals might be resilient to this noise (Duarte et al., 2021).

Fishes remain underrepresented in acoustic research (Popper and Hastings, 2009; Popper and Hawkins, 2019; Williams et al., 2015), and little is known about how boat noise affects their vocal communication. Vessel noise can mask the vocalizations of some marine fishes, and the presence of external noise decreases the ability of an individual to detect sound (Radford et al., 2014). Masking of conspecific communication due to vessel noise has been demonstrated in the Lusitanian toadfish (*Halobatrachus didactylus*) and brown meagre (*Argyrosomus regius*) (Vasconcelos et al., 2007; Vieira et al., 2021). Animals commonly react to masking by altering the characteristics—i.e. the quantity, amplitude, frequency, or duration—of their vocalizations (Feng et al., 2006; Lengagne et al., 1999). Decreased calling during artificial and real boat noise has been documented in painted gobies (*Pomatoschistus pictus*; de Jong et al., 2016), Atlantic croakers (*Micropogonias undulatus*; Luczkovich et al., 2012), oyster toadfish (*Opsanus tau*; Luczkovich et al., 2016, Mackiewicz et al., 2021), and in plainfin midshipman (*Porichthys notatus*; Brown et al., 2021; Woods et al., 2023). Increases in call amplitude (loudness) in response to anthropogenic noise have been documented in fish species such as the blacktail shiner (Holt and Johnston, 2014), oyster toadfish (Luczkovich et al., 2016), and plainfin midshipman (Brown et al., 2021). There is also some evidence that fishes can alter their call frequencies (pitch) in response to environmental (Amorim et al., 2011) and human-induced noise (Brown et al., 2021). Currently, most studies investigating the effects of noise on fish vocalizations have been conducted in the laboratory or have made use of noise playbacks, with some exceptions such as research with oyster toadfish (Luczkovich

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et al., 2016) and Atlantic croaker (*Micropogonias undulatus*) (Luczkovich et al., 2012). To better understand how boat noise truly impacts fish, it is necessary to examine fish acoustic communication in their natural environments and in response to true vessel noise.

In this study, we investigate the effects of real-world boat noise on the call characteristics of the plainfin midshipman fish. The plainfin midshipman is a useful animal model for this study because sound is its dominant communication modality for mate attraction and defense (Brantley and Bass, 1994; Cullis-Suzuki, 2016), and because the rocky intertidal zones used for breeding are subjected to high concentrations of pleasure and commercial boats (Fiorini et al., 2016; Halliday et al., 2018). Plainfin midshipman occur along the west coast of North America and are typically caught at depths >200 m in fall and winter (Hubbs and Schultz, 1939). In the early spring, plainfin midshipman migrate from their deep-water habitat to nest and breed in the intertidal zone (Arora, 1948). Once established in a nest that has been excavated under a large rock, plainfin midshipman males contract the sonic muscles attached to their physoclistous swim bladder to produce vocalizations known as hums, grunts, and growls (Greene, 1924). Hums, which facilitate mate attraction, are tonal sounds with a fundamental frequency ranging between 80 and 120 Hz that can last from a few minutes to an hour (Mohr et al., 2017; Halliday et al., 2018; Brantley and Bass, 1994; Zeddies et al., 2012). Female plainfin midshipman are sensitive to specific frequencies of the male hum (Bass and Ladich, 2008), therefore mate selection by females may be impacted if male plainfin midshipman alter their call characteristics to avoid masking by boat noise. Grunts and growls are primarily agonistic calls (Mohr et al., 2017). Grunts are short (<1 s) vocalizations with most energy concentrated below 500 Hz and can be emitted as an individual sound or successively as a ‘grunt train’ (McIver et al., 2014). Growls are more complex sounds, with fundamental frequencies within one call varying from about 50–120 Hz and often lasting >10 s (McIver et al., 2014).

In this study, we examined the effects of boat noise on plainfin midshipman vocalizations in situ during their reproductive season. We compared call characteristics during periods with and without boat noise. Our study provides important data on plainfin midshipman calling behaviour in the wild and helps quantify the effects of boat noise on this fish species and on the intertidal soundscape more generally.

2. Methods

2.1. Data collection

The soundscape of a plainfin midshipman breeding site in Brentwood Bay, British Columbia, Canada (48.5729°N, 123.4635°W) was monitored using two autonomous passive acoustic recorders (SoundTrap ST300 STD, Ocean Instruments, Auckland, New Zealand) between March 27–August 5, 2020. The recorders were situated within a small bay on the east coast of Saanich Inlet, adjacent to a local small vessel marina. This is a muddy subtidal zone, with bedrock along the shore (Halliday et al., 2018). The first recorder was retrieved and replaced with a second, identical recorder on June 30, 2020. The recorders were set to a duty cycle of 5 min recording followed by 10 min off, and recorded at a 48 kHz sample rate with the high gain setting activated. The acoustic recorder was fixed inside a 30-cm segment of PVC pipe, which was then strapped to a heavy sandbag. Mesh (1 cm^2 openings) was fixed over the ends of the PVC pipe to keep larger animals from entering the pipe. The recorders were placed roughly 10 m from shore at low tide at a depth ≈1 m below the annual lowest low water line (see Halliday et al., 2018 for a similar set up).

2.2. Bioacoustics analysis

Sound files were analysed in Raven Pro (version 1.5; Bioacoustics Research Program, Cornell University, Ithaca, New York, USA). Plainfin midshipman typically broadcast a chorus of hums just before dusk and can hum through the night until dawn (Halliday et al., 2018). We assumed recreational boat traffic was most likely to occur in daylight hours, so we reasoned that the timeframes around dawn and dusk would have the highest incidences of overlap between vessel noise and plainfin midshipman vocalizations. Hence, to maximise the presence of both plainfin midshipman calls *and* boat noise on the recordings, only files recorded 3 h before and 4 h after sunrise, and 4 h before and 3 h after sunset were selected for analysis. During these periods, all files (n = 7309) were first assessed for the presence or absence of boat noise. Spectrograms were set at a frequency range of 3000 Hz, a time range of 5 min, and with a window size of 7000 samples for this analysis. Boat noise was initially categorized as ‘quiet’ or ‘loud’ to investigate if louder boat noise differed in its impact from all boat noise, including very low amplitude or high frequency noise, on plainfin midshipman calls. When the presence of boat noise was visually confirmed, it was categorized as quiet or loud: boat noise <40 dB above ambient sound levels was considered to be quiet boat noise, and boat noise >40 dB above ambient was classified as loud boat noise. Examples of plainfin midshipman calls recorded during quiet and loud boat noise are shown in Fig. 1. Only files with no visual indication of boat noise (quiet or loud) were used in analyses of periods without boat noise. The number of files annotated was roughly similar between periods when boat noise was present (n = 3537) and absent (n = 3772).

Each group of files (with and without boat noise) was then assessed separately for plainfin midshipman calls by a single analyst (the first author, SO). Spectrograms were zoomed in so that frequency bands from 0 to 1000 Hz and a time range of 30 s was visible on the screen to identify plainfin midshipman calls, although the analyst zoomed in to annotate calls when required. Grunts were defined as calls <0.5 s, growls were calls ≥0.5 s and were further divided into short and long growls. Short growls were defined as calls ranging from 0.5 to 1.5 s long, and long growls were calls longer than 1.5 s. This was done because it allowed short growls to fit consistently with a Gaussian distribution. Long growls were more variable in length and did not fit any distribution. The long growl duration data were log-transformed and fit with a Gaussian distribution. The fundamental frequencies of growls and individual grunts were annotated to calculate their durations and frequency ranges. If the fundamental frequency was not visible, only the duration of the call was measured. The clearest (i.e. with the least background noise overlap) grunt in each grunt train was annotated, and the number of grunts within that train was counted. In each file containing hums, the clearest portion of the fundamental frequency (if visible), was annotated. Examples of each of the three call types are shown in Fig. 1.

2.3. Statistical analyses

2.3.1. Call presence/absence analysis

All statistical analyses were conducted in R (version 1.2.5042). Model error distributions were determined using histograms of the residuals. To ensure the distributions of fitted model residuals appropriately conformed to the assumptions of the fitted models, we examined quantile-quantile plots of residuals, and residual versus predicted response plots using the “simulateResiduals” function in the DHARMa package (Hartig, 2022). We considered vocalizations during quiet and loud boat noise (combined together as ‘all boat noise’) and compared these to vocalizations occurring when no boat noise was present. We performed a second set of analyses using vocalizations that just occurred during loud boat noise (referred to as ‘loud boat noise’) and also compared these to vocalizations occurring when no boat noise was present.

The presence versus absence of hums, growls, and grunts within each file were assessed using binomial generalized linear models (GLM; package: MASS; function: glm; Venables and Ripley, 2002). Grunts and growls were converted to presence/absence per file due to low numbers of grunts and growls in most files. Hums are analysed as presence/

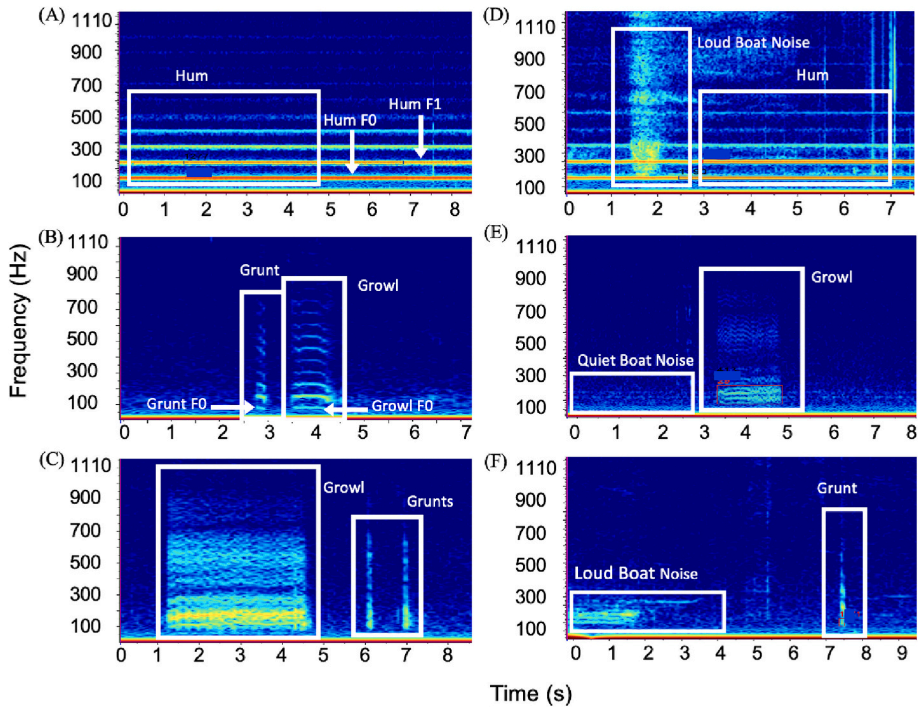

Fig. 1. Spectrograms of the three midshipman call types under various levels of boat noise. (A) through (C) do not contain any boat noise and panels (D) through (F) show calls overlapping with boat noise. Each spectrogram is an example of the following calls; (A) shows a hum, with the fundamental frequency (Hum F0) and first harmonic (F1), (B) shows one grunt followed by one short growl, with the fundamental frequency of each (Grunt F0, Growl F0), (C) shows a long growl followed by two grunts, (D) shows a hum overlapping with loud boat noise, (E) shows a growl overlapping with quiet boat noise, and (F) shows a grunt following loud boat noise. Sample rate = 48 kHz, window type = Hann, window size = 7000 samples, overlap = 50%.

absence because they often stopped and started outside of the recording period. For each of these three analyses, treatment (boat noise vs. no boat noise), time of day (dawn vs. dusk), deployment device (first or second acoustic recorder), week, and water temperature were included as independent variables. We included week and deployment to control for the seasonality effect and water temperature to control for these known environmental effect on plainfin midshipman vocalization characteristics (Halliday et al., 2018). A maximal model including all independent variables listed above and an interaction term for treatment × time of day was first fitted, along with additional models without the treatment, time, week, temperature, or deployment device. We used stepwise regression to find the best model using the lowest Akaike's Information Criterion (AIC) value. The significance of the best model was tested using a likelihood ratio test (package: car; function: Anova; Fox and Weisberg, 2019) and post-hoc tests were conducted to elucidate significant effects (package: emmeans; function: emmeans; Lenth, 2023).

2.3.2. Call characteristic analysis

Peak frequency was analysed for each call type, and call duration was assessed for grunts and growls (separated into short and long growls). Hum duration was not calculated because hums often lasted longer than each 5 min file and therefore could not be tracked between contiguous files. Each call characteristic (peak frequency and duration) was fit with a Gaussian linear model for each call type, except for growl peak frequency. Growl peak frequencies did not conform to the assumptions of any conventional error distribution, so these calls were assessed using a Kruskal-Wallis non-parametric test and a Dunn post-hoc test. For each parametric call characteristic analysis, models with time of day, treatment, deployment, and time of day × treatment interaction as fixed effects were compared using AIC using the same model selection procedures described in the paragraph above.

3. Results

3.1. Hum characteristics in the presence and absence of boat noise

The following results are for hums occurring during all boat noise pooled, compared to periods with no boat noise (Table 1). A total of 7309 sound files (609 h) were analysed for this study and of these, 2359 files contained hums. In 30% of files that contained hums, boat noise was also present. Of the files analysed, 3611 were at dawn and 3698 were at dusk; 20% of dawn files contained hums while 44% of the dusk files contained hums. The best model to describe hum presence included an interaction term between treatment and time, deployment, week, and water temperature. At dawn, hums were 11 times (95% CI: 8–15 times) more likely to occur in the absence of boat noise, while at dusk hums were 7 times (95% CI: 5–9 times) more likely to occur in the absence of boat noise (GLM: treatment×time; $\chi^2_1 = 7.91$, $p = 0.005$; Fig. 2).

The peak frequencies of all hums analysed ranged between 82 and 129 Hz. At dawn, 489 hums were analysed and 8.4% of these occurred during boat noise. At dusk, 1117 hums were analysed and 30.6% of these occurred during boat noise. The best model to describe hum peak frequency included an interaction term between treatment and time, deployment, week, and water temperature. At dawn, hum peak frequencies were approximately 2.6 Hz (95% CI: 1.1–4.0 Hz) higher when boat noise was present (GLM: treatment×time; $F_{1,156} = 13.95$, $p < 0.001$; Fig. 4). At dusk, hum peak frequencies did not differ significantly in the presence or absence of boat noise (estimate: 0.3 Hz; 95%CI: −0.3–0.9 Hz; GLM: treatment×time; $F_{1,156} = 13.95$, $p < 0.01$; Fig. 4). We detected no overall significant difference in hum peak frequencies between dawn and dusk when measured across both boat noise conditions (GLM: time; $F_{1,2} = 0.21$, $p = 0.60$).

The effect of loud boat noise on hum presence and peak frequency was similar to the effect of all boat noise. For detailed results on hums occurring during loud boat noise, see Supplementary Material S1.0.

Table 1

Summary of relevant results, organised by call type and call characteristic. 'Fewer calls' indicates significantly less calls in the given category. Rows labelled with "All boat noise" are analyses conducted using calls during quiet and loud boat noise pooled and the rows labelled "Loud boat noise" are the same analyses but only analyzing calls that occurred during loud boat noise. Statistical significance is denoted by the following codes: NS = not significant, *** = $p < 0.0001$, ** = $p < 0.01$, * = $p < 0.05$. NA = not applicable.

Call characteristic	Hums		Growls		Grunts	
	Noise effect	Noise and time of day interaction	Noise effect	Noise and time of day interaction	Noise effect	Noise and time of day interaction
Call rate (All boat noise)	Fewer calls during boat noise***	Fewer calls during boat noise at dawn and dusk**	Fewer calls during boat noise***	At dawn, fewer calls during boat noise**	Fewer calls during boat noise ***	NS
Call rate (Loud boat noise)	Fewer calls during boat noise***	NS	Fewer calls during boat noise***	At dawn, fewer calls during boat noise*	Fewer calls during boat noise**	NS
Peak frequency (All boat noise)	Higher during boat noise**	At dawn, higher during boat noise***	NS	Higher during boat noise at dusk compared to during boat noise at dawn**	Higher during boat noise*	At dusk, higher during boat noise*
Peak frequency (Loud boat noise)	Higher during boat noise **	NS	NS	Differed between periods with boat noise at dusk compared to periods with no boat noise at dawn*	Higher during boat noise*	At dusk, higher during boat noise*
Duration (All boat noise)	NA	NA	Short Growl: NS Long Growl: NS	Short Growl: NS Long Growl: NS	NS	NS
Duration (Loud boat noise)	NA	NA	Short Growl: NS Long Growl: NS	Short Growl: NS Long Growl: At dawn, shorter during boat noise*	NS	NS

3.2. Growl characteristics in the presence and absence of boat noise

The following results are for growls occurring during all boat noise pooled, compared to periods with no boat noise (Table 1). Of the total files analysed, 1076 files contained growls and 35% of these occurred when boat noise was present. The best model to describe growl presence included an interaction term between treatment and time, deployment, week, and water temperature. At dawn, the proportion of files containing growls was 2 times (95% CI: 1.5–2.5 times) lower in the presence of boat noise (GLM: treatment×time; $\chi^2_1 = 9.17$, $p < 0.01$; Fig. 2), while at dusk growl presence was not significantly affected by boat noise (95% CI: 0.9–1.6 times).

The peak frequencies of growls were more variable than those of hums, ranging from 47 to 141 Hz. Only the effect of treatment and time on growl peak frequency was assessed using non-parametric tests. At dawn, the average peak frequency of growls was 94.2 ± 19.7 Hz (mean ± sd) during periods without boat noise and 91.2 ± 18 Hz (mean ± sd) during periods of boat noise, though this difference was not statistically significant (Dunn test: z = 1.37, $p = 0.17$; Fig. 4). At dusk, the average peak frequency of growls was 96.3 ± 18 Hz (mean ± sd) during periods without boat noise and 101.0 ± 15.3 Hz (mean ± sd) during periods with boat noise (Dunn test: z = −2.18, $p = 0.18$; Fig. 4). In periods with boat noise, the peak frequency of growls was higher at dusk compared to dawn (Dunn test: z = −3.76, $p < 0.001$; Fig. 4), however there was no significant difference in dawn vs dusk growl peak frequencies during periods without boat noise (Dunn test: z = −1.02, $p = 0.30$; Fig. 4).

A total of 2126 growls were used for duration analysis, of which 635 were short growls and 1491 were long growls, and were on average 3.7 ± 3.3 s (mean ± sd) long. The best model to describe short growl duration included treatment, time, and week. The best model to describe long growl duration included an interaction term between treatment and time, deployment, week, and water temperature. The duration of short growls did not differ between times with and without boat noise, or by time of day (dawn vs dusk) (GLM: treatment; $F_{1,0.06} = 0.74$, $p = 0.39$, time; $F_{1,0.8} = 0.89$, $p = 0.34$). The duration of long growls varied between 1.5 and 27.1 s and also did not differ between periods with and without boat noise (GLM: treatment; $F_{1,0.25} = 0.74$, p = 0.39). Long growls were approximately 1.23 times (95%CI: 1.1–1.3 times) longer at dawn than at dusk (GLM: time; $F_{1,12.7} = 37$, $p < 0.0001$) regardless of boat noise condition. The effect of loud boat noise on growl presence, peak frequency, and duration was similar to the effect of all boat noise. For detailed results on growls occurring during loud boat noise, see Supplementary Material S1.0.

3.3. Grunt characteristics in the presence and absence of boat noise

The following results are for grunts occurring during all boat noise pooled, compared to periods with no boat noise (Table 1). A total of 276 files containing grunts were analysed, 34% of which also contained boat noise. The best model to describe grunt presence included treatment, time, and week. Grunts were 1.7 times (95%CI: 1.3–2.2 times) more likely to occur during the periods without boat noise compared to when boat noise was present (GLM: treatment; $\chi^2_1 = 14.5$, $p < 0.0001$; Fig. 3).

Peak frequencies were assessed for a total of 123 grunts, and these ranged 47–147 Hz. The best model to describe grunt peak frequency included an interaction term between treatment and time, deployment, week, and water temperature. At dusk, grunt peak frequencies were 11.7 ± 7.3 Hz (estimate ± sd) higher when boats were present compared to grunts that occurred during the periods without boats (GLM: treatment×time; $F_{1,541} = 5.23$, $p \leq 0.05$; Fig. 4). At dawn, grunt peak frequencies were 0.9 ± 2.7 Hz (estimate ± SE) higher when boat noise was present, though this difference was not significant (95% CI = −6.25–8.03 Hz; Fig. 4). Grunt durations ranged from 0.1 to 1.2 s. The model that best explained these differences did not include the treatment parameter, and time of day was not a significant explanatory variable (GLM: time; $F_{1,0.03} = 0.2$, $p = 0.63$). The effect of loud boat

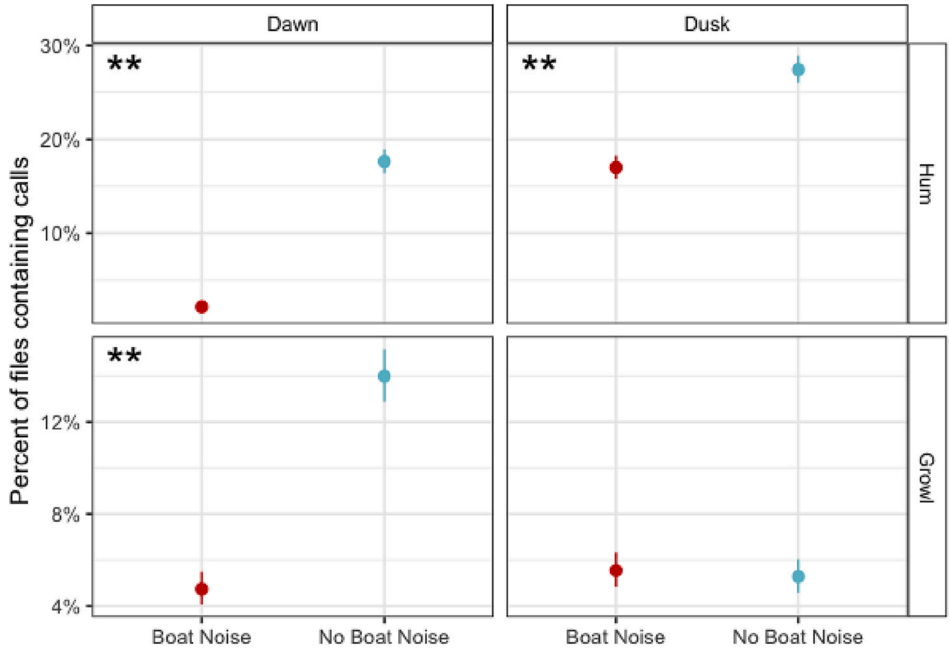

Fig. 2. The percent of files analysed that contained plainfin midshipman hums and growls in the presence and absence of boat noise, at dawn and at dusk. Percentage of files containing calls are calculated out of the total number of files analysed at dawn (n = 3611 files) and dusk (n = 3698 files). Error bars show 95% binomial confidence intervals, and stars represent significance between boat noise conditions where *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

noise on grunt presence, peak frequency, and duration was similar to the effect of all boat noise. For detailed results on grunts occurring during loud boat noise, see Supplementary Material S1.0.

4. Discussion

In this study, the rates and characteristics of plainfin midshipman vocalizations were measured in the wild in the presence and absence of boat noise. There were fewer plainfin midshipman vocalizations when boat noise was present and the peak frequencies of hums and grunts increased when they overlapped with boat noise. These results suggest the vocalizations of plainfin midshipman fish are impacted by anthropogenic boat noise at our study site.

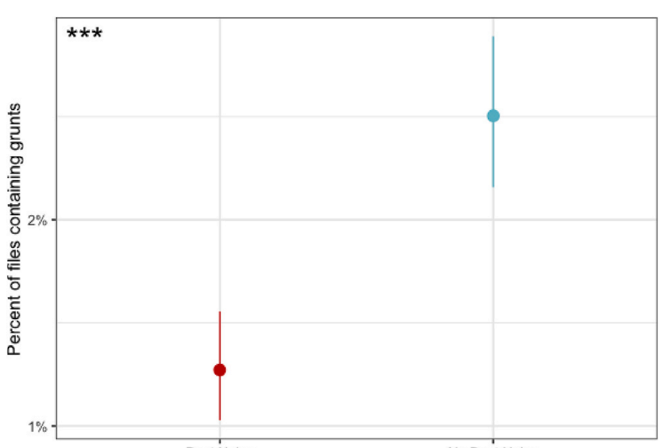

Fig. 3. The percent of files analysed that contained plainfin midshipman grunts in the presence and absence of boat noise. These data are shown with dawn and dusk pooled together because the interaction between treatment and time was not significant for grunts. Percentage of files containing grunts are calculated out of the total number of files analysed at dawn (n = 3611 files) and dusk (n = 3698 files). Error bars show 95% binomial confidence intervals, and stars represent significance between boat noise conditions where *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

The decrease in humming observed in our study is consistent with previous field-based studies that investigated a variety of soniferous fish species. For instance, Luczkovich et al. (2016) found that oyster toadfish made only 7.6 mating calls/min in a noisy boat channel compared to 12 mating calls/min in a remote strait. In addition, wild oyster toadfish exposed to boat noise playbacks decreased the number of mating calls by 31.6% following playback exposure (Mackiewicz et al., 2021). Similarly, Vieira et al., 2019 found that Lusitanian toadfish decreased from 0.57 mating calls/min to 0.22 mating calls/min when exposed to boat noise playbacks. Further, a previous study investigating plainfin midshipman found that incidences of hums, growls, and grunts decreased in the presence of an artificial tonal noise stimulus by 30–40% (Brown et al., 2021). In other toadfishes, a male's success in attracting females has been correlated with the amount of time it spent calling (Vasconcelos et al., 2012). Therefore, if boat noise reduces the amount of time males spend humming, this could affect their ability to attract mates. Future research is now required to determine whether noise-induced reductions in mating vocalizations can lead to subsequent declines in toadfish reproductive success.

The decrease in grunts we observed is consistent with previous field studies on plainfin midshipman. One study employed real boat noise trials and found that plainfin midshipman agonistic calls decreased during periods of boat noise exposure compared to periods with no boat noise exposure (Woods et al., 2023). We too observed a decrease in growls when boat noise was present, but only saw this effect at dawn. In plainfin midshipman, growls and grunts are used primarily for territory and offspring defense (Mohr et al., 2017). Males emit these calls in response to egg predators such as benthic invertebrates, as well as when encountering sneaker males or rival guarder males (Bose et al., 2014; Cogliati et al., 2013; Lee and Bass, 2004; Woods et al., 2022). In other species, such as the Lusitanian toadfish, these defensive calls can effectively ward off threats, causing predators to flee and decreasing the number of nest invasions (Amorim et al., 2015). If boat noise causes a reduction in defensive calls in plainfin midshipman, then the guarder male's ability to defend his eggs may be compromised in areas with high levels of boat noise. Plainfin midshipman egg predators such as red rock crab (*Cancer productus*), and various fishes are known to flee in the

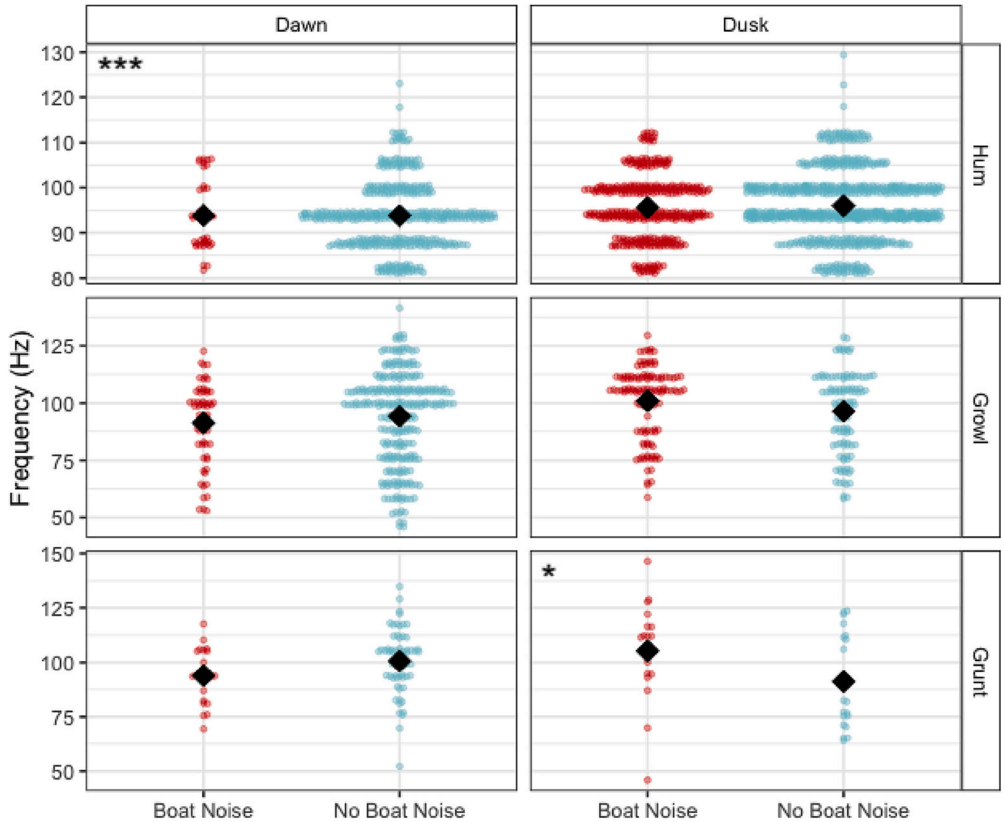

Fig. 4. The peak frequencies of hums, growls, and grunts in the presence and absence of boat noise, at dawn and dusk. The points are distributed approximately following the density estimate for the data. Black diamonds represent means and stars represent significance between boat noise conditions for each plot where *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

presence of boat noise (Cullis-Suzuki, 2016), so there may be fewer predation attempts overall during periods of boat noise. These predator responses to noise could explain the reduced number of growls and grunts observed while boat noise was present. In addition, it is currently unknown how sneaker or female plainfin midshipman respond to boat noise. Reduced growls and grunts by nest guarding males during boat noise could lead to more spawning opportunities or copulation attempts by sneaker males, which could alter the relative fitness of the two male morphs (Cogliati et al., 2013). However, further work is needed to examine how boat noise influences sneaker males and females.

It has been suggested that fishes are unable to alter their call frequencies in response to environmental conditions (Bass and Ladich, 2008), and some studies have reported no changes in the fundamental frequencies of fish vocalizations in response to anthropogenic noise (Holt and Johnston, 2014; Ladich, 2019; Luczkovich et al., 2016). However, our study provides clear evidence that plainfin midshipman alter the peak frequency of their calls in response to boat noise, although the change in peak frequencies was small relative to the observed natural variation in the mating calls. We observed that peak frequencies of plainfin midshipman hums and grunts increased (by 2.6 Hz for hums observed at dawn only and 11.7 Hz for grunts) when boat noise was present. Guarder males may be increasing the frequency of their calls to avoid masking by boat noise, and more effectively communicate with conspecific females. This behaviour in response to low frequency anthropogenic noise has also been reported in marine mammals (Tyack, 2008).

Our results contrast a recent study by Brown et al. (2021) that reported that plainfin midshipman decreased hum fundamental frequency by approximately 5 Hz in response to artificial tonal noise treatments. The difference between the two studies may reflect the divergent methods used, as Brown et al. (2021) had multiple acoustic recorders focused on small clusters of nests that were enclosed by mesh to ensure males remained present throughout the study period. Further, they used a 113–128 Hz artificial tonal noise as a stimulus. In our study, we used a single acoustic recorder to record the soundscape of a plainfin midshipman breeding ground with an unknown population size, and where the number of fish recorded may have varied from day to day and week to week. We also examined the effect of real boat noise, which differs dramatically in frequency range and amplitude depending on motor specifications and therefore varied widely throughout the study period. If it is favourable for plainfin midshipman to adjust their hums frequency up or down depending on the nature of the external noise they are exposed to, this may explain the differing results.

Guarder male plainfin midshipman use hums to court and attract females to their nest (Brantley and Bass, 1994) and female plainfin midshipman are highly sensitive to the fundamental frequency and first several harmonics of male hums, using these hums to locate nests in which to lay their eggs (Ibara et al., 1983; Sisneros, 2009; Sisneros and Bass, 2003). There is some evidence females have a hum fundamental frequency preference that is temperature dependent (McKibben and Bass, 1998), therefore if boat noise is causing males to alter the frequency of their hums, this could impact female mate selection. However, what a shift in hum frequency of ~3 Hz means for reproductive success and whether females can detect this relatively small frequency change potentially induced by boat noise remains unknown.

Growl peak frequencies were not significantly affected by boat noise conditions, while grunt peak frequencies increased during periods with boat noise. Specifically, at dusk, grunt peak frequencies were 12 Hz higher than when boat noise was present. Growls are the more dynamic of the two vocalizations with a much larger fundamental frequency range, potentially explaining why differences in growl frequencies could not be detected between periods with and without boat noise. Similar to hums, male plainfin midshipman may be altering to fundamental frequencies of their grunts during boat noise to avoid masking. Lower frequencies in Lusitanian toadfish agonistic vocalizations are correlated with superior male body condition (Amorim et al., 2015). The information contained in these calls may therefore be important when males establish territories, defend their nests against sneaker males and other usurping guarder males, as well as attract females (Bose et al., 2014). If the information in grunts is altered as a result of boat noise, the outcome of aggressive interactions or incursions may also be affected. In this case, the increase in grunt fundamental frequencies during boat noise could be portraying weaker condition to threats and potentially decrease the effectiveness of these calls.

The effects of boat noise on the presence, duration, and peak frequency of hums, grunts, and growls were assessed when files with quiet boat noise were included and excluded from the analysis. Interestingly, the differentiation between the amplitude of the boat noise signal did not affect the results of the majority of call characteristic analyses. The two notable exceptions are hum presence and long growl duration. When quiet boat noise was excluded, hums were even less likely to occur during boat noise, and this did not differ between dawn and dusk. In addition, at dawn, long growls were shorter in the presence of boat noise. These results highlight that boat noise, including noise with very low amplitudes, can have detectable effects on plainfin midshipman vocalization characteristics. This idea is consistent with the results of Brown et al. (2021) who detected midshipman vocal changes in response to even a relatively low amplitude pure tonal noise.

In our study, the effects of anthropogenic boat noise on fish vocalizations were observed in a wild population of plainfin midshipman. Our study adds to the research on plainfin midshipman bioacoustics and is one of the few studies to measure plainfin midshipman vocalizations in response to anthropogenic boat noise in situ. The quantities of all three call types were reduced in the presence of boat noise, and the peak frequencies of hums and grunts increased during boat noise. Because effective acoustic communication in many fish species is essential for reproductive success (Amorim et al., 2015; Vasconcelos et al., 2012), anthropogenic boat noise may affect the fitness of plainfin midshipman. Understanding the consequences of increasing boat noise on aquatic organisms and the ecological effects of increasing anthrophony in the ocean is critical for creating rational and effective noise mitigation strategies.

CRediT authorship contribution statement

Shaye Dana-Lynn Ogurek: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **William D. Halliday:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Mackenzie B. Woods:** Writing – review & editing, Supervision, Conceptualization. **Nick Brown:** Writing – review & editing, Visualization, Data curation. **Sigal Balshine:** Writing – review & editing, Supervision, Funding acquisition. **Francis Juanes:** Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.116412.

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