

The plainfin midshipman's soundscape at two sites around Vancouver Island, British Columbia

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ABSTRACT: The soundscape is an integral habitat component for acoustically sensitive animals. In marine environments, noise pollution from anthropogenic activities is pervasive, potentially leading to negative consequences for marine animals. To understand the impacts of noise pollution, one must first understand the soundscape in which these animals live. Using autonomous passive acoustic recorders, we examined the soundscape of plainfin midshipman fish *Porichthys notatus* at 2 breeding sites around Vancouver Island, Canada. Plainfin midshipman humming was recorded every night for the 4 wk long recording period; it was a main driver of sound pressure levels, adding more than 6 and 17 dB on average (SE \pm 0.8) at each site in the 80 Hz octave band. The fundamental frequency of the hum was temperature-dependent and varied between 76 and 111 Hz. At one site (Ladysmith Inlet), sound pressure level was consistently higher than at the other site (Brentwood Bay), and these differences appeared to be related to anthropogenic noise rather than to plainfin midshipman humming. Although most of the anthropogenic noise occurred during the day and fish humming occurred mostly at night, both anthropogenic noise and midshipman humming occasionally occurred at the same time, suggesting that noise pollution has the potential to impact this species. This study constitutes the first long-term *in situ* description of the soundscape for the plainfin midshipman. Our results will increase our understanding of teleost soundscapes, a currently critically understudied research area, and shed light on how anthropogenic noise pollution might affect fishes and coastal ecosystems.

KEY WORDS: Acoustic habitat · Ocean ambient noise · Passive acoustic monitoring · *Porichthys notatus* · Toadfish · Vocalization

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INTRODUCTION

The underwater soundscape is an important habitat feature for marine animals that rely on sound (Fay 2009, Bertucci et al. 2015, Pine et al. 2017). Generally, soundscapes represent all sounds that an animal is exposed to (Pijanowski et al. 2011), such as vocalizations of conspecifics (Brantley & Bass 1994) or sounds made by predators (Remage-Healey et al. 2006). The soundscape can be broken down into 3 components: (1) the geophony (sounds from physical processes

like wind, waves, and rain); (2) the biophony (sounds from biological sources such as cetacean or invertebrate vocalizations); and (3) the anthrophony (sounds generated by human activities like boating or underwater construction). The geophony and biophony represent the natural ambient sound levels that an organism must compete with for communication, whereas the anthrophony is a newer phenomenon for marine animals, and often elevates background sound levels more so than the geophony (Andrew et al. 2002, McDonald et al. 2006). Physical characteris-

tics of the environment, such as depth, sediment type, water chemistry, and temperature can all affect these components of the soundscape through their impacts on sound propagation and sound speed (Au & Hastings 2008). Different habitats are therefore dominated by different sounds, simply based on the sound propagation characteristics of the environment and the proximity of different sound sources.

Animals have evolved a variety of traits and strategies to counter the masking effects of natural sounds such as crashing waves or sounds made by other animals. However, they have had little time to adapt to the influence of anthropogenic activity on the soundscape (Williams et al. 2015), especially given the recent sharp rise in anthropogenic noise in the ocean (Andrew et al. 2002, McDonald et al. 2006). Anthropogenic noise can have a wide range of impacts on animals, including altering behaviour (Gomez et al. 2016), impairing acoustic communication and acoustic masking (Clark et al. 2009, Holt & Johnston 2014, Erbe et al. 2016b), increasing stress levels (Roland et al. 2012), and causing temporary or permanent hearing damage (Southall et al. 2007). To best mitigate against these deleterious effects, it is imperative to understand the soundscapes used by marine organisms, especially soniferous species that rely on sound for communication, foraging, reproduction, or other fitness-related tasks. While the acoustic sensitivity and characteristics of the vocalizations of some species have been relatively well-studied, studies examining the soundscapes in which these species hear and vocalize are lacking, especially for fish (Wall et al. 2014). Recent reviews highlight that underwater noise can have a wide range of negative impacts on fishes (Hawkins et al. 2015, Hawkins & Popper 2016, Cox et al. 2018), and that more work is needed to fully understand these impacts.

The plainfin midshipman *Porichthys notatus* is a soniferous fish and a member of the toadfish family, Batrachoididae (Greenfield et al. 2008). It lives along the Pacific coast of North America (Walker & Rosenblatt 1988) and produces 3 main types of vocalizations: a long-duration tonal hum (lasting several minutes to an hour); a short-duration grunt (~0.5 s in duration, which can be emitted individually or in quick succession as a 'grunt train'); and a medium-duration growl (lasting up to several seconds; Brantley & Bass 1994, McIver et al. 2014). There are 2 types of male plainfin midshipman. Guarder type I males, which are large in body size, actively build and defend nests under rocks, court females, and care for eggs (Arora 1948). Sneaker type II males, on the other hand, do not actively build or defend nests,

or vocally court females, but rather steal fertilizations from spawning guarder type I males by using stealth or satellite spawning tactics (Bass 1992, Cogliati et al. 2013, Bose et al. 2018). Plainfin midshipman vocalize by rapidly contracting specialized sonic muscles and 'drumming' on their inflated swim bladder (Bass & Marchaterre 1989a,b, Bass 1990). Sonic muscles of plainfin midshipman change seasonally; they are largest during the beginning of the breeding season (late April and May) and smallest during the non-breeding season (August to March; Sisneros et al. 2009). These sonic muscles are larger and more developed in guarder type I males than in sneaker type II males or females, and guarder males also vocalize more frequently (Bass 1990).

Guarder type I males hum nocturnally to attract females to their nests (Zeddies et al. 2012), and grunt and growl to warn off competitors (Ibara et al. 1983, Brantley & Bass 1994). Once attracted to a particular nest, females will lay their eggs on the nest ceiling of the chosen male and leave the care of young to the nesting guarder male (Brantley & Bass 1994, Cogliati et al. 2013). The fundamental frequency of the male hum is temperature-dependent (Brantley & Bass 1994), and is typically around 100 Hz at 15°C (Brantley & Bass 1994, McIver et al. 2014). However, hums have been shown to vary by as much as 20 Hz, and ranged between 84 and 104 Hz for the same fish over a period of 7 recording days (McIver et al. 2014). Vocalizations and acoustic communication are central to male mate attraction and intraspecific competition in the plainfin midshipman fish, and in other toadfishes (Greenfield et al. 2008).

Acoustics are central to the reproduction of plainfin midshipman, through both mate attraction and territoriality; therefore, the soundscape should play an integral role in the breeding ecology of this species. As such, it is important that we understand how this vocalizing fish contributes to, and is impacted by, the soundscapes in which it breeds. To assess this question, we examined the soundscape of plainfin midshipman at 2 sites around Vancouver Island, Canada, over a 4 wk period during their breeding season. We predicted that the plainfin midshipman hum will be a dominant feature of the nocturnal soundscape on the breeding grounds, and that wind speed and tide level would be important aspects of the geophony. As previous field observations have demonstrated a relationship between reproductive success (offspring development) and the lunar cycle (A. Bose unpubl. data), we also investigated whether the lunar cycle and nocturnal light levels were correlated with rates of humming, and the soundscape. This study is the

first long-term *in situ* examination of the shallow soundscape used by plainfin midshipman during their breeding season.

MATERIALS AND METHODS

Study site and instrument deployments

We deployed autonomous acoustic recorders (SoundTrap ST300; Ocean Instruments) at 2 sites with confirmed plainfin midshipman nests on Vancouver Island, British Columbia, Canada: Brentwood Bay (48.57°N, 123.46°W) and Ladysmith Inlet (49.01°N, 123.82°W). We confirmed that male plainfin midshipman were nesting at both of these sites; therefore, these sites each represent a possible soundscape in which plainfin midshipman live. The Brentwood Bay site was adjacent to a public marina and private docks, and had a muddy subtidal substrate with a shallow slope leading to a muddy intertidal zone with plenty of loose large rocks. The Ladysmith Inlet site was situated beside a private dock, but was only a few hundred meters away from a marina, with a lumber mill across the inlet. The subtidal substrate was quite muddy, with a shallow slope leading to a muddy intertidal zone with many larger loose rocks, which was then surrounded by a bedrock shoreline. We set the recorders with a 48 kHz sampling rate, 50% duty cycle (5 min recording every 10 min), a 16-bit depth, and the 'high gain' setting selected. Both recorders had a full-scale response of 171.5 dB re 1 μ Pa. We deployed the recorder at Brentwood Bay on 28 May 2017, and the recorder at Ladysmith Inlet on 30 May 2017. We secured each recorder inside a 10 cm diameter piece of PVC pipe with windows cut out around the hydrophone, and strapped the piece of PVC pipe onto a sandbag. We then placed the instrument into the water so that it was roughly 30 cm deeper than the lower low water of the month's spring tide, and positioned within at least 10 m of nesting male plainfin midshipman which were identified in intertidal nests. Tide ranged from 0.03 to 3.60 m during our study (Environment and Climate Change Canada 2017a). Recorders remained submerged for the entirety of their deployment. We collected both instruments after 4 wk of recording. The detection range for these recorders at these sites is unknown, but the propagation of low frequency sounds would have been inhibited at the shallow depths where we recorded. The soundscape that we recorded is only representative of the area directly around the recorders, but certainly includes

the areas where midshipman were nesting near the recorders.

Acoustic analyses

We processed all acoustic recordings using custom scripts in Matlab (version R2017a). We calculated power spectral densities (PSD) in 1 s bins with 50% overlap using a Hanning window. We also calculated sound pressure levels (SPLs) in octave bands from 20 Hz to 24 kHz (Table 1), and calculated the root mean squared SPL for each 5 min file. We did not analyze data below 20 Hz because the sensitivity of the hydrophone drops below this frequency. An octave band is defined as a range of frequencies where the highest frequency is double the lowest frequency. For example, the first octave band in our series was between 20 and 40 Hz, the second between 40 and 80 Hz, the third between 80 and 160 Hz, and so on (Table 1). We examined octave bands because fish have wider critical bandwidths than other vertebrates (Fay 1988), and full octaves represent a wider bandwidth than the 1/3 octaves used for other animals, such as marine mammals.

Plainfin midshipman hums were audible during all nights of recording. We manually analyzed the 5 min recording at 23:00 h during each day of recording at each site to obtain information on the fundamental frequency of the hums, using the software Raven (version 1.5; Cornell Lab of Ornithology). We selected 23:00 h because the humming consistently started before this time and ended after this time every night, and it allowed for a consistent sampling period for every day of the deployment. We extracted concurrent temperature data, which were recorded automatically by the acoustic recorder, and exam-

Table 1. Octave bands used for analysis of sound pressure levels. Note that statistical analyses were only performed on the 40 to 80, 80 to 160, and 1280 to 2560 Hz bands

Octave bands	Lower (Hz)	Center (Hz)	Upper (Hz)
1	20	30	40
2	40	60	80
3	80	120	160
4	160	240	320
5	320	480	640
6	640	960	1280
7	1280	1920	2560
8	2560	3840	5120
9	5120	7680	10 240
10	10 240	15 360	20 480

ined the relationship between temperature and fundamental frequency at each site using simple linear models in R (package 'stats', function 'lm'; R Core Team 2016), including temperature, site, and their interaction as independent variables. The acoustic recorder measured temperature once every minute while it was on, so it recorded temperature 5 times during each 5 min file.

We manually analyzed the first 2 d of recordings from each recorder/site to quantify the number of plainfin midshipman calls produced over a 48 h period, and also document the presence of anthropogenic noise such as propeller and engine noise from boats. As the purpose of this analysis was to examine which types of plainfin midshipman calls (i.e. hums, grunts, and growls) influenced SPLs, it was not necessary to exhaustively manually analyze our entire data set. Instead, we chose comparable data (i.e. the first 2 d of recording) from each site, and analyzed all data within a 48 h period. Within each 5 min recording, we noted the presence or absence of hums (constant energy around 100 Hz, typically with strong harmonics; Fig. 1) and anthropogenic noise, and counted the number of grunts and growls detected (defined by McIver et al. 2014; Fig. 1B). We then analyzed how each plainfin midshipman call type affected the SPLs in 3 octave bands: the 40 to 80 Hz octave band (henceforth referred to as the 40 Hz octave band), the 80 to 160 Hz octave band (henceforth referred to as the 80 Hz octave band), and the 1280 to 2560 Hz octave band (henceforth referred to as the 1280 Hz octave band) using linear models. We selected these bands specifically in relation to the fundamental frequency and harmonics of the plainfin midshipman hum. The 40 Hz octave band is below the frequency of plainfin midshipman hums, and therefore represents an octave that midshipman can likely perceive but one that they are not influencing with their vocalizations. The 80 Hz octave band overlaps with the fundamental frequency of the plainfin mid-

shipman hum (Brantley & Bass 1994), and is therefore likely to be greatly affected by plainfin midshipman vocalizations (as assessed in previous analyses). The 1280 Hz octave band is above the frequencies of the plainfin midshipman hum, including its harmonics, and should not be influenced by their vocalizations. This octave band may also be above the hearing ability of plainfin midshipman (e.g. Alderks 2013). All 3 octave bands may also include noise from anthropogenic activity. We used this analysis to assess the utility of using SPLs in each of these octave bands

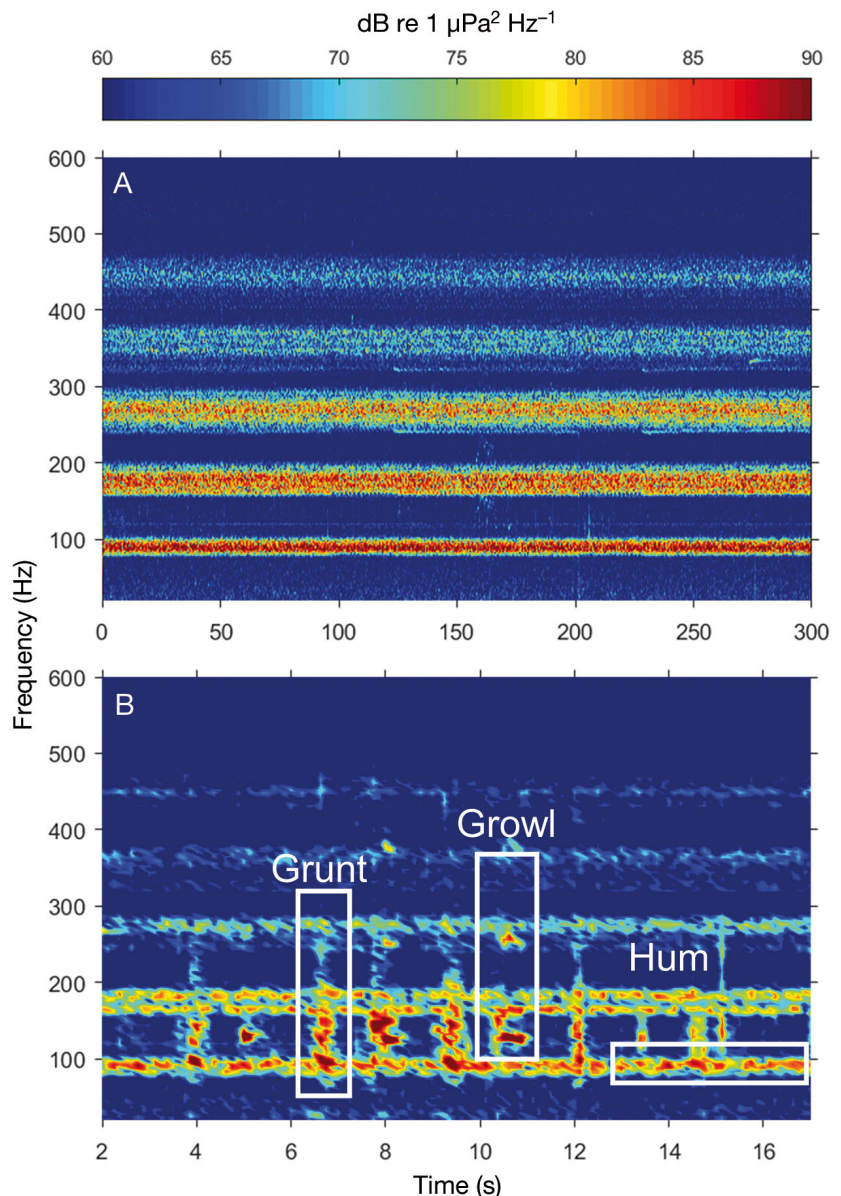


Fig. 1. Spectrograms of plainfin midshipman *Porichthys notatus* (A,B) hums and (B) hums, grunts and growls. Sample rate = 48 kHz. Fast Fourier transform (FFT) window size = 12 000 for (A) and 6000 for (B). Each spectrogram has a 50% overlap and uses a Hanning window

throughout the remainder of the deployment as a proxy for plainfin midshipman calls. We included SPL as the dependent variable, and presence of hums, counts of grunts and growls, and site as independent variables. We did not include the presence of anthropogenic noise in this analysis because we did not extract sufficient information on the type of anthropogenic activities taking place at each site. We also assessed if anthropogenic noise was more likely during the day (06:00 to 18:00 h) versus the night (18:00 to 06:00 h) using logistic regression in R (package 'stats', function 'glm', family 'binomial').

We conducted further statistical analyses to examine the SPLs to which plainfin midshipman are exposed. We examined SPLs in the same 3 octave bands used in the previous analysis: 40, 80, and 1280 Hz. We analyzed each band separately using linear models. We included hourly linear averages of SPL as the dependent variable, time of the day (broken down into 6 h quarters, see below), tide height, wind speed, site (Brentwood Bay or Ladysmith Inlet), moon phase, cloud cover, and all 2-way interactions as independent variables. We included tide height and wind speed because water depth and wind speed are known to impact underwater noise levels (Au & Hastings 2008); we did not differentiate between ingoing and outgoing tides. We included time of day because plainfin midshipman are known to produce their hums overnight (Brantley & Bass 1994). We included cloud cover and moon phase because many animals that are nocturnally active react to changing light levels. Plainfin midshipman reproduction also may be linked to the lunar cycle (A. Bose unpubl. data). We split each day into quarters of 6 h slots starting at 00:00, 06:00, 12:00, and 18:00 h. We used tide height data from Environment and Climate Change Canada's Tides, Currents, and Water Levels database (Environment and Climate Change Canada 2017a), and used observations from Patricia Bay for our data from both Ladysmith Inlet (~46 km away) and Brentwood Bay (~10 km away). We used wind speed data from Environment Canada's Weather and Climate database (Environment and Climate Change Canada 2017b), and used observations from Nanaimo Airport for our Ladysmith Inlet data (~8 km away), and data from Victoria International Airport for our Brentwood Bay data (~9 km away). We used a stepwise method to compare models with different parameters, compared models using Akaike's information criteria (AIC) (package 'stats', function 'AIC'), and selected the model with the lowest AIC as the best model.

RESULTS

General description of the soundscape

The soundscapes at both Brentwood Bay and Ladysmith Inlet were dominated by the plainfin midshipman's hum (Fig. 2), which was present every night of our deployments at both sites. The hum shows clearly on a spectrogram, with the fundamental frequency just below 100 Hz, and harmonics every ~100 Hz above that (Figs. 1A & 2). The median fundamental frequency of the hum at Brentwood Bay was 93.8 Hz (mean \pm SE = 93.0 \pm 1.1 Hz), while at Ladysmith Inlet the hum was at 99.6 Hz (102.1 \pm 1.5 Hz). The median temperature recorded at Brentwood Bay was 12.3°C (mean \pm SE = 12.1 \pm 0.2°C), whereas it was 13.6°C (13.7 \pm 0.2°C) at Ladysmith Inlet. At both sites, there was a significant relationship between the hum's fundamental frequency and temperature (pooled data: intercept = 28.66 \pm 8.82; slope = 5.34 \pm 0.68; $p < 0.0001$, $R^2 = 0.56$, $n = 48$; Fig. 3), and no significant difference in fundamental frequency between sites was detected ($p > 0.05$).

While the plainfin midshipman hum was the main signal that showed up on the 1 mo spectrogram for Brentwood Bay (Fig. 2A), the 1 mo spectrogram for Ladysmith Inlet also had considerable noise during the day caused by boats and other anthropogenic activity, which shows up as long vertical lines on the spectrogram (Fig. 2B). When examining spectral patterns at both sites (Fig. 4), clear peaks from the hum and its first harmonic are apparent in the 50th, 95th, and 99th percentiles of power spectral density. This implies that noise from the hum and its first harmonic are the strongest sounds in those frequencies (i.e. 80 to 120 Hz and 160 to 240 Hz). At Brentwood Bay, these peaks are also apparent for the second, third, and fourth harmonics (Fig. 4A). However, at Ladysmith Inlet the second, third, and fourth harmonics are present in the 50th percentile, the third and fourth in the 95th percentile, and none of these additional harmonics appear in the 99th percentile (Fig. 4B). These differences between Brentwood Bay and Ladysmith Inlet suggest that hums at Brentwood Bay are causing the strongest noises in the frequency bands of all of their harmonics, whereas at Ladysmith Inlet, other noises are stronger at the frequencies of the upper harmonics of the hum. The 95th and 99th percentiles were generally higher at Ladysmith Inlet than at Brentwood Bay between 100 and 1000 Hz (Fig. 4), and this was likely caused by increased anthropogenic noise at Ladysmith Inlet. Median power spectral density at both sites was around 60 dB

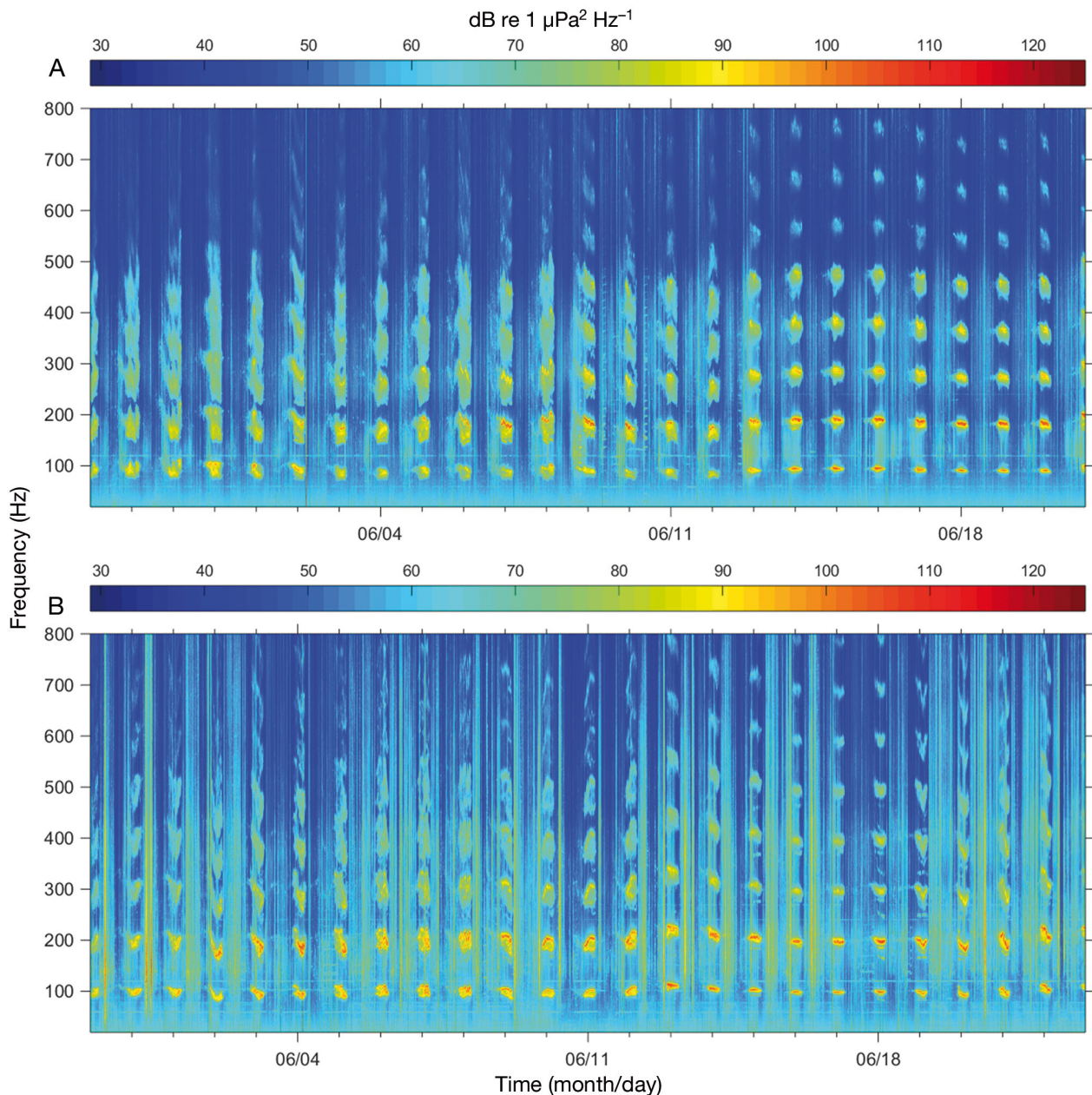


Fig. 2. Spectrogram for the full deployments at (A) Brentwood Bay and (B) Ladysmith Inlet, British Columbia, showing clear peaks in power spectral densities around 100 Hz every night throughout both deployments. The peaks are caused by the plainfin midshipman *Porichthys notatus* hum

re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ from 50 to 400 Hz, and then steadily decreased between 400 Hz and 24 kHz from 60 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ to just above 30 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ (Fig. 4).

Influence of plainfin midshipman calls on the soundscape

During the first 2 d of recordings at each site, there were plainfin midshipman hums present in 51% of the 5 min files that we examined (detected

in 293 of the 578 files, examples in Fig. 1). We also counted 263 grunts and 54 growls over the course of the 2890 min (present in 9.5 and 2% of files examined, respectively) that we analyzed (examples in Fig. 1B), with a maximum of 43 grunts and 11 growls in a file. Anthropogenic noise was present in 76% of recordings (442 files); 234 files at Ladysmith and 208 files at Brentwood Bay. Both midshipman hums and anthropogenic noise were present at the same time in 28% of files (160 files) (e.g. Fig. 5). Anthropogenic noise was more likely to be

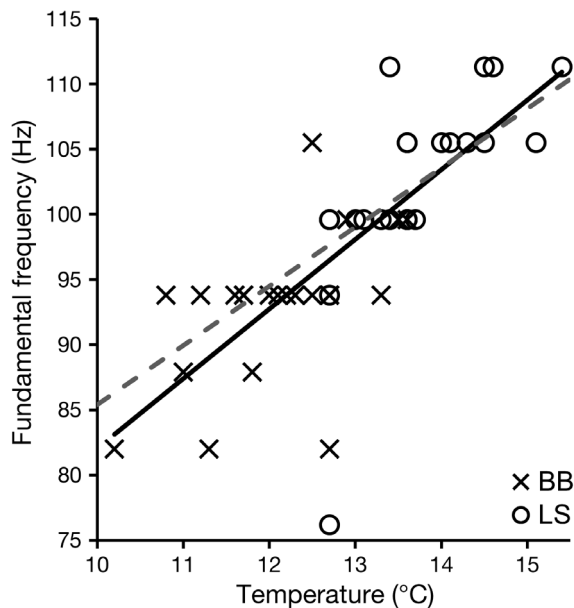


Fig. 3. Relationship between temperature and the fundamental frequency of the plainfin midshipman *Porichthys notatus* hum at Brentwood Bay (BB) and Ladysmith Inlet (LS) recorded near Vancouver Island, Canada. Solid black line: linear regression fit for the pooled data; grey dashed line: trend from Brantley & Bass (1994)

present during the day than overnight ($z_{576} = 7.44$, $p < 0.0001$).

In the 40 Hz octave band, SPL was 1.0 ± 0.4 and 2.3 ± 0.6 dB lower in the presence of midshipman hums at Brentwood Bay and Ladysmith Inlet, respectively, compared to when hums were absent ($t_{502} > 2.1$, $p < 0.03$, model $R^2 = 0.27$). In the 80 Hz octave band, when plainfin midshipman hums were present, SPL increased by 17.1 ± 1.1 and 6.8 ± 1.5 dB at Brentwood Bay and Ladysmith Inlet, respectively ($t_{502} > 6.90$, $p < 0.0001$, model $R^2 = 0.39$; Fig. 6A). In the 1280 Hz octave band, the presence of hums had no influence on SPL at Brentwood Bay ($t_{502} = 0.46$, $p = 0.64$), but SPL was 2.6 ± 0.9 dB re $1 \mu\text{Pa}$ lower at Ladysmith Inlet when midshipman hums were present ($t_{502} = 2.54$, $p = 0.01$, model $R^2 = 0.08$). Neither grunts nor growls had any influence on SPL in any of the octave bands ($t_{500} < 0.92$, $p > 0.36$).

Soundscape components that midshipman are exposed to

40 Hz octave band

SPL in the 40 Hz octave band decreased as tide levels increased, although this effect was only signifi-

cant between 12:00 and 18:00 h ($F_{1,1153} = 8.70$, $p < 0.01$). Changes in wind speed did not affect SPL in this octave band ($p > 0.05$). SPL was slightly higher between 12:00 and 18:00 h than between 00:00 and 06:00 h, although this trend only occurred when it was cloudy ($F_{3,1153} = 2.77$, $p = 0.04$). SPL did not differ across other times of day in this octave band (Fig. 6B). SPL was slightly lower on cloudy days than on clear days ($F_{1,1153} = 5.20$, $p = 0.02$). Ladysmith Inlet had generally higher SPLs than Brentwood Bay ($F_{1,1153} = 235.88$, $p < 0.0001$). Moon phase did not affect SPLs in this octave band.

80 Hz octave band

SPLs in the 80 Hz octave band showed a strong diurnal pattern ($F_{3,1151} = 336.22$, $p < 0.0001$), where SPL was highest between 18:00 h and midnight, followed by midnight to 06:00 h, with the lowest SPLs recorded between 06:00 and 18:00 h (Fig. 6C). This diurnal trend also varied with the phase of the moon ($F_{9,1151} = 12.93$, $p < 0.0001$), where the above pattern occurred during the full moon phase, but during the third lunar quarter, SPLs were highest from 18:00 h to midnight, and lower but equally so across the other 3 daily quarters (from midnight to 18:00 h). During the new moon and first lunar quarter, SPLs were highest all night from 18:00 to 06:00 h, and lowest during the daylight hours from 06:00 to 18:00 h. SPLs were also lower during the third lunar quarter when it was cloudy compared to both the first lunar quarter and new moon when it was cloudy ($F_{3,1151} = 6.44$, $p < 0.001$). Cloud cover did not affect any other aspect of the soundscape in this octave band ($F_{1,1151} = 2.14$, $p = 0.14$). As the tide increased (i.e. water was deeper), SPLs decreased (slope = -10.63 ± 0.90 , $t_{1151} = 11.81$, $p < 0.0001$). As wind speed increased, SPL increased (slope = 0.10 ± 0.04 , $t_{1151} = 2.40$, $p = 0.02$). This effect was most pronounced between midnight and 06:00 h and between 12:00 and 18:00 h. SPLs at the 80 Hz octave band were generally higher at Ladysmith Inlet than at Brentwood Bay ($F_{1,1151} = 131.23$, $p < 0.0001$).

1280 Hz octave band

SPL in the 1280 Hz octave band increased as wind speed increased (slope = 0.08 ± 0.03 , $t_{1154} = 3.04$, $p < 0.01$). Between 12:00 and 18:00 h, SPL decreased as tide increased ($F_{3,1154} = 3.07$, $p = 0.03$), but this effect did not occur at other times of the day. Tides also had a reduced effect at Ladysmith Inlet compared with

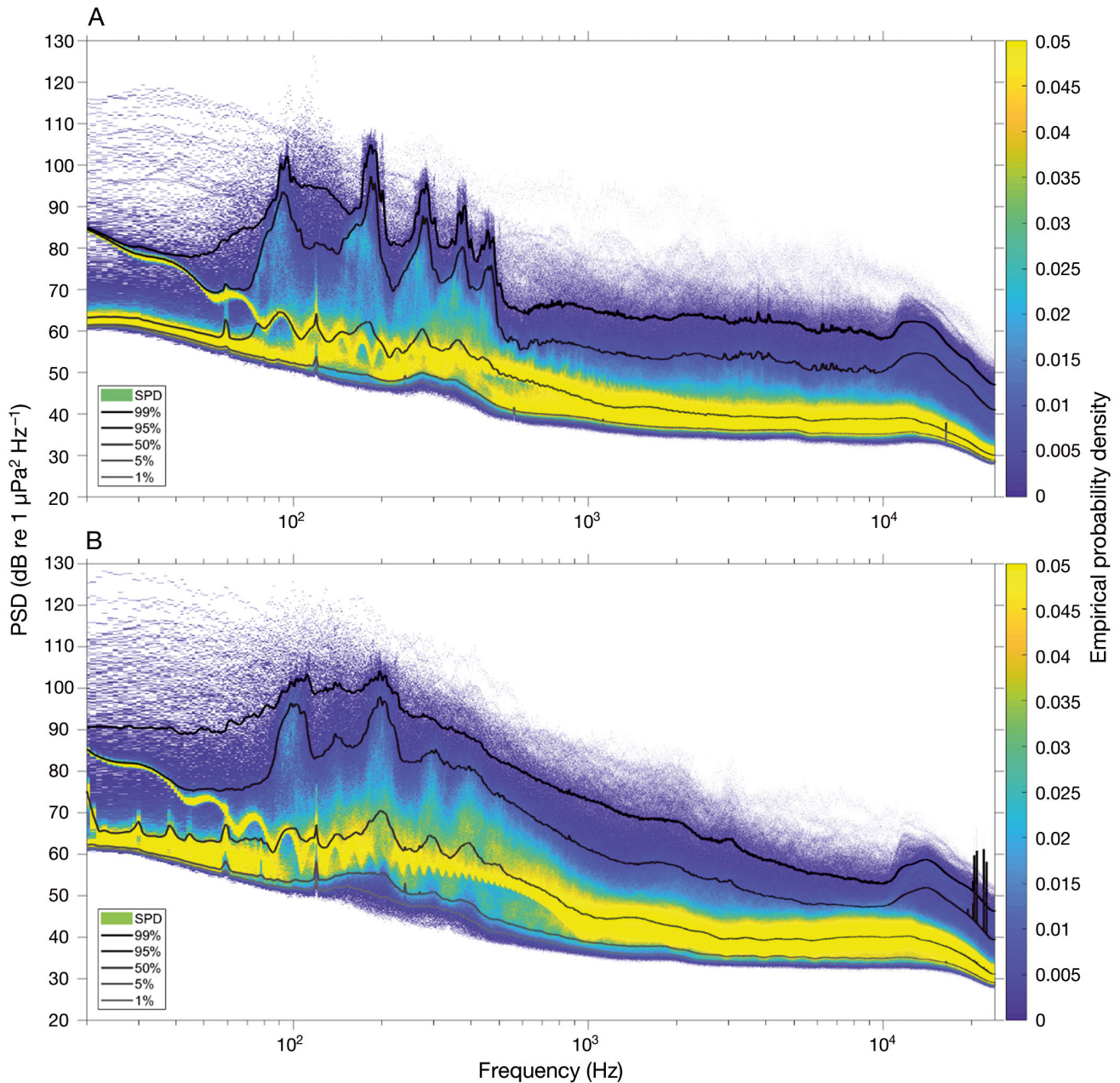


Fig. 4. Power spectral densities (PSD) and empirical probability densities at (A) Brentwood Bay and (B) Ladysmith Inlet from 50 to 24 000 Hz. Clear spikes from plainfin midshipman *Porichthys notatus* hums show up in the 50th, 95th, and 99th percentiles around 100 and 200 Hz at both sites. Clear spikes for the hum harmonics also show up at 300, 400, and 500 Hz at Brentwood Bay, but these harmonics only show up in the 50th percentile at 300 and 400 Hz at Ladysmith Inlet

Brentwood Bay ($F_{1,1153} = 28.51$, $p < 0.0001$). SPL was also generally higher at Ladysmith Inlet than at Brentwood Bay ($F_{1,1153} = 29.86$, $p < 0.0001$). SPL was lowest between 00:00 and 06:00 h compared to all other times of the day ($F_{3,1153} = 8.18$, $p < 0.0001$; Fig. 6D). SPL at this octave band was highest during the full moon and the third quarter, followed by the first quarter, and lowest during new moon ($F_{3,1153} = 21.87$, $p < 0.0001$).

DISCUSSION

The plainfin midshipman's soundscape is dominated by their hum, and this hum was also the main source of biophony identified in the 2 soundscapes. Grunts and growls were present in 9.5 and 2% of files examined, respectively, but they did not influence SPLs. The hum caused a strong diurnal pattern in the 80 Hz octave band that was stronger over-

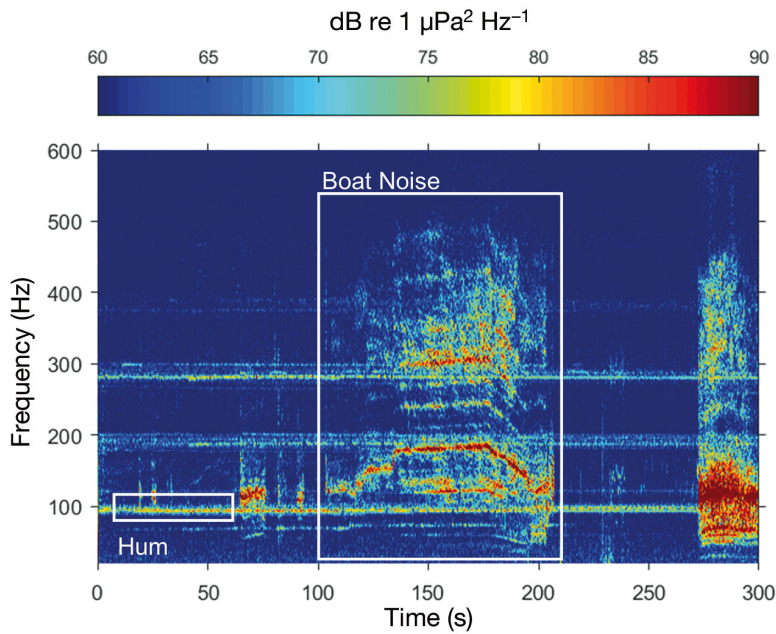


Fig. 5. Spectrogram of plainfin midshipman *Porichthys notatus* hum and boat noise present at the same time. Sample rate = 48 kHz. Fast Fourier transform (FFT) window size = 12 000. Each spectrogram has a 50% overlap and uses a Hanning window

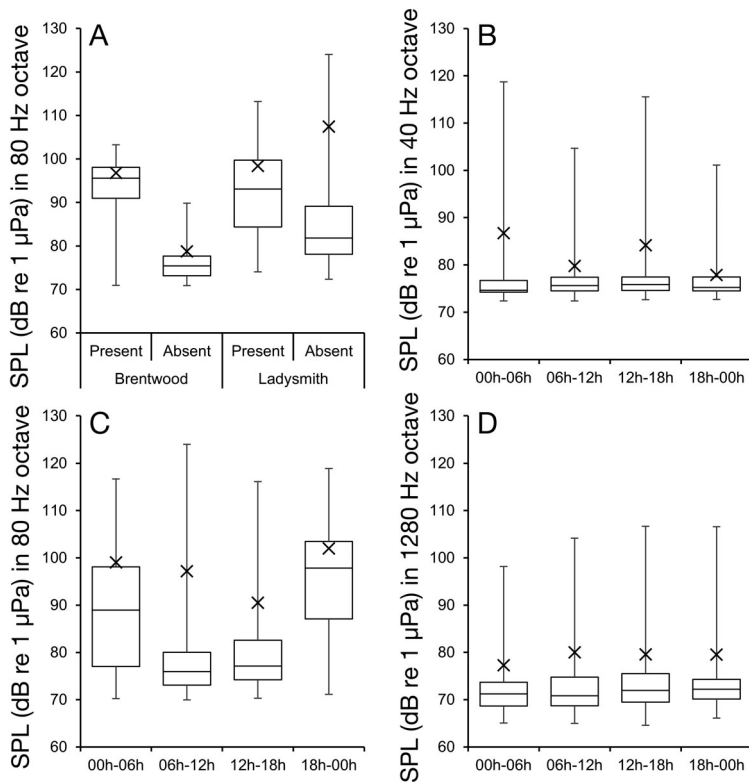


Fig. 6. Impact of the presence of plainfin midshipman *Porichthys notatus* hums at 2 deployment sites (Brentwood Bay and Ladysmith Inlet) on sound pressure levels (SPLs) in (A) the 80 Hz octave band, and trends in SPL in (B) 40, (C) 80, and (D) 1280 Hz octave bands throughout the deployments at Brentwood Bay and Ladysmith. Boxes: interquartile range; lines within the boxes: median values; whiskers: minimum and maximum values. × symbols: arithmetic means

night, and that was not present in the other 2 octave bands examined. The presence of hums added an average of 6.8 and 17.1 dB to the 80 Hz octave band at both of our sites. Conversely, SPLs in the 40 and 1280 Hz octave bands were generally higher during the day than overnight. These patterns in both the 40 and 1280 Hz octave bands may be driven by anthropogenic noises (i.e. the anthrophony) such as boat noise; anthropogenic noises were present more during the day than at night (18:00 to 06:00 h). The sites where we recorded were likely too shallow for the noise to have come from commercial shipping or larger vessels, but the Brentwood Bay site was adjacent to a marina, and the Ladysmith Inlet site was surrounded by private docks and also had tug boat traffic from a local lumber yard. Other activities at the lumber yard were also quite noisy, and could be heard clearly in the air from our recording site, and likely similarly influenced the underwater soundscape. Small boats can cause substantial noise above 1 kHz (Scholik & Yan 2002), but also in the low frequencies below 100 Hz (Erbe 2002, Erbe et al. 2016a). An interesting future research avenue would be to assess the spatial distribution of plainfin midshipman hums within the coastal soundscape, how far the hum chorus propagates, if its intensity changes throughout the season, and how it is potentially masked by anthropogenic noise. The plainfin midshipman's contribution to the soundscape is likely to have a strong seasonal signature, since males arrive on the breeding ground in late April, peak breeding season occurs between late April and mid-June, and then although paternal care continues, much of the spawning activity and male-male competition subsides in late June and July (Bose et al. 2014). Future work could explore how the soundscape varies over the course of the entire breeding season and with male density, and connect signalling capacity to the ability to attract mates and successfully reproduce.

The fundamental frequency of the hum was temperature-dependent: greater than 50% of the variation in fundamental frequency was explained by water temperature. This pattern was first described by Brantley & Bass (1994), although in that study, the authors manipulated water temperature in the lab. In our study, we examined changes in fundamental frequency as water temperature varied naturally. Brantley & Bass (1994) varied temperature between 14 and 26°C, and recorded the fundamental frequency shifting from ~90 to 140 Hz, with a relationship of $y = 40 + 4.54x$. McIver et al. (2014) also measured the temperature dependence in fundamental frequency in the field, and found that an increase of 1°C corresponded with an increase of 5 Hz. In our study, temperature varied between 10 and 15.5°C, and fundamental frequency varied between 82 and 111 Hz, with a relationship of $y = 28.7 + 5.3x$. Although the relationship that we measured was not identical to the one measured by Brantley & Bass (1994), there is a clear overlap (see comparison in Fig. 3), and the relationship described by McIver et al. (2014) is intermediate. It is possible that the relationship between fundamental frequency and temperature may be non-linear, such that at lower temperatures, fundamental frequency increases at a different rate as temperature increases compared to at higher temperatures. Still, we clearly demonstrate the temperature-dependence of the fundamental frequency of the plainfin midshipman hum in the wild over a 30 d period, and confirm previous results from McIver et al. (2014) based on a shorter field recording and from Brantley & Bass (1994) in the laboratory.

Grunts and growls did not affect the SPLs of the soundscape. These vocalizations occur much more intermittently and are likely to have much lower source levels (i.e. they are quieter calls) than the hum, although to the best of our knowledge no one has measured these source levels. Although grunts and growls are important local social signals for midshipman (Brantley & Bass 1994), they do not need to propagate far because they are likely used only in close encounters between competitors or to warn off predators (A. Bose & S. Balshine pers. comm.). Because the purpose of the hum is to attract potential mates (Ibara et al. 1983), to be useful it must propagate much greater distances than these aggressive vocalizations. Hence, grunts and growls likely affect the small-scale soundscape directly around a midshipman nest, but they are unlikely to contribute to the overall coastal soundscape where midshipman live during the breeding season.

Wind speed (i.e. bubble formation and wave action) (Kerman 1984, Wille & Geyer 1984, Ma et al. 2005), precipitation (rain drops hitting the water) (Ma et al. 2005), and water flow (sounds generated as water interacts with the bottom substrate and shoreline) are all important drivers of underwater noise levels, and are all the main components of the geophony at our study site. On Vancouver Island, there is very little precipitation during the summer months (May to September) (Government of Canada 2018). For this reason, we did not examine precipitation in our analysis because there was virtually none during our study. However, we did examine the impacts of wind speed and tide height on SPLs. We found a positive relationship between wind speed and SPL in the 80 and 1280 Hz octave bands, but not in the 40 Hz octave band. The relationship between wind speed and SPL had a slope of 0.1 and 0.08 dB $\text{km}^{-1} \text{h}^{-1}$ in the 80 and 1280 Hz bands, respectively. Although statistically significant, this relationship is relatively weak compared to studies conducted in deeper water (Knudsen et al. 1948, Wenz 1962). For example, researchers found the relationship between SPL and wind speed to be between 0.18 (wind speed < 20 km h^{-1}) and 0.56 dB $\text{km}^{-1} \text{h}^{-1}$ (wind speed > 20 km h^{-1}) in a deep-water study conducted in California (McDonald et al. 2006). Another study conducted in the Arctic at 30 m depth found a relationship between SPL and wind speed to be above 0.4 dB $\text{km}^{-1} \text{h}^{-1}$ (Insley et al. 2017). Both of our recorder sites were relatively sheltered in the back of narrow bays, which would thereby limit fetch and the level of wind-driven noise. Plainfin midshipman appear to select such sites to breed (S. Balshine pers. obs.). The lack of trend in the 40 Hz octave band may be related to cut-off frequency (i.e. only frequencies greater than x can propagate in water depth y). Low frequencies have a longer wavelength, and therefore require deeper water to propagate than higher frequencies. Our shallow recorders likely only recorded the low frequencies that were nearby. Low frequency sounds created by wind and waves would therefore have to be occurring very close to the recorder, which likely diminished their overall effect on the soundscape compared to sounds at higher frequencies.

Tide height had a negative relationship with SPL, where SPL was highest when tide height was lowest. We found this relationship in both the 80 and 1280 Hz octave bands, but not in the 40 Hz octave band. This relationship may be due to flow noise around the hydrophone, where in shallower water there is greater water movement around the hydrophone as

the tide comes in and goes out, but less movement around the hydrophone in deeper water. If this relationship is due to flow noise, then it is not related to actual ambient sound levels, but rather to hydrodynamic noise around our instrument. If there is flow noise from the tide in our recordings, it may be similar at both of our sites given that the tides were similar at both sites. More work is needed to tease apart the sources of the tide-related sounds in our recordings.

The soundscape is a critical aspect of midshipman habitat. Mating success relies on male hums effectively being received by females (Zeddies et al. 2012), and on males competing (in part vocally) and winning nests. Plainfin midshipman hums are a continuous band of energy that occupies a similar frequency band to other continuous noise sources, such as boat noise. This overlap may lead to acoustic masking if humming occurs at the same time as the anthropogenic noise. When inspecting spectrograms, we observed noise from small boats at both sites and clearly documented higher levels of anthropony at Ladysmith Inlet than at Brentwood Bay. We also detected anthropogenic noise occurring simultaneously to midshipman hums during some (28%) of our recordings (Fig. 5). Boat noise may have large impacts on the midshipman soundscape, and may even affect reproductive outcomes if female phonotaxis is impaired in noisy environments. Female plainfin midshipman can home in on the hums of male plainfin midshipman with remarkable precision (Zeddies et al. 2012), and it is unknown how masking from anthropogenic noise may affect this behaviour. Our study presents the first continuous assessment of the plainfin midshipman's soundscape in the field, and acts as a good starting point for future investigations of the impacts of noise pollution on mating success in this soniferous fish species. Understanding how natural processes such as the tidal cycle and lunar cycle affect this soundscape will facilitate future studies that examine the impacts of the anthropony on the soundscape and on the fitness of plainfin midshipman.

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