Vol. 595: 245–252, 2018
https://doi.org/10.3354/meps12572

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 14

NOTE

First description of a glass sponge reef soundscape reveals fish calls and elevated sound pressure levels

Stephanie K. Archer[1,*,], William D. Halliday[2,3,**], Amalis Riera[2], Xavier Mouy[4], Matthew K. Pine[2,3], Jackson W. F. Chu[5], Anya Dunham[1], Francis Juanes[2]**

[1]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada
[2]University of Victoria, Department of Biology, Victoria, BC V8W 2Y2, Canada
[3]Wildlife Conservation Society Canada, Whitehorse, YT Y1A 0E9, Canada
[4]University of Victoria, School of Earth and Ocean Sciences, Victoria, BC V8W 2Y2, Canada
[5]Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, BC V8L 4B2, Canada

ABSTRACT: Structured biogenic habitats are biodiversity hotspots that host a wide range of soniferous species. Yet in deep-water systems, their soundscapes are largely undescribed. In September of 2016 we deployed 3 underwater acoustic recorders for approximately 4 d in and around a glass sponge reef in the Outer Gulf Islands sponge reef fishing closure, British Columbia, Canada. The 2 recordings from the reef (within and at the margin of the reef footprint) were significantly louder in the mid- and high-frequency bands (100 to 1000 Hz and 1 to 10 kHz, respectively) than the recordings made in soft-bottom habitat away from the reef. These frequency bands are known to correlate with aspects of the biological community as well as benthic cover in shallow-water systems; visual surveys conducted in the area confirmed the presence of several known soniferous species. More fish sounds were recorded on the reef compared to the off-reef site. Our results suggest that this glass sponge reef has a distinct soundscape and that future work linking aspects of the soundscape to the ecology of the ecosystem are warranted.

KEY WORDS: Acoustics · Biophony · Glass sponge reefs · Anthrophony

INTRODUCTION

Soundscapes are an important yet understudied trait of marine environments. A variety of marine organisms, from whales to shrimp, make noise either incidentally or for communication or navigation (Rountree et al. 2006). For example, fish use sounds during courtship as a way to distinguish conspecifics (Danley et al. 2012) and assess mate quality (Verzijden et al. 2010). Monczak et al. (2017) recently used the frequency and spatial distribution of fish calls and choruses to identify when and where soniferous fish were spawning. Therefore, studying the biophony (sounds generated by organisms within an ecosystem) can give us clues about the identity, relative abundance, and behaviors of species present in an ecosystem (Širovi et al. 2009). Additionally, soundscapes can provide information on, and help to maintain the health of an ecosystem. For example, the specific acoustic signature of both coral and oyster reefs are used by juveniles to gauge the quality of a habitat and as a settlement cue (Simpson et al. 2008, Lillis et al. 2013, Butler et al. 2016). Consequently, analysis of soundscapes may provide ecosystem-level information in difficult-to-study marine systems.

Sound is an important sensory cue for organisms living in deep-water systems (Wall et al. 2014), but deep-water soundscapes have received minimal

*Corresponding author: stephanie.archer@dfo-mpo.gc.ca
**These authors contributed equally to this work

Publisher: Inter-Research · www.int-res.com

attention (Rountree et al. 2012). Anthrophony (noise from human activities such as shipping) is increasing, and this can affect the behavior of benthic organisms. For example, Solan et al. (2016) found that increased anthropogenic noise altered the behavior of multiple sediment-dwelling invertebrates and that this had cascading consequences for benthic nutrient cycling. Thus, it is important to study the soundscape and contribution of anthropogenic noise in these deep-water systems.

Glass sponge reefs (GSRs) are built by dictyonine hexactinellid sponges which have skeletons made of glass fused into a rigid but fragile 3-dimensional structure (Leys et al. 2007). Similar to coral reefs, GSRs are built by larval sponges settling on the skeletons of previous generations of sponges (Dunham et al. 2018). This process results in the construction of large bioherms with live reef-building sponges at the reef's surface that support diverse communities of fish and invertebrates (Cook et al. 2008, Chu & Leys 2010, Dunham et al. 2015). GSRs have only been documented in shelf habitats in the Northeast Pacific from Portland Canal to the Strait of Georgia, British Columbia, Canada (Dunham et al. 2018). Here, we provide the first description of the soundscape on a GSR including a discussion of the anthrophony potentially influencing this system.

MATERIALS AND METHODS

Site description

We deployed 3 autonomous acoustic recorders (SoundTrap 300 STD Model, Ocean Instruments) on the Galiano sponge reef within the northern portion of the Outer Gulf Islands fishing closure (48° 54.70′ N, 123° 19.56′ W; Fig. 1) (DFO 2015) on 28 and 29 September 2016 using Fisheries and Oceans Canada's (DFO's) Phantom remotely operated vehicle (ROV). The recorders were attached to 1 m of rope and suspended 0.3 m off of the bottom with a buoy. This reef was surveyed in detail by Chu & Leys (2010) and has consistently been found to have high average sponge cover (~26%) (Dunham et al. 2015, 2018). A total of 59 species from 7 phyla have been reported from the reef (Cook et al. 2008, Chu & Leys 2010, Dunham et al. 2015). Two recorders were placed within the reef; one in an area of high sponge cover (reef-center; depth = 87 m, deployed 28 September 2016 for 108.7 h) and the other on the edge of the reef (reef-margin; depth = 94 m, deployed 28 September 2016 for 118.5 h). A third recorder was placed well outside the reef (off-reef; depth = 185 m, deployed 29 September 2016 for 98.6 h; Fig. 1). The reef-center recorder was placed in an area of >35% live sponge cover. Both the reef-margin and off-reef recorders were not immediately adjacent to live sponge cover: the reef-margin recorder was approximately 60 m from live sponge, while the off-reef recorder was over 500 m from the nearest live sponge. The sediment consisted of soft-bottom sediments at the off-reef site and a combination of siliciclastic soft sediments and buried sponge skeletons at the 2 within-reef sites. Sponge percent cover was estimated for the reef-center and reef-margin locations using the data and methods described in Chu & Leys (2010) and confirmed using the ROV. Each instrument recorded continuously (96 kHz, 16 bit) on 'high gain' setting.

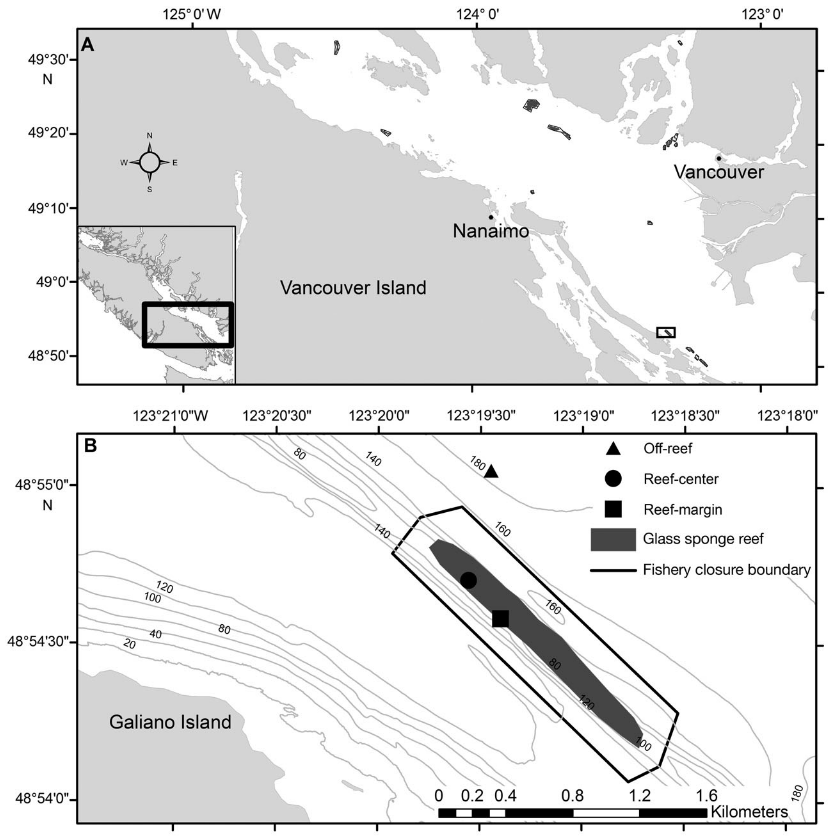

Fig. 1. Overview of protected glass sponge reef locations in (A) the Strait of Georgia, British Columbia and (B) the northern section of the Outer Gulf Islands fishing closure, the footprint of the sponge reef, and the location of the recorders. Contour lines in (B) represent 20 m contours

Biological sounds

Trained bioacousticians manually analyzed all recordings looking for calls matching the characteristics of confirmed fish calls they were familiar with. We amplified the recordings by 30 dB and then searched for fish sounds by viewing spectrograms (10 000 fast Fourier transform [FFT], Hann window, 50 % overlap) in Raven Pro (Bioacoustics Research Program 2017) displaying frequencies between 0 and 1400 Hz, in 10 s windows. We verified all fish sounds aurally.

Ambient noise levels

We processed all acoustic recordings in PAMGuide using MATLAB version R2016b (Merchant et al. 2015). All 3 recorders were calibrated by the manufacturer and had 'high gain' clip levels of 171.7, 172, and 172.2 dB re 1 µPa. We measured power spectral densities (PSDs) between 20 Hz and 48 kHz based on 1 min averages from FFTs of 1 s of data in 1 Hz bins with 50 % overlap using a Hann window. From these PSDs, we calculated sound pressure levels (SPLs; in dB re 1 µPa) in different frequency bands (20 to 100 Hz, 100 to 1000 Hz, 1 to 10 kHz, 10 to 48 kHz, and broadband from 20 Hz to 48 kHz). We did not include data below 20 Hz in SPL calculations because the recorders used were not sensitive below 20 Hz. We compared the SPLs using 2 data sets; the first was restricted to the times when all recorders were deployed, the second used the full duration of deployment for each recorder. The results did not differ. Therefore, the data presented here are from the full deployment for all recorders. We examined PSDs for each recorder based on exceedance percentiles. We compared SPLs from the different locations and in different frequency bands using analysis of variance in R (R Core Team 2016), with band level, location, and their interaction as independent variables.

We analyzed the influence of vessel traffic on SPLs in each frequency band. We estimated the vessel traffic in the area using an automated identification system (AIS) receiver located on the Iona Island Causeway (49° 12.96′ N, 123° 12.33′ W) operated by Ocean Networks Canada. All received AIS messages were decoded following the NMEA 0183 standard (NMEA 2002) using a custom MATLAB script and provided the unique identification (MMSI number), position, course, and speed of each AIS-equipped vessel in the area. Then we calculated the number of vessels and the distance of the closest vessel within a 10 km radius around each recorder for each minute of the monitoring period. We used linear regressions in R to examine the impact of vessel traffic on SPL, with the SPLs in each frequency band as the dependent variable, and number of vessels, distance to the nearest vessel, location of the recorder, and all 2-way interactions were the independent variables.

RESULTS

Biological sounds

We detected fish sounds at all 3 locations, but variability in the number of fish sounds between sites was high (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m595p245_supp.pdf). We counted 41 fish sounds at the reef-center location, consisting of 19 grunts and 22 knocks. At the reef-margin site, we counted 120 fish sounds (36 grunts and 84 knocks). At the off-reef site, we only counted 7 knocks and no grunts. Grunts and knocks were occasionally isolated, but typically came in a succession of one grunt followed by multiple knocks (Fig. 2). Grunts had an average peak frequency of 129.4 Hz (1st quartile = 58.6, median = 70.3, 3rd quartile = 143.6) and a duration of 0.37 s (1st quartile = 0.30, median = 0.36, 3rd quartile = 0.47) while the peak frequency of knocks averaged 210.7 Hz (1st quartile = 76.2, median = 175.8, 3rd quartile = 316.4) and a duration of 0.16 s (1st quartile = 0.09, median = 0.11, 3rd quartile = 0.14) (Table S1).

Ambient noise levels

Ambient noise levels at all 3 locations generally stayed between 60 and 100 dB re 1 $\mu Pa^2\ Hz^{-1}$ from 20 to 100 Hz, and then steadily decreased between 100 Hz and 48 kHz (Fig. 3). There were many small peaks in PSD between 20 and 1000 Hz at all 3 locations, likely caused by shipping noise. The largest peaks occurred between 20 and 40 Hz, which were likely caused by propeller cavitation noise (Lourens & du Preez 1998). An additional large peak, which was also related to vessel noise, occurred at 400 Hz. Shipping noise was visible on the spectrograms at all hours of the day (Fig. 4). Large peaks in PSD between 10 and 20 kHz at the reef-center and reef-margin recorders were due to nearby surveys with the ROV. These peaks were missing from the off-reef recorder because ROV surveys did not take place at this site. When statistically comparing median PSD

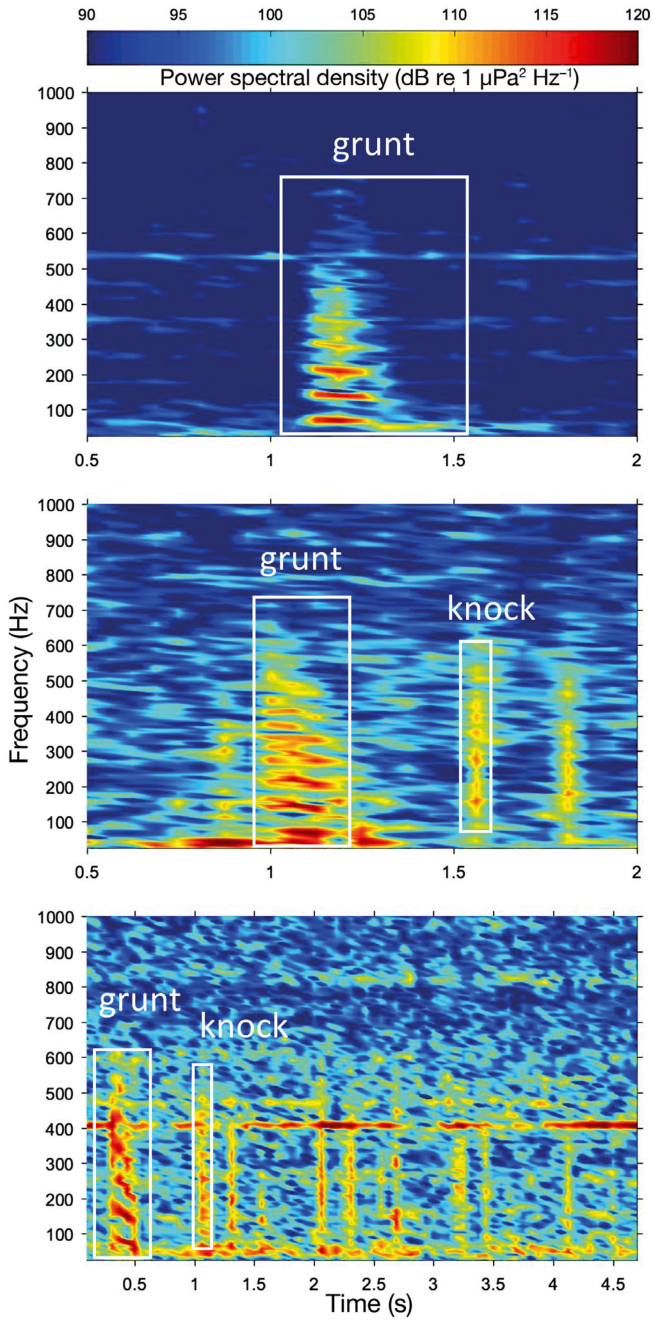

Fig. 2. Spectrograms of example fish sounds detected on the glass sponge reef. Grunts and knocks are identified with white boxes. Horizontal lines (blue line at ~550 Hz in the top panel, red line at ~400 Hz in the bottom panel) represent ship noise

levels, the reef-margin had higher levels than the reef-center between 20 and 100 Hz ($p < 0.01$), and both reef-center and reef-margin locations had higher levels than off-reef from 100 Hz to 10 kHz ($p < 0.001$). All locations had similar noise levels above 10 kHz ($p > 0.94$). Median broadband levels (20 Hz to 48 kHz) were similar at each site, and were 103.0 dB re 1 µPa at reef-center, 103.6 dB re 1 µPa at reef-margin, and 100.6 dB re 1 µPa at the off-reef site.

An increase in the number of vessels within 10 km caused increased SPLs in all bands and at all recorder locations (see Tables A1 & A2 in the Appendix), with the largest effect at the reef-margin, followed by reef-center, and with the off-reef location having the lowest effect. As the distance to the closest vessel increased, SPL increased in the 20 to 100 Hz band, but decreased in the 100 to 1000 Hz and 1 to 10 kHz bands, and did not change in the 10 to 48 kHz band.

DISCUSSION

We showed that this GSR likely possesses a distinct soundscape. The off-reef recording was quieter than the on-reef recordings in the mid (100 to 1000 Hz) and high (1 to 10 kHz) frequency bands. These bands correlate with the presence of soniferous organisms and benthic cover in shallow-water systems (Bertucci et al. 2016, Butler et al. 2016). The 2 on-reef recordings had more fish sounds than the off-reef recording. We cannot identify the fish producing these sounds at this point; however, over 700 species of fish are known to produce detectable vocalizations, typically in the mid-frequency band (Kaatz 2002, Rountree et al. 2006). Previous visual surveys conducted in close proximity to the location of our recorders have documented 12 species of fish (Cook et al. 2008, Chu & Leys 2010, Dunham et al. 2015, 2018). Of these, 6 are confirmed soniferous species or are from known soniferous families: *Sebastes elongates*, *S. ruberrimus*, *S. flavidus*, *S. proriger*, *Theragra chalcogramma*, and an unidentified Cottidae species (Fish 1948, Fish & Mowbray 1970, Nichols 2005, Širovic & Demer 2009, Wall et al. 2014, Mooney et al. 2016). The higher number of fish sounds recorded on the GSR suggests that this ecosystem has a different biophony than the surrounding habitat.

Although we do not have visual observations paired with our sound recordings, there is strong evidence that fish and invertebrate communities differ between the on- and off-reef deployment sites. The large sponges that form the reefs attract fish (Chu & Leys 2010, Du Preez & Tunnicliffe 2011, Dunham et al. 2018). Fish and invertebrate (hereinafter megafauna) abundance is higher on reefs than in the surrounding areas (Chu & Leys 2010), and both fishes and decapod crustaceans are abundant on the Galiano sponge reef, particularly in areas of live sponges (Chu & Leys 2010, Dunham et al. 2015). The

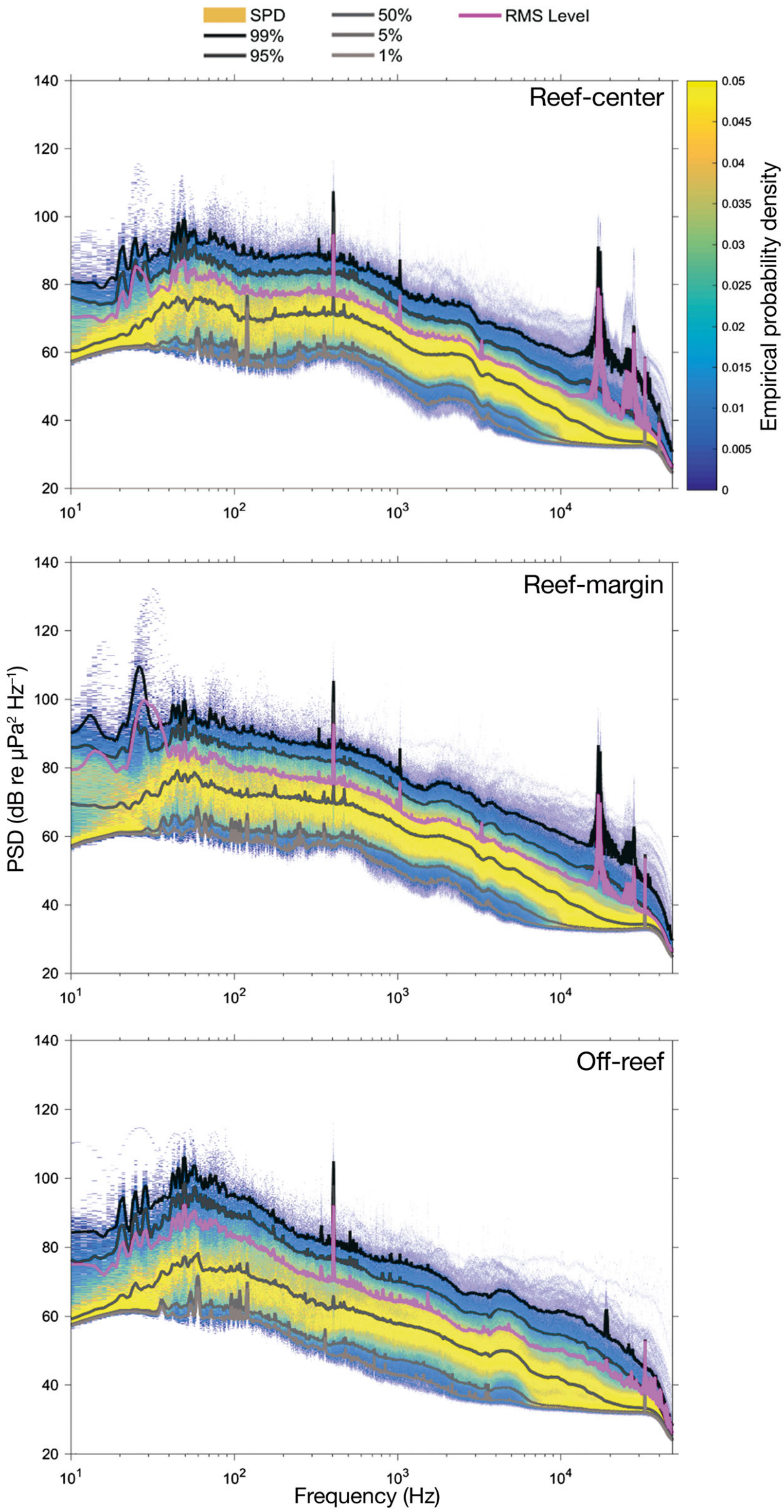

Fig. 3. Power spectral densities (PSDs) and spectral probability densities (SPDs) recorded around a glass sponge reef at 3 locations (reef-center, reef-margin, and off-reef). Exceedance percentiles and the mean (root mean square [RMS] level) are displayed for each location. Analyses focused on levels above 20 Hz due to decreased sensitivity below 20 Hz

megafauna observed during recorder deployment and retrieval support these patterns. No megafauna were observed during the deployment or retrieval of the off-reef recorder, while 6 species were observed at the reef-margin site, and 13 species were observed in close vicinity of the reef-center recorder (see Table A3 in the Appendix). Although we cannot make quantitative comparisons of the megafauna that were present at each of our deployment sites at the time of our study, the published literature, our qualitative observations, and the patterns of fish calls we observed suggest that megafauna abundance (and therefore, likely the biophony) is higher on the reef.

The fish sounds we detected were likely too quiet and transient to significantly influence the sound levels that we measured. However, other biological activity may contribute to the 2 on-reef recordings being louder than the off-reef in the mid- and high-frequency bands. Many invertebrates common on GSRs are from orders known to produce sounds (e.g. decapod crustaceans; Schmitz 2002). Invertebrates can generate noise within the high-frequency bands (Simpson et al. 2008). Additionally, increased SPLs in both mid- and high-frequency bands have been linked with aspects of the benthic structure (Bertucci et al. 2016). We need to investigate what sounds are made by invertebrates in this ecosystem to fully assess their contribution to the soundscape.

Given the short distance between the reef-center and reef-margin sites, the difference between the 2 recordings in the 20 to 100 Hz frequency band was initially surprising. However, this difference can be largely attributed to vessel traffic, as both the number of vessels and the distance to the nearest vessel increased SPLs in this frequency range more on the reef-margin than the reef-center recordings. Despite the large difference in depth between the on- and off-reef hydrophones (98 m), vessel traffic had a similar effect on SPLs recorded by these 2 hydrophones. Our study area is just north of Active Pass, an area of high ship traffic including large vehicle-carrying ferries, and based on vessel locations, at least one AIS-equipped vessel was within 10 km of the

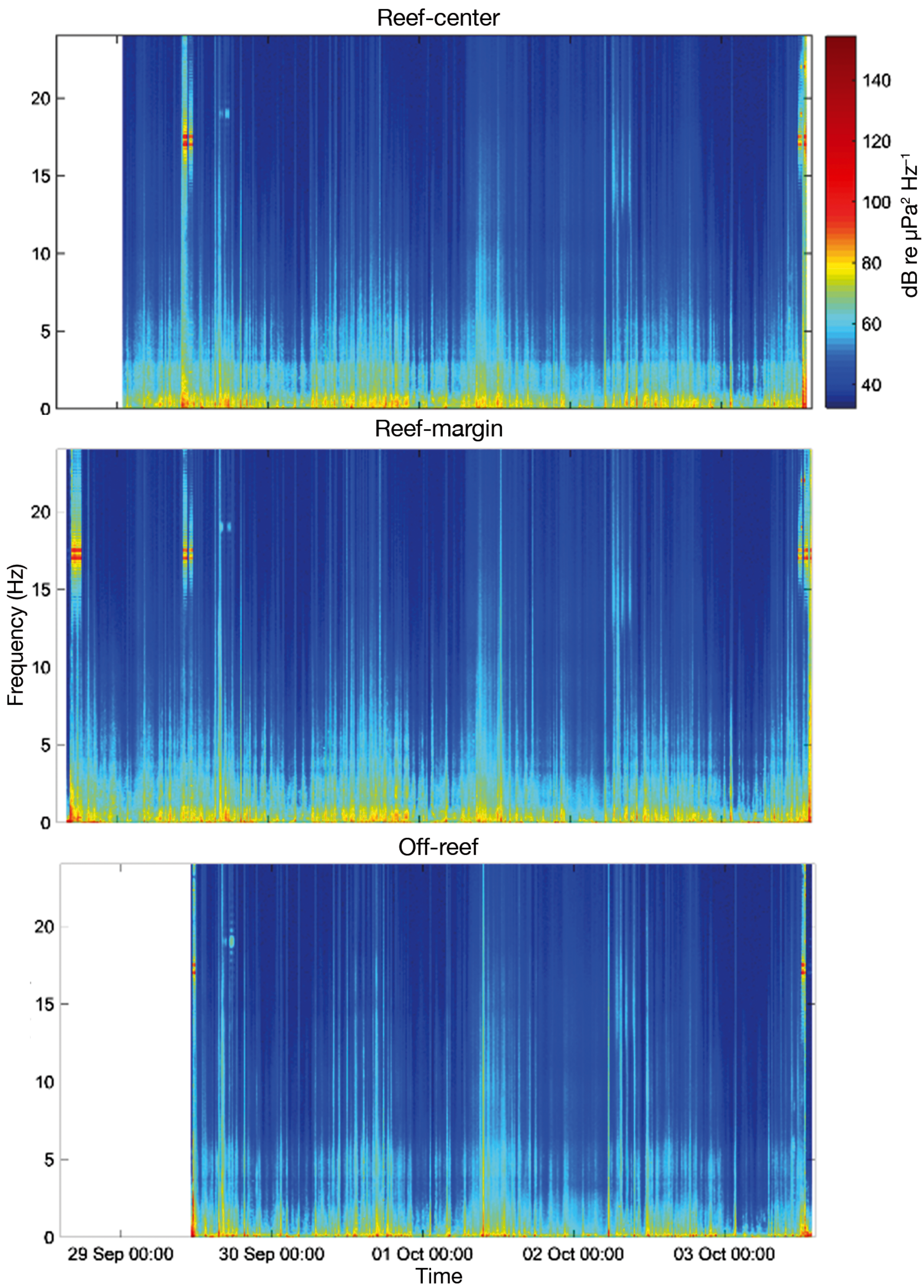

Fig. 4. Long-term spectrograms for 3 locations (reef-center, reef-margin, off-reef) on or near a glass sponge reef. Colors range from blue (quiet) to red (loud). Vertical bars: sounds made from ships at their closest point of approach; high frequency noise (~17.5 kHz) at the beginning and end of the recordings is noise from the remotely operated vehicle (ROV)

recorders 85% of the time. We saw a significant difference in the influence of vessel traffic on SPLs at the 3 locations across all frequency bands, with the greatest influence in the low frequency band at the reef-margin location. However, noise caused by vessel traffic does not explain the difference between the recordings on the reef versus off the reef, since vessel traffic always had a similar influence on the reef-center and off-reef recordings.

Our results suggest that this GSR has a distinct biophony, thereby indicating that passive acoustics may complement traditional visual surveys. Longer deployments combined with fine-scale community mapping would allow us to fill knowledge gaps regarding temporal changes in community structure and habitat use. We also found that vessel traffic increased noise levels on the GSR. Further work is needed to determine how vessel noise reaching the reefs is impacting the community. Future work should also allow us to identify fish calls recorded on the reef to species level, bolstering our understanding of the fish community on the reefs. This pilot study represents the first description of the soundscape of a GSR, and shows that further research into the relationship between sound production, community structure, and ecosystem health is warranted.

Acknowledgements. We thank the crew of the CCGS Neocaligus for support during hydrophone deployment, James Pegg and Wolfgang Carolsfeld for customizing, maintaining, and co-piloting the Phantom ROV, Ocean Networks Canada for providing their AIS data, and James Pilkington and Svein Vagle (DFO) for their comments on earlier versions of the manuscript. Funding was provided by DFO, NSERC VF, CFI/BCKDF and the Liber Ero Foundation. This research was sponsored by the NSERC Canadian Healthy Oceans Network and its Partners: Department of Fisheries and Oceans Canada and INREST (representing the Port of Sept-Îles and City of Sept-Îles). (NETGP 468437-14, CHONe Project 2.1.4)

LITERATURE CITED

Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D (2016) Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Sci Rep 6:33326

Bioacoustics Research Program (2017) Raven Pro: interactive sound analysis software (version 1.5). Cornell Lab of Ornithology, Ithaca, NY

Butler J, Stanley JA, Butler MJ (2016) Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. J Exp Mar Biol Ecol 479:89–96

Chu JWF, Leys SP (2010) High resolution mapping of community structure in three glass sponge reefs (Porifera, Hexactinellida). Mar Ecol Prog Ser 417:97–113

Cook SE, Conway KW, Burd B (2008) Status of the glass sponge reefs in the Georgia Basin. Mar Environ Res 66: S80–S86

Danley PD, Husemann M, Chetta J (2012) Acoustic diversity in Lake Malawi's rock-dwelling cichlids. Environ Biol Fishes 93:23–30

DFO (2015) Fishery notice FN0415 www-ops2.pac.dfo-mpo.gc.ca/fns-sap/index-eng.cfm?pg=view_notice&DOC_ID=183964&ID=all (accessed 12 Feb 2017)

Du Preez C, Tunnicliffe V (2011) Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. Mar Ecol Prog Ser 425:217–231

Dunham A, Pegg J, Carolsfeld W, Davies S, Murfitt I, Boutillier J (2015) Effects of submarine power transmission cables on a glass sponge reef and associated megafaunal community. Mar Environ Res 107:50–60

Dunham A, Mossman J, Archer SK, Davies S, Pegg J, Archer E (2018) Glass sponge reefs in the Strait of Georgia and Howe Sound: status assessment and ecological monitoring advice. DFO Canadian Science Advisory Secretariat Research Document RES2018/010. Fisheries and Oceans Canada, Ottawa

Fish MP (1948) Sonic fishes of the Pacific. Woods Hole Oceanographic Institution, Woods Hole, MA

Fish MP, Mowbray WH (1970) Sounds of western North Atlantic fishes: a reference file of biological underwater sounds. Johns Hopkins University Press, Baltimore, MD

Kaatz IM (2002) Multiple sound-producing mechanisms in teleost fishes and hypotheses regarding their behavioural significance. Bioacoustics 12:230–233

Leys SP, Mackie GO, Reiswig HM (2007) The biology of glass sponges. Adv Mar Biol 52:1–145

Lillis A, Eggleston DB, Bohnenstiehl DR (2013) Oyster larvae settle in response to habitat-associated underwater sounds. PLOS ONE 8:e79337

Lourens JG, du Preez JA (1998) Passive sonar ML estimator for ship propeller speed. IEEE J Oceanic Eng 23: 448–453

Merchant ND, Fristrup KM, Johnson MP, Tyack PL, Witt MJ, Blondel P, Parks SE (2015) Measuring acoustic habitats. Methods Ecol Evol 6:257–265

Monczak A, Berry A, Kehrer C, Montie EW (2017) Long-term acoustic monitoring of fish calling provides baseline estimates of reproductive timelines in the May River estuary, southeastern USA. Mar Ecol Prog Ser 581:1–19

Mooney TA, Kaplan MB, Izzi A, Lamoni L, Sayigh L (2016) Temporal trends in cusk eel sound production at a proposed US wind farm site. Aquat Biol 24:201–210

NMEA (National Marine Electronics Association) (2002) NMEA 0183: standard for interfacing marine electronic devices, version 3.01, January 1, 2002. www.nmea.org/content/nmea_standards/nmea_0183_v_410.asp

Nichols B (2005) Characterizing sound production in near-shore rockfishes (*Sebastes* spp.). MSc thesis, University of South Florida, Tampa, FL

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rountree RA, Gilmore RG, Goudey CA, Hawkins AD, Luczkovich JJ, Mann DA (2006) Listening to fish. Fisheries (Bethesda, MD) 31:433–446

Rountree RA, Juanes F, Goudey CA, Ekstrom KE (2012) Is biological sound production important in the deep sea? In: Popper AN, Hawkins A (eds) The effects of noise on

aquatic life. Advances in experimental medicine and biology, Vol 730. Springer, New York, NY, p 181–183
Schmitz B (2002) Sound production in Crustacea with special reference to the Alpheidae. In: Wiese K (ed) The crustacean nervous system. Springer, Berlin, p 536–547
Simpson SD, Meekan M, Jeffs A, Montgomery J, McCauley R (2008) Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise. Anim Behav 75:1861–1868
Širovic A, Demer DA (2009) Sounds of captive rockfishes. Copeia 2009:502–509
Širovi A, Cutter GR, Butler JL, Demer DA (2009) Rockfish sounds and their potential use for population monitoring in the Southern California Bight. ICES J Mar Sci 66:981–990
Solan M, Hauton C, Godbold JA, Wood CL, Leighton TG, White P (2016) Anthropogenic sources of underwater sound can modify how sediment-dwelling invertebrates mediate ecosystem properties. Sci Rep 6:20540
Verzijden MN, van Heusden J, Bouton N, Witte F, ten Cate C, Slabbekoorn H (2010) Sounds of male Lake Victoria cichlids vary within and between species and affect female mate preferences. Behav Ecol 21:548–555
Wall CC, Rountree RA, Pomerleau C, Juanes F (2014) An exploration for deep-sea fish sounds off Vancouver Island from the NEPTUNE Canada ocean observing system. Deep Sea Res I 83:57–64

Appendix

Table A1. Counts of vessels within 10 km of each recorder and distance (m) of the closest vessel to each recorder for each minute of recording

Location	Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
Number of vessels						
Reef-center	0	1	2	1.9	3	8
Reef-margin	0	1	2	1.9	3	8
Off-reef	0	1	2	1.9	3	8
Minimum distance						
Reef-center	14	3817	4952	5253	6785	9998
Reef-margin	19	3983	5122	5355	6761	10653
Off-reef	8	3611	4800	5132	6795	10262

Table A2. Slope estimates (mean ± SE) for the impact of the number of vessels within 10 km and the distance to the nearest vessel on sound pressure levels (dB re 1 µPa) in 4 frequency bands for each recorder deployed at the reef-center, reef-margin, and off-reef of the Galiano sponge reef

Location	20–100 Hz	100–1000 Hz	1–10 kHz	10–48 kHz
Number of vessels				
Reef-center	1.01 ± 0.15	0.64 ± 0.13	0.79 ± 0.12	1.14 ± 0.14
Reef-margin	1.45 ± 0.16	0.89 ± 0.14	0.79 ± 0.12	1.44 ± 0.15
Off-reef	0.8 ± 0.15	0.58 ± 0.13	0.79 ± 0.12	1.11 ± 0.14
Minimum distance				
Reef-center	$0.59\times10^{-4} \pm 7.90\times10^{-5}$	$-2.72\times10^{-4} \pm 6.18\times10^{-5}$	$-2.80\times10^{-4} \pm 5.49\times10^{-5}$	0.00
Reef-margin	$2.54\times10^{-4} \pm 7.30\times10^{-5}$	$-2.72\times10^{-4} \pm 6.18\times10^{-5}$	$-2.80\times10^{-4} \pm 5.49\times10^{-5}$	0.00
Off-reef	$0.23\times10^{-4} \pm 8.24\times10^{-5}$	$-2.72\times10^{-4} \pm 6.18\times10^{-5}$	$-1.56\times10^{-4} \pm 6.20\times10^{-5}$	0.00

Table A3. Species observed during recorder deployment and retrieval at each location

Off-reef	Reef-margin	Reef-center
No species observed	*Cribrinopsis fernaldi*	*Acantholithodes hispidus*
	Crossaster papposus	*Chorilia longipes*
	Hydrolagus colliei	*Gephyreaster swifti*
	Metridium sp.	*Henricia* sp.
	Munida quadrispina	Unidentified Lithodidae sp. 1
	Pandalus platyceros	*Munida quadrispina*
		Unidentified Osmeridae sp. 1
		Pandalus platyceros
		Peltodoris lentiginosa
		Sebastes elongatus
		Sebastes sp. 1
		Sebastes sp. 2
		Unidentified Asteroidea sp. 1

Editorial responsibility: Christine Erbe, Bentley, Western Australia, Australia

Submitted: December 4, 2017; Accepted: March 20, 2018
Proofs received from author(s): April 26, 2018