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This paper describes song production by the eastern North Pacific right whale (NPRW, *Eubalaena japonica*) in the southeastern Bering Sea. Songs were localized in real-time to individuals using sonobuoys. Singers whose sex could be determined were all males. Autonomous recorder data from 17 year-long deployments were analyzed to document and characterize song types. Four distinct song types were documented over eight years (2009–2017) at five distinct locations. Each song type consists of a hierarchical structure of 1–3 different repeating phrases comprised predominantly of gunshot sounds; three of the four songs contained additional sound types (downsweep, moan, and low-frequency pulsive call). Songs were detected annually (July–January); all song types remained consistent over eight years. Two different songs often occurred simultaneously, produced by different individuals; the same song was never detected simultaneously at the same location. The same song type was detected on the same day and time at two distant locations, indicating multiple individuals can produce the same song. These findings provide support that males produce song; it remains unknown if females also sing. NPRW is the first right whale species documented to produce song. Based on current knowledge about song in mysticetes, it is hypothesized that these songs are reproductive displays. https://doi.org/10.1121/1.5111338

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I. INTRODUCTION

In several species across many different taxa, males use acoustic displays in reproductive contexts (Burk, 1983; Payne, 1983; Searcy and Andersson, 1986; Fischer *et al.*, 2004). One of the most recognizable forms of acoustic display is song, which can serve to attract females, defend territories, or mediate intrasexual encounters (Searcy and Andersson, 1986; Croll *et al.*, 2002; Cholewiak *et al.*, 2018). There are numerous and varying definitions of song, yet they all share the same basic commonalities. Probably the most commonly referenced definition is by Catchpole and Slater (2008), who describe bird songs as "long, complex vocalizations produced by males, in the breeding season." While this definition references seasonality and production by males, most definitions of song in marine mammals refer only to the structural and temporal characteristics, with no reference to function (e.g., Payne and McVay, 1971; Clark, 1990; Würsig and Clark, 1993; Stafford *et al.*, 2008). In one of the earliest studies on cetacean song, Payne and McVay (1971) characterized in detail the structure of humpback whale (*Megaptera novaeangliae*) song. They compared it with song in birds, stating that "one of the characteristics of bird songs is that they are fixed patterns of sounds that are repeated," and "…vocalizations occur in long, fixed sequences and are repeated with considerable accuracy every few minutes."

There is a wide range of complexity in cetacean song. The most complex is humpback whale song, where there is a strict hierarchical structure consisting of several repeated sound units comprising a phrase, phrases repeated to comprise a theme, and several unique themes comprising a song (Payne and McVay, 1971). All male humpback whales within a given population sing the same version of song, which changes progressively throughout a single season (Payne *et al.*, 1983). Bowhead whales (*Balaena mysticetus*) also produce complex songs with hierarchical structures, similar to humpback whales (Würsig and Clark, 1993). However, unlike humpbacks, bowhead whales produce a staggering number of complex song types (as many as 76 distinct types) within a season, and songs appear to change every year (Würsig and Clark, 1993; Delarue *et al.*, 2009a; Stafford *et al.*, 2018).

Songs can be complex, despite being comprised of only a few call types. North Atlantic walrus (*Odobenus rosmarus*) songs are comprised of a series of pulses (knocks or taps) with occasional bell calls (Stirling *et al.*, 1987; Sjare *et al.*, 2003). The predominant call types are both impulsive sounds; as such, the distinguishing feature among each song type is the specific timing and pattern of the knocks and taps, and their timing relative to the bell production. Additionally, individuals can vary the length of their song

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both during a singing session as well as throughout the season (Sjare *et al.*, 2003).

Less complex songs are common among mysticetes. Blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) produce relatively simple songs that can be used to distinguish among different populations. For example, blue whale songs are composed of a series of phrases, with each phrase containing one to five call units (Cummings and Thompson, 1971; McDonald *et al.*, 2006). These songs remain constant over many years, even decades. Fin whale song is even more simple, comprised of sequences of short low-frequency pulses, with several sequences forming a song (Watkins *et al.*, 1987; Croll *et al.*, 2002; Delarue *et al.*, 2009b). While lacking the hierarchical complexity of humpback whale song, the songs of fins and blues still have the consistent patterning and timing definitive of cetacean song.

Some species have both complex and simple songs. Bowhead whales, in addition to their complex songs, also produce call sequences that are sometimes referred to as "simple song," defined as a repetition of simple moans (Stafford *et al.*, 2008; Delarue *et al.*, 2009a). These simple songs are less constrained structurally, and vary considerably in number of units, phrases, and order and timing of phrases (Delarue *et al.*, 2009a). Because of this lack of complexity and consistency, there is still some debate as to whether these are considered song (Würsig and Clark, 1993; Stafford *et al.*, 2018). Previous to our study, no species of right whale has been observed producing song.

Currently, three species of right whales are recognized: the southern right whale (SRW, *Eubalaena australis*); the North Atlantic right whale (NARW, *E. glacialis*); and the North Pacific right whale (*E. japonica*). The latter species is divided into eastern and western populations. Sightings and acoustic detections of the eastern North Pacific population (hereafter NPRW) in the southeastern Bering Sea in recent decades (Shelden *et al.*, 2005; Wade *et al.*, 2006; Ivashchenko and Clapham, 2012) led to the federal designation of Critical Habitat in 2008 (pentagon, Fig. 1). The critically endangered status of this small population ($n \approx 30$ individuals; Wade *et al.*, 2011) has led to long-term monitoring of NPRW within the Bering Sea shelf.

Right whales make a variety of tonal signals, including upsweeps, downsweeps, down-upsweeps, and moans, as well as other non-tonal broadband sounds such as screams and gunshots (Clark, 1983; Matthews *et al.*, 2001; McDonald and Moore, 2002; Parks *et al.*, 2012; Crance *et al.*, 2017). The gunshot sound (hereafter "gunshot") is the predominant sound type observed for the NPRW, with maximum recorded individual call rates of 425 calls h^{-1} (Crance *et al.*, 2017). The gunshot is a broadband, impulsive sound, ranging in frequency from 20 Hz up to 20 kHz, with a short duration of approximately 200 ms (Matthews *et al.*, 2001; Parks and Tyack, 2005; Crance *et al.*, 2017). The gunshot is produced by both sexes in all three species of right whale (Clark, 1983; Gerstein *et al.*, 2014; Crance *et al.*, 2017), although gunshot production by females was only very recently documented for both NPRW

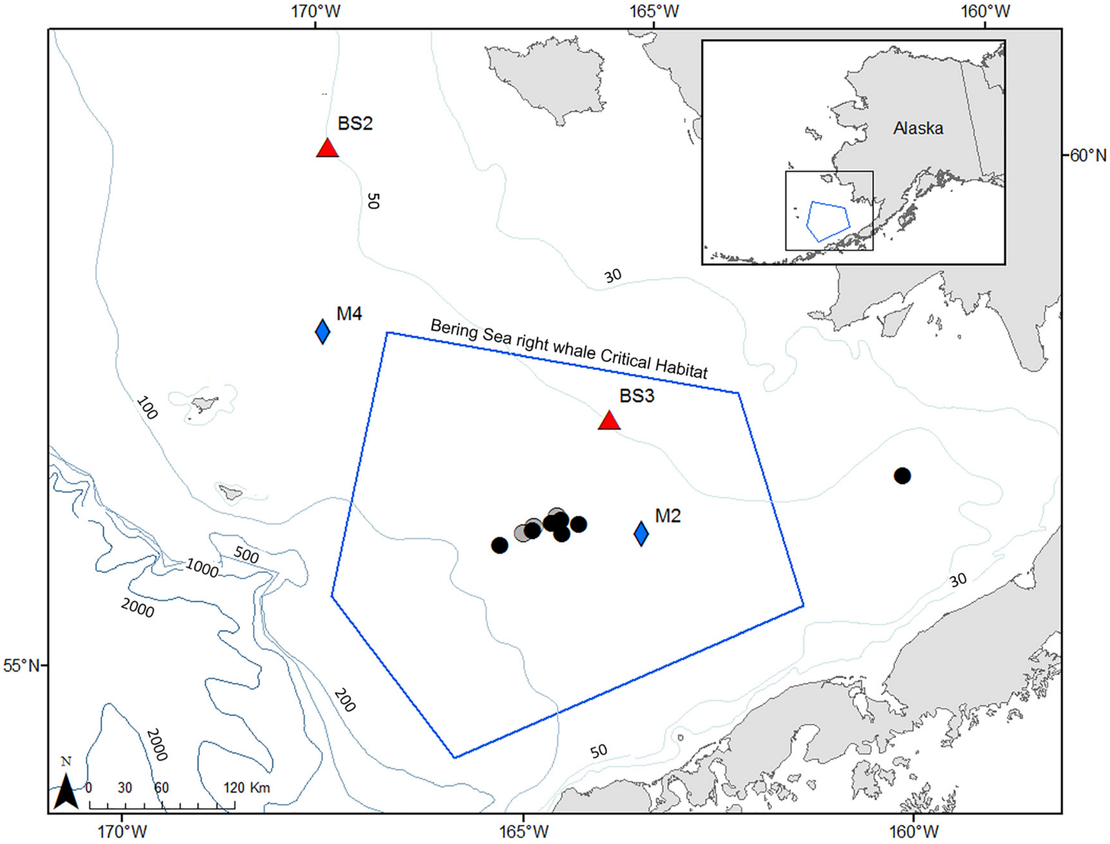

FIG. 1. (Color online) Location of the long-term passive acoustic recorders (2009–2016) and sonobuoy deployments (2010, 2017) in the southeastern Bering Sea, Alaska (inset). Blue diamonds = passive acoustic moorings co-located with oceanographic moorings; red triangles = passive acoustic moorings only. Circles = sonobuoys on which gunshot songs were detected: gray = 2010, black = 2017. Blue pentagon = Federally Designated right whale Critical Habitat.

and NARW (Gerstein *et al.*, 2014; Crance *et al.*, 2017). Gunshots appear to be produced at much higher rates by males for both NPRW (year-round) and NARW (seasonally), and as such researchers have suggested that their primary function is as a reproductive display (Parks *et al.*, 2012; Crance *et al.*, 2017).

Both NPRW and NARW have been reported producing long bouts of gunshots, where the same call type is produced for periods lasting from 30 min to 7 h (Parks *et al.*, 2012; Crance *et al.*, 2017). However, these bouts are not stereotyped, and calling rates, inter-call intervals, the patterning of calls, and number of gunshots vary considerably among bouts. Here, we present evidence of stereotyped, repeated, and rhythmically patterned gunshot and other calls produced by NPRW. These patterns have a distinct hierarchical structure, consistent timing between and number of units, and characteristics that are in line with the definition of song, and therefore represent the first documented occurrence of song in right whales.

II. METHODS

A. Data collection

Since 2007, the Alaska Fisheries Science Center's Marine Mammal Laboratory has deployed year-long passive acoustic recorders at eight sites throughout the southeastern Bering Sea using sub-surface moorings. Data were obtained from four of the eight mooring locations (including two within the Critical Habitat and two northwest of the Critical Habitat). Recordings were also made from short-term sonobuoy deployments inside the Critical Habitat (Fig. 1). A summary of all sampling effort, including details of recording device specifications and sample rates, is presented in Table I. Eight years of data (2009–2016) were obtained from Autonomous Underwater Recorder for Acoustic Listening[1] (AURAL) recorders for this study. These recorders were placed 6 m above the seafloor on either a subsurface oceanographic mooring located on the 70 m isobath (Fig. 1, diamonds) or a subsurface passive acoustic mooring on the 50 m isobath (Fig. 1, triangles). These instruments sampled at either 8 or 16 kHz on a 30%–86% duty cycle, depending on deployment year (Table I). From 2009 to 2012, duty cycles were either 26 min on every 30 min, or 40 min on every 60 min (Table I). From 2012 to 2016, duty cycles ranged from 80 to 180 min on every 300 min (Table I). Two years of data (2010–2011) were obtained from an Ecological Acoustic Recorder (EAR; Lammers *et al.*, 2008) deployed 4 m above the seafloor on a subsurface mooring located on the 50 m isobath. This instrument sampled at 4 kHz on a 6.7% duty cycle (4 min on every hour; Fig. 1, triangle).

Acoustic data were also recorded using sonobuoys deployed for two summer (July–September 2010, 2017) vessel surveys in the southeastern Bering Sea to monitor for the presence of large whales (Fig. 1, circles). Sonobuoys are free-floating, expendable, short-term passive acoustic devices that transmit audio signals to receivers on a vessel in real time using VHF radio waves. Sonobuoys used in this study were AN/SSQ 53F (Undersea Sensor Systems) and 77C (Sparton). For more details regarding sonobuoy data collection protocols and the complete system used, see Crance *et al.* (2017). In summary, sonobuoy cable lengths were shortened for deployment, so that hydrophones would not drag or rest on the shallow Bering Sea shelf floor. In-air (i.e., ship-to-sonobuoy) reception range was approximately 20–30 km, dependent on sea state conditions, age and condition of the sonobuoy, height of the receiving antenna, and sonobuoy VHF transmission frequency. Although the probability of detection in this region is unknown, the maximum

TABLE I. Summary of acoustic recording effort for both long-term moored recorders and short-term sonobuoy deployments, and song types and number of complete songs detected. RWCH = Right Whale Critical Habitat.

Mooring	Year	Instrument	Recording time frame	# Days of recordings	Sample rate (kHz)	Record. Mins/ Cycle time	Song types detected	Total # songs detected
BS2	2012-13	AURAL	12 Aug 12–17 Aug 13	371	16	85/300		-
	2015-16	AURAL	27 Sept 15–27 Sept 16	365	16	80/300	GS1-PF, GS4-DG	10
M4	2012-13	AURAL	5 Sept 12–12 Sept 13	373	16	85/300		0
	2013-14	AURAL	18 Sept 13–17 Oct 14	395	16	80/300	All four	56
	2014-15	AURAL	19 Oct 14–26 Sept 15	343	16	80/300	GS2-TP, GS3-PU	32
BS3	2010-11	EAR	18 Sept 10–5 July 11	291	4	4/60	GS1-PF, GS2-TP	28
	2011-12	EAR	6 Sept 11–7 June 12	276	4	4/60	GS1-PF, GS2-TP, GS4-DG	122
	2013-14	AURAL	18 Sept 11–5 Oct 13	18	16	80/300	GS1-PF, GS4-DG	133
	2014-15	AURAL	20 Oct 14–27 Sept 15	343	16	80/300	GS2-TP, GS4-DG	147
	2015-16	AURAL	28 Sept 15–28 Sept 16	365	16	80/300	All four	101
M2	2009-10	AURAL	6 May 09–7 Mar 10	287	8	26/30	All four	392
	2011	AURAL	19 May 11–27 Sept 11	132	8	40/60	GS1-PF, GS2-TP, GS3-PU	270
	2012-13	AURAL	12 May 12–5 May 13	344	8	40/60	GS2-TP, GS3-PU	252
	2013	AURAL	11 May 13–25 Nov 13	138	16	165/300	GS4-DG	49
	2014-15	AURAL	18 May 14–30 Apr 15	347	16	165/300	GS2-TP, GS3-PU, GS4-DG	214
	2015-16	AURAL	2 May 15–4 May 16	367	16	165/300		-
	2016	AURAL	14 May 16–29 Sept 16	139	16	180/300		-
RWCH	2010	Sonobuoy	July–Sept 2010	26	48[a]	Cont.	GS1-PF	33
	2017	Sonobuoy	July–Sept 2017	55	48[a]	Cont.	GS2-TP, GS3-PU	144

[a] Although sonobuoys were sampled at 48 kHz, there was usable audio only up to 2.5 kHz.

range of NPRW calls obtained on sonobuoys was approximately 75 km, based on localization of calling animals and associated visual sightings, when possible (Crance *et al.*, 2017).

Sonobuoys were set in Directional Frequency Analysis and Recording mode, with an audio frequency range of 10 Hz–2.5 kHz (higher frequencies used in bearing calculation), to obtain directional bearing information (calibrated using the ship as a sound source; Crance *et al.*, 2017). All recording settings were sufficient to capture the frequency range of NPRW calls (i.e., peak energy is from 50 to 2000 Hz). Sonobuoys were monitored in real time using ISHMAEL software (Mellinger, 2001). When NPRW calls were detected, up to two additional sonobuoys were deployed, so that a cross-fix to the whale's approximate location could be obtained. Demultiplexing software (to decode the bearing information), a custom MATLAB interface,[2] and a MATLAB-based tracking and plotting program were used to process signals from the sonobuoys and obtain localizations in near-real time. All audio data were recorded in ten-minute increments to an external hard drive using ISHMAEL (48 kHz sampling rate).

B. Data analysis

Sonobuoy data were monitored in real-time for the presence of marine mammal calls, and all species acoustically and visually detected were noted. Repeated sonobuoy deployments, localizations, and increased signal strength of the calls as sonobuoys were deployed closer to the animal, and subsequent visual sighting of the calling animal were used to attribute calls to an individual and classify calls and other sounds to species. All of the long-term recorder data (100%) were reviewed manually by experienced analysts for the presence of five species of marine mammals (NPRW; humpback whale; bowhead whale; gray whale, *Eschrichtius robustus*; walrus) as well as anthropogenic (seismic airgun; vessel) signals (for full details see Wright *et al.*, 2019). For both sonobuoy and long-term data analyses, there were observations of rhythmic patterning and regular timing within some gunshot bouts; these dates/times were noted for further investigation. During these *post hoc* analyses, it became clear that these patterns were extremely consistent, repeated for up to hours at a time, and that they could be categorized into visually distinguishable pattern types. The predictability of these patterns, the specific and consistent timing between gunshot units, and their repetition over time were key factors in distinguishing songs from other non-song gunshot sequences. Sequences determined to be song were then analyzed further for spectral and temporal characteristics. Analyses of songs were conducted using Raven Interactive Sound Analysis Program (Version 1.4, Cornell Lab of Ornithology)[3]. Spectrograms were generated (Hamming window, 95% overlap, and either 256, 512, or 1024 point fast Fourier transform (FFT) depending on sampling rate required to obtain ∼20 ms time analysis resolution). All recordings were visually and aurally reviewed for the presence of gunshot songs.

A NPRW song was defined as a series of units that are repeated in a stereotyped, rhythmic manner (i.e., consistent number of gunshots and temporal patterning). Song sessions were defined as continuous repetitions of the same song, and inter-unit interval (IUI) was defined as the start of one call to the start of the next consecutive call. To test the inter-observer reliability of our classification of song types, seven naive analysts of varying acoustic experience were asked to match 25 clips (portion of a song session that included at least one complete song) to one of the four song types, presented to the observers as spectrograms. The 25 clips included five each of the four song types as well as five non-song gunshot clips that were extracted from recordings made on multiple mooring locations and years. Overall, there was 86% agreement among observers. There was no evidence that any one song type was more difficult to classify than others. In all but two incorrect answers, the observers erred on the side of caution, labeling a song as random, rather than mis-classify a song.

For each song session, start and end times of each song, number of phrases, number and type of units (e.g., gunshot, moan, upcall, etc.), peak frequencies, and IUIs were measured. Because the recorders were programmed on a duty cycle, we were unable to calculate every inter-song interval or the start and end of every song session, and so those values are not presented here. There were often multiple conspecifics singing or calling simultaneously, or vessel noise present, and songs were often cut off as a result of the duty cycle. As such, only those songs with clear gunshots with good signal to noise ratio, where individual singers were easily identified, and where the entire song was present were included for analyses. It should also be noted that the exact number of singers could not be determined, due to the nature of bottom-mounted autonomous recorders.

Propagation modeling was conducted using the Monterey-Miami Parabolic Equation (Smith *et al.*, 2007) with a water column sound speed profile obtained from conductivity, temperature, depth (CTD) data at the M2 mooring (P. Stabeno), ambient noise levels of 80 dB re 1 μPa (Munger *et al.*, 2011), sediment velocity of ∼1600 m s^{-1} (Wiggins *et al.*, 2004), source depth of 10 m (Munger *et al.*, 2011; Thode *et al.*, 2017), water depth of approximately 70 m, a source level of 195 dB re 1 μPa (Parks *et al.*, 2005), and a detection threshold of 0 dB (Au *et al.*, 2001).

III. RESULTS

Stereotyped gunshot patterns (later classified as songs) were first detected and identified while monitoring sonobuoys on 19 September 2010 during a summer/fall field survey in the right whale Critical Habitat (Fig. 1). The detection of this song (GS1-PF, described below) led to a more thorough investigation of the data collected over eight years on long-term recorders in the southeastern Bering Sea. Four different song types have been detected on multiple long-term passive acoustic recorders every year from July to early January, when right whales inhabit the area. Additionally, these song types were detected on directional sonobuoys during the 2017 summer field survey, where they were localized and associated with visually-sighted NPRW on three separate occasions.

A. North Pacific right whale song description

The main phrase was defined as the song phrase that was present in all songs, had the longest duration, and occurred

TABLE II. Comparison of structural components of songs. PP = Preliminary phrase; MP = Main phrase; TP = Terminal phrase; IUI = Inter-call interval.

Song type	GS1-PF	GS2-TP	GS3-PU	GS4-DG
Total # songs detected (Total # analyzed)	288 (180)	571 (213)	540 (218)	451 (277)
# Songs with PP	—	213 (100%)	208 (95.4%)	—
# Songs with TP	23 (7.9%)	213 (100%)	143 (67%)	—
# IUI's PP	—	2	1	—
# IUI's MP	2	3	1	3
# IUI's TP	1	2	1	—
Amplitude modulation	Increasing	Alternating	Increasing	N
Defining characteristics	Peak freq. around 630 Hz	PP and TP always present	Low-freq. pulsive calls in PP	Doublet gunshot
Months detected	Aug, Sept, Oct	Jun, Jul, Aug, Sept, Oct, Dec	Jul, Aug, Sept, Oct	Aug, Sept, Oct, Nov, Dec, Jan
Years detected	2009, 2010, 2013, 2014, 2015	2009, 2010, 2011, 2012, 2014, 2015, 2017	2009, 2011, 2012, 2014, 2015, 2017	2010, 2011, 2013, 2014, 2015

only once within a song. The preliminary phrase was defined as any phrase that occurred before the main phrase. Likewise, the terminal phrase was defined as any phrase that occurred immediately after the main phrase. Based on this terminology and the observed phrase syntax, four different gunshot song types were observed. Two song types had all three phrases, one type had main and terminal phrases, and one type consisted of only a main phrase (Table II). One song consisted entirely of gunshots (GS4-DG), while the other three contained additional unit types (e.g., low-frequency pulsive calls, moans, downsweeps). A summary of the parameters of each unit or phrase within a song are presented in Table III. Due to duty cycling, multiple conspecifics singing simultaneously, or poor signal to noise ratio, the number of songs analyzed ($n = 888$) is considerably less than the total number of songs detected ($n = 1983$). The overall number of singers is also unknown due to the nature of single-element, duty-cycled, autonomous recorders.

The first gunshot song type, GS1-PF [PF = Predominant Frequency; Figs. 2(a) and 3(a)], was detected a total of 288 times ($n = 180$ analyzed) and was composed of two phrase types, the main phrase and occasionally a terminal phrase. The main phrase was composed of an average of 15.2 gunshots (±4.0) followed by a downsweep from 250 to 120 Hz [Table III; Fig. 2(a)]. The average IUI for song type GS1-PF was 1.1 s (±0.1); the average IUI from the terminal gunshot to the downsweep was 2.3 s (±0.5). The average duration of the downsweep was 1.0 s ± 0.1, and the average sweep rate was 104.7 Hz/s ± 24.9. This song type consistently showed a predominant frequency centered at 630 Hz [Fig. 2(a)]. The terminal phrase was present in 23 of the analyzed songs (7.9%), occurring in multiple different song sessions in three different years, and always consisted of only one iteration of the phrase. The number of gunshots in the terminal phrase was variable (8.4 ± 3.2), while the average IUI was similar to the main phrase (1.0 s ± 0.1). The overall duration for song type GS1-PF was 17.8 (±5.3). A portion of a song session of song type GS1-PF is shown in Fig. 3(a).

The second song type, GS2-TP [TP = Terminal Phrase; Figs. 2(b) and 3(b)], was detected a total of 571 times ($n = 213$ analyzed), and consisted of a preliminary phrase of 3.0 (±0) gunshots, a main phrase with an average of 16.2 (±1.1) gunshots, followed by a repeating terminal phrase with an average of six gunshots per phrase [±0.8; Table III, Fig. 2(b)]. The song always begins with a preliminary phrase of three gunshots of decreasing amplitude in rapid succession with two different IUIs (1.4 s ± 0.1, 1.6 s ± 0.1). These were then followed by the main phrase, consisting of 12–20 gunshots of alternating amplitude with a consistent IUI (1.6 s ± 0.1), ending with two gunshots with an increasing

TABLE III. Duration, frequency, and unit parameters of phrases and songs. All values presented as mean ± standard deviation. IUI = inter-unit interval .

		Preliminary phrase			Main phrase		Terminal phrase	
Song type	Duration (s)	Call type	# Units	IUI (s)	# Units	IUI (s)	# Units	IUI (s)
GS1-PF ($n = 180$)	17.8 ± 5.3		N/A		15.2 ± 4.0 ($n = 2052$)	1.1 ± 0.1 2.3 ± 0.5	8.4 ± 3.2 ($n = 210$)	1.0 ± 0.1
GS2-TP ($n = 213$)	112.6 ± 27.7	GS ($n = 639$)	3.0 ± 0	1.4 ± 0.1 1.6 ± 0.1	16.2 ± 1.1 ($n = 3188$)	1.6 ± 0.1 3.1 ± 0.1 3.5 ± 0.2	5.9 ± 0.7 ($n = 5493$)	1.5 ± 0.1 3.1 ± 0.1 3.5 ± 0.1
GS3-PU ($n = 218$)	132.1 ± 29.9	LF pulsive call ($n = 1974$)	8.9 ± 1.7	2.6 ± 0.3	17.8 ± 2.8 ($n = 3818$)	3.9 ± 0.3	3.8 ± 0.9 ($n = 1103$)	3.8 ± 0.2
GS4-DG ($n = 277$)	40.0 ± 6.7		N/A		7.9[a] ± 1.3 ($n = 2174$[a])	0.5 ± 0.1 9.4 ± 0.3 5.0 ± 0.1	N/A	

[a] Units refers to number of doublets, not each individual gunshot.

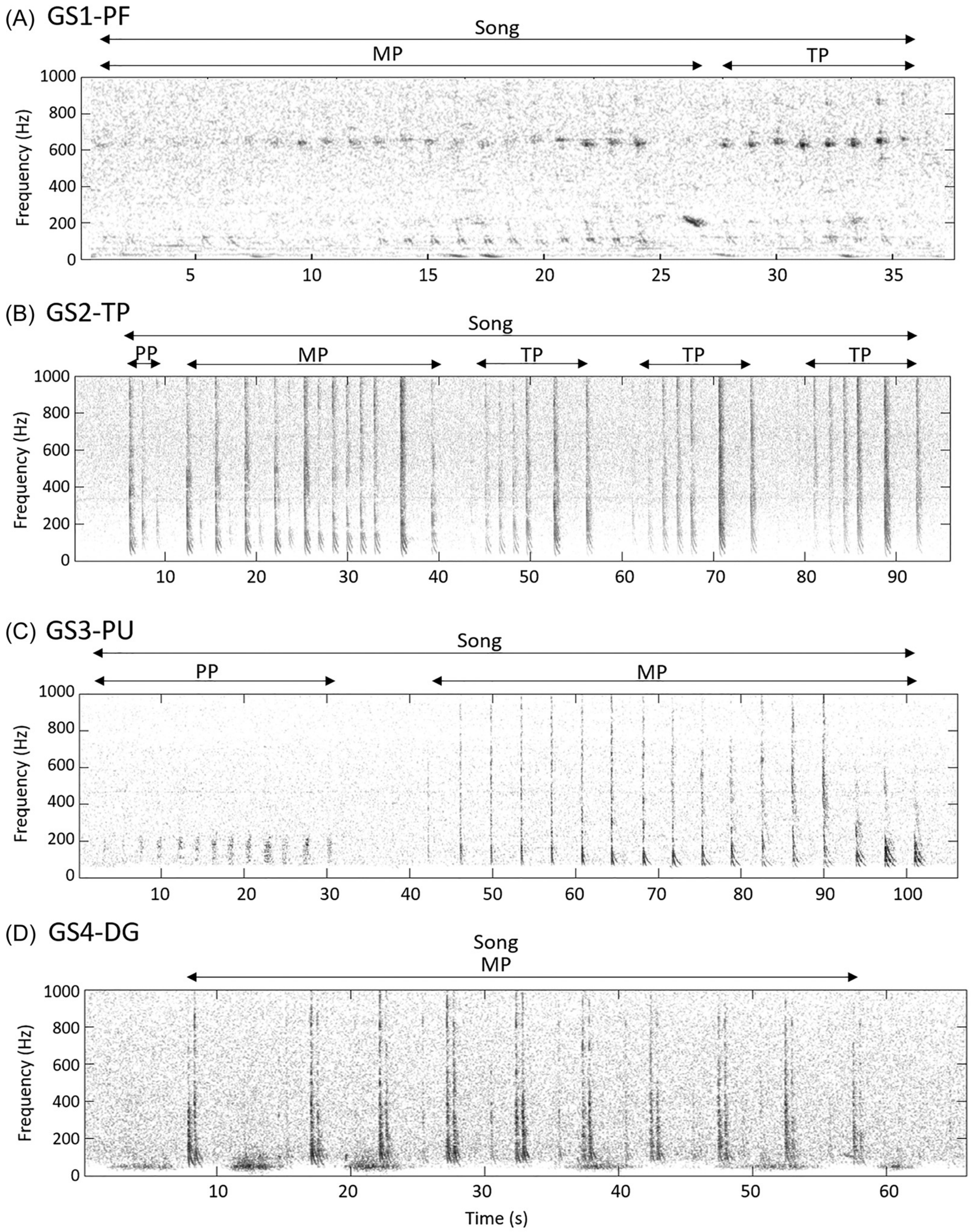

FIG. 2. Spectrogram of four North Pacific right whale gunshot song types. (A) GS1-PF, clip from sonobuoys, 19 September 2010. (B) GS2-TP, clip from BS3, 6 October 2010. (C) GS3-PU, clip from M2, 29 July 2011. (D) GS4-DG, clip from BS3, 1 December 2015. Note presence of some distant gunshots in between the doublets (e.g., at 31 s). PP = preliminary phrase. MP = main phrase. TP = terminal phrase. All spectrograms FFT 1024 (B) or 2048 (A, C, D), 95% overlap, Hamming window. Clips for (C) and (D) were high-pass filtered at 70 Hz to reduce noise.

IUI [3.1 s ± 0.1 and 3.5 s ± 0.2; Table III; Fig. 2(c)]. The terminal phrase had an average of 5.9 (± 0.8) gunshots of increasing amplitude and three IUIs similar to the final three IUIs of the main phrase. The first IUI of the terminal phrase was 1.5 s (±0.1), while the IUI of the final three gunshots was greater (3.1 s ± 0.1 and 3.5 s ± 0.1). The overall duration for song type GS2-TP was 112.6 s (±27.7). A portion of a song session of song type GS2-TP is shown in Fig. 3(b).

The third song type, GS3-PU [PU = Pulses; Figs. 2(c) and 3(c)], was detected a total of 540 times ($n = 218$ analyzed), and consisted of a preliminary phrase of low frequency pulsive calls (i.e., frequency range 30–240 Hz, average duration = 0.6 s ± 0.1) followed by the main phrase of gunshots [Table II; Fig. 2(c)]. Of the 218 songs analyzed, only 143 (65.5%) contained a terminal phrase of gunshots; additionally, the preliminary phrase was missing in ten songs (4.6%). The preliminary phrase consisted of an average of 8.9 (±1.8) low frequency pulsive calls with an average IUI of 2.6 s (±0.3; Table III). The main phrase was composed of an average of 17.8 gunshots (±2.8), which increased in amplitude throughout the phrase. The average IUI of the gunshots in the main phrase was 3.9 s (±0.3). The average duration between the end of the preliminary phrase and the start of the main phrase was 14.1 s (±2.2). The terminal

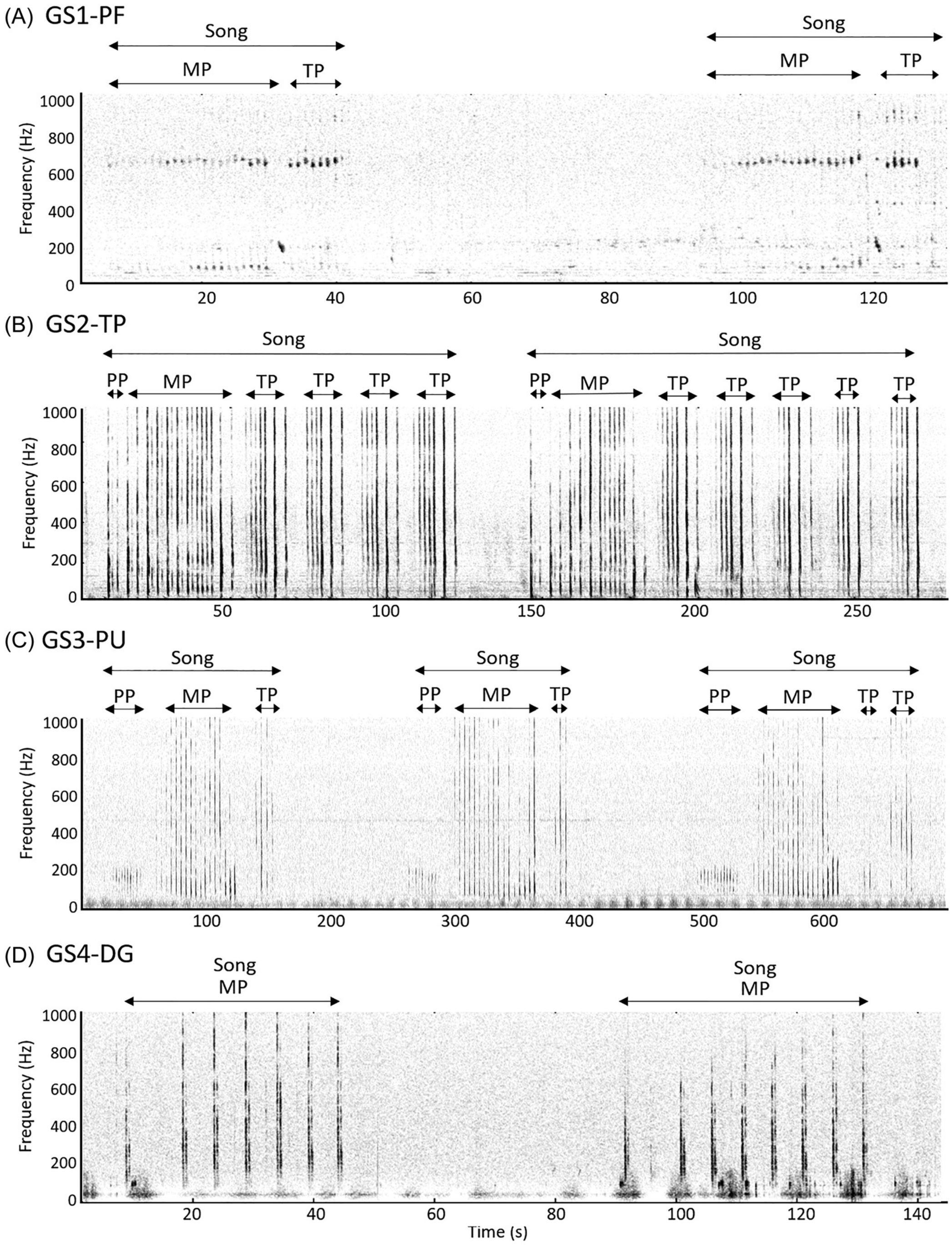

FIG. 3. Spectrogram of a portion of a singing session of all four song types with different phrases delineated. (A) GS1-PF, clip from BS3 on 5 October 2011. (B) GS2-TP, clip from M2 on 30 August 2011. (C) GS3-PU, clip from M2 on 29 July 2011. (D) GS4-DG, clip from BS3 on 30 November 2015. PP = preliminary phrase. MP = main phrase. TP = terminal phrase. All spectrograms FFT 2048 (C) or 4096 (A, B, D), 95% overlap, Hamming window.

phrase consisted of an average of 3.8 gunshots (±1.0) with a similar IUI of 3.8 s (±0.2). The main phrase terminated in a moan for only 11 songs (5.0%), all of which occurred on the same day [10 September 2017; Fig. 5(c)]. The frequency range of the moan was 160–100 Hz, with an average duration of 1.9 s (±0.4). The overall duration for song type GS3-PU was 132.1 s (±29.9). An example of a portion of a song session of song type GS3-PU is presented in Fig. 3(c).

The final song type, GS4-DG [DG = Doublet Gunshots; Figs. 2(d) and 3(d)], was detected a total of 451 times ($n = 277$ analyzed) and consisted of a single main phrase; no preliminary or terminal phrases were detected [Table II; Fig. 2(d)]. The defining characteristic of this song is that all gunshots produced in the song consisted of "doublets," defined as two distinct gunshots that are produced in rapid succession (i.e., <1 s). The IUI between the two gunshots, the water depth (50–70 m), and average sound speed ($\sim$1470 m s^{-1}) support that these are independent units, not echoes. Song type GS4-DG consisted of an average of 7.8 doublets (±1.3), with three discrete IUIs. The average IUI within each doublet was 0.5 s (±0.1; Table III). The IUI between the first and second doublets was 9.4 s (±0.3), while the average IUI between the remaining doublets was 5.0 s (±0.1). The overall duration for song type GS4-DG was 39.9 s (±6.7). A portion of a song session of song type GS4-DG is shown in Fig. 3(d).

B. Spatio-temporal distribution of song detections

The four different songs described above were detected as early as July, and as late as early January (corresponding to their seasonal distribution), over eight years and five different locations throughout the southeastern Bering Sea (Fig. 4). NPRW songs were detected in every year, and all four song types were detected within a season at the same location in three separate years (2009, 2014, 2015; Fig. 4). These songs have remained consistent over eight years, as illustrated by the consistent IUI and low standards of deviation. Figure 5 presents a spectrogram showing the consistency of song type GS3-PU over several different years and locations, with the only difference being the presence of a moan or number of terminal phrases [Fig. 5(c)]. Of a total 4975 days of recordings (i.e., number of days with acoustic recordings), the total number of days with NPRW calls (song and non-song) was 1340 (26.9%). Of these 1340 days, singing was detected on 84 different days (6.3%). Singing was always detected on days when other non-song gunshots or upcalls were detected. The three months with the greatest number of days with songs detected (summed across years) were August (24 days), September (23 days), and October (15 days).

There were fewer days with detections and fewer total songs detected at the two northern sites, BS2 and M4 (Table II, Fig. 1). Songs were detected on only two days at BS2 and eight days at M4, while songs were detected on 35 and 34 days at BS3 and M2, respectively. At the northernmost site (BS2), only two song types (GS4-DG and GS1-PF) were detected, and only in one year (2015). Song type GS4-DG was produced on 13 October 2015 until 02:00 UTC on 14 October. Twenty hours later, at 22:00 UTC on 14 October 2015, song type GS1-PF was produced, indicating either two singing right whales or one individual producing two different song types.

There were multiple instances of two different song types occurring simultaneously, in almost all possible pairwise combinations. This indicates that multiple individuals produce songs. Interestingly, the same song type was not produced simultaneously by two callers at the same location. However, on one occasion, the same song type (GS2-TP) was detected on the same day at two different recording sites (M2 and M4). At site M2 within the Critical Habitat, song type GS2-TP was detected on 20 August 2014 from 17:14 to 21:48 UTC. This same song type was detected at site M4 that same day beginning at 21:53 UTC, indicating multiple individuals can produce the same song type.

C. Attribution to male NPRW

In the summer 2017, songs were localized using directional sonobuoys and associated with visually-sighted pairs of NPRW on three separate occasions. Given the close proximity of the paired animals, it is unclear whether both animals were vocalizing, or only one animal within the pair. The animal(s) continued to sing both during the encounter and after the vessel left the area. There was no noticeable behavior while the whales were at the surface (e.g., no sexual behavior, no evidence of feeding) during any of the encounters. In all instances, the individuals of known sex were all males (known from previously collected biopsy data); it is unknown whether the non-sex determined animals were female or male. One of the pairs consisted of two males, with no other species visually sighted nearby, or detected on the sonobuoys, confirming that male NPRW produce these songs. However, it is unknown whether female NPRW also produce songs.

IV. DISCUSSION

A. Song classification

We provide the first documentation that North Pacific right whales produce songs. On three separate occasions in 2017, gunshot songs were localized using directional sonobuoys. Because song has not yet been attributed to any population of right whale, it is reasonable to question whether the sounds observed in this dataset constitute song as defined in the literature for other baleen whale species. As mentioned previously, there are many definitions of song, but the main commonality among all is the rhythmically patterned series

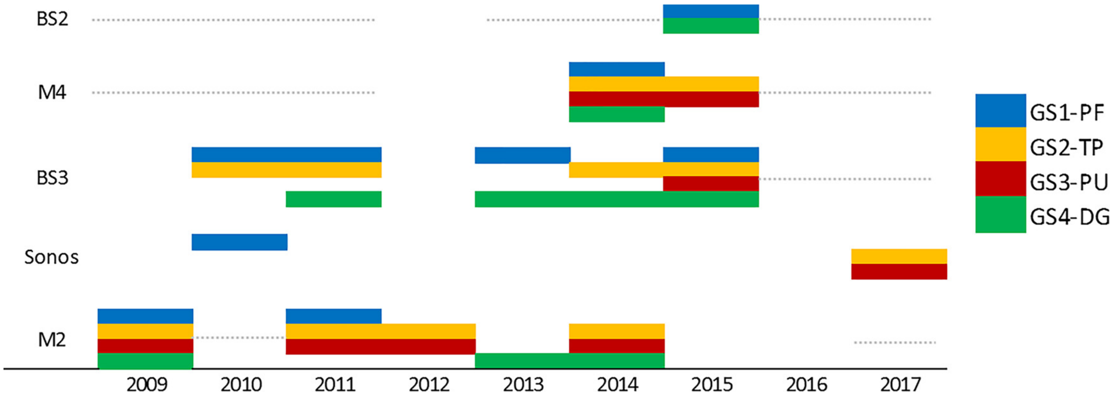

FIG. 4. (Color online) Spatio-temporal distribution of North Pacific right whale gunshot songs at five locations in the southeastern Bering Sea in summer and fall (July to early January). Plot is oriented geographically from north to south. Sonos = sonobuoys. Gray dotted lines = data not yet analyzed. Note: This plot only denotes when songs were detected, and makes no reference to the number of songs detected in a year at a recording site.

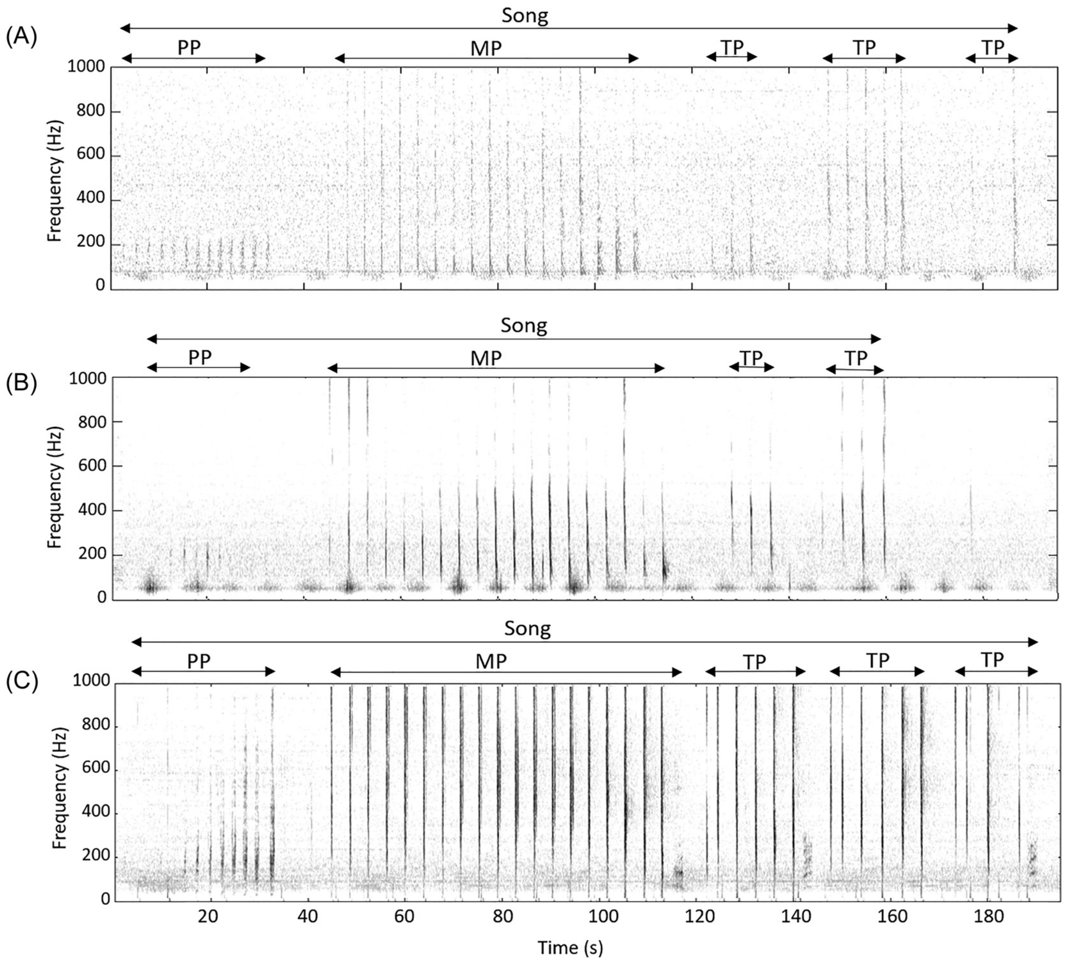

FIG. 5. Spectrogram of multiple songs of gunshot song type GS3-PU recorded over eight years, three different locations, and three different months with different phrases delineated. (A) Clip from M2, 29 July 2011. (B) Clip from BS3, 19 October 2015. (C) Clip from sonobuoys, 10 September 2017, localized to calling male NPRW. All spectrograms FFT 2048, 95% overlap, Hamming window. Clips for (A) and (B) were high-pass filtered above 70 Hz to reduce noise; all three examples time aligned on the same scale.

of units produced in a consistent manner to form clearly recognizable patterns. For more complex songs like those produced by humpback and bowhead whales, these units are repeated in the same order to comprise phrases, multiple phrases comprise themes, multiple themes comprise a song, and multiple songs produced in succession form a song session (Payne and McVay, 1971; Delarue *et al.*, 2009a). The patterns presented here likewise follow this same hierarchical structure, and as such should be classified as song.

The NPRW songs presented here share many similarities with several other mysticete species. As with blue and fin whales, NPRW song types remain constant over many years. Similar to humpback whales, these songs have a hierarchical structure of units and phrases (Payne and McVay, 1971). Similar to bowhead whales, in NPRW there are multiple song types that occur within a season or across years (Delarue *et al.*, 2009a; Stafford *et al.*, 2018). Bowhead whales also produce what has been referred to as "simple song," which is defined as the repetition of simple frequency-modulated calls (Delarue *et al.*, 2009a; Tervo *et al.*, 2009). While there are similarities between simple songs of bowhead whales and the songs produced by NPRW, the main difference is in the amount of variability. Bowhead whale simple songs vary greatly in both the number of units, the presence of phrases, and the order of phrases (Delarue *et al.*, 2009a). Conversely, the songs of NPRW have a clear hierarchical structure, do not vary their phrase order, the variability in number of units per phrase was less than in bowhead whale song, and the proportion of units relative to other phrases in a song did not change.

Interestingly, NPRW song characteristics are perhaps most similar to those produced by male Atlantic walrus, a large pinniped that is restricted to Arctic seas, including the Bering Sea where the NPRW occurs. Like NPRW songs, walrus songs are comprised of a series of impulsive calls, whose defining features are the temporal patterning of the pulses (Stirling *et al.*, 1987; Sjare *et al.*, 2003). Furthermore, each walrus song is easily recognized and categorized despite the variations in length that occur both during a singing session as well as throughout the season (Sjare *et al.*, 2003). The songs presented here likewise are comprised predominantly by a single call type, although all four songs are noticeably different from each other. And despite each song having subtle variations in song length or number of gunshots, it is easily recognized as being the same song. It is the specific timing of these calls relative to one another that defines each song.

One main commonality among mysticete song is that, for species in which the sex of the calling animal has been determined, it is always produced by males (e.g., humpbacks: Payne and McVay, 1971; fin whales: Croll *et al.*, 2002; blue whales: McDonald *et al.*, 2006). Several of the song detections in our study were localized to calling male NPRW. Male NPRW have previously been reported producing bouts of gunshots with consistent timing (Crance *et al.*, 2017). It is therefore clear that male NPRW produce these songs. Female NPRW have been shown to produce gunshots, albeit at considerably lower calling rates than males, and without rhythmic patterning of units (Crance *et al.*, 2017). Additionally, female humpback whales produce individual song units as social calls outside of the breeding grounds (Rekdahl *et al.*, 2013). The function of gunshots produced by female NPRW remains unknown. It is assumed that the NPRW songs presented here are produced exclusively by males; however, there are limited data on vocalizing female NPRWs. As such, we cannot rule out the possibility of song production by female NPRW.

B. Shared song type from spatially distant conspecifics

Although the same song type was never produced simultaneously by two callers at the same location, there was an instance of the same song type (GS2-TP) being detected on the same day at two different recording sites (M2 and M4). These two sites are approximately 310 km apart. At site M2 within the Critical Habitat, song type GS2-TP was detected on 20 August 2014 from 17:14 to 21:48 UTC. This same song type was detected at site M4 that same day beginning at 21:53 UTC, indicating multiple individuals can produce the same song type. Propagation modeling suggests that gunshots had a maximum detection range of approximately 120 km. Additionally, similar studies in the Bering Sea at this time of year have reported detection distances in the tens of kilometers for NPRW calls (McDonald and Moore, 2002; Munger *et al.*, 2011; Crance *et al.*, 2017; Wright *et al.*, 2019).

Given this song was detected on recorders located approximately 310 km apart, even if the singer was located between the two, it would have had to travel 70 km in 5 min to be detected on both recorders. In addition, the amplitude of the gunshots at both locations did not change, suggesting the callers remained a similar distance from the recorder for the duration of their song sessions. Furthermore, the 120 km range is conservatively high because it assumes the song received level is at the same as the ambient noise level; however, the signal to noise ratio of the gunshots at M2 and M4 were 16 and 18 dB, respectively. Altogether, this suggests that this was not one calling individual being detected on two different moorings, but rather two different callers, indicating multiple animals can produce the same song type.

C. Possible functions of right whale song

As we have observed no associated behavior coinciding with NPRW song production, theories about its function remain speculative. One probable function is an acoustic reproductive display. It has already been hypothesized that NARW produce gunshots in long bouts in a similar manner as reproductive displays in other species (Parks *et al.*, 2005). However, it has long been assumed that the primary mating strategy for NARW is sperm competition, based on the relatively large size of the testes and simultaneous copulation (Brownell and Ralls, 1986; Mate *et al.*, 2005). Although the mating strategies of NPRW remain unknown, it is thought they share similar mating strategies to the congeneric NARW and SRW. Perhaps NPRW employ multiple mating strategies, and these songs serve as a pre-copulatory acoustic display. During one encounter with two male singing NPRW, there were no females present and no sexual behavior (e.g., surface-active group behavior, belly-to-belly behavior, genitalia observed, etc.) observed. However, this is also seen in humpback whales, and one hypothesis is its function in male social ordering (Darling and Bérubé, 2001; Darling *et al.*, 2006). With limited focal follow data of singing male NPRW, the function of song as it relates to organizing males cannot be definitively determined.

Another aspect of sexual selection and possible function of NPRW song is a territorial display, or a display of dominance toward other males, as has been suggested for other species (e.g., Darling and Bérubé, 2001). Within the eastern population of NPRW, the sex ratio is currently 2:1 male to female. With so few females, it is possible that males must employ acoustic displays towards their conspecific competitors to remain competitive for potential mates. Alternative functions include to stimulate ovulation, as has been hypothesized for humpback whales (Herman, 2017), or as an indicator of size, and thus suitability, of males as a mate, as is seen in sperm whale (*Physeter macrocephalus*) clicks (Gordon, 1991). However, all of these hypothesized functions deal with sexual selection or reproduction and would presumably be taking place at the breeding grounds of the respective species. The songs produced by NPRW were all recorded on their summer feeding grounds. Humpbacks have been known to produce song on their feeding grounds, although these are typically shorter, abbreviated versions of their full song, sometimes referred to as "aberrant song" (McSweeney *et al.*, 1989; Clark and Clapham, 2004). The detection of song on feeding grounds led the authors to hypothesize that courtship and breeding are not confined to lower latitudes but may extend into feeding grounds. As this is the first documentation of songs for NPRW, it remains unknown whether these are abbreviated versions of longer songs.

Yet another possible function is that the songs contain information about the individual caller. The same song was detected on the same day at two locations 310 km apart, suggesting there may not be individual-specificity with regard to song choice. However, individual-specific information may be encoded in the subtle characteristics within each song (e.g., number of gunshots, slight variation in IUIs, etc). In male Atlantic walrus, individual callers can be distinguished based on the timing of each particular pulse pattern (Stirling *et al.*, 1987; Sjare *et al.*, 2003). It is possible the songs produced by NPRW have individual-specific information encoded in the subtle differences of IUIs. Or perhaps the information is encoded within the calls themselves. Upcalls recorded from known NARWs showed sufficient differences to allow for individual discrimination (McCordic *et al.*, 2016); similar discriminatory features may likewise occur in the calls within the songs described here.

Alternatively, there may be individual-preference in choosing songs. There were no two callers at the same location producing the same song simultaneously, so the choice of which song is produced may impart some knowledge about the animal, its behavior, or possibly its fitness. In humpback whales, male singers will alter their acoustic behavior in the presence of another singer (Cholewiak *et al.*, 2018). When in a dyad, male singers would overlap their themes, in a manner similar to song matching, which the authors hypothesize is indicative of competition between males, rather than mate attraction (Cholewiak *et al.*, 2018). As all male humpback whales share the same song, the competition lies in the variations made to that song; however, NPRW produce multiple song types. Perhaps in NPRW, repertoire size is seen as an indicator of fitness. Large repertoires have been documented in bowhead whales (Stafford *et al.*, 2018), although it remains unknown if this is related to mate suitability. Although the paucity of behavioral observations of many species of singing whales makes it difficult to assess the function of repertoire size, in the great tit (*Parus major*), song repertoire size was correlated with reproductive success (McGregor *et al.*, 1981). The larger the male's song repertoire, the greater lifetime reproductive success of the singer (McGregor *et al.*, 1981); similarly, it is possible that male NPRW may be seen as more fit, and therefore a better mate, if they have a larger song repertoire.

One other possible function relates to the availability of resources. Pflumm *et al.* (1984) found that yellow-bellied sunbirds (*Nectarinia venusta*) altered the type and number of elements in the initial and terminal part of the song, respectively, depending on the concentration of the sucrose solution provided. These authors hypothesized that song in yellow-bellied sunbirds encodes information regarding the availability or quality of resources. Additionally, it has been hypothesized that fin whales sing songs as a means of attracting females to aggregations of prey (Croll *et al.*, 2002), signifying their ability to find food resources, and thus fitness to a potential mate. Perhaps similar information regarding resource availability is encoded in the songs of NPRW. This may explain the high variability present in the terminal phrase, as well as their production on feeding grounds. Future analyses should include modeling song distribution and timing with oceanographic and prey parameters to determine whether correlations exist between singing and prey availability.

Regardless of the function of these songs, they likely play an important role in the summer vocal activity of NPRW, with detections numbering in the hundreds for each song type. Right whale acoustic behavior is characterized by periods of high calling activity followed by extensive periods of silence (Matthews *et al.*, 2001; Parks and Tyack, 2005; Crance *et al.*, 2017; Wright *et al.*, 2019). As such, the number of songs detected and presented here are likely an underrepresentation of total song production, due to both the duty cycling of the recorders as well as the scarcity of animals in this population, and the highly mobile nature of this species.

D. Management implications

Currently, the breeding/calving grounds and migration routes of NPRW remain unknown. However, there is considerable passive acoustic monitoring effort along the west coast of the US, and in possible breeding or migratory areas. Given that gunshot songs are a clear indicator of NPRW presence, the detection of these songs in areas outside their known feeding grounds would be instrumental in determining the location of migration routes or breeding grounds.

Additionally, although bowhead whales also produce gunshots (Würsig and Clark, 1993), there are no records of bowheads producing them at high calling rates or in distinctive patterns. As such, these songs may be used to distinguish between the two species at times and locations where the two species may overlap (i.e., Bering Sea shelf in late fall/early winter). It remains unknown whether a portion of the NPRW population remains overwinter in the southeastern Bering Sea. If these songs are detected overwinter, it would indicate NPRW presence, and improve our understanding of the spatio-temporal distribution of NPRW.

E. Conclusions

The findings presented here represent the first documentation of song production by the eastern North Pacific right whale. The four song types detected remained constant over eight years, and overlapped in space and time, indicating multiple animals can produce the same song type. This is the first record of song production in any right whale species. Given its known attribution to male NPRW, and what is known about song in other mysticetes, it seems likely that these songs are reproductive displays. Dedicated focal follow studies are needed to confirm this hypothesis. In addition, future work will attempt to quantify what proportion of their repertoire these songs comprise, determine any diel calling patterns, as well as investigate whether subtle differences within each song encode individual-specific information. Finally, future work should be conducted to determine if seasonally-dependent changes occur (i.e., if there are subtle changes in song production, if terminal phrases change, and whether certain songs are produced at different times within a season). Results from these future studies may allow for more focused research and conservation efforts for this critically endangered population.

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[1] Multi-Électronique, Rimouski, Quebec. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] For more information, see www.birds.cornell.edu/raven.

[3] Greeneridge Sciences, Inc. and Mark McDonald, Whale Acoustics

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