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INTERNATIONAL WHALING COMMISSION

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Salvatore Cerchio[1,2], Andrew Willson[3,4,5], Charles Muirhead[1,6], Suaad Al Harthi[7], Robert Baldwin[3], Marco Bonato[8,9], Tim Collins[10], Jacopo Di Clemente[11], Violaine Dulau[12], Vanessa Estrade[12], G. Latha[13], Gianna Minton[14], Maia Sarrouf Willson[7]

[1] *New England Aquarium, Anderson Cabot Center for Ocean Life, Boston, MA, USA*
[2] *Woods Hole Oceanographic Institution, Woods Hole, MA, USA*
[3] *Five Oceans Environmental Services, Ruwi, Sultanate of Oman*
[4] *University of Exeter, Environment and Sustainability Institute, Cornwall, UK*
[5] *University of Exeter, Centre for Ecology and Conservation, Exeter, UK*
[6] *University of Massachusetts Boston, School for the Environment, Boston, MA, USA*
[7] *Environment Society of Oman, Ruwi, Sultanate of Oman*
[8] *University of Padova, Department of Biology, Padova, Italy*
[9] *University of Torino, Department of Life Science and Systems Biology, Torino, Italy*
[10] *Wildlife Conservation Society, Ocean Giants Program, Bronx, NY, USA*
[11] *Accademia del Leviatano, Rome, Italy*
[12] *Globice, Reunion Island, France*
[13] *National Institute of Ocean Technology, Chennai, India*
[14] *Megaptera Marine Conservation, Den Hague, Netherlands*

ABSTRACT

Existing genetic, demographic and behavioral evidence indicates that Arabian Sea humpback whales represent an isolated and unique population. The population exhibits a Northern Hemisphere breeding cycle, is believed to feed year-round, and lacks the typical latitudinal migrations and seasonal separation of breeding and feeding ecology exhibited by other populations of humpback whales globally. A key feature of humpback whale breeding behavior is the male acoustic breeding display, song, studied extensively around the world. Key characteristics of humpback whale song include: all males within a population share the same song patterns (phrases); a population's song changes progressively over time; and populations that do not overlap or exchange individuals have distinctly different songs, whereas populations in contact share some or all phrases. Here we use long-term acoustic monitoring off the coast of Oman to further assess the isolation of the Arabian Sea population. A total of 76 samples (amounting to 4,434 minutes of recording) of Arabian Sea song collected between 2011 and 2013 were examined, and phrase content was characterized and compared to 23 samples (totaling 202 min of recording) collected during the same years in the Southwest Indian Ocean from Reunion Island and the Comoros Islands. Song from the Arabian Sea and the Southwest Indian Ocean was distinct across the entire study period, with no evidence for shared phrases in any year. In addition, song fragments recorded off western India in 2011 were composed of two phrases present in the Oman song, suggesting continuity across the Arabian Sea. Moreover, the Arabian Sea song exhibited a markedly atypical low level of temporal variation, with song phrases remaining virtually unchanged during the three examined breeding seasons. Notably, Southwest Indian Ocean song was recorded off the coast of Oman in August 2012 (Boreal summer, Austral winter). This song was recorded on multiple days and included multiple simultaneous singers over a 25 day period indicating the presence of more than a single accidental vagrant Southern Hemisphere animal. We suggest that these Southern songs were produced by Southwest Indian Ocean animals moving into the Arabian Sea, and that this may be more common than is currently thought. The low level of temporal variation shown by the Arabian Sea males along with the lack of adoption of the Southwest Indian Ocean song material, further indicate the uniqueness and distinct nature of this population. It seems possible that isolation mechanisms exist that may inhibit the mixing of the Arabian Sea population with Southern Hemisphere animals, and that this may be reflected in the observed atypical song behavior.

INTRODUCTION

Humpback whales are known for the diversity and complexity of their vocalizations, which can be broadly classified into three categories: *Song*, a male breeding display (Payne & McVay 1971, Winn and Winn 1978); *Social sounds*, produced by all subclasses and likely having social communicative function (Silber 1986, Dunlop et al. 2007); and *Feeding cries*, currently documented only from southeast Alaska and apparently having a prey herding and/or foraging coordination function (Cerchio & Dalheim 2001). Humpback whale song has received considerable research focus due to its ubiquitous presence on breeding grounds and intriguing complexity, with several fundamental features shared among populations globally. Only males sing and it is considered a breeding display important to male reproductive success (Herman and Tavolga 1980, Glockner 1983, Darling et al. 1983). It consists of a complex hierarchal sequence of stereotyped patterns, first described and categorized by Payne & McVay (1971), in a classification system that is still used by most authors today (Figure 1). The basic building block of the pattern is termed a "Unit", analogous to a note, and a phonation that appears continuous to the human ear. Units vary markedly in temporal and frequency characteristics, with fundamental frequencies spanning a broad spectrum from ca. 20-10,000 Hz, complex harmonic structures, and both frequency and amplitude modulation. Different units are arranged into distinctly stereotyped and recognizable patterns termed "Phrases" that are typically 10-30sec in duration. The same (or very similar) phrase is repeated a variable number of times in an uninterrupted sequence to comprise a "Theme", each theme having its own diagnosable phrase type. A series of themes, most commonly from four to eight, are uttered in sequence to comprise a "Song", which typically lasts from 5-30 minutes. The sequence order of themes within a song is often, but not always, consistent within and between individuals. Songs are repeated one after the other without breaks, at times for many hours. Although Payne and McVay (1971) chose to call the long repeating and hierarchical sequence of phrases a song, Cholewiak et al. (2013) noted that in comparison to birdsong, the humpback phrase is more analogous to a single song of a songbird. Moreover, the Paynian humpback whale song is analogous to the complete run-through of the repertoire of a bird exhibiting the singing behavior of "eventual variety" (Kroodsma 1982); in this behavior a singer will repeat a song several times in a sequence (as humpbacks do with phrases in a theme) before switching to a different song (a different theme in humpback song) and eventually sing through their entire repertoire (a humpback whale song). Therefore, we consider the phrase to be the fundamental element of humpback whale song, a principal that guides our approach towards analysis; moreover, challenges in defining what constitutes a Paynian humpback whale song due to high levels of intra- and inter-individual variation results in distinct inconsistencies between researchers on the classification of songs (Cholewiak et al. 2013); this ambiguity is much reduced at the phrase level, due to the far greater stereotypy of individual phrases.

All males in a population sing the same (or very similar) patterns, and the patterns change over time with all males learning and incorporating the changes, thus maintaining continuity within the population (Payne and McVay 1971, Payne et al. 1983, Guinee et al. 1983). It is believed that cultural transmission via vocal learning is the process by which males maintain consistency across individuals, and populations that have demographic exchange of individuals culturally transmit and share songs; therefore, the propensity to share song types among neighboring populations provides the opportunity to utilize song as an indicator of population connectivity and interchange between populations (Payne & Guinee 1983, Cerchio et al. 2001, Garland et al. 2011). This was first described in the North Pacific and North Atlantic Oceans (Winn et al. 1981, Payne & Guinee 1983, Cerchio et al 2001), and has been the focus of more recent work in the southern hemisphere (Noad et al. 2000, Garland et al. 2011). Relating to geographic variation among the Indian Ocean populations, extensive song similarity has been documented between Madagascar and the South Atlantic populations off Gabon and Brazil, indicating relatively extensive interaction in the South Indo-Atlantic region (Darling and Sousa-Lima 2005, Razafindrakoto et al 2009). There were few similarities documented between Madagascar and Western Australia, indicating limited interaction but still some exchange (Murray et al. 2012). Whitehead (1985) originally suggested that song recorded in the North Indian Ocean off Oman and Sri Lanka was similar, but distinct from North Pacific song. Moreover, a cursory assessment of existing data from 2001 to 2003, songs from Oman showed no similarities with the SWIO population (S. Cerchio, personal observation based on unpublished data collected by Environment Society of Oman and partners in the Arabian Sea and Wildlife Conservation Society in Madagascar), providing further support for the genetic (Pomilla, Amaral et al. 2014), demographic and behavioural (Minton et al 2011, Willson et al. 2016, 2017) lines of evidence for isolation of the Arabian Sea population.

Together, these studies on regional variation globally illustrate the power of song analysis for making inferences on population connectivity. In this study we use song as a means to further explore the isolation of the Arabian Sea humpback whale population, by conducting a more robust comparison than previously possible utilizing a large sample size of recordings collected from the coast of Oman with those collected off Reunion Island and the Comoros Islands, as well as the coast of India.

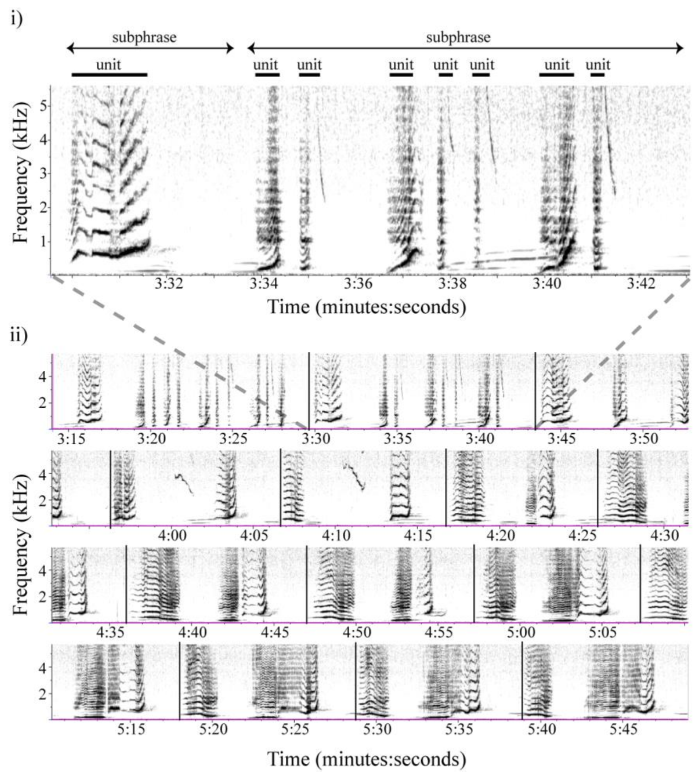


Figure 1. Spectrogram of humpback whale song sequence illustrating hierarchal song structure (adapted from Cholewiak et al. 2013). Time on the x-axis is in minutes:seconds, while frequency on the y-axis is in kHz. i) One phrase consisting of two subphrases. The first subphrase is composed of one unit, while the second subphrase is composed of a repeating pattern of 2-3 individual units. ii) 155-second sequence of song, in which multiple types of phrases can be observed. Phrases have been delineated by vertical lines.

METHODOLOGY

Oman Arabian Sea Song

Archival recorders and sample characteristics

Three autonomous archival acoustic recorders, Wildlife Acoustics model SM2M (www.wildlifeacoustics.com), were deployed in 2011/2012 in the Hallaniyats Bay region, the site of previous boat surveys focusing on the population of Arabian Sea humpback whales (Figure 2). The sites are referred to as: Hal 1 – Hasakiyah, furthest east; Hal 2 – Ras al Hamrah, furthest to the north; and Hal 3 – Ras al Hasik, furthest to the south (Figure 2C). Distance between deployment sites ranged from 20km to 31km and depth at deployment sites ranged from 16m to 33m. Given these distances and reduced sound propagation in the shallow water shelf habitat, it was considered that each recorder had independent listening space. From November 2011 to October 2012, three separate deployments were conducted, with varying recording parameters and durations (Table 1). The first two deployments from November 2011 to March 2012 recorded continuously at sample rates of 16kHz (8kHz recording bandwidth) and 32kHz (16kHz recording bandwidth), respectively. The third deployment was duty cycled to record 10min every 30min (10min on / 20min off) at 22kHz, in order to have a longer recording endurance from March until October 2012.

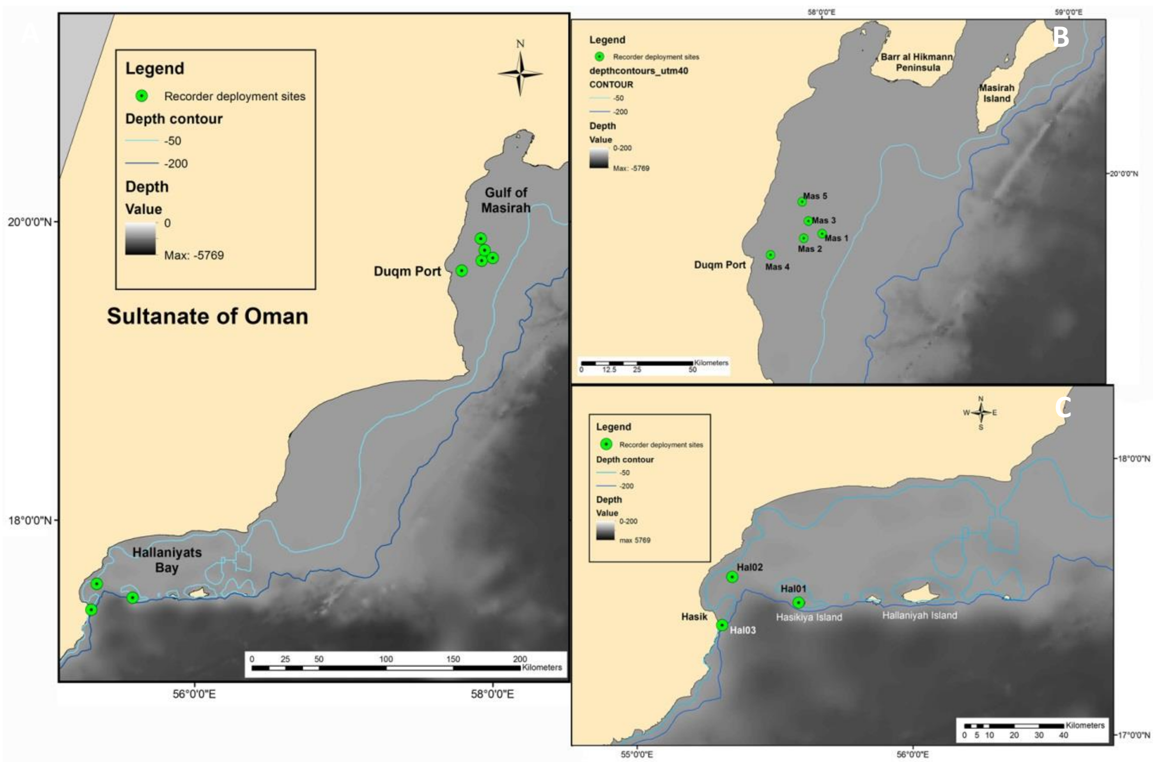


Figure 2. Study region off the cost of Oman (A), showing positions of deployed recorders in the Gulf of Masirah / Duqm site (B) and the Hallaniyats Bay site (C).

During 2012/2013 the recorders were deployed in the Gulf of Masirah near the port of Duqm, with the intention of documenting presence of whales at this more northerly site and with consideration of the port development occurring at Duqm (Baldwin *et al*., 2015). Two deployments were conducted with different spatial arrangements and deployment sites. The first deployment from November 2012 to April 2013 was placed in a triangle formation at sites referred to as Mas 1, Mas 2 and Mas 3, with 8km spacing between each unit at depths from 24m to 27m, and ranging from approximately 20km to 27km from the mainland coast near Duqm (Figure 2B). Given the relatively close spacing of this deployment, it is likely that the recorders had overlapping listening spaces. Recordings were made on a duty cycle different than in Hallaniyats Bay, recording 15min every 30min (15min on / 15min off). After this deployment, the units were redeployed between April 2013 and Mar 2014 in a different spatial arrangement covering a greater range, maintaining one unit at Mas 2, and deploying the others at new sites, Mas 4, and Mas 5 (Figure 2B). Distance between sites ranged from 16km to 27km and depths were all ca. 24m; given these distances it was considered that each recorder had independent listening space.

Table 1. Description of acquired data for each deployment at each site, accounting for only complete days of data. See text and Figure 5 for description of site names and positions of sites.

	Deployment 1				Deployment 2				Deployment 3			
Site	First Day Data	Last Day Data	Days Data	Duty Cycle Min on/off	First Day Data	Last Day Data	Days Data	Duty Cycle Min on/off	First Day Data	Last Day Data	Days Data	Duty Cycle Min on/off
Hal 1	11/24/2011	1/19/2012[1]	48[1]	Continuous								
Hal 2	11/24/2011	2/18/2012	87	Continuous	2/25/2012	3/25/2012	30	Continuous	3/30/2012	9/25/2012	180	10/20
Hal 3	11/24/2011	2/2/2012	71	Continuous	2/25/2012	3/25/2012	30	Continuous	3/30/2012	10/20/2012	205	10/20
Mas 1	11/23/2012	4/12/2013	141	10/20								
Mas 2	11/23/2012	4/12/2013	141	10/20	4/15/2013	8/13/2013	73[2,3]	15/15				
Mas 3	11/23/2012	4/12/2013	141	10/20								
Mas 4					4/15/2013	7/28/2013	105[3]	15/15				
Mas 5					4/15/2013	8/9/2013	117[3]	15/15				

[1] The Unit deployed at Hal 1 experienced a catastrophic failure due to electrical shorting and stop recording entirely on 1/31/2011. Signal interruptions starting on 12/14/2011 caused the loss of complete hours of data on 21 days resulting in only 48 complete days of data between the indicated dates during Deployment 1. Thereafter the unit was not functional and thus there were no Deployments 2 or 3 at Hal 1.

[2] Mas 2, Deployment 2 experienced an unexplained gap in recording from 5/23/2013 to 7/9/2013, resulting in only 73 complete days of data.

[3] Mas 2, 4 and 5, Deployment 2, stopped recording well short of anticipated 211 days due to suspected failure of logging unit circuitry.

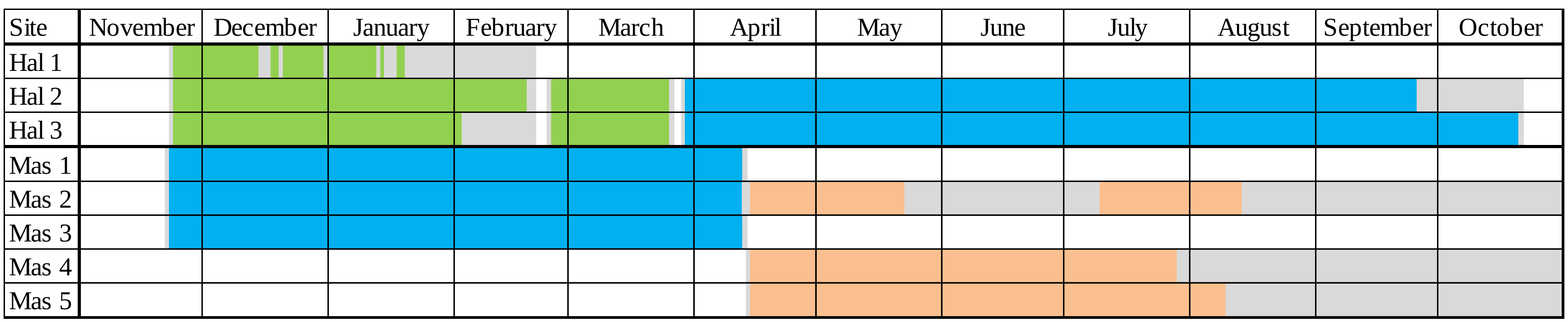


Figure 3. Temporal map of available recordings from deployments off Oman. The entire recording period for Hallaniyats Bay (Hal 1, 2 and 3) and Gulf of Masirah (Mas 1, 2, 3, 4 and 5) are aligned by month of the year, despite the former being sampled in 2011/2012 and the latter in 2012/2013. Days for which there were complete days recorded are color coded for recording schedule: green being continuous, blue duty-cycled 10min on and 20min off, and orange duty-cycled 15min on and 15min off. Grey indicates periods for which the unit was deployed but either no data were recorded, or an incomplete day (<24hrs) was recorded.

The performance of the recorders varied from expectations among the different deployments, with some deployments providing data at, near or exceeding expected recording duration and others manifesting technical failures that yielded reduced data (Table 1, Figure 3). In Hallaniyats Bay, the unit deployed at site Hal 1 had a catastrophic failure during Deployment 1 due to an internal electrical short partway through the deployment, resulting in no data from Hal 1 for Deployments 2 and 3. In the Gulf of Masirah, all three units during Deployment 1 performed as expected; however, during Deployment 2 the units performed inconsistently and for less than the expected duration, with the last data-day recorded between late July and mid-August 2013, well before the mid-November expectation, and Mas 2 experienced an unexplained gap in recording between mid-May and mid-July. Considering only days for which data were collected in all 24-hour blocks, the total sample included 651 complete data days in Hallaniyats Bay and 718 complete data days in Gulf of Masirah. As a visual overview of the entire sample, Figure 3 displays a temporal chart of all deployments, indicating when the units were deployed, when data were recorded, when failures resulted in no data collection, and the programmed duty cycle for the collected data.

Relevant to this analysis of song structure, there were several consequences of the sampling scheme and unit failures. All deployment sample rates provided a frequency bandwidth great enough to record the complete bandwidth of humpback whale song for the region (considering fundamental frequencies of units) and readily allowed classification of phrase types. Continuous recording deployments (Hallaniyats only, blue in Figure 3) provided complete and extended sequences of song; duty cycled deployments provided only segments of song sequence equivalent to the sampling period (10 or 15min). Unit failures resulted in reduced data for some periods, and consequently lower probability of recording high signal-to-noise ratio (SNR) songs samples. Of some consequence to the interpretation of results, the Hallaniyats deployments covered nearly the entire year from late November 2011 to mid-October 2012, whereas the Masirah deployments only covered late November to mid-August, consequently missing part of the Boreal summer and autumn (the Austral winter and spring, or Southern Hemisphere breeding/singing season). As will be described, although song was recorded during August and September 2012 in Hallaniyats, we did not have the sample to assess this for 2013 in Masirah.

Acoustic detection analysis

As described in Cerchio et al. 2016b, presence/absence of humpback whale vocalizations was documented in each hour of each deployment by manually browsing spectrograms with a frequency band of 0-1,000 Hz; this band encompasses the majority of humpback whale song signals and standardized detection across the variety of sampling bandwidths. In order to standardize assessment of the presence of humpback whales across recording schemes, we examined ten minutes starting at the beginning and half-hour point of every recorded hour, which was the maximum sample length common to all recording sites and deployments. Each 10-minute recording period was logged as either containing humpback whale song or social sounds or as being devoid of humpback vocalizations. Given that humpback whales characteristically sing for hours continuously, by examining two 10-minute windows separated by 20min, we are confident that we would detect song in every hour in which it was audible at the recording site. The SNR for detected song varied markedly, from cases where complete phrases and details of all units were obvious and clear, to cases where only one or two units in each phrase could be faintly detected and phrases could not be consistently classified (Figure 4). During browsing, all detections were qualitatively graded on a scale from A to D for high to low SNR. In terms of the current analysis of song structure, this provided a “roadmap” of the entire sample facilitating the identification of high SNR song samples that were suitable for classification of phrase types. A second pass was then made through all detections assigned an “A” quality rating to further classify them in terms of length and consistency of high SNR over an extended period. The goal was to identify a set of samples that were ideally 30-60min or greater in length with high enough SNR to confidently classify different phrase types for the entire sample sequence. These were in turn rated on a scale of 4 to 1 for high to low SNR, and served as the sample for song structure analysis.

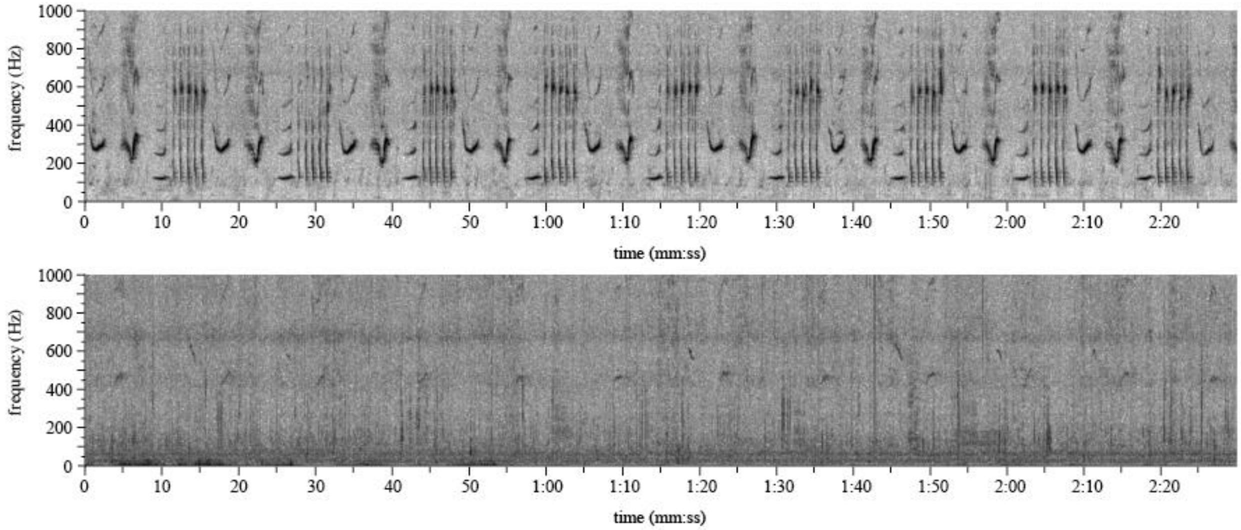


Figure 4. Example spectrograms of humpback whale song detected during browsing of recorder data, illustrating the range in signal quality, with a high quality, high signal-to-noise ratio exemplar (top panel), and a low quality, low signal-to-noise ratio exemplar (lower panel). Spectrograms are displayed with a 1000Hz bandwidth and 2.5min length, as each line was displayed during the browsing.

Each song sample consisted of an unbroken phrase sequence without extended complete "fade-outs" where song could not be detected. Such a song sample was considered to be a single individual male for continuously recorded data. For those deployments that were duty cycled, if there existed a series of 10 or 15min sample periods that maintained a high SNR without fading, they were lumped together to represent a single song sample. Ultimately, it is impossible to be confident if each separate recording sample was from the same individual due to the intervening periods of no recording, so there is an assumption on individual identity. Data from the continuously recording deployments indicated that individual singers were heard for extended periods at a consistent SNR and cases of multiple singers were rare (particularly singing at similar SNRs), therefore we believe this to be a reasonable assumption. However it is important to note that it was impossible to determine if a given male was represented multiple times throughout the dataset, either in consecutive samples or across days and months, and therefore there is a degree of non-independence for which it is impossible to control.

Qualitative Phrase Classification and Logging

Initially a few high quality samples from both 2012 and 2013 were examined in order to classify and numerically label different phrase types according to general guidelines presented in Cholewiak et al. (2013). In all cases the shift from one phrase type to another was unambiguous based upon markedly different arrangements of different units. In cases where there was minor variation, comprised of a change in unit type within the same general phrase type, and that variation was consistent across a sequence of several phrases, a phrase variant was alphabetically labeled (e.g., Phrase 1a and 1b). A phrase guide was then created with exemplars for each phrase type to aid in the logging of phrases across the song sample. A subset of the best recordings, based on the 4 to 1 quality rating, were chosen for detailed logging of phases, in which every phrase in as long of a continuous sequence as possible was classified and logged. A minimum of 5 samples were chosen for logging during each of the early (December to March) and late (April to June) singing seasons in both 2012 and 2013. The remaining song samples were scanned to assess for consistency across samples in song structure and to detect any previously unidentified phrases. In addition to the archival recorder data from 2012 and 2013, a single boat-based recording from Oman in 2011 was classified and logged to assess consistency and change across the three seasons.

Southwest Indian Ocean Song

A small sample of boat-based recordings was obtained from colleagues that were opportunistically recording humpback whale song in the Southwest Indian Ocean (SWIO) during the same years of the Oman recording effort. Several samples recorded off Reunion Island during the Austral winters (Boreal summers) of 2011, 2012 and 2013 were provided by V. Dulau (unpublished data), and several samples recorded off Grande Comore, Comoros Islands during the Austral winter of 2013 were provided by M. Bonato and J. Di Clemente (unpublished). These years bracketed the years of the Oman deployments, being collected in the Southern Hemisphere singing seasons. Recording gear, quality and length varied greatly among the contributed samples. All recordings of sufficient quality for phrase classification were logged as described above for Oman recordings. Once all samples were classified and logged, exemplar phrases were qualitatively compared to assess for similarities or differences between regions and years.

Arabian Sea Song from the west coast of India

In addition to the primary song samples described above, fragments of humpback whale song recorded in the southeastern Arabian Sea were provided by G. Latha and M.M. Mahanty (Mahanty et al. 2015). These data consisted of ten 30-second samples recorded during January (n=3), February (n=6) and March (n=1) of 2011 by an autonomous ambient noise recorder situated off the southwestern coast of India near Cochin, Kerala; details of recording system and protocol were reported in Mahanty et al. (2015). These song fragments were examined to assess similarity of songs across the Arabian Sea during 2011.

RESULTS

Humpback whale detections and song sample in Oman

Humpback whale vocalizations were detected at all Oman recording sites at some point during all deployments, and were predominantly song. A total of 43,848 10min samples were scanned, representing 23,424 hour-blocks, and resulting in 5,802 hour-blocks with humpback whale detections across all sites and deployments. As an overview of detections in the two study areas, data from each were lumped into a composite depiction of hourly presence (Figure 5). For this assessment, if a whale was detected in a given hour-block at any of the three sites at which units were simultaneously deployed, that hour was scored as having a whale present (essentially "in the study area" as a whole). For each hour block in which song was detected, a subjective quality score was assigned, and all hours with the highest "A"-quality rating were examined to determine sequences that were suitable for analysis and identify individual song sequence samples. We identified a total of 32 samples during the Boreal winter of 2012 from the Hallaniyats sites, and 33 samples during the Boreal winter of 2013 from the Masirah sites (Table 2) for a total of 4,307min of song that were reviewed. In addition 11 samples totaling 126.5min of recording were identified during the Boreal summer of 2012 from Hallaniyats Site Hal2 between 10-August and 3-September.

Humpback whale song sample in the Southwest Indian Ocean

A total of 17 boat-based recordings were contributed from Isle Reunion recorded during the Austral winters of 2011, 2012 and 2013; of these 11 samples proved to be of adequate length and quality to classify and log phrases for a total of 170.1 min of recording (Table 3). A total of 6 boat-based recordings were contributed from the Comoros Islands recorded during the Austral winter 2013; of these 2 samples proved to be of adequate length and quality to classify and log phrases for a total of 32.1 min of recording (Table 3). This amounted to the review of 4, 3 and 6 samples from 2011, 2012 and 2013, respectively, from the Southwest Indian Ocean.

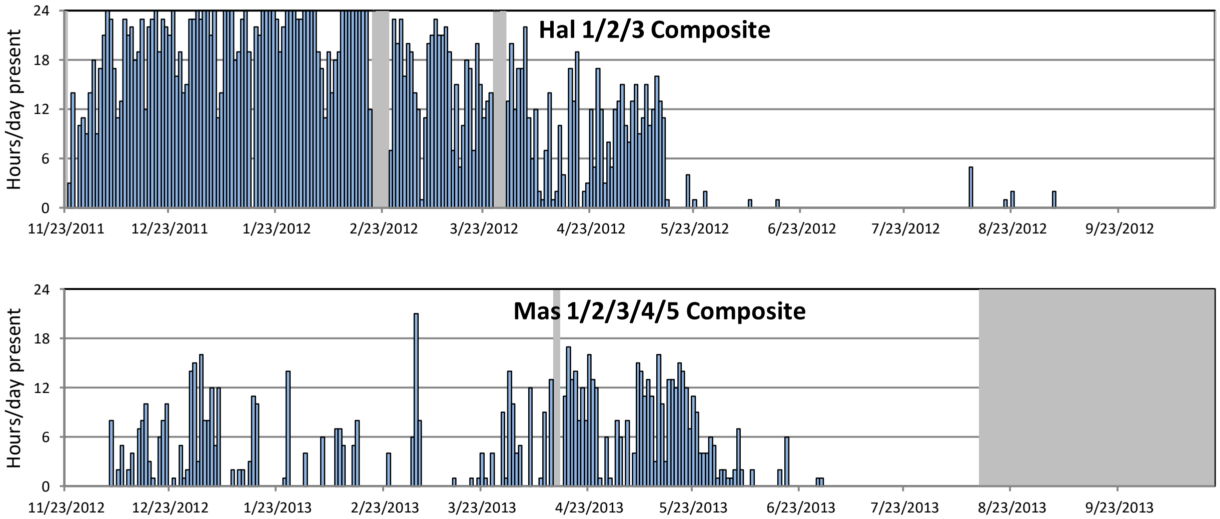


Figure 5. Daily occurrence of humpback whale vocalizations as shown by composite histograms for all sites in Hallaniyats Bay (Hal 1, 2 and 3) and Gulf of Masirah / Duqm (Mas 1, 2, 3, 4 and 5), showing the number of hours in a given day in which humpback whales were detected during complete days for which recordings were available. Since these sites within each region were not close enough to record the same whales, the composite histogram combining the data from all sites represents a general indication of presence in the region as a whole. Grey indicates no data.

Table 2. Summary of sample of humpback whale song recorded off Oman in 2012 and 2013.

Season	Analysis	Samples	Min Date	Max Date	Mean Sess Dur (min)	Mean Rec Len (min)	Total Rec (min)	Mean Log Rec (min)	Total Log (min)
Winter 2012		***32***	***12/6/2011***	***5/1/2012***	***100.8***	***86.3***	***2761.2***		
	Logged	13	12/30/2011	5/1/2012	103.5	78.0	1014.3	47.4	615.6
	Scanned	19	12/6/2011	4/6/2012	98.8	91.9	1746.9		
Summer 2012		***11***	***8/10/2012***	***9/3/2012***	***30.5***	***11.5***	***126.5***		
	Logged	6	8/10/2012	9/3/2012	42.9	15.1	90.5	6.1	36.6
	Scanned	5	8/20/2012	9/3/2012	15.6	7.2	36.0		
Winter 2013		***33***	***12/5/2012***	***5/23/2013***	***105.0***	***46.9***	***1546.1***		
	Logged	10	12/5/2012	5/22/2013	114.7	46.7	467.1	32.4	323.7
	Scanned	23	12/28/2012	5/23/2013	100.8	46.9	1079.0		
Total		***76***	***12/6/2011***	***5/23/2013***	***92.4***	***58.3***	***4433.8***		***975.9***

Table 3. Summary of sample of humpback whale song recorded off Reunion and Comoros Islands in 2011, 2012 and 2013.

Region / Year	Samples	Min Date	Max Date	# Samples Logged	Mean Log Rec (min)	Total Log (min)	Total # Phrases
Reunion 2011	***6***	***8/19/2011***	***10/19/2011***	**4**	***10.1***	***40.4***	***117***
Reunion 2012	***5***	***7/24/2012***	***8/26/2012***	**3**	***16.9***	***50.8***	***293***
Reunion 2013	***6***	***8/23/2013***	***9/05/2013***	**4**	***19.7***	***78.9***	***348***
Comoros 2013	***6***	***8/8/2013***	***8/15/2013***	**2**	***16.0***	***32.1***	***135***
Total	***23***			***13***		***202.2***	***893***

Song Structure and Phrase Types in the Oman Boreal Winter Samples

Of the 65 song samples identified in the initial review of the 2012 and 2013 Boreal winter Oman data, 23 were chosen for logging phrases based on quality and length (Table 4). These were chosen to divide each yearly sample into early and late season, in order to assess change during the singing season, with at minimum 5 samples in each period; for late season 2012, seven samples were logged due to the short duration of some of the samples (Table 4). In total, 939 min were reviewed with individual samples ranging from 5 to 251 minutes, and 5143 phrases were logged with individual samples ranging from 28 to 700 phrases. Figure 6 illustrates a 12 min section of recording from site Hal 2 on 19 Feb 2012 with all phrases logged for a complete song sequence.

Oman song phrases were classified into five distinct phrases, two of which had two variants, for a total of seven readily identifiable phrase types (Figures 6 and 7). For each of the logged song samples, a set of high SNR exemplar phrases were selected to represent the repertoire of the singer, and from those the most clear exemplars were chosen to illustrate the phrase types for the period (Figure 7). The pattern of units comprising Phrase Types 1, 2, 3, 4 and 5 were all distinctly different with no ambiguity or graded signals that would confuse qualitative categorization of a phrase (Figure 7). For Phrases 1 and 5, two variants were identified for each. In Phrase Type 1, the presence of a frequency oscillation in either or both units 3 and 4 was classified as Phrase Type 1a, whereas the absence of the oscillation in both units was classified as 1b; in most sequences where both Phrase Types 1a and 1b were present, it progressed from 1a to 1b without reversal (e.g., as in Figure 6). In Phrase Type 5, a series of 3-5 low frequency grunts occurred at the end of the phrase; when these were upswept it was classified as Phrase Type 5a, whereas when they were downswept it was classified as 5b (Figure 7). Most of the seven phrase types were present in the logged samples with only one sample having four of the phrase types and the remainder having between five and seven (Table 4). After the classification of all phrases in the 23 logged samples, the 42 samples that were not logged were carefully scanned for phrase content, indicating no new phrases that were not identified in the 23 logged samples, and congruity with the described phrase types. Therefore we are confident that we have identified all phrase types present in the 2012-2013 Oman song.

The single 22min boat-based recording from 2011 was also logged after the classification of phrase types from the extensive 2012 and 2013 season samples (Figure 8). All five major phrase types were identified among 101 phrases logged in the 2011 recording, however Phrase Type variants 1a and 5a were not identified. In addition, Phrase Type 4 was represented by two variants, 4a with a strong oscillation in the first unit, and 4b which was equivalent to Phrase Type 4 of 2012 and 2013 (Figure 8). Also an additional distinct phrase was identified and labeled Phrase Type 6 (out of numerical order) although it occurred only twice between a sequence of Phrase Types 3 and 4b (Figure 8).

Table 4. Details of humpback whale samples logged for phrase content during the winters of 2012 and 2013.

Singer#	Site	Dep	Date	Qual Index	Sess Dur (min)	Rec Len (min)	Logged (min)	Total # Phrases	# Phrase Types
Boreal Winter 2012									
2011-12-30-A	Hal 2	1	30-Dec-11	3	240.1	238	101.9	454	7
2012-02-02-A	Hal 3	1	2-Feb-13	2	109.6	110	31.6	181	6
2012-02-02-B	Hal 3	1	2-Feb-13	4	85.8	86	59.1	440	6
2012-02-02-C	Hal 3	1	3-Feb-13	4	36.9	37	35.5	330	7
2012-02-17-A	Hal 2	1	17-Feb-12	4	113.1	113	105.4	494	7
2012-02-19-A	Hal 2	1	19-Feb-12	4	253.2	251	138.7	700	7
2012-04-18-A	Hal 3	3	18-Apr-12	4	210.2	76	65.6	482	4
2012-04-22-A	Hal 2	3	22-Apr-12	4	9.5	11	9.0	39	5
2012-04-22-B	Hal 2	3	22-Apr-12	4	4.9	5	4.6	28	5
2012-04-23-A	Hal 2	3	23-Apr-12	4	37.4	17	9.1	46	5
2012-04-24-A	Hal 2	3	24-Apr-12	3	121.0	39	17.3	87	6
2012-04-25-A	Hal 2	3	25-Apr-12	4	55.0	14	12.7	67	5
2012-05-01-A	Hal 2	3	1-May-12	4	69.4	28	25.2	142	6
Boreal Winter 2013									
2012-12-05-A	Mas 3	1	5-Dec-12	4	150.0	50	33.2	179	6
2013-02-23-A	Mas 3	1	23-Feb-13	4	97.4	37	27.6	127	5
2013-03-02-A	Mas 3	1	2-Mar-13	4	230.0	70	58.7	276	5
2013-03-04-A	Mas 2	1	4-Mar-13	4	157.2	34	34.1	199	4
2013-03-22-A	Mas 1	1	22-Mar-13	4	40.0	20	9.7	45	5
2013-04-22-C	Mas 5	2	22-Apr-13	4	73.5	43	37.2	204	5
2013-05-15-B	Mas 5	2	15-May-13	4	81.8	37	35.7	173	5
2013-05-16-B	Mas 5	2	16-May-13	4	76.8	32	28.3	134	5
2013-05-20-A	Mas 5	2	20-May-13	3	180.0	90	30.0	155	5
2013-05-22-A	Mas 4	2	22-May-13	4	60.4	30	29.2	161	5

A marked aspect of the Oman song structure is the consistency and minimal amount of temporal change across the three examined years (Figures 7 and 8). This low level of variation across three years is striking in relation to typical humpback whale song behavior documented in other regions globally. There were several apparent “extinction” events; Phrase Type 4a and 6 which occurred in 2011 were definitively not present in any of the large sample of 2012 and 2013, so clearly disappeared; Phrase Type 5b was present in both the single 2011 sample and in the early 2012 samples, but disappeared thereafter; and Phrase Type 1a was not identified in any of the late 2013 samples, so may also have disappeared. The absence of Phrase Types 1a and 5a in the 2011 sample suggests that these may have been innovations in 2012; however the 2011 sample is too small to be conclusive. Irrespective of these changes in the repertoire of phrase types, those phases that occurred in all years showed very little change in their specific phrase structure across the three year period (Figures 7 and 8).

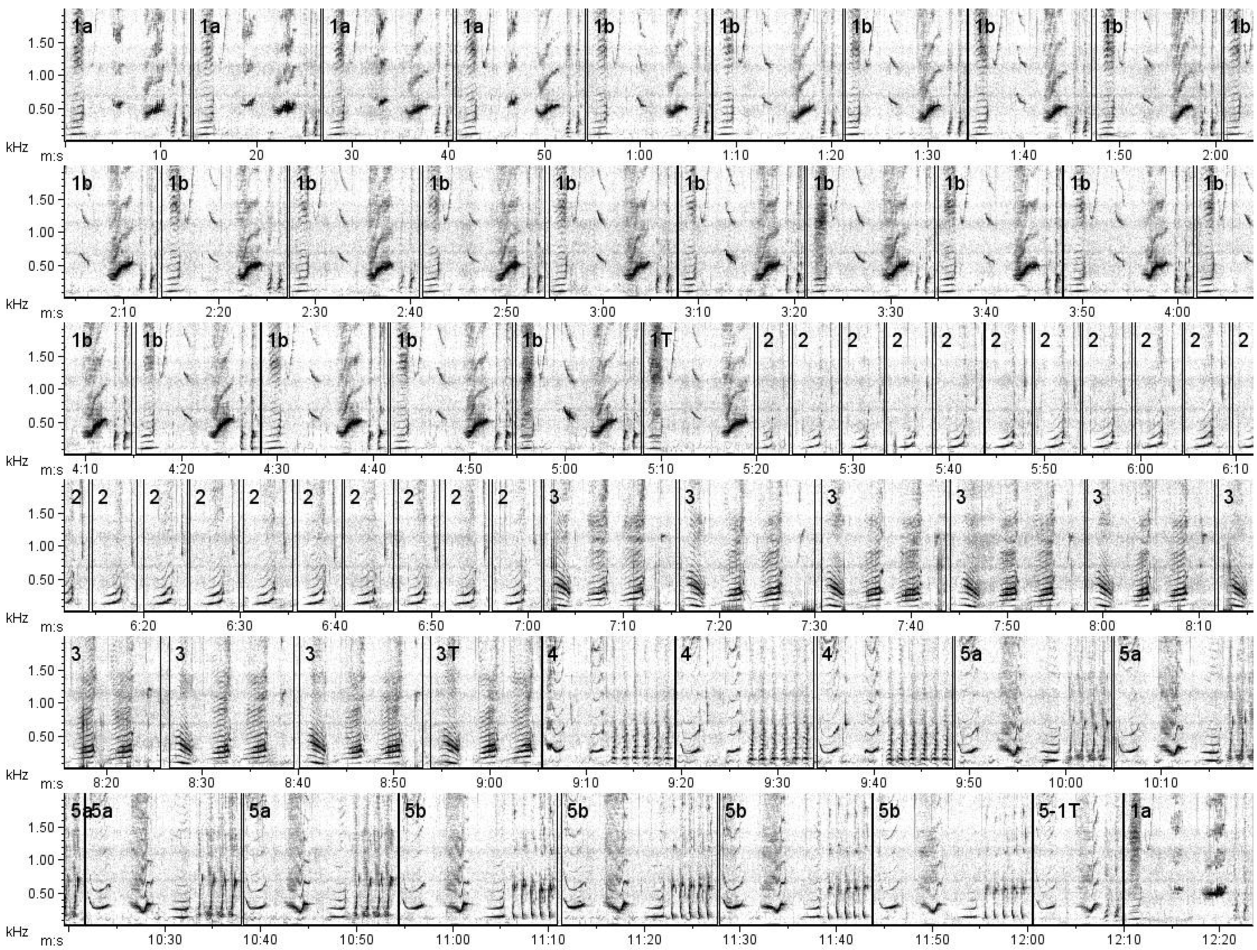
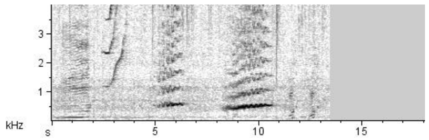
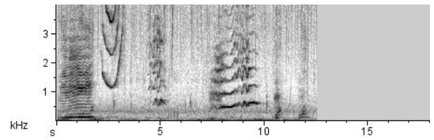
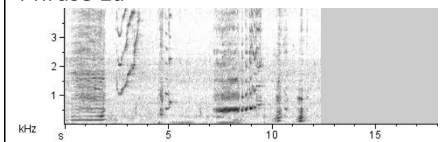
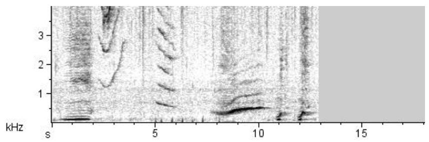
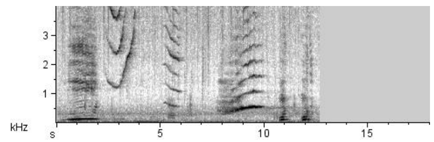
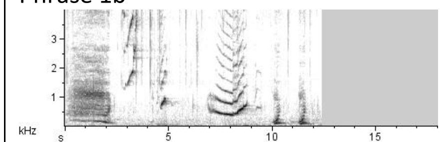
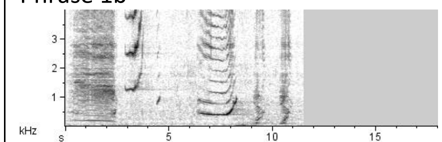
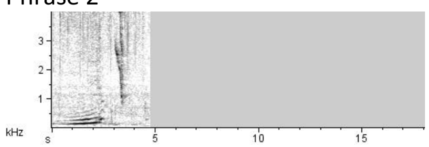
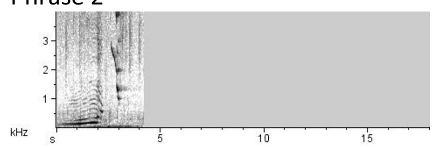
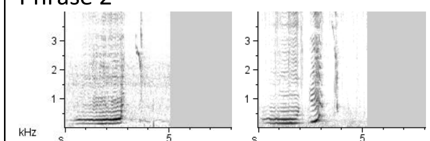
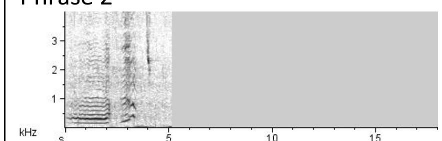
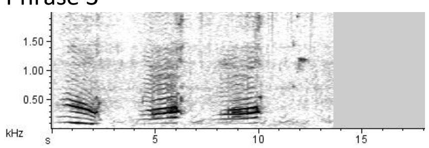
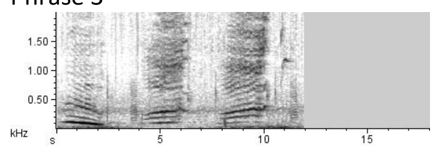
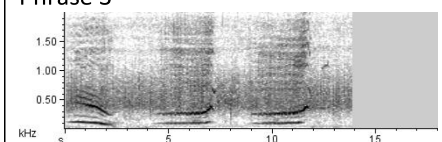
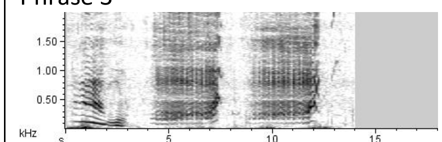
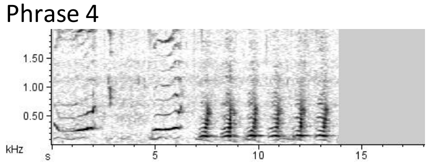
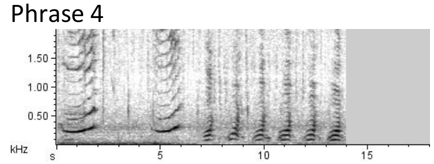
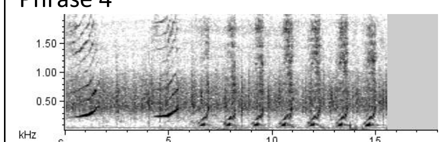
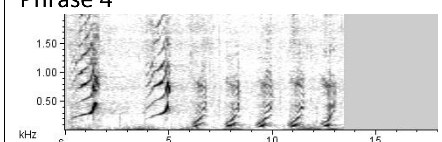
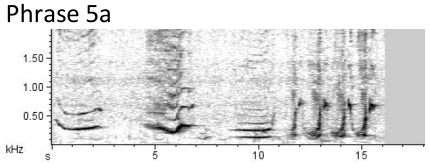
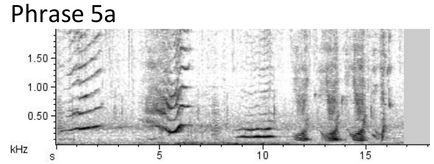
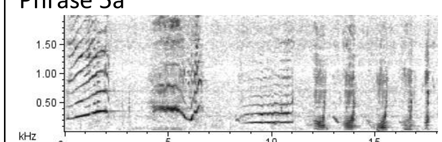
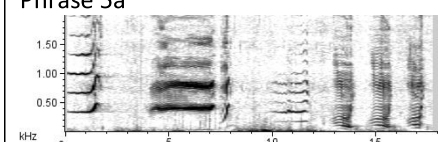
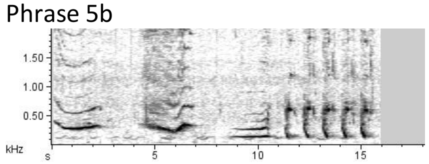


Figure 6. Spectrogram of song recorded off Oman at site Hal 2 on 19 Feb 2012, illustrating a complete song sequence of 66 consecutive phrases and the seven different phrase types and variants (Phrases 1a,1b, 2, 3, 4, 5a and 5b) classified for the year. Each phrase is delineated with a line and labeled in the top right corner; repetitive sequences of the same phrase type making up "themes" are evident; phrase labels with "T" represent a transition phrase between different themes, as is typical in humpback song globally.

Figure 7. (Next page) Exemplar phrases from Hallaniyats Bay, Oman in 2012, and Gulf of Masirah, Oman in 2013. For each year phrases are illustrated from early season (Dec 2011-Feb 2012, and Dec 2012-Mar 2013) and late season (Apr-May 2012, and May 2013). Spectrograms generated at resolution of ca. 45ms and 10Hz, and frequency bandwidth of 0-4kHz (Phrases 1a, 1b, 2) or 0-2kHz (remainder).

Oman 2012 - early	Oman 2012 - late	Oman 2013 - early	Oman 2013 - late
Phrase 1a 	Phrase 1a 	Phrase 1a 	Phrase 1a Not present
Phrase 1b 	Phrase 1b 	Phrase 1b 	Phrase 1b 
Phrase 2 	Phrase 2 	Phrase 2 	Phrase 2 
Phrase 3 	Phrase 3 	Phrase 3 	Phrase 3 
Phrase 4 	Phrase 4 	Phrase 4 	Phrase 4 
Phrase 5a 	Phrase 5a 	Phrase 5a 	Phrase 5a 
Phrase 5b 	Phrase 5b Not present	Phrase 5b Not present	Phrase 5b Not present

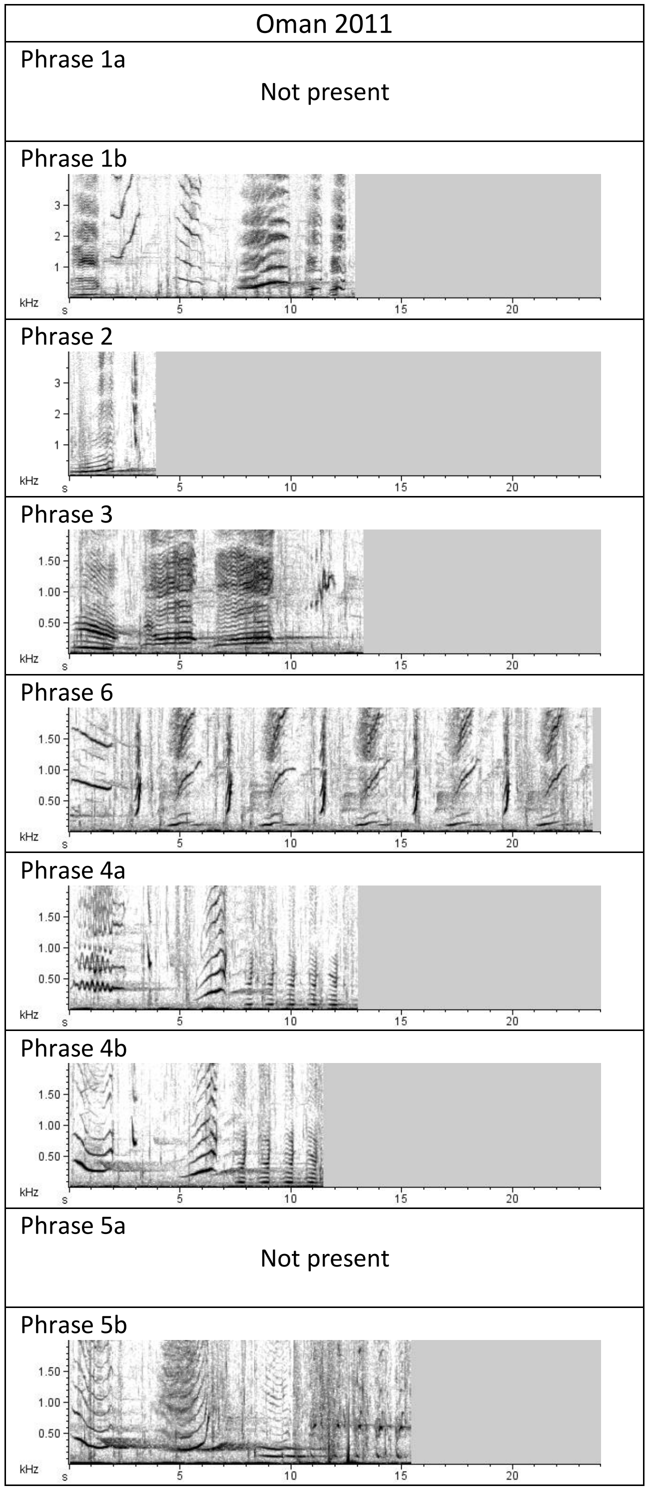


Figure 8. Exemplar phrases from a single male recorded in Hallaniyats Bay, Oman on March 18, 2011. Phrases were labelled giving priority to 2012 recordings, such that some incongruities exist in the naming protocol for this year: Phrases 1a and 5a of 2012/2013 were not found in this 2011 recording; Phrase 6 was not found in 2012/2013 (an apparent extinction event), but is illustrated in its relative sequence order between Phrase 3 and 4a; Phrase 4a of 2011 was not found in 2012/2013, and thus Phase 4b of 2011 is equivalent to Phrase 4 of 2012/2013. Spectrograms generated at resolution of ca. 45ms and 10Hz, and frequency bandwidth of 0-4kHz (Phrases 1b, 2) or 0-2kHz (remainder).

Phrase Types in the India Boreal Winter Samples

As reported in Mahanty et al. (2015), among the 10 short samples of song recorded in the southeastern Arabian Sea during the Boreal Winter of 2011, a total of two different phrase types were identified. Each 30-second sample contained two to three repetitions of a single phrase type at relatively low SNR. Examination of these samples revealed five samples that matched Oman Phrase Type 1b (Figures 7 and 8; Theme-I of Mahanty et al 2015, see Figure 4 of that article), and five samples that matched Oman Phrase Type 5b (Figures 7 and 8; Theme-II of Mahanty et al. 2015, see Figure 5 of that article). Given the fragmentary nature of this sample, it is difficult to draw any firm conclusions about the similarity of songs across the Arabian Sea; however, the fact that the two identified phrases are part of the Oman song supports the expectation of consistency of song between the eastern and western Arabian Sea. This is congruent with the findings of Whitehead (1985) who reported that songs recorded from Oman and Sri Lanka during winter 1982 had the same phrase content.

Song Structure and Phrase Types in the SWIO Austral Winter Samples

Classification of phrases in the 13 logged SWIO recordings from 2011-2013 revealed no overlapping phrase types with Oman 2011-2013 Boreal winter recordings (Figures 9 and 10). Despite the much smaller sample size than that from Oman, there was much more variation apparent across years in the SWIO recordings. Thus, phrases were labeled with a prefix representing the year (11-, 12-, or 13-). The song recorded off Reunion in 2011 was characterized by seven distinct phrase types most of which contained multiple subphrases (Payne and McVay 1972) and several of which were markedly long in excess of 20 sec duration (Figure 9). Phrase Type 11-4 was classified as a shifting theme (Payne and Payne 1985) in which each repetition of the phrase progressively changed so that the first and the final phrase of the theme are notably different (represented in Figure 9). Due to the brevity of the individual recordings, no sample contained all phrase types; however, all samples had overlap in content with other samples, such that no sample contained unique phrases. Therefore, the identified repertoire appears to represent the region in 2011, although it is possible that some phrase types were missed.

Between 2011 and 2012 there was a complete change in all phrase types recorded off Reunion, with no phrases from 2011 readily identifiable in the 2012 and 2013 samples (Figure 10). Therefore, phrase type numerical labels from 2012 and 2013 have no relationship to the same number in 2011. The Reunion 2012 song was characterized by a series of short phrases with the same general simple structure: a single introductory unit that was relatively low frequency, narrow band with little frequency modulation, and harmonically rich; this was followed by two to three repetitions of a second unit or motif (Figure 10). The phrase types at times graded into each other, making it somewhat challenging to classify distinct phrase types. Between 2012 and 2013 there was distinct change and diversification, however enough similarity remained to allow inference as to which phrase types represented the same lineage. In total five major phrase types were classified, and each had from two to four variants (a-d) in either 2012 or 2013, yielding 9 different phrase types in 2012 and 13 phrase types in 2013 (Figure 10). Some variants represented a change in the structure of a unit (e.g., frequency oscillation in the last two units of 12-2c vs. 12-2d), whereas others represented the addition of units (e.g., addition of high frequency chirps following the lower frequency upsweeps of 12-4a vs 12-4b). Review of the short Comoros sample from 2013 revealed strong similarities with the Reunion 2013 songs, despite the ca. 1800km distance between the two sites (Figure 9). Of the 13 phrase types identified in Reunion 2013 song, 10 were also identified in Comoros 2013, with no novel phrases; given the small Comoros sample, it is likely that some of the three missing phrase types were actually present, and in one poor recording that was not logged the missing Phrase Type 13-4 appeared to be present.

Unlike the thorough sample collected and reviewed from Oman, the SWIO sample is relatively small and temporally patchy; therefore it is not possible to be confident that all phrase types and variation within the region were captured. Despite this caveat, an adequate sample of phrase types was identified to show a degree of variation that was greater than observed in Oman during the same years, and moreover that no overlap in phrase types existed between the SWIO Austral winter songs and the Oman Boreal winter songs.

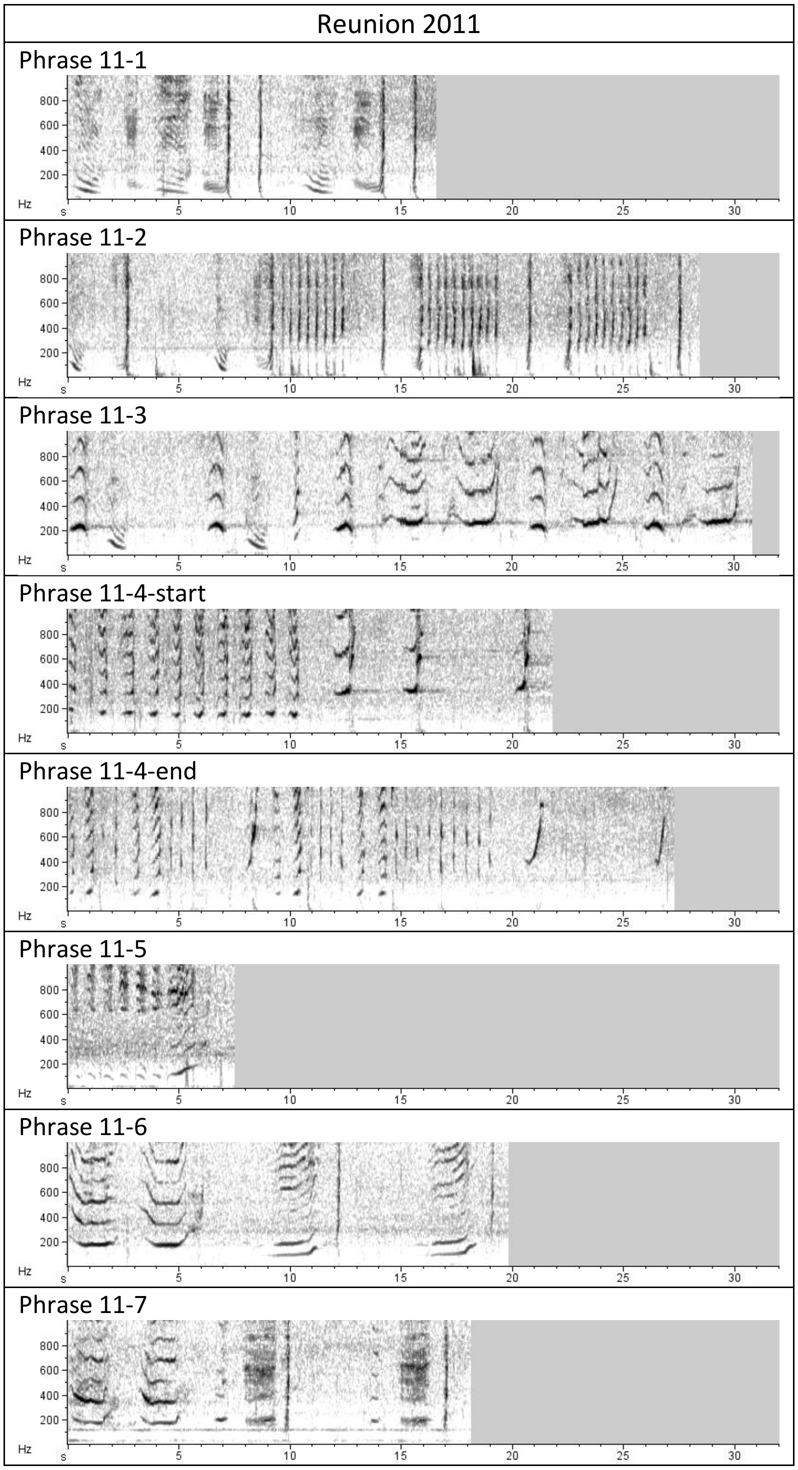


Figure 9. Exemplar phrases from Reunion Island in 2011. Spectrograms generated at resolution 46.4ms and 10.8Hz. Due to the absence of any units with fundamental frequencies above 1kHz, all phrases are illustrated on a 0-1kHz bandwidth.

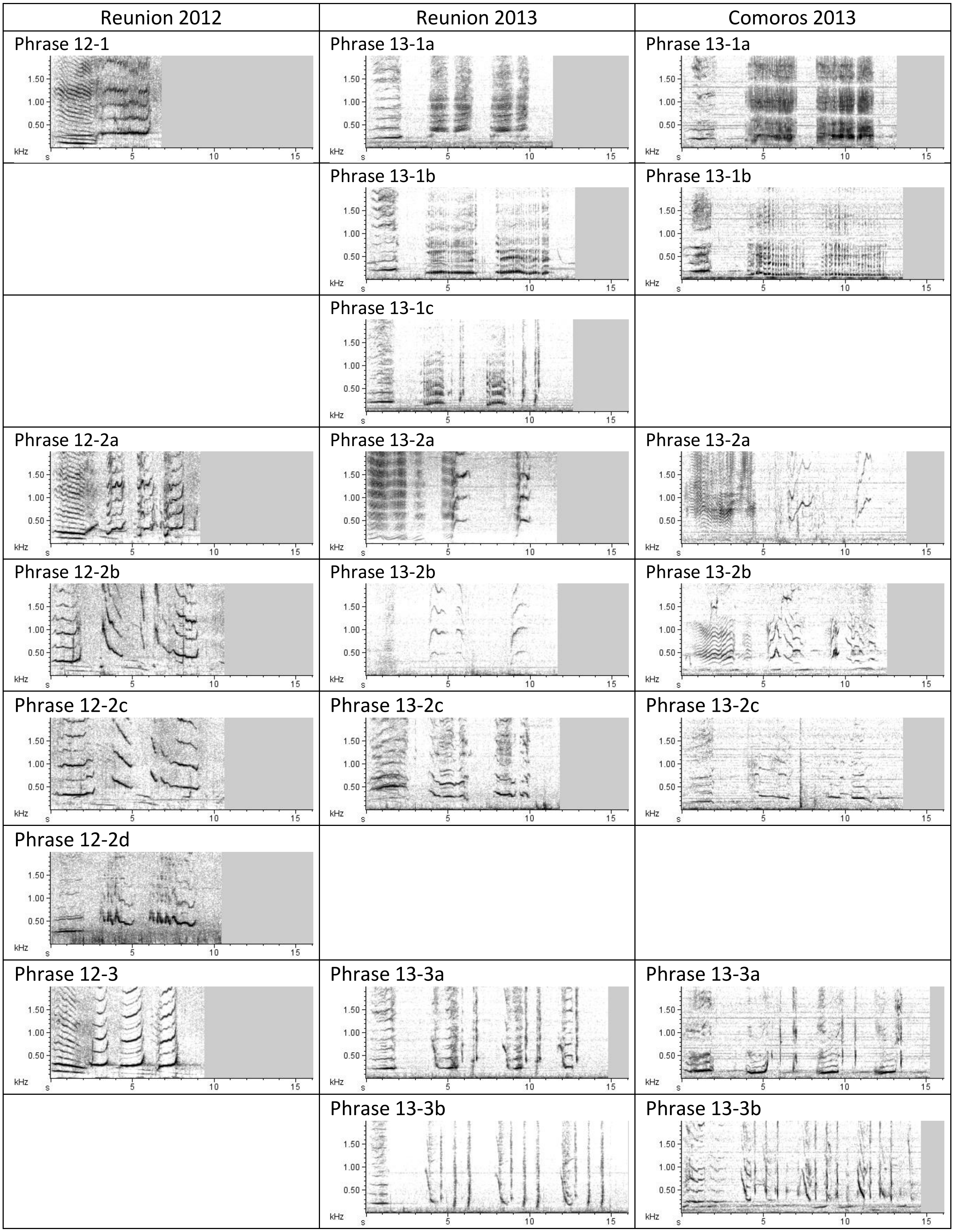


Figure 10. Exemplar phrases from Reunion Island in 2012 and 2013 and Comoros in 2013. Spectrograms generated at resolution of 46.4ms and 10.8Hz, and frequency bandwidth of 2kHz.

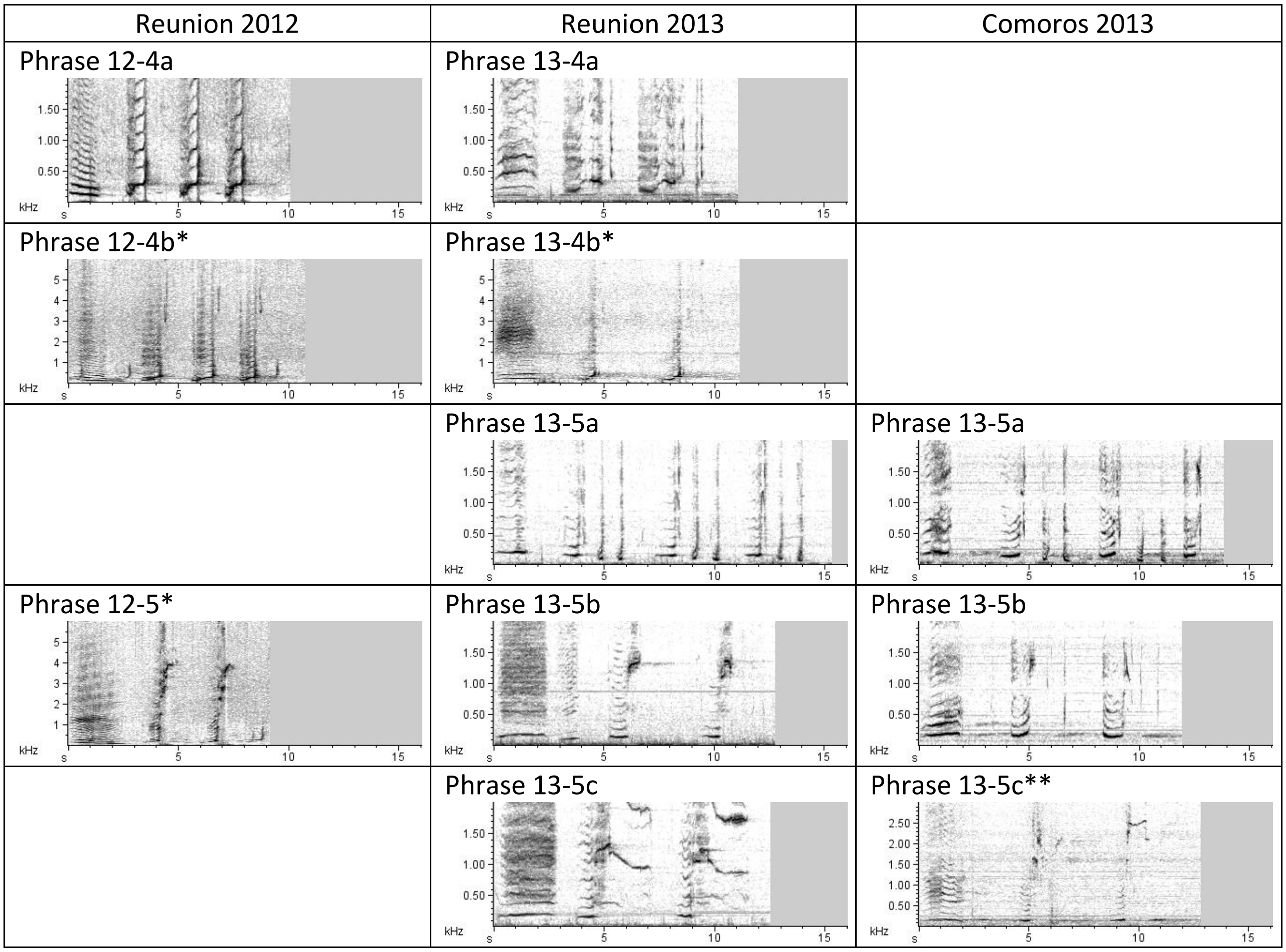


Figure 10 (continued). Exemplar phrases from Reunion Island in 2012 and 2013 and Comoros in 2013. Spectrograms generated at resolution of 46.4ms and 10.8Hz. Note: some phrases have expanded frequency scale of 6kHz* or 3kHz** (otherwise at scale of 2kHz).

Song Structure and Phrase Types in the Oman Boreal Summer (Austral Winter) Samples

Between 10 August and 3 September 2012, song was recorded off Oman at site Hal2 on five separate days, approximately two months after the last previous singing was detected on 15 June 2012 (Figure 5, Table 5). The SNR of these recordings was poor with extended fade outs as singers appeared to come in and out of range of the recorder, making it difficult to discern and classify all phrases. The low SNR indicates that these singers were relatively distant; however, given the propagation characteristics of humpback whale song in shallow water it is safe to assume that they were within tens as opposed to hundreds of kilometers. Eleven different samples were identified ranging from 1.7min to 46.3min of recording, although it is likely that different samples on a single day represent the same singers. The longest of these spanned five consecutive 10min duty cycles (the recorder being on a 10min every 30min recording cycle) and 150min of actual clock time (Table 5).

Of these 11 Boreal summer samples, six contained sections in which phrase types could be discerned and classified for a total of 124 phrases spread across the samples (Table 5). In every case the phrase matched a SWIO phrase type from Austral winter 2012, and there were no indications of phrases from the Oman Boreal winter song. At least four different SWIO phrase types were identified: 12-2b and/or 12-2c (difficult to distinguish between these variants in the low SNR Oman recording, see Figure 11 for examples and comparison); 12-2d (quality too poor to adequately represent in a figure); 12-3 (quality too poor to adequately represent in a figure); and 12-4a and/or 12-4b (impossible to distinguish between these variants due to low SNR Oman recording and likely attenuation of the high frequency unit diagnostic to 12-4b, see Figure 12 for examples and comparison). Despite the low quality of these distant and degraded songs, we are confident that all 124 discernable phrases could be classified as one of the SWIO phrase types. Moreover, on at least one day (10 August) there were clearly two different singers present, as documented through overlapping sequences of Phrase Types 12-2c and 12-4a/b (Figure 13).

Table 5. Details of humpback whale song samples recorded in Hallaniyats Bay, Site Hal2 during the Boreal Summer (Austral Winter) 2012.

Singer#	Date	Time	Qual Index	Sess Dur (min)	Rec Len (min)	Logged (min)	Total # Phrases	# Phrase Types	Review
Boreal Summer 2012									
2012-08-10-A	10-Aug-12	15:39	0	150.7	46.3	28.0	124	4-6	Logged
2012-08-10-B	10-Aug-12	20:30	0	4.1	4.1	1.0	5	1	Logged
2012-08-10-C	10-Aug-12	21:06	0	32.6	11.7	0.4	2	1	Logged
2012-08-11-A	11-Aug-12	0:32	0	63.5	21.7	1.7	9	1	Logged
2012-08-11-B	11-Aug-12	2:08	0	1.7	1.7	1.4	4	1	Logged
2012-08-20-A	20-Aug-12	23:31	0	7.6	7.6		n.a.	n.a.	Scanned
2012-08-22-A	22-Aug-12	3:34	0	27.4	6.4		n.a.	n.a.	Scanned
2012-09-03-A	3-Sep-12	16:30	0	34.8	13.8		n.a.	n.a.	Scanned
2012-09-03-B	3-Sep-12	20:04	0	5.0	5.0	4.1	15	2	Logged
2012-09-03-C	3-Sep-12	20:37	0	1.8	1.8		n.a.	n.a.	Scanned
2012-09-03-D	3-Sep-12	21:33	0	6.4	6.4		n.a.	n.a.	Scanned

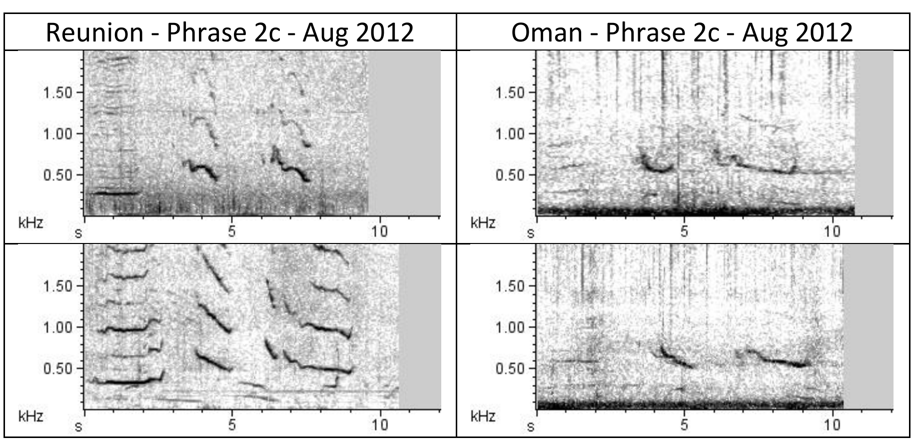


Figure 11. Examples of SWIO Phrase 12-2c as recorded off Reunion Island during August 2012 (left), and off Hallaniyats Bay, Oman on August 10, 2012 (right).

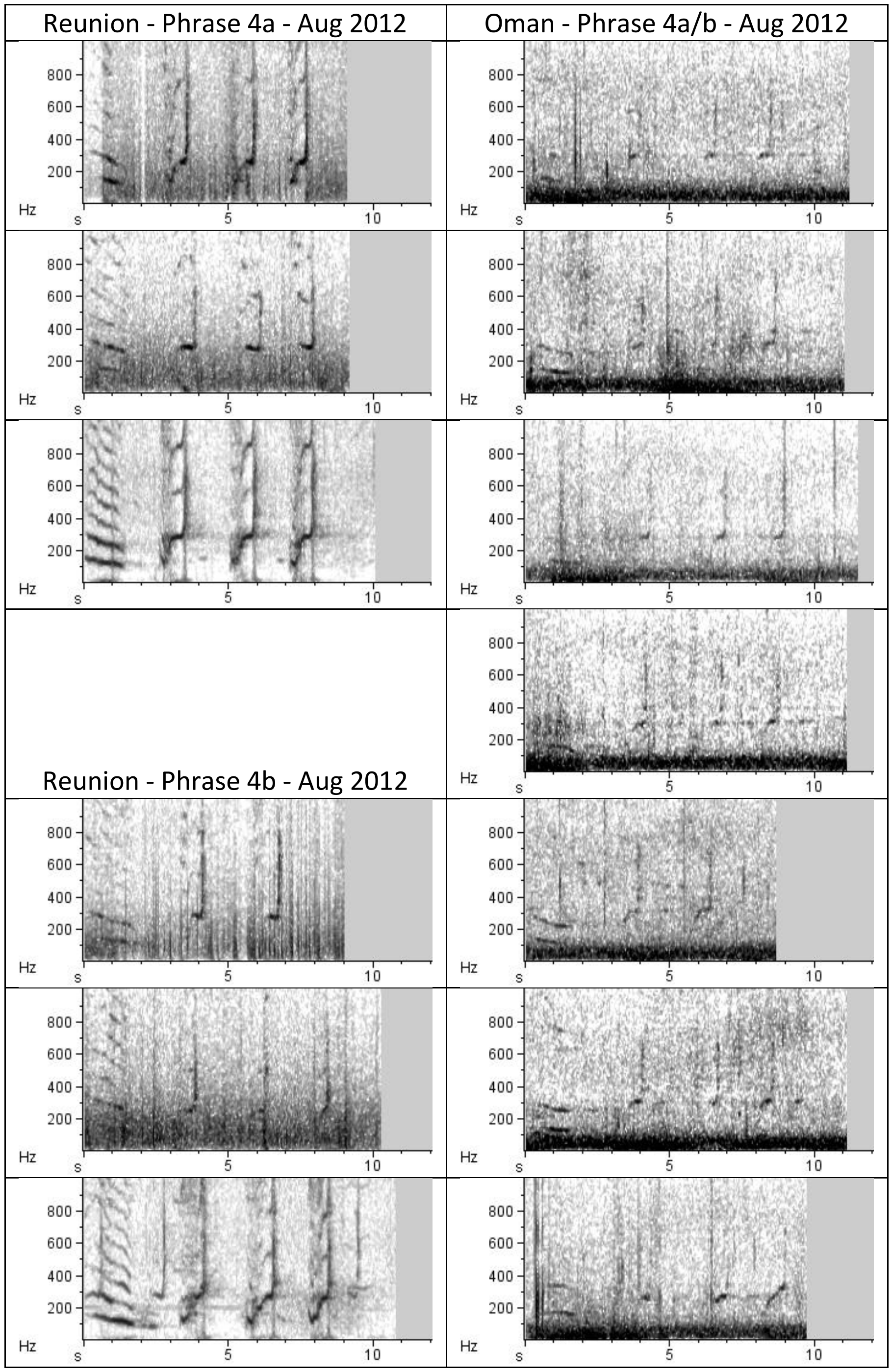


Figure 12. Examples of SWIO Phrase 12-4a and 12-4b as recorded off Reunion Island during August 2012 (left), and SWIO Phrase 12-4a/b off Hallaniyats Bay, Oman on August 10, 2012 (right). Note that the difference between Phrases 12-4a and 12-4b is the presence of high frequency chirping units at 3-5kHz (see Figure 10); since these units would not be audible in the low SNR recordings from Oman, the frequency scale is zoomed in to a 0-1kHz bandwidth to better discern the detail in the lower frequencies. Phrase examples are not arrange in any specific order, but are presented to illustrate the range of SNRs.

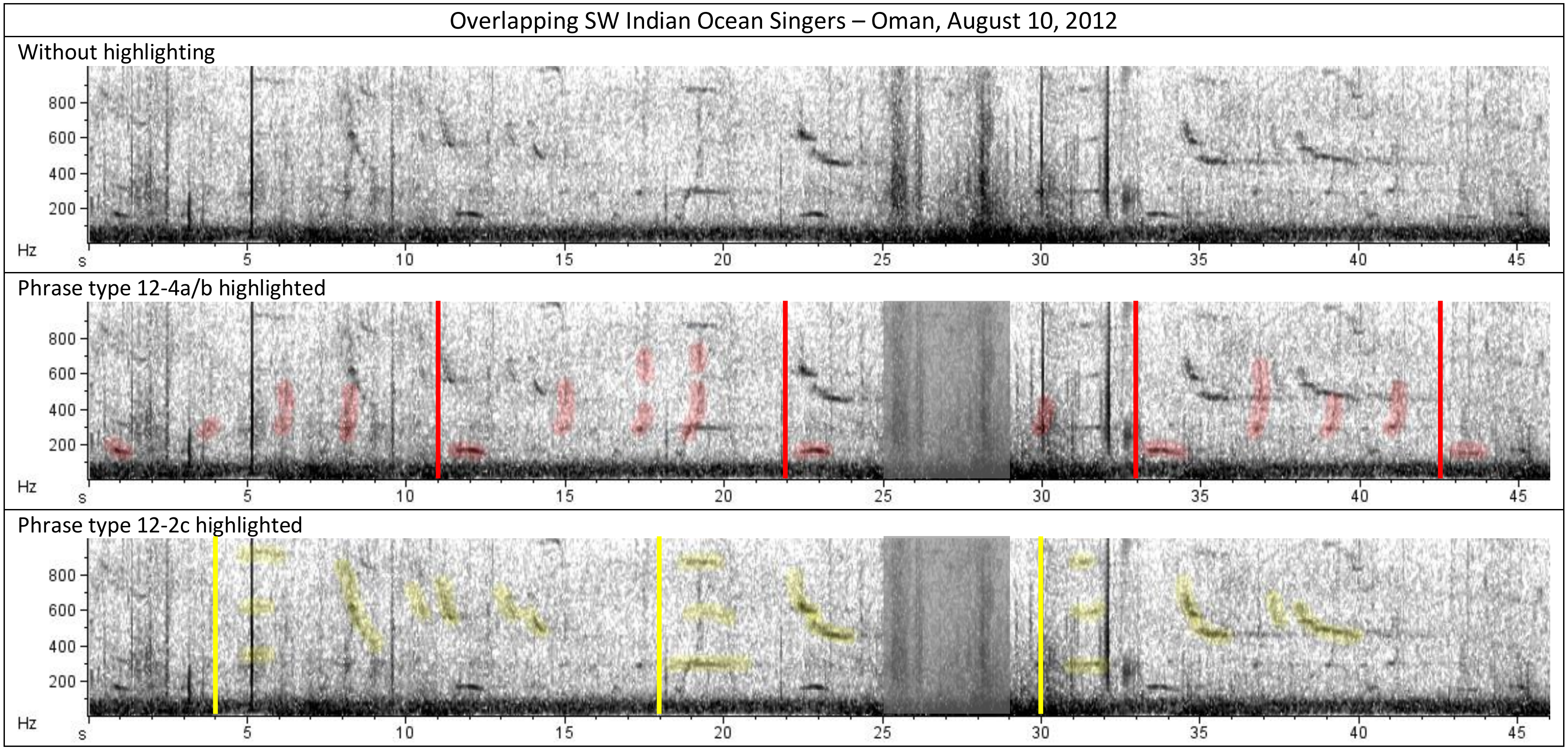


Figure 13. Spectrogram segment illustrating the presence of two SWIO singers off the coast of Oman on August 10, 2012, as indicated by overlapping sequences of different phrases (top panel). The first singer is in Phrase 12-4a/b displaying a sequence of 4 phrases starting at 0s, 11s, 22s, and 33s (highlighted and demarcated in red in middle panel); the second singer is in Phrase 12-2c displaying a sequence of three phrases starting at 4s, 18s and 30s (highlighted and demarcated in yellow in lower panel). Note that the broad spectrum ambient noise at 25-29s obscures (masks) portions of the 3rd 12-4a/b phrase and 2nd 12-2c phrase (indicated in grey).

DISCUSSION

Humpback whale song geographic variation

Geographic variation in humpback whale song has been used globally for over three decades to infer connectivity between regions, and as an indication of mixing versus isolation of populations or sub-populations. Initial studies in the Northern Hemisphere demonstrated connectivity of populations within the North Pacific and isolation from the North Atlantic (Winn et al. 1981, Payne & Guinee 1983), and later studies explored the patterns of connectivity in the North Pacific in greater detail (Cerchio et al. 2001, Darling et al 2014). In the Southern Hemisphere, connectivity was shown between the western and eastern South Atlantic and across to the Southwest Indian Ocean (Darling & Sousa-Lima 2005, Razafindrakoto et al. 2009), whereas minimal similarity was shown between the Southwest and Southeast Indian Ocean (Murray et al. 2012). In the western South Pacific, complex patterns of both isolation and periodic connectivity leading to diffusion of songs across subpopulations have been demonstrated (Noad et al. 2000, Garland et al. 2011). Given this background along with the observation of apparent long-term genetic isolation of the Arabian Sea humpback whale population (Pomilla, Amaral et al. 2014), we expected to find distinct differences between songs from the Arabian Sea and the SWIO. Our results are in part congruent with this expectation, with continuity inferred between Oman and India within the Arabian Sea, and isolation indicated by consistent song differences with the SWIO over three years. However, the scenario is more complex, with the presence of SWIO song in Oman waters during the Boreal summer suggesting the potential for trans-equatorial population mixing. There are four major findings of consequence in the results of this study that will be highlighted individually: the distinct difference between Oman Boreal winter song and SWIO Austral winter song; the temporal stasis of Oman song over the three monitored years; the presence of SWIO song off Oman during the Boreal summer; and the lack of diffusion of SWIO song into the Arabian Sea population's song.

1. Boreal winter songs indicate isolation of Arabian Sea humpback whales

It was found that the Boreal winter song of Oman humpback whales was completely different from the Southwest Indian Ocean song over a three year period, with no overlapping phrase content. This in itself supports the current understanding that the Arabian Sea population of humpback whales is isolated from the southern hemisphere populations as supported by photographic (Minton et al 2010) and genetic data (Pomilla, Amaral et al 2014), as well as the observed asynchrony of breeding cycles between the Northern and Southern Hemisphere populations (Mikhalev 1997, 2000). When compared with levels of song sharing and diffusion in other ocean basins, this suggests that there is little to no mixing of the populations or otherwise we would expect to find some song sharing.

2. Minimal change in Oman song over three years indicates unique temporal stasis

Many of the Oman phrases described (e.g., Phrase Types 1b and 3), were virtually unchanged from 2011 to 2012 to 2013, and those that did exhibit some change (e.g., Phrase Types 2, 4 and 5a) had only very minor changes in unit structure, repetitions of units, or addition of a unit (Figure 7 and 8). Although the current assessment is qualitative, this level of continuity across years has never been documented in any previously studied population. Distinct changes in phrase structure are much more evident in all studies to date that have looked at temporal change over a span of several years (e.g., Payne et al. 1983, Garland et al. 2011, Darling et al. 2014) or even within a single season (Payne et al. 1983, Cerchio et al. 2001) (see Figure 14 for an example). This observation is worthy of a detailed quantitative study to compare rates of progressive change in the Arabian Sea animals with other populations. If, as apparent from the qualitative assessment, Oman humpback whale song exhibits pronounced temporal stasis, then this would represent a unique behavioral condition among humpback whale populations globally. It is possible that the very small population of adult males within the Arabian Sea population results in a low level of innovation and novelty in song structure (i.e., fewer males making fewer innovations), the processes believed to drive progressive change in song (Payne et al. 1983, Cerchio et al. 2001). Alternatively, it may indicate a loss in the Arabian Sea population of the tendency to innovate and/or adopt novel material that appears widespread through all other studied populations.

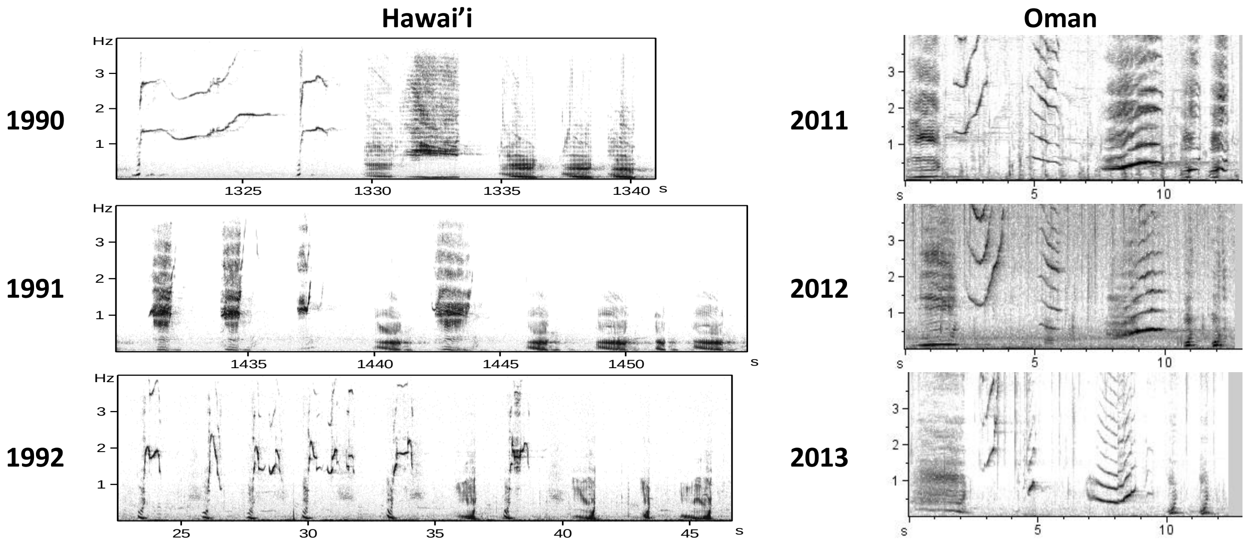


Figure 14. Qualitative example of typical progressive change in phrase structure of humpback whale song, as evident across three years in Hawai'i, in comparison to relative stasis exhibited in Oman song from 2011 to 2013. The Hawai'ian phrases were recorded off Kaua'i (Cerchio et al. 2001 and unpublished data; Phrase 3B), and verification of the three exemplar phrases for each year being from the same lineage (i.e., homologous) come from many intermediate versions of the phrase across the three-year period.

3. Presence of SWIO song off Oman during the Boreal summer indicates SH migrants

SWIO song was heard off Hallaniyats Bay, Oman during the Boreal summer (Austral winter) of 2012, with a minimum of four distinct SWIO phrase types discernable from low SNR recordings. These SWIO phrase types were never documented during the Boreal winter singing seasons of the Oman humpbacks in either 2012 or 2013, straddling the summer in which they were recorded. Therefore, we assert that the most parsimonious explanation is that these songs were not made by Arabian Sea whales, but rather Southern Hemisphere whales that moved into the Arabian Sea during their Austral winter breeding season. Whether these animals represent accidental vagrants or actual "migrants" is a matter of interpretation and impossible to determine with any certainty at this point. However, given that SWIO songs were documented on five different days across a 25 day period, and that on at least one day there were at least two different animals singing, this movement may be more common than previously considered. Unfortunately sampling did not occur in the appropriate time frame to assess whether this phenomenon was repeated during 2013 in Gulf of Masirah.

There have been several historic and recent indications supporting the hypothesis that SWIO humpback whales occasionally or regularly visit the Arabian Sea during the Southern Hemisphere breeding season. During the Austral winter of 2012 (the same season under consideration here) a male humpback whale satellite tagged in Madagascar on 24-July moved into the Northern Hemisphere (Cerchio et al. 2016a). When the tag stopped transmitting on 24-August off the coast of Somalia at 3ºN latitude, the whale had traveled over 2800km and was within 1200km of the Gulf of Aden (a calculated 8 days of swimming at its last documented travel speed) (Cerchio et al. 2016a), or within 1900km and 13 days of Hallaniyats

Bay. Given this timing, if the whale continued to move north it would have arrived off Oman after the last SWIO song was recorded, so this specific individual could not have been one of the singers documented prior to 3-September; however, it may very well have reached the Arabian Sea, and its movements may have been typical of a wider cohort of animals displaying similar behaviour. In addition to this direct evidence of movement from the Southern to Northern Hemisphere, there are historical and modern observations of whales off the north Somali coast, in the Gulf of Aden, and the Red Sea during the Austral winter, and suggestion that they may represent Southern Hemisphere seasonal migrants or vagrants (Brown 1957, Notarbartolo di Sciara et al. 2017), due in part to their colouring and scarring patterns which are more typical of Southern Hemisphere than Arabian Sea humpback whales (Mikhalev 1997). In addition, a stranded animal off the coast of Oman on 26-August 2016 had a very white-dominant pigmentation and many barnacle scars, typical Southern Hemisphere characteristics that are rare or absent in the Arabian Sea (Mikhalev 1997, 2000, Minton 2004). Unfortunately it was not possible to collect genetic material from this stranding to confirm the specimen's population identity (Al-Jabri et al. in prep; ESO unpublished data). It is worth noting that trans-equatorial migration of humpback whales from the Southern Hemisphere into breeding areas in low latitudes of the Northern Hemisphere has now been documented in several ocean basins, including the eastern South Pacific (Rassmussen et al. 2007) and the eastern South Atlantic (Rosenbaum et al. 2014). Given the sum total evidence, it seems plausible that Southern Hemisphere whales may be relatively regular visitors to Arabian Sea waters, even if infrequent and seasonally restricted.

4. SWIO song did not culturally diffuse into the Arabian Sea song

Arabian Sea humpback whales recorded off Oman did not incorporate phrases from the SWIO into their song. Songs recorded during the Boreal winter of 2013 closely followed all phrase lineages that were present in the Boreal winters of 2011 and 2012, without any evidence of copying and singing the SWIO phrases that were recorded during the intervening Boreal summer of 2012. Cultural diffusion is the process by which behavioral traditions, such as song, are transferred between individuals and populations through the process of learning and copying (Mundinger 1980, Whiten et al. 2016). Movements of individual humpback whales between breeding areas and the process of cultural diffusion is one mechanism believed to explain how distant populations within ocean basins maintain continuity in song despite gradual progressive change (Payne et al. 1983, Payne & Guinee 1983, Cerchio et al. 2001, Garland et al. 2011), as well as explain the complete replacement of a population's phrase types by that of a neighboring population (Noad et al. 2000, Garland et al. 2011). Even within our SWIO sample, albeit small, there is evidence for a complete replacement of phrase types between 2011 and 2012 in Reunion, likely due to cultural diffusion from a neighboring population.

Given the apparent propensity for humpback whales to adopt and incorporate novel material into their song, at times to the level of complete replacement, it is noteworthy that this did not happen in Oman during our study period. We propose three hypotheses that could account for this. (1) During the Boreal summer months, the Arabian Sea humpback whales depart the waters of Oman for other areas, such as the coast of Pakistan and/or India, and therefore were not there to be influenced by the SWIO singers. Little is known about the movements of humpback whales within the Arabian Sea; however, this suggestion is somewhat incongruent with the observation of at least one humpback whale satellite tagged in March 2015 remaining within the western Arabian Sea off the coasts of Yemen and Oman into late August 2015 (Willson et al. 2016). Although the monsoon conditions make it difficult to conduct cetacean surveys off the coast of Oman during the peak Boreal summer months, shore-based and other incidental sightings records from Oman also indicate that humpback whales are present during this time (Minton 2004, Minton et al 2011, ESO unpublished data). (2) There is some as yet unquantified threshold of exposure to novel song before cultural diffusion would take place and a recipient population would copy and incorporate elements of the song. It is conceivable that if such a threshold exists it was not reached during this study period, i.e., too few SWIO singers were present to influence the Oman animals. Although this is plausible, it is noted that the SWIO song was recorded over a relatively extended period of 25 days, and at times with multiple singers present, suggesting the presence of SWIO whales did not represent a single accidental vagrant. (3) The Arabian Sea humpback whales were not receptive to learning and incorporating songs during the period when SWIO singers were present (the Boreal summer, the off-season for singing), or the population has partially lost the trait for adoption of novel material that is common to all other populations. Such sensitive periods for learning are well documented in some songbirds, during which birds are more susceptible to learning song (e.g., Nottebohm et al. 1986). Another fundamental observation of this study is the low variation of Oman song across three years described above. These separate observations (temporal stasis in Arabian Sea song and lack of adoption of SWIO song) suggest that Arabian Sea humpback whales may be less flexible learners than is typically associated with humpback whales, and thus less subject to song copying. It is conceivable that assessment of songs in the years following 2012 will indicate diffusion of SWIO song material in the Arabian Sea song; however, it remains clear that this diffusion did not occur during our study period, despite the opportunity for it to occur.

Implications for population status and conservation

The findings of this song comparison only underscore the enigmatic nature of the Arabian Sea population of humpback whales. Pomilla, Amaral et al. (2014) established the genetic distance and isolation of the Arabian Sea humpback whale from its Southern Hemisphere counterparts using both mitochondrial (mtDNA) and nuclear microsatellite (mSAT) DNA evidence. Based on mtDNA a divergence time from Southern Hemisphere (the most likely source population being Stock C, SWIO) was estimated at 70,000 years; gene flow after divergence was estimated to be highest with the Madagascar population, but still very low (on the order of 1/5 to 1/6 of that between Southern Hemisphere populations). In addition, mSAT nuclear data indicated high levels of divergence with strong and distinct population structure. Overall, the observed divergence of the Arabian Sea population was the highest that has been documented globally when comparing populations of humpback whales. In addition, genetic diversity based on both mtDNA and mSAT data was found to be reduced compared to Southern Hemisphere populations and there was evidence for both ancient and recent bottlenecks. Pomilla, Amaral et al. (2014) concluded that the Arabian Sea humpback whale is likely the most isolated and distinct population of the species globally, and that although there has been some gene flow with the Southern Hemisphere since divergence, it is unlikely that there is currently migrants being exchanged.

The presence of SWIO singers (males) in the Arabian Sea presents somewhat of a conundrum for this current understanding. If male humpback whales from the SWIO are moving into the Arabian Sea on a level beyond that of occasional accidental vagrants, then there is potentially the opportunity for gene flow. In other documented areas of range overlap between Southern and Northern Hemisphere in the eastern North Pacific (Rassmussen et al. 2007) and eastern North Atlantic (Rosenbaum et al. 2014), asynchronous latitudinal migration means that the Northern populations are absent from the low latitudes during the Austral winters, whereas in the Arabian Sea the residency of the population increases the likelihood of interaction, notwithstanding the low number of individuals in the population. There are a few key points to consider when assessing this. The divergence estimates and rates of migration in Pomilla, Amaral et al. (2014) were based on maternally inherited mtDNA, so it is possible that male-mediated gene flow may have been underestimated; however, bi-parentally inherited mSAT data also indicated strong divergence and population structure, offsetting this concern to some degree. It is recommended that higher resolution modern techniques for nuclear DNA (i.e., RADseq) be applied to the dataset to assess more rigorously the potential for male-mediated gene flow. This hypothetical aside, it is noteworthy that despite the presence of these SWIO singers, the Arabian Sea song maintained its distinct nature over the monitored three years. Less-detailed song comparisons from previous years have also indicated distinct differences between Arabian Sea and Southern Hemisphere songs (S.Cerchio pers.

observ.). In the context of song behavior of humpback whale populations globally, these observations alone would argue for isolation of the Arabian Sea whales.

The movements of SWIO whales into the Arabian Sea may be a relatively recent historic occurrence as the Southern Hemisphere populations recover from 20th century whaling and undergo range expansion; however, the genetic differentiation data indicate that the isolation of the Arabian Sea animals is ancient. Since the modern whaling-induced reduction of the SWIO population was a brief event relative the inferred period of isolation of the Arabian Sea population (70,000 years), then it is expected that for the vast majority of this period the SWIO population was at or above its current abundance. Therefore it seems unlikely that movement of whales from a large SH population is a novel phenomenon due solely to recent population expansion. Opportunities for mixing would have occurred throughout the existence of the Arabian Sea population, unless some other novel phenomenon is present. One obvious possibility is changes in ocean circulation patterns associated with human-induced climate change; however, it is not clear if such changes exist in low latitudes that would promote trans-equatorial migration, and it is beyond the scope of this manuscript to assess such physical parameters. It is also conceivable that 2012 represents a highly anomalous year, and that movement by the SWIO may be exceedingly rare; only continued monitoring in the future can assess this.

Given the combined evidence and evaluation presented here, it seems possible that isolation mechanisms exist that have maintained the distinction of the Arabian Sea population, and that this is reflected in the lack of adoption of the SWIO song by Arabian Sea males. A clear and obvious factor is the asynchrony of the breeding cycles, reinforced by the findings of our long-term acoustic monitoring effort which indicated unequivocally that song production is exclusively during the Northern Hemisphere breeding cycle (Cerchio et al. 2016b). Moreover, the observed lack of temporal variation documented in the Arabian Sea song, with song phrases being virtually unchanged across three breeding seasons, is completely unprecedented and extraordinary. This may reflect the small population size of singing males, and reduced levels of innovation, the “raw material” for temporal change. However, the presence of SWIO song presents the opportunity for abundant new song material to be heard by and incorporated by Arabian Sea males. That it is not, suggests some other undescribed and novel mechanism, such as a lack of song learning flexibility in the Arabian Sea that is the standard in other populations globally. From a behavioral ecology perspective, this is a fascinating premise that warrants further work examining long-term change, individual variation and comparative rates of change of song elements. From a conservation perspective, our findings only underscore and emphasize the uniqueness of the Arabian Sea humpback whale. The current IUCN Red List status for the population is “Endangered” based on the current understanding of population status and threats. Pomilla et al (2014) explicitly recommend that the status be revised to “Critically Endangered”, noting that the population is “genetically and demographically unique, and exhibit atypical behavior for humpback whales”. It is apparent that in song behavior as well, the population is atypical and divergent from other populations globally, reinforcing this recommendation.

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