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The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*)

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Although the songs of humpback whales have been extensively studied, other vocalizations and percussive sounds, referred to as “social sounds,” have received little attention. This study presents the social vocalization repertoire of migrating east Australian humpback whales from a sample of 660 sounds recorded from 61 groups of varying composition, over three years. The social vocalization repertoire of humpback whales was much larger than previously described with a total of 34 separate call types classified aurally and by spectrographic analysis as well as statistically. Of these, 21 call types were the same as units of the song current at the time of recording but used individually instead of as part of the song sequence, while the other 13 calls were stable over the three years of the study and were not part of the song. This study provides a catalog of sounds that can be used as a basis for future studies. It is an essential first step in determining the function, contextual use and cultural transmission of humpback social vocalizations.

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I. INTRODUCTION

Acoustic signaling is often significantly more effective than using only visual cues in the marine environment because sound is attenuated far less than light in that medium. Humpback whales (*Megaptera novaeangliae*) in particular use many acoustic signals of which the long, complex, stereotyped, repetitive “song” is the best studied (Payne and McVay, 1971). Song units are highly variable in frequency range and usually lie between 100 Hz and 4 kHz (Tyack and Clark, 2000). However, other studies of humpback whale song have found fundamental frequencies of units as low as 30 Hz (Payne and Payne, 1985), and others with harmonics extending beyond 24 kHz (Au *et al.*, 2006).

In addition to song, humpback whales produce another set of sounds known as “social sounds” which include surface-generated percussive sounds (e.g., breaches, pectoral flipper slaps, tail slaps) and social vocalizations. For the purpose of this study, “vocalizations” are any sounds that are produced internally by the animal and include sounds that may be generated from the blow hole. These vocalizations are not produced in the highly complex structural format of the humpback song and many of the social vocalization units are not heard in the characteristic breeding population song. Song is only produced by males, whereas social vocalizations are produced by both males and females (Winn *et al.*, 1979; Mobley *et al.*, 1988). However, other reports have sug-

gested that social vocalizations are rarely heard from lone humpback whales or mother and calf pairs (Tyack 1983; Silber 1986). Social sounds are commonly produced on the feeding grounds (Thompson *et al.*, 1977; Jurasz and Jurasz, 1979; D’Vincent *et al.* 1985; Mobley *et al.* 1988; Sharpe *et al.* 1998) and breeding grounds (Silber 1986) though these sounds are yet to be reported in migrating humpback whales.

Quantification of a species’ acoustic repertoire is an essential first step before investigating its function, contextual use, geographic variation and cultural transmission. However, a comprehensive catalogue of humpback whale social vocalizations has not yet been produced. Categorizing and cataloguing the vocalization repertoire of any marine mammal is difficult. Studies on dolphin vocalizations have attempted to statistically quantify the acoustic repertoire using multivariate techniques such as principal components analysis (PCA) and discriminant function analysis (DFA) (e.g. Biosseau 2005) to eliminate subjectivity. However, the wide variation both within each sound type and between different sounds made classification difficult. Clark (1982) proposed a repertoire description for southern right whales (*Eubalaena australis*), which included vocal and nonvocal calls. In it, sounds were divided into eight broad categories (one of which was “slaps”) using spectrographic and aural properties, but there was no individual call analysis or description in this study. Humpback calls are also highly variable and acoustically complex making them difficult to classify objectively. Chabot (1988) proposed a quantitative technique to classify humpback song sounds based on a clustering technique on binary data, in an attempt to eliminate the subjec-

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tivity of aural classification. Other studies have attempted to quantitatively compare humpback whale song units over time and measure the variability within these units (e.g., Mercado *et al.*, 2005). In this study, specific frequency and temporal variables within the song units were selected and measured to obtain an objective characterization of their acoustic features. One of the few studies on humpback social vocalizations associated with feeding aurally categorized these sounds into “moans,” “grunts,” “pulse-trains,” “blow-hole-associated sounds” and “surface impacts” (Thompson *et al.*, 1986), making a total of five different sound types. However, no statistical methods were applied to categorize them.

In all of the above studies, broad categories such as “tonal,” “noisy” and “pulsive” were used to classify sounds. Placing sounds into broad categories such as these has its problems, for example, sounds may form a structured continuum rather than fall into discrete categories resulting in a misinterpretation of the animal’s communication system (Tyack, 1997). Clark (1983) found that southern right whale calls did indeed form an acoustic continuum consisting of two functional subdivisions; a set of discrete frequency-modulated calls and a set of highly variable intergraded signals. Therefore, placing sounds into such broad categories may not be a biologically relevant way of classifying sounds; rather sounds should be analyzed as discrete and separate call types.

The east Australian population of humpback whales (part of the Group E metapopulation; IWC 2005) migrates annually along the east Australian coastline between feeding grounds in the Antarctic and breeding grounds inside the Great Barrier Reef off central and northern Queensland (Chittleborough, 1965; Dawbin, 1966). Humpbacks were acoustically recorded for three years during the southward migration, which occurs from August to November, with a peak in early October at the latitude of our study area. The aims of this paper are to (i) describe and quantify the whales’ nonsong social vocalizations and (ii) classify and categorize these using multivariate techniques to propose a social vocalization repertoire of east Australian migrating humpback whales.

II. METHODS

A. Visual and acoustic data

1. Visual data collection

Data were collected during the Humpback Whale Acoustic Research Collaboration (HARC) Project, in September/October 2002–2004 during the humpback whale southward migration (for detailed methods see Noad *et al.*, 2004). The study site was located at Peregrine Beach, 150 km north of Brisbane, on the east coast of Australia (26°29’S, 153°06’E) and about 400 km south of the Great Barrier Reef (Fig. 1(a)). Land-based behavioral observations were collected on a daily basis (7 am–5 pm, weather permitting) from an elevated survey point, Emu Mountain (73 m), adjacent to the coast (Fig. 1(b)). A theodolite (Leica TM 1100) was connected to a notebook computer running CYCLOPES software (E. Kniest, Univ. Newcastle, Australia) and used to track and observe passing whales. CYCLOPES recorded the

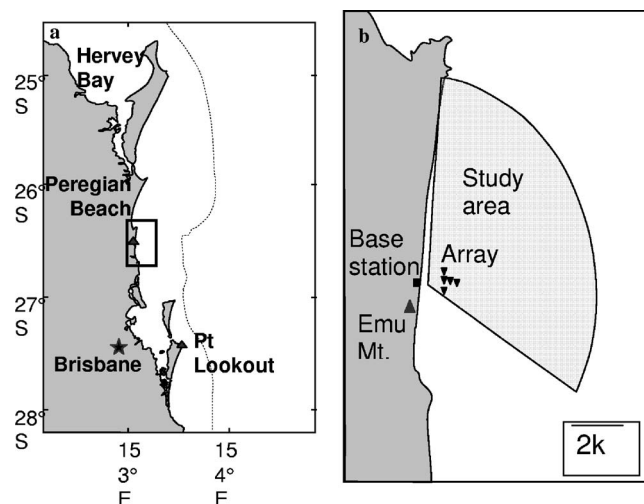


FIG. 1. Map showing the position of the study site at Peregrine Beach, southeast Queensland, Australia (Fig. 1(a)) and (Fig. 1(b)) the arrangement of the base station, visual station (Emu Mountain) and hydrophone array within the study site (see inset, Fig. 1(a)).

positions of whales from the theodolite elevation and azimuth in real time and these were annotated with observed behaviors and group compositions (e.g., adult and calf, two adults, etc.) out to the 10 km limit of the study area.

2. Acoustic data collection

Acoustic recordings of both humpback song and humpback social sounds were made from five hydrophone-buoy systems anchored in 18–28 m of water and arranged in a T shape. Each hydrophone buoy consisted of a surface buoy with attached solar panel, a preamplifier (+20 dB) and VHF radio transmitter. At the seabed, each buoy was held in place by a concrete mooring. A High Tech HTI-96-MIN hydrophone with built-in +40 dB preamplifier was attached to a separate subsurface float a meter off the bottom and cabled to the surface buoy. Buoys 1–3 were 1.5 km from the beach and parallel to the shoreline and approximately 0.7 km apart. Buoys 4 and 5 extended seaward from buoy 2 in a line perpendicular to the shore and were approximately 0.5 km apart (Fig. 1(b)). Accurate positions of hydrophones were obtained by a careful shore-based theodolite survey of the surface buoys (Noad *et al.*, 2004).

3. Acoustic tracking

Radio transmissions from the buoys are received at a base station just behind the beach (Fig. 1(b)) on a large, vertically orientated Yagi antenna attached to a four channel, low noise, VHF receiver (type 8101) and (in 2003) a Winradio receiver. Two computers equipped with National Instruments E-series data acquisition cards and using ISHMAEL software (Mellinger, 2001) were used to record the acoustic signals received from the hydrophone buoys (one computer) and track the sound sources in real time using the arrival time differences of the sounds as they are received at the various hydrophones (the other computer). On each channel digital recordings were made at 22.05 kHz sampling rate. Tracking was performed either in the field in real time, si-

multaneously with the theodolite tracking, or during postfield analysis. Although the bearings to the sound sources calculated by ISHMAEL were accurate, there were small errors in the range estimates. At a range of 2 km from the array, the range error for a single sound position was less than 50 m. At 10 km from the array, the error was less than 1 km. However, sound location accuracy was significantly improved by using the mean position of several estimates calculated over a brief period. The array was validated by comparing acoustically calculated positions with theodolite positions of visually identified singers within the study area (for further validation experiments see [Noad et al., 2004](#)).

Acoustic tracks of vocalizing whales were overlaid on the visual tracking map in CYCLOPES and the combined acoustic/visual data was shared between the base and hilltop stations using a wireless network. This provided almost real time superposition of acoustic and visual tracks out to the 10 km limit of the study area. There were rarely more than six groups migrating through the 10-km-radius study area at any one time, and these were usually widely dispersed, unless a joining interaction between two groups was occurring. Given the accuracy of the system and the way in which groups could be simultaneously visually and acoustically tracked in real time, there was no doubt as to which groups were vocalizing at any time. Within groups, however, it was not possible to determine which animal was vocalizing.

B. Data analysis

1. Spectrographic analysis

Humpback whale vocal sounds (surface-generated sounds are not included in this analysis) with average/good signal-to-noise ratios (vocalizations in which the signal was at least 10 dB higher than the background noise) were extracted from recordings for further analysis. Every pod analyzed was represented by a minimum of five vocalizations. Spectrograms of vocalizations were produced either using Spectrogram 14 (R. Horn, Visualization Software) with 4096 point fast Fourier transforms (FFTs) and 5.4 Hz frequency resolution or Raven 1.2 (Cornell Lab of Ornithology) with 1024 point FFTs, Hamming window, 21.5 Hz resolution and 75% overlap. The higher frequency resolution spectrograms tended to be used for the lower frequency sounds.

2. Vocalization classification and statistical analysis of vocalization type

Vocalizations were classified into a series of vocalization types based on aural and spectrographic characteristics. A series of variables, listed in Table I, were measured from the spectrographic samples of each vocalization for statistical analysis. The variables measured included the vocalization duration, the number of vocalizations in a bout for repetitive sounds, the number of inflections, the frequency of the spectral peak and frequency properties. Measurements of the lowest frequency component of the vocalization (the fundamental in harmonic sounds) were: start and end frequencies, minimum and maximum frequencies, ratio of start to end frequency (frequency trend ratio), ratio of maximum to minimum frequency (frequency range ratio), and the percentage

TABLE I. Measurements and a description of the measurements made on all vocalizations. Some of the measurements are illustrated in Fig. 2.

Measurement	Abbreviation	Description
Variables measured on lowest frequency component F_0		
Duration (s)	Dur F_0	Vocalization length
Minimum frequency (Hz)	Min F_0	Minimum frequency
Maximum frequency (Hz)	Max F_0	Maximum frequency
Start frequency (Hz)	Start F_0	Start frequency
End frequency (Hz)	End F_0	End frequency
Percentage to maximum (%)	%	Percentage of duration to the maximum frequency
Frequency range (as ratio)	Range F_0	Max freq/min freq
Frequency trend (as ratio)	Trend F_0	Start freq/end freq
Inflections	Inflec	Number of reversals in slope
Other variables measured		
Peak frequency (Hz)	Peak F	Frequency of the spectral peak
Number of units per bout	No./bout	Equals one for nonrepetitive sounds
Pulse rate (/s)	Pulse rate	for pulsative sounds

of duration to the maximum frequency. Ratios of frequencies were measured rather than the differences since ratios better match mammal perception of frequency differences ([Richardson et al., 1995](#)). All frequency measurements were initially made on a linear scale (shown in Table II and Table III). They were then converted to a logarithmic scale for analysis, as this better matches the perception of pitch ([Richardson et al., 1995](#)). The measured variables were used in a principal component analysis (PCA) which can describe the variation of a set of multivariate data in terms of sets of uncorrelated factors, each of which is a particular linear combination of the original variables ([Pearson 1901](#)). This reduced the variables into a number of factors that were used in place of the original variables during some subsequent analyses. A varimax rotation was applied to maximize loading scores and facilitate interpretation of the data. These factors and the original measured variables were used in discriminant function analysis (DFA) with cross validation to determine the probability of sounds being correctly classified to each of the possible groups determined by aural and spectrographic characteristics.

III. RESULTS

Acoustic recordings of 61 vocal pods were made between 2002 and 2004 and from these 660 social vocalizations were extracted for analysis. Group compositions from which sounds were recorded included singletons ($n=15$), mother and calf pairs ($n=12$), pairs of adults ($n=8$), mother, calf and escort ($n=18$), three adults ($n=3$), four adults ($n=1$) and mother, calf and three escorts ($n=4$). All escorts were assumed to be males ([Glockner and Venus, 1983](#); [Clapham et al., 1992](#)). The sexes of adults other than moth-

TABLE II. Mean (SD) spectrogram parameters (see Table I) of measured low-frequency, amplitude-modulated, noisy, complex and repetitive sounds, the number measured of each vocalization and the number of groups in which they were heard (see Figs. 2–4 for associated spectrograms). All frequency measurements are shown in the linear scale (Hz). Social vocalizations which were also part of the song structure are highlighted along with the song year of which they were part.

	Wop	Thwop	Snort	Grumble	Sigh	Siren	Short moan	Horn	Violin	Groan	Ascend moan	Mod moan	Cry	Mod cry	Ascend cry	Trumpet	Ascend shriek	Des shriek	Squeak
N (sounds)	64	67	43	73	2	5	7	18	12	12	4	13	8	2	8	27	2	7	6
N (groups)	24	15	17	20	1	1	5	5	4	5	2	5	2	1	1	6	1	3	3
Dur F_0	0.748 (0.196)	0.949 (0.244)	0.284 (0.107)	1.509 (1.362)	2.533 (0.901)	2.309 (0.584)	0.353 (0.060)	0.365 (0.126)	0.312 (0.057)	1.262 (0.630)	1.854 (0.510)	1.212 (0.418)	1.623 (0.194)	2.204 (0.517)	1.773 (0.119)	0.732 (0.345)	1.252 (0.021)	2.297 (1.192)	0.213 (0.132)
Min F_0	43 (15)	42.2 (13)	51 (25)	43.6 (12)	30 (10)	95 (33)	161 (34)	180 (51)	548 (185)	139 (39)	162 (24)	201 (24)	338 (138)	524 (193)	171 (46)	231 (80)	714 (0)	809 (84)	1431 (302)
Max F_0	73 (16)	83.1 (20)	53 (25)	48.5 (15)	327 (23)	337 (48)	206 (60)	430 (116)	908 (239)	172.6 (50)	271 (29)	618 (182)	709 (202)	1415 (32)	437 (68)	854 (124)	2268 (20)	1373 (138)	2420 (746)
Start F_0	52 (34)	43.6 (18)	53 (26)	44.2 (14)	183 (226)	162 (79)	168 (37)	180 (51)	884 (246)	156.7 (54)	162 (24)	206 (31)	352 (163)	534 (179)	259 (41)	234 (77)	714 (0)	889 (107)	1649 (506)
End F_0	73 (16)	83.0 (20)	52 (25)	46.7 (15)	174 (193)	272 (78)	199 (64)	401 (133)	616 (256)	160.0 (41)	233 (36)	610 (188)	627 (226)	1415 (32)	406 (79)	836 (135)	2268 (20)	932 (90)	2227 (897)
% duration	100	100	7 (25)	26.0 (44)	0	9.5 (2)	59 (43)	100 (0)	8 (29)	53.1 (31)	100 (0)	64 (35)	21 (10)	100 (0)	13 (1)	77 (35)	17 (3)	16 (15)	55 (44)
Peak F	80 (19)	94.6 (27)	84 (41)	62 (24)	86 (7)	168 (18)	178 (55)	302 (32)	700 (152)	156.4 (41)	229 (38)	364 (50)	516 (89)	588 (458)	354 (29)	471 (140)	953 (8)	1083 (239)	1478 (265)
Inflect	1	2	0	0	0	6	0	1	0	0	0	2	0	2	3	0	0	1	0
No./ bout																			
Pulse rate (/s)																			
Song unit yr	No	No	No	No	02	02	02	02	02	02, 03, 04	02, 03, 04	02, 03, 04	No	No	No	02	02, 03, 04	02	02, 03, 04

TABLE III. Mean (SD) spectrogram parameters (see Table I) of measured repetitive and harmonic sounds, the number measured of each vocalization type and the number of pods they were heard in (see Figs. 5–7 for associated spectrograms). All frequency measurements are shown in the linear scale (Hz). Social vocalizations which were also part of the song structure are highlighted along with the song year in which they were heard.

	Purr	Growl	Trill	Blow	Bark	Bellow	Creek	Screech	Scream	Grunts	Croaks	Yap	Yelps	Pulses	Low yap
N															
(sounds)	16	14	6	6	50	4	4	4	8	90	17	10	21	25	5
N															
(groups)	4	5	3	3	13	4	1	1	3	9	3	4	1	2	1
Dur F_0	1.566 (0.575)	2.253 (1.268)	2.194 (0.468)	0.281 (0.152)	0.205 (0.119)	0.939 (0.415)	1.723 (0.614)	1.366 (0.336)	1.179 (0.288)	0.221 (0.110)	0.522 (0.255)	0.372 (0.101)	0.251 (0.074)	0.062 (0.027)	0.129 (0.037)
Min F_0	56 (43)	60 (18)	245 (83)	45.5 (15)	139 (98)	382 (117)	29 (7)	119 (42)	678 (156)	43 (20)	75 (45)	230 (94)	95 (42)	139 (11)	243 (128)
Max F_0	59 (41.8)	73 (17)	427 (92)	45.5 (15)	346.9 (204)	403 (100)	102 (26)	221 (39)	1436 (270)	45 (23)	120 (61)	2480 (875)	372 (158)	294 (152)	820 (310)
Start F_0	56 (43.9)	62 (18)	261 (72)	45.5 (15)	153.4 (104)	379 (114)	29 (7)	125 (51)	684 (149)	43 (20)	75 (45)	2480 (875)	236 (118)	191 (102)	712 (85)
End F_0	59 (41.8)	70 (18)	342 (127)	46.3 (20)	350.4 (201)	404 (100)	102 (26)	216.0 (45)	1157 (248)	43 (20)	120 (61)	250 (94)	173 (111)	188 (39)	268 (383)
%	0	14	34	0	100	75	100	57	38	0	100	0	100	0	10
Duration		(36)	(36)			(50)		(15)	(18)						(22)
Peak F	206 (62)	73 (36)	360 (42)	191 (57)	225.7 (106)	437 (97)	243 (15)	365 (38)	1177 (166)	74.8 (39)	193 (62)	1325 (611)	170 (46)	171 (63)	488 (330)
Inflects	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0
No./ bout										5	4 or 5 (3 - 8)	6 - 8	3 or 4	7 - 15	6
Pulse rate	21.6 (6.1)	67.3 (3.9)	40.5 (3.4)												
Song unit yr	02	02, 03, 04	02	No	02	No	02	02	No	03, 04	02	02	No	No	No

ers and escorts were usually not known unless they had been heard singing, in which case they were males (Winn *et al.*, 1973; Glockner-Ferrari and Ferrari, 1981).

Initial subjective aural and spectral analysis classified the social vocalizations as 34 separate types. The humpback whale song structure for the three study years was also aurally and visually inspected. Song structure was similar in 2003 and 2004 with the same units being used in the song in both years, but the 2002 song was very different from the 2003/2004 song. A sample of each song unit was extracted from the song recordings and used as a template to subjectively aurally and visually compare each social vocalization type (a match between a song unit and a social vocalization was obvious from very similar aural and spectrogram properties). Of the 34 different social vocalizations, 21 were similar to units of the song current at the time of recording, but used individually or in a small bout (of less than six vocalizations) instead of part of the song sequence (usually lasting more than 5 min). Some of these were observed over the three years of recording while others were evident only for one or two years. The remaining 13 vocalizations were not part of the song and were observed in three years.

A. Initial vocalization classification and individual call description

Most of the calls are harmonic and have been separated arbitrarily into three frequency bands for ease of presentation (Figs. 2–4). Low-frequency harmonic sounds had fundamentals below 100 Hz, mid-frequency sounds 160–550 Hz and high-frequency sounds above 700 Hz. There are also ampli-

tude modulated calls (Fig. 5), calls that have been classified as “noisy and complex,” either broadband or harmonic with additional noise like (broadband) characteristics or broadband (Fig. 6), and repetitive calls that always occur as a repetition of individual sounds (Fig. 7).

1. Low-frequency sounds

Vocalizations were aurally and visually categorized into separate call types and measured. The most common vocalizations heard were “wops” and “thwops” (Figs. 2(a) and 2(b)), which were brief harmonic upsweeps at a low frequency (fundamental generally below 60 Hz) compared to other humpback vocalizations. These two vocalizations were similar; the primary difference being that the “thwop” was broken into two parts (“ther-wop”) and had two inflection points, whereas the “wop” was one sound and had one inflection point (Table II). “Snorts” (Fig. 2(c)) and ‘grumbles’ (Fig. 2(d)) were also relatively common sounds with a fundamental frequency generally below 60 Hz (Table II). Where the fundamental frequency could not be distinguished from the background noise, the frequency recorded was that of the lowest detectable frequency above noise limit. These vocalizations were not similar to any units heard in the song for the three study years (Table II). The “sigh” (Fig. 2(e)), though heard only twice in one pod, was part of the 2002 song structure (Table II).

2. Mid-frequency harmonic sounds

“Sirens” (Fig. 3(a)), “short moans” (Fig. 3(b)), “horns” (Fig. 3(c)) and “violins” (Fig. 3(d)) were similar to sounds in

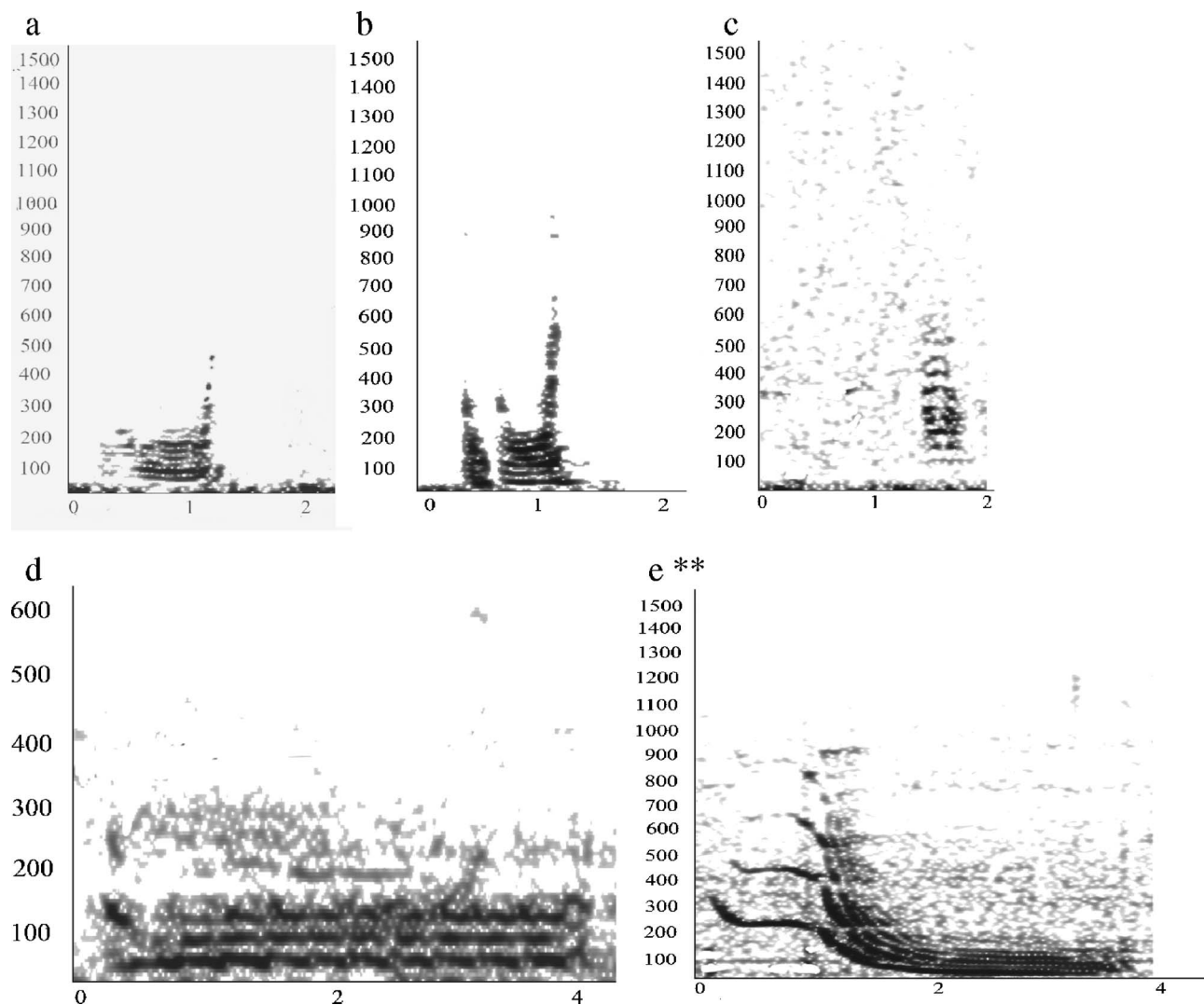


FIG. 2. Spectrogram (x =time (s), y =frequency (Hz)) of sounds in the nonsong, low-frequency, narrowband category; “wop” (a), “thwop” (b), “snort” (c) “grumble” (d) and “sigh” (e). Spectrograms were generated using a FFT of 4096 and frequency resolution of 5.4 Hz. Social vocalizations which were also part of the song structure are identified by**.

the 2002 song, though only heard in later years (2003 and 2004) as part of the social vocalization repertoire (Table II). Longer harmonic sounds such as “groans” (Fig. 3(e)), “ascending moans” (Fig. 3(f)) and “modulated moans” (Fig. 3(g)) were a relatively common part of the humpback song and social vocalization repertoire during all three study years (Table II). “Modulated moans” were particularly common in the 2003/2004 song and were one of the more common song-unit social vocalizations. Higher frequency harmonic sounds such as “cries” (Fig. 3(h)), “modulated cries” (Fig. 3(i)) and “ascending cries” (Fig. 3(j)) were not similar to any units in the song structure for the three study years (Table II).

The most common sound in this group was the relatively loud harmonic upswEEP “trumpet,” similar to a major unit found in the 2002 humpback song structure (Fig. 3(k)) (Table II), though heard in all three years as part of social vocalization repertoire.

3. High-frequency harmonic sounds

“Shrieks,” the highest frequency long, harmonic sound, were either ascending (Fig. 4(a)) (similar to units in the

song structure in all three study years) or descending (Fig. 4(b)) (similar to units in the 2002 song) (Table II). “Squeaks” (Fig. 4(c)) were the shortest and highest frequency sounds heard in the social vocalization repertoire and were part of the song structure in all three years. All of these social vocalizations were heard in all three study years (Table II).

4. Amplitude-modulated sounds

“Growls” (Fig. 5(a)) were heard in all three analyzed years, in both the song and as part of the social vocalization repertoire. These vocalizations were a combination of harmonic and amplitude-modulated components, the modulation being close to the fundamental frequency (Table III). “Purrs” (Fig. 5(b)) were low-frequency amplitude-modulated sounds in which the sound energy was distributed over a broad spectrum. These vocalizations were heard in all three years as part of the social vocalization repertoire, but were heard only in the 2002 song (Table III). “Trills” (Fig. 5(c)) were long, highly amplitude-modulated sounds also similar to units heard in the 2002 song, though were heard in other years as part of the social vocalization repertoire (Table III).

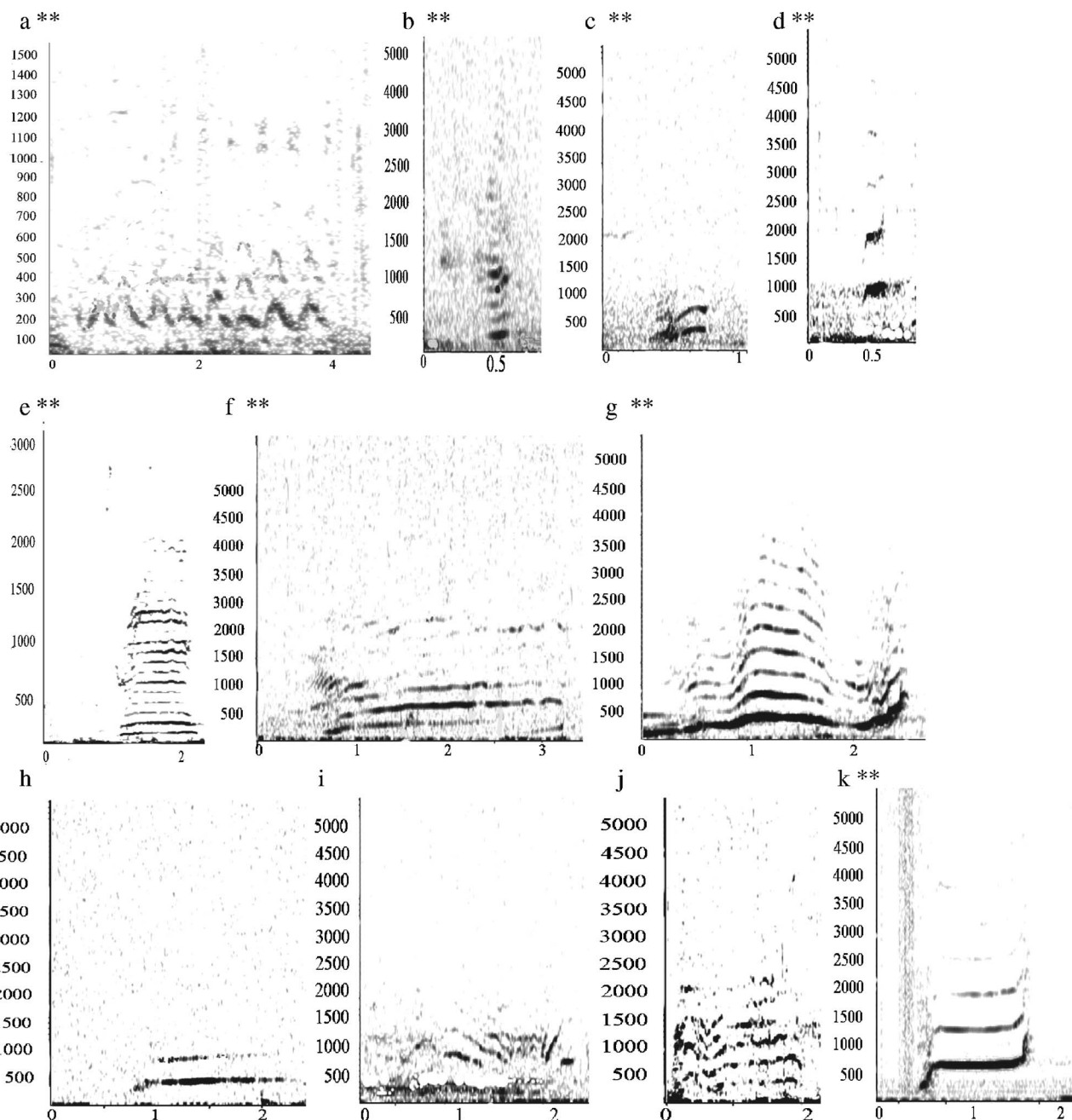


FIG. 3. Spectrogram (x =time (s), y =frequency (kHz)) of mid-frequency harmonic sounds; “groan” (a), “siren” (b), “short moan” (c), “ascending moan” (d), “modulated moan” (e), “horn” (f), “cry” (g) “modulated cry” (h), “ascending cry” (i), “violin” (j) and “trumpet” (k). Spectrograms were generated using a FFT of 1024 samples and frequency resolution of 21.5 Hz. Social vocalizations which were also part of the song are identified by “**”.

5. Broadband, “noisy” and complex sounds

Sounds which were presumed to be underwater blows were brief, high level, broadband sounds with energy spread over a wide frequency range (45–>10,000 Hz) (Fig. 6(a), Table III). Other sounds in which energy was distributed over a broad spectrum, though with a harmonic component, (complex sounds) were “barks,” “bellows,” “creaks” and “screeches” (Figs. 6(b)–6(e)). “Bellows,” “creaks” and “screeches” had a harmonic structure but with considerable bandwidth so energy distributed over a wide frequency range creating “smearing” around the frequency bands. All of these sounds were similar to units heard in the 2002 song (Table III), but were heard in the social vocalization repertoire

throughout the three analyzed years; “barks” being particularly common. The “scream” (Fig. 6(f)), heard in multiple pods, was a unique sound consisting of a high-frequency carrier which shifted upward in frequency over the duration (from about 800 to 2500 Hz) with some overlying a broadband component (Table III). It was not heard in the song over the three years.

6. Repetitive sounds

Repetitive sounds were short, low-frequency, discrete sounds that occurred in groups or bouts. “Grunts” (Fig. 7(a), Table III) were one of the most commonly heard vocalizations in the repertoire throughout the three years and oc-

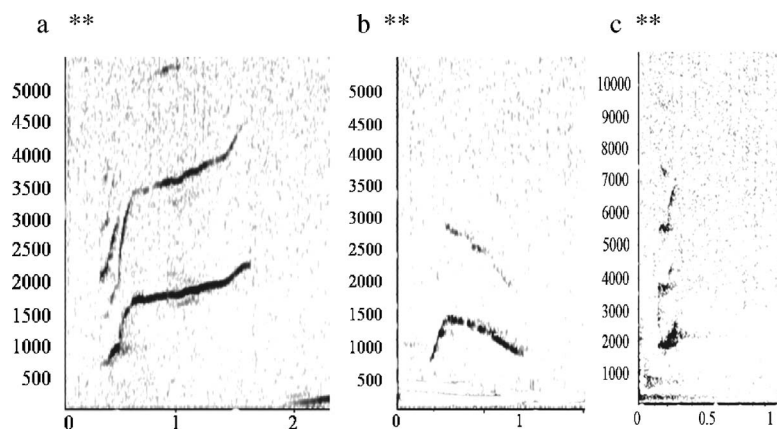


FIG. 4. Spectrogram (x =time (s) v y =frequency (KHz)) of high-frequency harmonic sounds; “ascending shriek” (a), “descending shriek” (b) and “squeak.” Spectrograms were generated using a fast Fourier transformation size of 1024 samples and a frequency resolution of 21.5 Hz. Social vocalizations which were also part of the song are identified by **.

occurred in the 2003 and 2004 song. “Croaks” (Fig. 7(b)) and “yaps” (Fig. 7(c)) were part of the 2002 song (Table III) though were only heard in 2003 and 2004 as part of the social vocalization repertoire. “Yelps” (Fig. 7(d)), “pulses” (Fig. 7(e)) and “low yaps” (Fig. 7(f)) were not heard in the song during the three years (Table III) and were comparatively uncommon vocalizations (Table III).

B. Statistical analysis of vocalization type

1. Comparison of signal types

A one-factor analysis of variance (ANOVA) was conducted on all of the measured parameters to compare between subjectively categorized signals. The means of all measured parameters were significantly different between the 34 proposed signal types ($P < 0.001$). Of the measured frequency parameters (start and end frequencies, minimum and maximum frequencies, frequency trend ratio, frequency range ratio, frequency of the spectral peak) the highest F value was for the maximum frequency of the lowest frequency component of the sound, suggesting this frequency parameter varied most between signal types (Fig. 8). The maximum frequency of the lowest frequency component of the sounds ranged from 40 to 2500 Hz. High F values (> 100) were also obtained for the end frequency of the lowest frequency component (range of 40–2500 Hz), which also suggests a high degree of variability in this parameter among signal types. Of all the sounds parameters, F values for the

number of inflections was highest ($F = 1126$) reflecting the large range of number of inflection points between different vocalization types (range 0–6).

2. Principal components analysis

Principal component analysis using the measured parameters in Table I generated four factors accounting for 80.3% of the variation, eigenvalues for the first four factors being greater than 1. Therefore, using these four factors resulted in 19.7% of the information being lost. Factor loading scores showed that factor 1 was most closely correlated with minimum, maximum, start and end fundamental frequency and peak frequency, reflecting the frequency characteristics of the signal. Factor 2 was most closely correlated with percentage of duration to the maximum frequency, the number of inflections and frequency trend ratio, reflecting the frequency modulation characteristics. The number of sounds per bout was also included in this factor. Factor 3 correlated with the duration of the sound and pulse rate of amplitude-modulated sounds. Factor 4 contained the frequency range ratio only. The mean values for the mean components differed significantly between signal types (ANOVA, $F > 155$, $p < 0.001$).

3. Discriminant function analysis

The DFA process correctly classified 78.6% of calls ($n = 660$) correctly when using the factor scores generated by

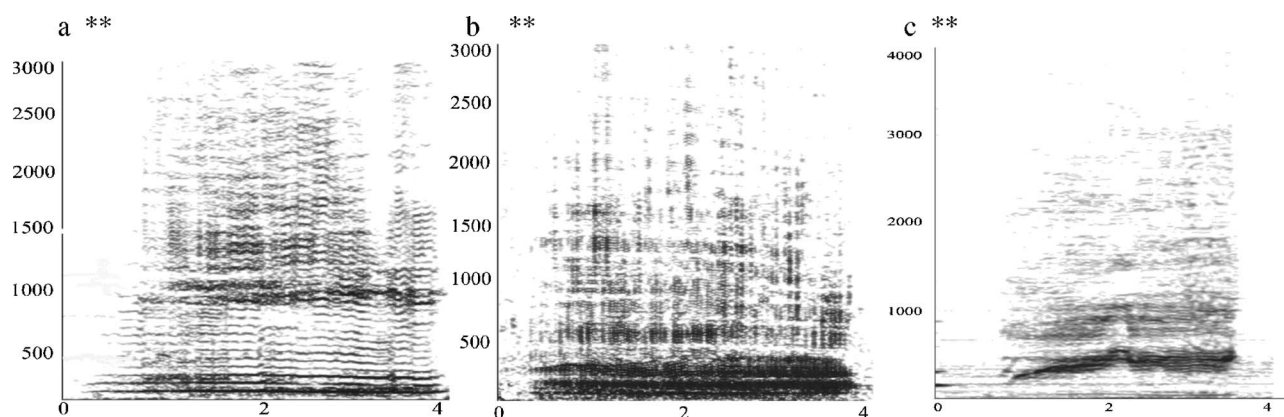


FIG. 5. Spectrogram (x =time (s), y =frequency (Hz)) of amplitude-modulated sounds; “growl” (a), “purr” (b) and “trill” (c). Spectrograms were generated using a FFT of 4096 and frequency resolution of 5.4 Hz (Figs. 4(a)–4(c)) and FFT of 1096 and frequency resolution of 21.5 Hz (Fig. 4(d)). Social vocalizations which were also part of the song are identified by **.

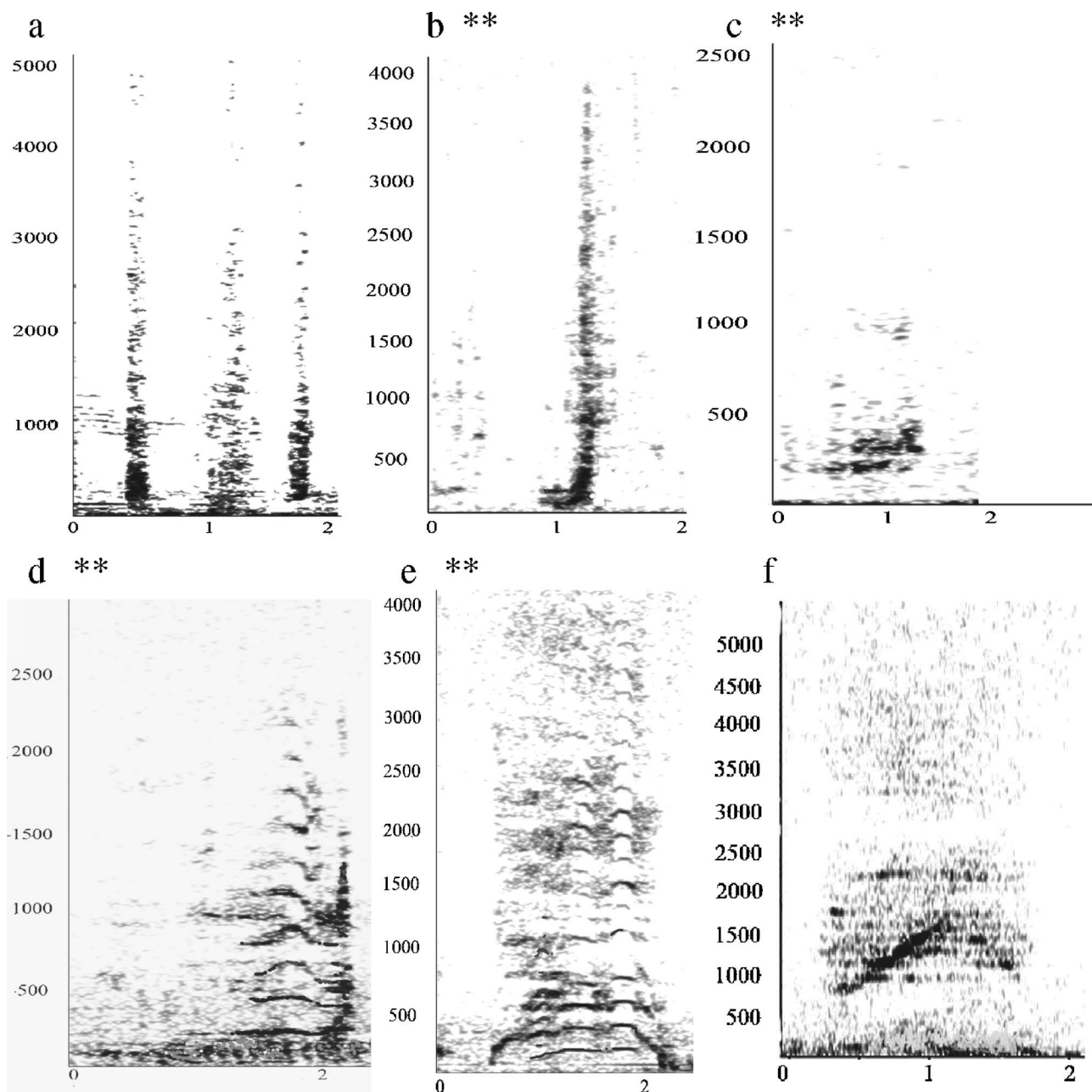


FIG. 6. Spectrograms (x =time (s), y =frequency (Hz)) of “broadband,” “noisy” and complex sounds; “presumed underwater blow” (a), “bark” (b), “bellow” (c), “creek” (d) and “screech” (e) and “scream” (f). Spectrograms were generated using a FFT of 4096 and frequency resolution of 5.4 Hz. Social vocalizations which were also part of the song are identified by **.

the PCA. Predicted classifications were over 67% correct in all but five of the sound groups (presumed underwater blows were classified as “snorts,” “creeks” were classified as “thwops,” “horns” were classified as “barks,” “screeches” were classified as “barks” or “groans” many of the “short moans” were classified as “barks”). However, generating factor scores from sound measurements may lose important information about that sound. When using the sound measurements as independent variables, the DFA process correctly classified 89.4% of the sounds and predicted classifications were over 60% correct for all groups. The DFA output showed that all measurements were significantly different between sound type ($P < 0.0001$). In this analysis, the number of inflections ($F = 720$) and the pulse rate ($F = 1484$) dis-

criminated most between vocalizations (according to the F values), followed by the number in the bout ($F = 76$). Of the fundamental frequency parameters, the end frequency had a slightly higher F value than the rest of the measurements ($F = 36$).

IV. DISCUSSION

Humpback whales are infamous for their varied and diverse song repertoire. This study shows that humpback social vocalizations are also extremely diverse in structure. Frequencies ranged from less than 30 Hz to 2.5 kHz and initial subjective qualitative visual and acoustic assessment of the number of different vocalizations produced 34 different vo-

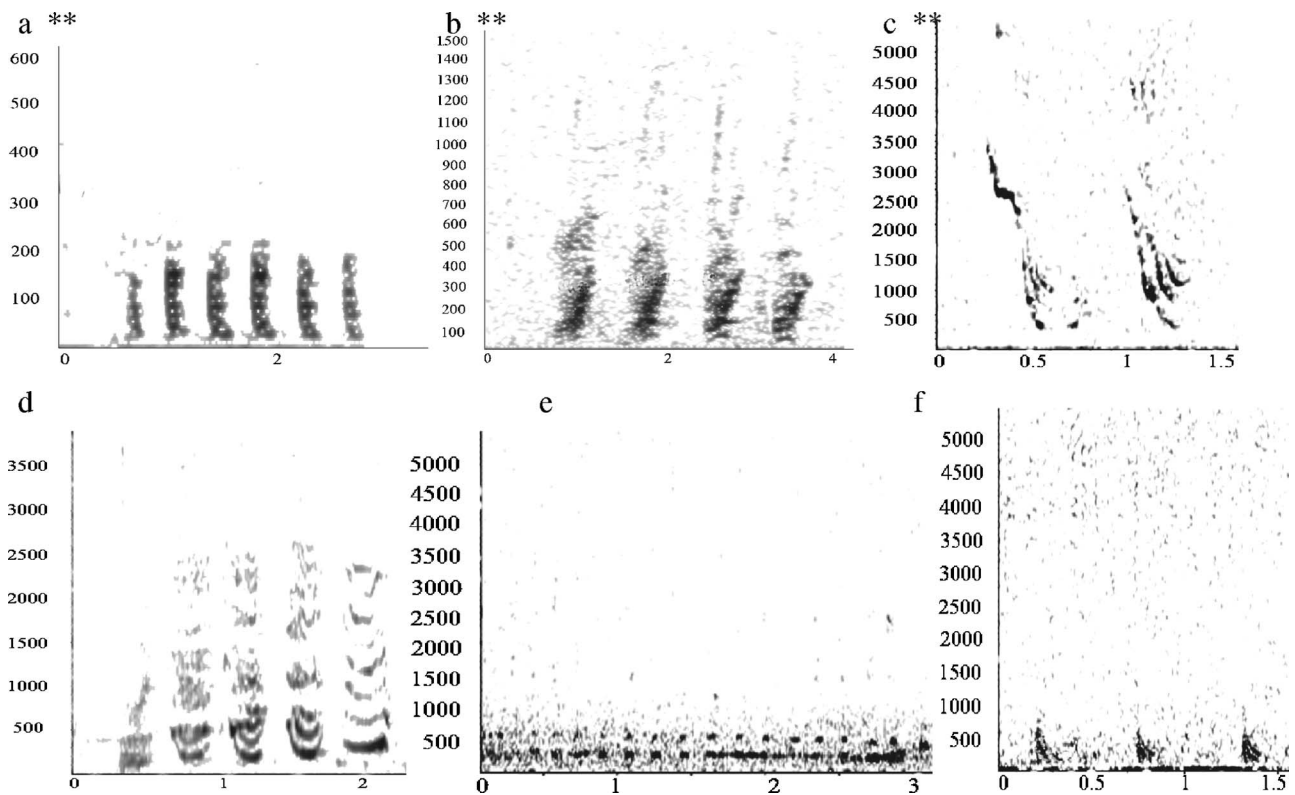


FIG. 7. Spectrograms (x =time (s), y =frequency (Hz)) of repeated sounds; “grunts” (a), “croaks” (b) and “yelps” (c). Spectrograms were generated using a FFT of 4096 and frequency resolution of 5.4 Hz. “Pulses” (d), “low yaps” (e) and “yaps” (f) spectrograms were generated using a FFT of 1024 samples and frequency resolution of 21.5 Hz. Social vocalizations which were also part of the song are identified by **.

calization types, of which 27 were heard from more than one group. This catalogue is much larger than previously described social vocalization repertoires (e.g. Thompson *et al.*, 1986). Contrary to previous suggestions (e.g. Tyack 1983; Silber 1986), they were commonly heard in mother and calf pairs and single animals as well as in other social groups such as mother-calf and escorts, pairs of adults, groups of three and groups of four adults. The use of social vocalizations within these different group compositions will be the subject of a further study. However, there are problems with subjectively analyzing sounds. There is a degree of both in-

dividual and between-group variation in similar vocalizations and it may be difficult to decide if similar calls are classified as one vocalization, or two separate vocalization types. Measuring sound parameters and statistically analyzing them helps in making objective decisions.

The PCA arranged vocalizations primarily by the frequency characteristics and secondly by the frequency modulation characteristics and the number of vocalizations within a bout. A third factor contained the duration of the vocalization and pulse rate (where applicable in amplitude-modulated vocalizations) and the fourth factor contained only the frequency range ratio. The highest source of variation between different vocalization groups came from the pulse rate, which separated amplitude-modulated vocalizations (e.g., “purrs,” “growls” and “trills”) from harmonic, complex and “noisy” vocalizations. Also, the number of inflection points in the sound was a source of high variation, separating highly modulated vocalizations (e.g., the “siren,” “modulated moan,” “ascending cry” and “modulated cry”) from unmodulated, upsweep or downsweep vocalizations. Another source of variation was the number of vocalizations within a bout, which separated vocalizations that were heard as single sounds from those that were heard in bouts (i.e., repetitive sounds, e.g., “grunts,” “croaks” and “yelps”). The most variable of the fundamental frequency characteristics was the maximum frequency (highlighted in the ANOVA) and end frequency of the sound (highlighted in the DFA). These features are obvious and easily recognizable and it is likely they are relevant in the contextual use of different acoustic signals. Fundamental frequency characteristics and frequency

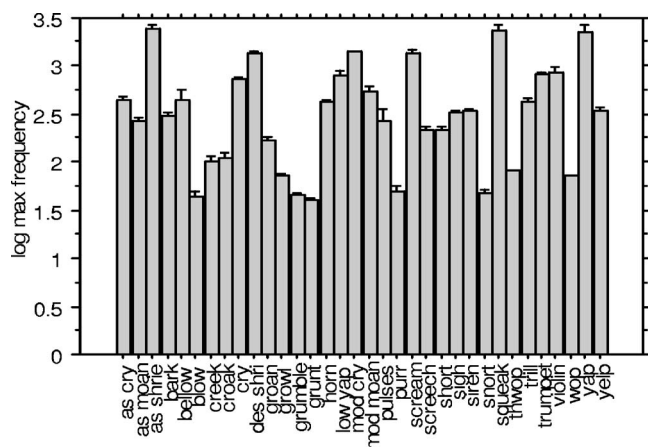


FIG. 8. Mean ($\pm$ scanning electron microscopy) plot of log maximum frequency of the 34 proposed different vocalization types. The maximum frequency was significantly different between vocalization type (ANOVA: $P < 0.0001$).

TABLE IV. Synopsis of humpback whale nonsong vocalizations recorded from previous studies (including the fundamental frequency and duration measurements if stated). Visual comparisons of spectrograms for vocalizations recorded in the following studies were made to spectrograms generated for vocalizations recorded in this study.

	Signal type	Fund freq (Hz)	Duration (s)	Spectrogram similar to
Watkins 1967	Wheezing blow	Complex	1.5–2.0	Scream
			0.72–3.48	One similar to a wop
Winn <i>et al.</i> , 1979	Pulsed moans		(variable)	
	Moans		2.1	Short moan
	Yups		(variable)	As moan
	Short cry	1625–1775	0.14–0.2	
	Chirps	1923–5520	0.23	Squeak
	Clicks		0.05–0.08	
D’Vincent <i>et al.</i> , 1985	Feeding cry	400–800	0.006	
Thompson <i>et al.</i> , 1986	Simple moans	25–30	3	
	Complex moans	35–360	0.8	Wop
	Grunt trains	25–80	0.3–0.4	Grunts
	Broadband pulse trains	400–5000	0.001	
	Shrieks	555–2000	0.42	Scream
	Trumpets	410–420	0.55	
Cherchio and Dahlheim 2001	Feeding cry	360–988	>0.5	As cry

modulation characteristics probably play important roles in humpback signal perception, though to test this, further behavioral studies should be carried out.

Although most of the sounds were separated into discrete groups with a DFA, using PCA generated factor scores does not accurately capture the entire acoustic repertoire. Also, some of the vocal repertoire formed a continuum rather than falling into discrete clusters of sounds, as was found previously in the southern right whale calls (Clark, 1982). For example, long, amplitude-modulated “growls” sometimes merged into amplitude-modulated “purrs.” “Growls” were sometimes very similar to “grumbles” and “snorts” were arbitrarily divided from “grumbles” based on the duration of the vocalization. What also must be remembered from this kind of statistical analysis is that measured sound parameters are selected subjectively. These parameters, believed to be important to human observers, may not necessarily be of importance to the whales.

Measured variables in a DFA are “independents,” that is, are a set of uncorrelated variables and PCA scores are usually used in lieu of raw data in a DFA (e.g., Boisseau 2005). However, the condensation of all sound measurements into four factors may not be appropriate given that the forced correlations in PCA may lose important acoustic aspects of the sound. The factor scores assume that sound components are correlated, for example, factor 1 assumes the fundamental frequency components (start, end, maximum, minimum frequency) are all highly correlated. Though this may be true in many sounds (the start and end frequencies must lie between the maximum and minimum frequencies), one frequency measurement is not necessarily the predictor of another frequency measurement in all sounds. A majority of the sounds were upsweeps or unmodulated, accounting for the high correlation between the start and minimum frequency (or the end and maximum frequency). However, this correlation is not true in downsweep sounds, therefore an impor-

tant acoustic property of these sounds was eliminated when using factor scores in lieu of raw data. Using all sound measurements as a set of uncorrelated independent variables in a DFA produced a set of 34 discrete calls and seemed to accurately support the aural and spectrographic categorization of sounds. Clark (1983) tested southern right whale sound categories to determine their biological significance. The same testing should be carried out on both the proposed humpback sound categories and separate calls to validate this proposed acoustic repertoire.

Vocalizations were either heard multiple times in multiple groups (the most common being the “thwop” and “wop”), or heard in only one group (though always multiple times within that group). Single males joining other groups were found to switch from low-frequency sounds to higher frequency song-like harmonic sounds, often in short, repeated sequences with similarity both in structure and sound type to song phrases, but lacking the continuity and highly structured themes of true song. Winn *et al.* (1979) referred to sounds which were similar to song units recorded from two entrapped humpback whales, a male and female. In the three study years reported here, 21 of the 34 vocalization types were part of the song repertoire at some time during the three study years; 14 of these 21 vocalization types were part of the 2002 song and only one vocalization was part of the 2003/04 song (the song changed little between 2003 and 2004) with six vocalization types heard in the song during all three study years. However, the social vocalization song units were not only part of the social vocalization repertoire in the year they were heard in the song. For example, units that were only part of the 2002 song were heard in the social vocalization repertoire during 2002, 2003 and 2004. Therefore, song units and social sounds are not discrete categories but seem to be interchangeable, and it is possible that all social vocalization units were present in a song at some

stage, or *vice versa*. This will be the subject of a further and more detailed investigation.

Some of the vocalizations recorded in this population of humpbacks also seemed to be similar to vocalizations recorded from other humpback populations. For example, the “wop” has similar frequency characteristics and spectrogram characteristics to the “simple moans” recorded from humpbacks in southeast Alaska (Thompson *et al.*, 1986) (Table IV). “Grunt trains” were also present in these recordings and “blowhole-associated shrieks” seem to be structurally similar (based on similarities in the spectrogram) to the “screams” recorded from the east Australian humpbacks (Watkins, 1967) (Table IV). A particular rhythmic series of eight repeated cries (named “ascending cries”) recorded in one particularly vocal mother-calf and escort group, were of a similar structure (though at a lower frequency) to a series of cries described in feeding humpbacks in Alaska (Cerchio and Dahlheim, 2001) (Table IV). These are initial and tentative comparisons and further comparative work should be carried out to investigate the similarity of these calls between populations.

This study provides the first comprehensive catalogue of social vocalization calls in the migrating humpback whales of eastern Australia. The catalogue includes 34 different vocalization types which are extremely varied in terms of structure. Most of the vocalization types were repeatable (i.e. heard in multiple groups), stereotyped among groups and were commonly heard in all social groups. This catalogue provides a necessary basis for subsequent analysis, for example, the changes of the social vocalization repertoire over time, and how frequently, if at all, new sound units are incorporated into and eliminated from the repertoire. Comparisons can also be made with the repertoire of other humpback populations, especially those on the feeding or breeding grounds. The significance of song units being used as social vocalizations is not known and should also be the subject of future studies.

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