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Disproportionate emission of bubble streams with killer whale biphonic calls: Perspectives on production and function

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Abstract: Stereotyped pulsed calls were attributed to 11 killer whales (*Orcinus orca*) with and without synchronous bubble streams in three datasets collected from two facilities from 1993 to 2012. Calls with and without synchronous bubble streams and divergent overlapping high frequency components ("biphonic" vs "monophonic") were compared. Subjects produced bubbles significantly more often when calls had divergent high frequency components. However, acoustic features in one biphonic call shared by five subjects provided little evidence for an acoustic effect of synchronous bubble flow. Disproportionate bubbling supported other evidence that biphonic calls form a distinct category, but suggested a function in short-range communication.

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1. Introduction

Although all killer whales produce similar types of vocalizations (whistles, clicks, and pulsed calls), repertoires of stereotyped pulsed calls are specific to populations and social groupings (Ford, 1991; Filatova *et al.*, 2012). Despite intergroup differences, killer whale pulsed calls worldwide share structural features. They are made up of components, including pulse bursts and relatively tonal pulse-modulated "screams." Most calls have at least one lower frequency scream component (LFC), while some also have an overlapping, relatively divergent high frequency component (HFC; Miller, 2002). These independent or loosely coupled components are evidence for

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production using two sound sources (Miller, 2002; Filatova *et al.*, 2007), hence the term "biphonic."

Detailed examinations of stereotyped pulsed calls support the presence of two sources in many cases (Grebner, 2009), but there is greater or lesser synchrony between the sources depending on call type. Thus, the distinction between monophonic and biphonic might be a measure of the degree of coupling rather than the number of sources operating. Here, the focus will be on calls with a strongly divergent high frequency component, termed DHFC calls (those without are no-DHFC calls).

Several lines of evidence support separation of calls with the DHFC into a functional category. Miller reported they were higher in amplitude than other pulsed calls, and also directional (Miller, 2002, 2006). Filatova *et al.* (2012) reported that they were emitted preferentially in large aggregations, while calls with a non-divergent or absent HFC were more likely to be emitted locally among pod members. These authors hypothesized that DHFC calls are long-range contact calls and signals of group identity.

Spectral analysis shows varying degrees of frequency and amplitude difference between the two sources within and between calls (Ford, 1991; Miller, 2006; Filatova *et al.*, 2007). For example, the two signal contours found in the Northern Resident killer whale N4 call, characterized by Miller as biphonic, can be separated by several kilohertz (Grebner, 2009; Grebner *et al.*, 2011), but they are not strongly divergent; the time-frequency contour of the HFC often closely follows that of the LFC.

Previous studies of DHFC calls in wild killer whales have not been accompanied by detailed behavioral observations, but they are possible under controlled conditions. Crance *et al.* (2014) observed behavioral events and states, including synchronous bubble streams, while collecting vocalizations attributed to individuals. In similar observations at another facility, Musser *et al.* (2014) noted that several DHFC calls seemed to be associated disproportionately with synchronous bubble streams. It seemed possible that DHFC calls as a class were bubbled preferentially. The present study was designed to test this hypothesis using a larger corpus of calls.

2. Methods

Three datasets (A, B, and C) of acoustic and video recordings were examined, including 3988 stereotyped pulsed calls attributed to 11 individual whales in 3 facilities from 1993 to 2012. The subjects and methods are summarized below and in Crance *et al.* (2014) and Musser *et al.* (2014).

2.1 Subjects and datasets

Dataset A subjects were two killer whale females of Icelandic origin recorded in Facility 2 ($F$2 and $F$9) in 1993 and 1994. They shared a repertoire.

Dataset B and C subjects were housed in Facility 1 and recorded from 2001 to 2012. They were four adult females ($F$1, $F$3, $F$4, and $F$13), two juvenile females ($F$7 and $F$14), two juvenile males ($M$4 and $M$6), and an adult male ($M$8). $F$7, $F$14, $M$4, and $M$6 were born in Facility 1 and 2. $F$3, $F$4, $F$7, $F$14, $M$4, and $M$6 shared a repertoire of Icelandic origin. $F$1 originated from the Pacific Northwest and had a repertoire from the Northern Resident A-5 pod (Crance *et al.*, 2014). $M$8 and $F$13 were also of Icelandic origin, but had unique and distinct repertoires.

Dataset A acoustic and video recordings were collected from 1993 to 1994 in Facility 2 with a single International Transducer Corporation ITC 6050C hydrophone (Santa Barbara, CA) suspended in the water column at least 1.3 m from any surface. Proximity and surface acoustic cues were used to attribute calls to individuals as well as synchronous behaviors. In the case of proximity cues, only calls with features indicating emission toward and near the hydrophone were accepted. Voice observations and the hydrophone track were recorded simultaneously with the signal from an underwater CCD camera (Princeton Instruments, Trenton, NJ) onto an EVO9500 VHS video recorder (Sony Electronics, Inc., Minato, Japan).

The other two datasets were recorded in Facility 1. Dataset B was collected from September 2001 to November 2006. An 8-element array of ITC 6050H and ITC 8212 hull-mounted hydrophones (ITC, Santa Barbara, CA) was used to record and locate calls of individual subjects (Crance *et al.*, 2014). Simultaneous behavioral recordings were collected on video, with signals passed to a Robot MV94 multiplexer from two underwater and two overhead video cameras (Sensormatic Video Products, San Diego, CA) and recorded on a Panasonic digital video recorder (Panasonic Consumer Electronics, Secaucus, NJ). Potential callers were separated from other whales by at least one body length. The calls could not overlap with others, show distortion or have a low signal-to-noise ratio (SNR).

Multiple procedures were developed for attributing vocalizations to individuals with low error. First, acoustic localization was used to attribute calls and check the reliability of attributions obtained using other methods (Crance *et al.*, 2014). Second, attributions were made by ear at the surface and when whales were alone in the pool.

For Dataset C, collected from November 2006 to September 2012, a third method was used, dialect attribution. Observations focused on individuals known to associate but having distinct repertoires of stereotyped pulsed calls ($F$1/$M$4, $F$1/$M$6, $F$1/$F$13). The dialect attribution method was ground-truthed using calls localized by observers at the surface or collected when whales were in the test pool alone. $M$4 was capable of learning calls (Crance *et al.*, 2014), but had not acquired calls that could be confused with $F$1's repertoire.

Although none of the attribution methods was perfectly unbiased, a balanced sample of calls emitted with and without synchronous bubbling could be collected in all three datasets (~50% of the calls were not bubbled). Bubble streams were readily detected on video and were associated with vocalizations if initiated within 300 ms of call onset.

2.2 Analysis

Recordings were digitized and processed as described in Crance *et al.* (2014). Calls in all three datasets were separated into two categories, those with a DHFC and those without (Table 1). Data for $F$7 were not included in the categorical analysis because her sample was too small, but were included in the comparison of call features.

Table 1. Summary of bubble streams produced synchronously with DHFC calls.

Dataset	Whale	Years	DHFC Calls	DHFC Bub.[§]	Prop*	No-DHFC Calls	No-DHFC Bub.[§]	Relative Prop	G^2
B	$F$1	01–06	23	3	0.13	193	0	All	—
C	$F$1	06–12	94	39	0.42	1144	0	All	
A	$F$2	93–94	80	65	0.81	40	12	2.71	373.1
B	$F$3	01–06	37	33	0.89	15	1	13.38	187.7
B	$F$4	01–06	62	37	0.60	24	1	14.32	156.6
A	$F$9	93–94	83	75	0.90	79	7	10.20	434.5
C	$F$13	12	23	3	0.13	107	0	All	—
B	$F$14	01–06	81	77	0.95	11	4	2.61	476.1
B	$M$4	01–06	147	90	0.61	77	1	47.14	448.8
C	$M$4	06–12	216	47	0.22	818	8	22.25	
B	$M$6	01–06	114	59	0.52	98	2	25.36	244.0
C	$M$6	06–12	24	7	0.29	62	0	All	
B	$M$8	01–06	222	77	0.35	114	0	All	—
	Totals		1206	612	0.51	2782	36	39.22	2388.2

Notes: [§] Count of subset bubbled. Expected values assumed a raw bubbling rate of 4%. *Prop—proportion of bubbled calls. Relative Prop—ratio of bubbled DHFC to no-DHFC calls. All—all bubbled calls were in the DHFC category. G^2 indicates the deviance statistic.

SD1-1 was the DHFC call used most frequently by the six Dataset B whales with a common Icelandic-origin dialect (Fig. 1 inset). It was composed of an initial pulse burst, followed by a scream with overlapping LFC and HFC, and could be terminated with a short, down-swept chirp. A tonal often overlapped the initial burst, and could extend into the transition between burst and scream for a few tens of milliseconds.

SD1-1 call samples were collected from five whales (*F*3, *F*4, *F*7, *M*4, and *M*6); those from *F*14 were eliminated because of an inadequate sample without bubble streams. Spectrograms were prepared (44.1 kHz sampling; 256 [bursts] or 512 [screams] points; 50% overlap) and acoustic features extracted (Fig. 1) from a subset ($N = 67$) with a high SNR and minimal distortion in Raven Pro 1.4 (Cornell Laboratory of Ornithology, Cornell, NY). The samples were balanced between bubbled and not-bubbled (35 bubbled, 32 not-bubbled).

Statistical analyses were conducted in the R statistical programming environment (Version 3.0.3, R Foundation for Statistical Computing, Auckland, NZ) and Statistica 6.1 (StatSoft, Inc., Tulsa, OK). Deviance statistics (G^2) for the proportions of calls bubbled were calculated based on the assumption that 4% of calls in both categories (DHFC and no-DHFC) should have been bubbled (estimated from all unattributed pulsed calls). If whales had bubbled both categories with equal frequency, the expected relative ratio would be 1.0 (1:1).

Acoustic features were compared between calls with and without synchronous bubble streams. The total sample of high-quality SD1-1 calls was small and potentially biased by individual differences. It was used to determine whether there were first order differences between bubbled and not-bubbled calls and to assess which features were most stereotyped. Categorical variables were compared using the deviance statistic (G^2) in R. Mean and range plots were used to check for biases by individual and bubbling categories, and an exploratory multivariate analysis of variance (MANOVA) was conducted in Statistica 6.1. Given the small sample, confidence intervals (CIs) provided a more interpretable measure of differences (bubbled vs not bubbled) than hypothesis-testing. Therefore, descriptive statistics and Wald 95% CIs were calculated for the continuous acoustic variables (all individuals pooled).
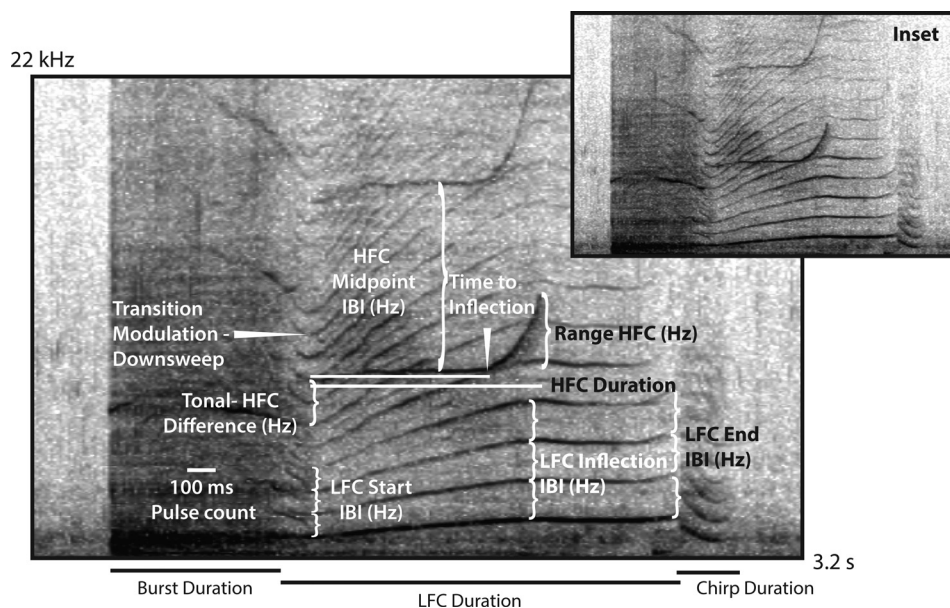

Fig. 1. Acoustic variables measured from SD1-1 calls (SD1-1a call shown in the inset). IBI indicates interband interval. LFC and HFC refer to the low frequency and high frequency components of the scream.

3. Results

Of the 1206 DHFC calls in the dataset, 612 (51%) were produced synchronously with bubble streams (Table 1), but only 36 (1.3%) of the 2782 no-DHFC calls were bubbled. The difference was significant ($G^2 = 2388.2$, $df = 2$, $p \ll 0.0001$). The deviance statistic is additive, and where within-whale values could be calculated, differences were all significant as well ($p \ll 0.0001$). Three whales ($F1$, $F13$, and $M8$) bubbled only DHFC calls ("ALL" in Table 1). Relative proportions of bubbled DHFC to no-DHFC calls were in excess of ten for all but $F2$ and $F14$, both young adult females.

Acoustic variables provided only weak evidence for an effect of bubble streams on SD1-1 calls. Possible differences were centered on the transition from the burst to scream, where there was generally a downward half-cycle of modulation in the LFC (50 of 67 samples), as of a brief overshoot and correction. However, a few calls with bubble streams began with a full sinusoidal cycle, with the positive excursion first. The difference in modulation between bubbled and not-bubbled calls was marginal ($G^2 = 6.2786$, $df = 3$, $p = 0.0988$), largely because variants were rare. Of the 67 calls, sinusoidal onset was seen in 6 bubbled calls and 1 not-bubbled. A half cycle of upward modulation was seen in 1 bubbled and 5 not-bubbled calls.

These differences could be interpreted as evidence that the onset of the scream was difficult to control or controlled differently when a bubble stream was present. This hypothesis is consistent with the only other differences observed. When a tonal overlapped the initial burst, it could extend into the LFC briefly. Presence of the tonal was not affected by bubbling ($G^2 = 0.4276$, $df = 1$, $p = 0.5132$), nor was persistence of the tonal after LFC onset ($G^2 = 1.6903$, $df = 1$, $p = 0.1936$). However, based on 95% CIs, duration of the overlap with the LFC was longer in bubbled calls (mean 144 ms vs 71 ms, 95% CI 87–201 ms vs 53–89 ms).

Calls with features suggesting an influence of the bubble stream were uncommon. The exploratory mean and range plots showed that differences were most parsimoniously explained by imbalances in samples and individual differences. For example, unusual overlap between the burst tonal and following scream was seen only in $M4$'s and $F7$'s samples. Both were young (juvenile to sub-adult age classes) during data collection.

Confidence intervals for the remaining variables overlapped, suggesting that call features were unaffected by bubble streams. The most parsimonious interpretation of the analysis was that bubble streams did not affect acoustic features of the SD1-1 call, with the possible exception of an influence on the burst-scream transition in young whales. MANOVA analysis found no significant difference ($F = 0.8503$, $df = 10$, $p = 0.6964$) and indicated that bubbling explained less than 15% of the variance in acoustic features.

4. Discussion and conclusions

Previous reports have suggested that killer whale calls with a DHFC are specialized for long-range communication (Miller, 2006), and may be important for maintaining group cohesion in large aggregations (Filatova *et al.*, 2012). However, the association between DHFC calls and bubble streams suggests a function within visual and/or echo-location range. A generalized hypothesis about the function of DHFC calls is needed.

Miller (2002) reported directionality in the HFC detectable at ranges up to 200–500 m, while the LFC was detected omnidirectionally. For free-ranging killer whales, these distances are fairly short. Miller did not study degradation of the directional cue at greater distances, so it was unclear how the HFC would function at long range. Other observations of pulsed calls have shown degradation of acoustic characteristics at ranges >2 km, with spectral elements missing at the onset and end portions of calls and loss of upper sidebands or harmonics (Grebner, 2009). This type of degradation is to be expected in a high-frequency acoustic component with a narrow source beam.

Miller found that calls with an HFC had greater source levels than LFC calls. However, he also found variations in level within call types of 20–30 dB re 1 μPa @ 1 m

(Miller, 2006), suggesting considerable amplitude scope. Vocal exchanges with relatively high source levels have been measured at close (i.e., within 100 m) to long range, so DHFC calls could serve as generalized congregation signals in addition to contact calls (Grebner, 2009). Miller (2002) also suggested that the directional HFC was a cue for swim direction. A high amplitude HFC would serve to emphasize swim direction locally.

The association between DHFC calls and bubble streams suggests that killer whales have substantial control over sound production. Based on work with the bottle-nose dolphin, vocalizations in odontocetes are pneumatically-driven by flow from the air sacs over the dorsal bursae (Madsen *et al.*, 2011). In order to produce a DHFC call with synchronous bubbles, a killer whale would have to control the flow of air and the two sources fairly independently while also controlling the flow of air out its blow-hole. Here, analysis of bubbled and not-bubbled SD1-1 calls suggested that if there was an influence on the call, it was limited to the burst-scream transition.

Evidence from the present study showed that 94% of the bubble streams observed were synchronized with DHFC calls. In the authors' experience, bubbling is associated not only with maintaining contact, but also in close-range, high activity states. Thus, DHFC calls may have multiple functions, associated not only with group cohesion, but bonding, maintaining social stability, and group action. Bubbling would draw attention to DHFC calls, making them easier to localize and follow, particularly for group members to the side or rear of the caller and out of the HFC beam. The strong association between short-range displays (bubble streams) and DHFC calls supported evidence from free-ranging studies that biphonic calls are in a special class. However, it did not suggest that the calls are specialized for long-range communication. Instead, DHFC calls are likely to be used at varying distances and in a range of behavioral contexts, wherever group connection and cohesive action are important.

Acknowledgments

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