

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/5506246>

Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii

Article in *The Journal of the Acoustical Society of America* · April 2008

DOI: 10.1121/1.2836750 · Source: PubMed

CITATIONS

57

READS

572

8 authors, including:



Ann M. Zoidis

Cetos Research Organization

14 PUBLICATIONS 157 CITATIONS

SEE PROFILE



Mari Ann Smultea

Smultea Environmental Sciences, Preston, WA USA

101 PUBLICATIONS 713 CITATIONS

SEE PROFILE



Adam S Frankel

Marine Acoustics, Inc.

74 PUBLICATIONS 1,903 CITATIONS

SEE PROFILE



Amy Whitt

Duke University

12 PUBLICATIONS 120 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Effects of ATOC [View project](#)



Behavioral Profiles [View project](#)

Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii

Ann M. Zoidis^{a)}

Cetos Research Organization, 11 Des Isle Avenue, Bar Harbor, Maine 04609

Mari A. Smultea^{b)}

Smultea Environmental Sciences LLC, 29333 SE 64th Street, Issaquah, Washington 98027
and Cetos Research Organization, 29333 SE 64th St., Issaquah, Washington 98027

Adam S. Frankel^{c)}

Hawaii Marine Mammal Consortium, P.O. Box 6107, Kamuela, Hawaii, 96738-6107

Julia L. Hopkins,^{d)} Andy Day,^{e)} and A. Sasha McFarland^{f)}

Cetos Research Organization, 11 Des Isle Ave, Bar Harbor Maine 04609

Amy D. Whitt^{g)} and Dagmar Fertl^{h)}

Geo-Marine, Inc., 2201 Avenue K, Suite A2, Plano, Texas 75074

(Received 17 July 2007; revised 12 December 2007; accepted 27 December 2007)

Although humpback whale (*Megaptera novaeangliae*) calves are reported to vocalize, this has not been measurably verified. During March 2006, an underwater video camera and two-element hydrophone array were used to record nonsong vocalizations from a mother–calf escort off Hawaii. Acoustic data were analyzed; measured time delays between hydrophones provided bearings to 21 distinct vocalizations produced by the male calf. Signals were pulsed (71%), frequency modulated (19%), or amplitude modulated (10%). They were of simple structure, low frequency (mean = 220 Hz), brief duration (mean = 170 ms), and relatively narrow bandwidth (mean = 2 kHz). The calf produced three series of “grunts” when approaching the diver. During winters of the years 2001–2005 in Hawaii, nonsong vocalizations were recorded in 109 (65%) of 169 groups with a calf using an underwater video and single (omnidirectional) hydrophone. Nonsong vocalizations were most common (34 of 39) in lone mother–calf pairs. A subsample from this dataset of 60 signals assessed to be vocalizations provided strong evidence that 10 male and 18 female calves vocalized based on statistical similarity to the 21 verified calf signals, proximity to an isolated calf (27 of 28 calves), strong signal-to-noise ratio, and/or bubble emissions coincident to sound.

© 2008 Acoustical Society of America. [DOI: 10.1121/1.2836750]

PACS number(s): 43.80.Ka [WWA]

Pages: 1737–1746

I. INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) produce song, nonsong social vocalizations, and nonvocal, surface-generated percussive sounds (e.g., caused by breaches, fluke slaps, pectoral fin slaps, etc.) during migration (e.g., Kibblewhite *et al.*, 1966; Payne and McVay, 1971; Norris *et al.*, 1999; Dunlop *et al.*, 2005, 2006; Dunlop and Noad, 2007), on low-latitude winter breeding/calving grounds (e.g., Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981, 1982; Darling, 1983; Silber, 1986; Payne, 1983; Helweg *et al.*, 1992; Au *et al.*, 2000), and on higher-latitude summer feeding grounds (e.g., Thompson *et al.*, 1977; Jurasz and Jurasz,

1979; D’Vincent *et al.*, 1985; Sharpe *et al.*, 1998). Songs are well-documented vocalizations produced by males predominantly on the wintering grounds where they appear to be part of breeding displays (e.g., Payne and McVay, 1971; Winn *et al.*, 1973; Tyack, 1981; Darling, 1983; Helweg *et al.*, 1992; Au *et al.*, 2000; Darling and Bérubé, 2001; Darling *et al.*, 2006). Singers are typically alone but may also accompany other whales including a mother and calf (e.g., Tyack, 1981; Darling, 1983; Glockner and Venus, 1983; Darling and Bérubé, 2001). Songs are characterized by continuous, repetitive, highly structured phrases and themes that contain units with harmonics above 15 kilohertz (kHz) and sounds above 24 kHz (Payne and McVay, 1971; Darling, 1983; Payne, 1983; Helweg *et al.*, 1992; Au *et al.*, 2000, 2001, 2005, 2006; Fristrup *et al.*, 2003; Potter *et al.*, 2003).

On the wintering grounds, nonsong social vocalizations have been documented among adults (Tyack, 1981; Silber, 1986). In contrast to song, adult nonsong vocalizations (i.e., “social sounds”) are produced erratically (variable through time, often interrupted by silent periods), are unpredictable, do not contain the rhythmic, consistent, and continuous pat-

^{a)}Electronic mail: ann@cetosresearch.org

^{b)}Electronic mail: msmultea@msn.com

^{c)}Electronic mail: adam.frankel@marineacoustics.com

^{d)}Electronic mail: julie@cetosresearch.org

^{e)}Electronic mail: andyday69@hotmail.com

^{f)}Electronic mail: sasha@cetosresearch.org

^{g)}Electronic mail: awhitt@geo-marine.com

^{h)}Current address: Ziphys EcoServices, 8112 Springmoss Drive, Plano, Texas 75025. Electronic mail: dfertl@gmail.com

tering of song, and are known to range from 50 hertz (Hz) to over 10 kHz, with dominant frequencies below 3 kHz (Tyack, 1981; Silber, 1986). Early publications on nonsong vocalizations in surface-active groups of wintering humpbacks coined the term social sounds to describe that specific behavioral context (Payne, 1978; Tyack, 1982, 1983; Tyack and Whitehead, 1983; Silber, 1986). These social sounds have been reported to occur predominantly in groups of three or more adults composed of a mature female accompanied by a male “principal escort” and other males aggressively vying for a position near her (Tyack and Whitehead, 1983; Silber, 1986; Clapham *et al.*, 1992). Common behaviors include chasing, charging, inflated head lunges, underwater blows, aggressive contact, and fast surface traveling (e.g., Darling, 1983; Tyack and Whitehead, 1983; Baker and Herman, 1984). Although the full function of social sounds in these surface-active groups remains uncertain, they appear to invoke approach or avoidance responses from other whales, depending on sex and composition (Tyack, 1983). They also seem to signal aggression or agitation among males fighting for dominance or proximity to a female (Silber, 1986).

Despite numerous underwater and/or acoustic studies of humpback whale groups containing a mother–calf pair in Hawaiian waters (e.g., Glockner and Venus, 1983; Tyack, 1983; Silber, 1986; Glockner-Ferrari and Ferrari, 1990; Zoidis and Green, 2001; Cartwright, 2005; Zoidis *et al.*, 2005), only recently have vocalizations been attributed to individual calves based on observational evidence and underwater videoacoustic data recorded with a single omnidirectional hydrophone (Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005). Reported evidence includes vocalizations recorded in closest proximity to a calf with no other whales nearby, strong signal-to-noise ratio, and/or vocalizations produced coincident to underwater bubble production by the calf. Although this is strong evidence that humpback calves vocalize, it cannot be ruled out that the sounds did not come from another source/whale that was nearby or not visible (i.e., the omnidirectional hydrophone used in those studies could not provide measurable evidence, such as directional bearings, linking acoustic data to a source). Published documentation that individual calves of other baleen whale species vocalize is limited to one calf from each of three different species (the first two of which were captive animals): gray (*Eschrichtius robustus*) (Wisdom *et al.*, 2001), Bryde’s (*Balaenoptera edeni*) (Edds *et al.*, 1993), and North Atlantic right whales (*Eubalaena glacialis*) (Parks and Tyack, 2005; Parks and Clark, 2007).

Dunlop *et al.* (2005, 2006) and Dunlop and Noad (2007) remotely recorded nonsong vocalizations among migrating humpback mother–calf pairs and other groups with a calf off eastern Australia using an array of five separately anchored hydrophone buoys; however, it was not possible to differentiate which individual vocalized. Dunlop and Noad (2007) collectively termed these and other nonsong vocalizations recorded from any migrating humpback as “nonsong social vocalizations,” although songs were also recorded. Vocalizations were further defined as being internally produced by a whale, including sounds generated from the blowhole. For the purpose of this paper and terminology consistency, we

use the term “nonsong vocalizations” for sounds attributed to humpback calves that did not meet the aforementioned definition of song and were not percussively generated by body contact with the water surface.

In this paper, directional acoustic data from a two-element hydrophone array combined with underwater video empirically confirm that a male humpback whale calf produced nonsong vocalizations. Additional data indicate that both male and female calves vocalize. Descriptions of these vocalizations are presented and compared to earlier reports and vocalizations from calves of other large whale species. Contexts of some calf vocalizations are also described.

II. METHODS

Underwater humpback vocalizations and behavior were recorded during the winters of 2001–2006 off southwest Maui and Kauai, Hawaii. Data were collected by one or two snorkelers off a 6–8 meter (m) inboard or outboard vessel and by personnel above water. Divers used two systems: a Panasonic GS200 and/or GS300 digital underwater video camera equipped with a single omnidirectional hydrophone (Biomon BM 8263-3c mounted 1 m below the camera, hydrophone sensitivity to 80 kHz), and a two-element hydrophone array used one day in March 2006. The two-element array consisted of two HTI MIN-96 hydrophones (frequency response 2 Hz to 30 kHz) mounted 1.5 m apart on a bar perpendicular to the optical axis of the camera. This configuration was used to determine left–right bearings to the source of sounds produced in mother–calf groups (i.e., the offset of a sound source from the plane between the two hydrophones was measured by the time delay of the signal arriving at the two hydrophones). The unit was held parallel to the water’s surface. A zero offset would indicate that the sound source was equidistant from the two hydrophones and located on a vertical plane parallel to the optical axis of the camera. Verification that sound(s) were produced by a calf for the two-element array was defined as repeated measurements of signals within a 10° angle of the plane bisecting the two hydrophones, with the calf centered in the video frame and no other whales present in that plane. Frequency response curves were obtained from the manufacturer specifications for the hydrophones and recording equipment. Hydrophones were calibrated by the manufacturer.

To analyze acoustic data, the recorded videotapes were connected to an Apple Mac Mini and raw video data were transferred to hard disk using the program IMOVIE HD. Recordings were divided into a series of video clip files. The digital video files were aurally and visually reviewed for potential acoustic signals. Visual inspection of spectrograms was useful, particularly if signals were low frequency or pulsed. All digital video clips with audible pulses were exported as audio interchange file format files. Clips downloaded from mini digital video tapes were processed using audio editing software. The sample rate of acoustic recordings was 32 or 48 kHz. Single-element recordings were downsampled by a factor of 3 to allow more detailed visualization of relatively low-frequency sounds, although the

original sampling rate data were used to determine the time delay differences.

Audio data were reviewed in RAVEN 1.2.1 (Charif *et al.*, 2004) in 30 s segments. Individual analog/digital samples were plotted and reviewed as a function of time. Detected pulses were copied and pasted into two different files to allow separate analyses of the same data. In the first file, data were low-pass filtered and decimated to allow higher resolution of low-frequency components. These data were used to create spectrograms to provide descriptive measurements of sounds. Spectrograms were calculated with a 1024 fast Fourier transform (FFT), 75% overlap, and a Hamming window. In the second file, the same original sounds recorded with the two-element array were band-pass filtered between 100 and 3000 Hz to allow more accurate measurement of time delays of each sound between the two left and right channels. Time delays were determined by hand-measuring the temporal differences between a wave form's arrival time at each sensor in milliseconds (ms). Time delays and angles were converted to bearings relative to the sound source assuming far-field propagation. Resultant bearings indicated the angular position of the sound source relative to a plane parallel to the camera's optical axis and normal to the line between the two hydrophones. These bearings are actually cones (or hyperbolic surfaces) relative to the plane parallel to the optical axis of the camera. Video from both divers was then examined to determine the position of the animal(s) in the frame at the time of sound production. The relationship between the time delay and the angle from the plane parallel to the optical axis of the camera to the sound source consists of the simple linear formula:

$$\text{angle} = \arcsin[(\Delta t \times c)/A], \quad (1)$$

where Δt =time difference between elements (s), c =speed of sound in water (m/s), and A =aperture (distance) between elements (m). Any single-measured angle could represent a source in any direction on the hyperbolic surface defined by the array geometry and the time delay differences (not necessarily the object in view of the camera, i.e., the sound source could be directly behind the camera). This was addressed by conducting both underwater and surface constant scans for animal presence and locations in relation to the recording diver. We inferred that the source animal was the one in front of the diver if no animal occurred behind the diver and no animals were visually detected on the same plane as the source animal. In addition, during calf vocalizations, no other groups were visible underwater or at the surface within 300 m.

Representative spectrograms were selected from clips to illustrate typical acoustic parameters attributable to calf vocalizations (Fig. 1). Clips were downsampled by a factor of 8, reducing the sample rate to 6 kHz. Spectrogram illustrations were made with a Hann window, a 512 FFT size, and a 98% overlap. A subsample of vocalizations with loud signal-to-noise ratios (10 dB, indicating close proximity), and data supporting the proximal position of the calf relative to other whales was selected for further analyses. Sounds with low signal-to-noise ratios, repetitive sounds similar to song, and/or sounds with more than one animal in the same plane

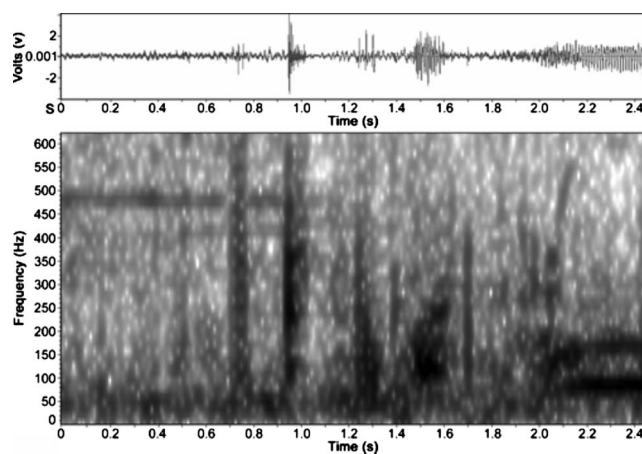


FIG. 1. Spectrograms of typical signal types attributed to a humpback whale calf based on sounds recorded with the two-element array. Five pulses are seen between 0.7 and 1.7 s. These are followed by a long tonal [or slight frequency-modulated (FM)] signal starting at 2.1 s. Above each spectrogram is a representation of the signal wave form (i.e., the recorded time series of voltages from the hydrophone shown on the y axis; time on the x axis).

based on video and field notes were discarded. Selected sounds were divided into pulsed, amplitude-modulated (AM), and frequency-modulated tonal (FM) signals. Pulsed signals had a distinct amplitude onset as opposed to the sinusoidal amplitude envelope of a typical AM signal. Duration and bandwidth, initial and ending AM and FM frequencies, number of pulses in a pulsed signal, and the first and last interpulse intervals were measured. It was noted if the interval was constant, increasing, or decreasing with time. It was not possible to calculate amplitude of sound from the source animal because we did not have the precise distance measurements necessary to estimate transmission loss with any degree of certainty.

Statistical analyses were conducted to compare vocalizations produced by the one calf recorded with the two-element hydrophone versus the selected subsample of 60 calf-attributed vocalizations recorded with the single hydrophone. Three measures of three signal types (AM, FM, and pulsed) were considered: lowest frequency, bandwidth, and duration. These measures were chosen as they are independent of each other. A mean value for each whale, measurement type, and signal type was calculated. Means were used to avoid unequal representation of one animal compared to another, as the number of vocalizations produced by each animal varied between focal sessions. Means were compared using a multivariate analysis of variance (MANOVA), with the three dependent measures compared for the two-element hydrophone array recordings of one calf in 2006 against the single-element hydrophone recordings of 21 different calves in 2001–2005.

Underwater behavior from the recorded video of all whale groups was analyzed using a modified behavioral sampling methodology based on Mann (1999). Behavioral state, individual behaviors, and vocalizations were noted for 30 s periods that the calf was in view for at least 15 s. Distance between mother, calf, and diver and depth of animals below the water surface were estimated in mother-whale body lengths similar to Glockner and Venus (1983), assuming an

average body length of approximately 13 m for a Hawaiian mother humpback per Spitz *et al.* (2000). For example, if a calf was separated from its mother by two mother-body lengths this separation distance was estimated to be approximately 26 m; the margin of error was not measured but was believed to be approximately ± 2 m based on the standard deviation and range of measured body lengths of 26 mother whales per Spitz *et al.* (2000). The mother was identified based on its closer consistent contact with the calf and genital morphology, the latter which was also used to determine sex of calves (True, 1904; Glockner, 1983).

III. RESULTS

Underwater video recordings of 170 groups containing a mother-calf humpback were filmed off Maui and Kauai from January to March for 1–3 months of each of the following years: 2001, 2002, 2004, 2005, and 2006. A total of 1007 min of videotape was recorded (mean=5.0 min per group, SD=4.9, range=< 1–30 min). Nonsong vocalizations were recorded in 110 (65%) of the 170 groups with a calf. Of the total 170 calf pods, nonsong vocalizations were detected in 87% or 34 of 39 lone mother-calf pairs and 68% or 76 of 111 mother-calf escorts; no calf nonsong vocalizations were detected among the 20 mother-calf pairs with two or more escorts. Many vocalizations were of relatively low amplitude and were not detected until later aural and spectral analyses of video and acoustic data.

The two-element array system was used off Maui for one day on 9 March 2006 for a total of 51 min on three separate mother-calf groups. Quality acoustic data were obtained for one group, a male calf accompanied by a mother and escort; they were observed and recorded for 38 continuous min of which 18 min was recorded with the two-element array set up simultaneous with a second underwater video camera and single hydrophone. The remaining 109 (95%) calf groups with nonsong vocalizations were recorded using the single hydrophone-video camera set up. Nearly all (97%) of these 109 groups and videotape (96%) were recorded near Maui; the remaining 3% were near Kauai. Acoustic data and videotape were analyzed for the one calf recorded with the two-element array and for a selected subsample of 28 calves from 109 groups as described here. All 29 calves consisted of different individuals based on examination of physical attributes of both the calf and mother [e.g., fluke, pectoral fin, and body pigment patterns, body creases, sex, and/or scarring (e.g., Katona *et al.*, 1979; Glockner and Venus, 1983)]. The one vocalizing calf recorded by the two-element array was male, whereas the 28 calves recorded with the single hydrophone consisted of 10 males and 18 females. All 29 whales assessed to be mothers based on close association with the aforementioned calves were sexed via underwater video data as females.

A. Two-element array recording of one calf

Directional bearings were determined for 21 distinct biological sound signals from the one male calf based on measured time delays of recordings between the two hydrophones of the two-element array (Table I). We analyzed nine

TABLE I. Distribution of signal types recorded from the one humpback whale calf with the two-element array and attributed to 28 humpback whale calves recorded with the single hydrophone. No significant differences were found between sounds recorded with the two-element array vs the single hydrophone for the three signal types based on lowest frequency, bandwidth, and duration parameters as indicated here. AM=amplitude modulated, and FM=frequency modulated.

Signal type	Two-element array (2006) (n=1)	Single hydrophone (2001–2006) (n=28) ^a	Total n (%)	MANOVA statistics
AM	2	12	14 (17)	$F(2, 1)=0.1285$, $p=0.8919$
FM	4	30	34 (42)	$F(2, 4)=0.2483$, $p=0.7914$
Pulsed	15	18	33 (41)	$F(2, 3)=1.7988$, $P=0.3066$
Total number of signals	n=21	n=60	n=81	

^aExcludes duplicative sounds recorded by a single hydrophone simultaneous to the two-element array for the one calf recorded with the two-element array in 2006.

different representative video clips (separate time segments from the 18 min data series) of this encounter providing real-time visual corroboration that the calf was the only animal present in the area of the recorded sounds. The calf is clearly visible in the center of all these frames. For example, a signal identified as a grunt occurred 160.8 s into clip 15 (Fig. 2). The measured time delay between the left and right hydrophones was 0.104 ms, corresponding to an angle of -6.14° , just slightly offset from the plane between the two hydrophones. No other animals were behind the calf being videoed or behind the first diver, verifying that the calf in front of the hydrophone made the sounds. A different animal behind the first diver is the only other scenario in which this time delay difference and resulting acoustic signals could possibly have been recorded. This was ruled out based on analysis of underwater video taken by the second diver, by constant vessel observer scans confirming that no other animals were nearby,

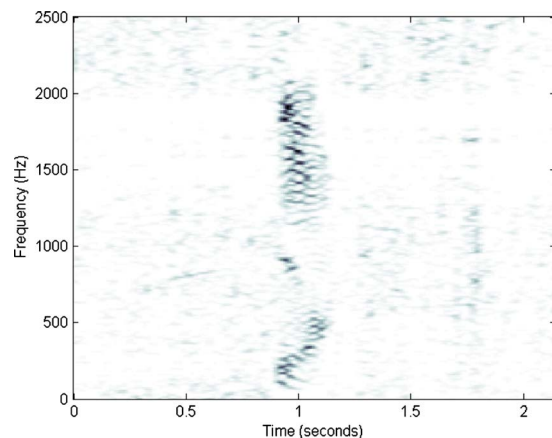


FIG. 2. (Color online) Spectrogram of an amplitude-modulated “grunt” signal produced by the humpback whale calf recorded by the two-element array.

TABLE II. Summary statistics for the amplitude-modulated (AM), frequency-modulated (FM), and pulsed signals for a male humpback whale calf recorded with the two-element (T), hydrophone array (n=21 signals), and 60 signals attributed to 28 humpback calves recorded with the single hydrophone (S). The mean value is provided for each measure with the standard deviation in parentheses. AM=amplitude modulated, FM=frequency modulated, Hz=hertz, and ms=milliseconds.

Signal type	Lowest frequency (Hz)	Highest frequency (Hz)	Bandwidth (Hz) ^a	Starting frequency (Hz)	Ending frequency (Hz)	Duration (ms)	Number of pulses	Interpulse interval (ms)	n
AM (T)	140 (39)	1442 (221)	1305 (182)	NA	NA	469 (276)	NA	NA	2
AM (S)	279 (506)	4000 ^b (2482)	3519 (2608)	NA	NA	765 (614)	NA	NA	12
FM (T)	409 (705)	1430 (685)	1024 (395)	468 (668)	1196 (706)	253 (200)	NA	NA	4
FM (S)	405 (414)	936 (736)	531 (677)	531 (677)	583 (489)	582 (502)	NA	NA	30
Pulsed (T)	181 (315)	2536 (2115)	2359 (243)	NA	NA	164 (66)	11.3 (5.6)	14.1 (3.5)	15
Pulsed (S)	140 (244)	2948 (2118)	2808 (2136)	NA	NA	384 (237)	14.1 (11.4)	31.0 (21.8)	18

^aMeasured bandwidth of the AM signals is larger than that of the FM signals, as only the fundamental was measured and harmonics were excluded.

^bLarge AM value of the category highest frequency is the result of measuring all side bands of the 12 AM sounds.

and data indicating that the mother and escort were resting at deeper water depth and were not within the angle offset range.

The types and structures of the 21 vocalizations measurably attributed to the same calf via the two-element array were predominantly pulsed signals (71%), followed by 19% FM and 10% AM signals (Tables I–III). All 21 signals were relatively short in duration (<1 s; mean=208 ms, SD=147, range=89–664 ms) and of predominantly low frequency (Table II). Mean lowest frequency of the 21 signals was 220 Hz (SD=391.5, range=10–1464 Hz). Mean highest frequency was 2221 Hz (SD=1861.4, range 312–7719 Hz). Vocalizations had a relatively narrow bandwidth (2004 Hz, SD=1891, range=238–7118 Hz) with a mean maximum frequency of 2.22 kHz (range=239–7719 Hz). Table II shows summary statistics for the AM, FM, and pulsed signals recorded from this calf. “Grunt” vocalizations were the most commonly heard signal (90% of 21) from this calf based on aural analyses (Fig. 2).

The calf made a total of four close (1–5 m) approaches to the diver, once during each of four surfacing bouts. During three approaches, the calf emitted 4–8 repetitive “grunts” and looked directly at the diver at its closest point of approach. The group (consisting of the mother, calf, and adult escort) remained in the same approximate location, resting near the shallow (<30 m) bottom.

Supplemental information providing a detailed description of this encounter, including behaviors associated with calf vocalizations and types of vocalizations, is available at the Cetos Research Organization website (2007).

B. Single hydrophone recordings of calves

A subsample of 28 of the 109 calf groups with non-song vocalizations recorded only with the single hydrophone was selected for detailed analyses based on quality of videotape and acoustic signals. These 28 groups yielded a subsample of 60 sound signals considered of reasonable quality and cir-

cumstance to be attributable to a calf using methods similar to previous reports (Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005) and data from the two-element array as follows: (1) The same 21 vocalizations made by the calf verified with the two-element array were recorded simultaneously by the single hydrophone, i.e., the omnidirectional hydrophone had coincident sounds that were verified separately as coming from the calf by the two-element array data. (2) No significant differences were found between the characteristics of three acoustic parameters of selected single-hydrophone vocalizations and those recorded and linked to the calf by the two-element array (Table II). (3) 27 of the 28 calves that produced vocalizations were alone (defined as isolated with no other whales in view within at least 15 m for at least 15 min and no humpback song sounds recorded). (4) Nonsong vocalizations were detected significantly more frequently when the calf was at or near its closest point of approach to the single hydrophone (<5 m) facing the diver/recorder whereas the mother and/or escort were resting in deeper water >10 m from the diver and calf (n=49, $X^2=49.0$, $p=0.002$, $df=2$). (5) The vocalizations had a relatively strong signal-to-noise ratio (10 dB). (6) Two different calves emitted bubbles concurrent with the time of the vocalizations.

Most (90%) of the above 60 signals were short in duration (<1.1 s, mean=559 ms, range=75 ms–2.5 s) and of predominantly low frequency (overall mean low frequency of all 60 was signals=306 Hz, range=10–1710 Hz). FM signals were most common (50%) followed by pulsed (30%) and AM (20%) signals (Table I). Of the 30 FM signals, eight were simple upsweeps, six were simple downsweeps, eight had near-flat frequency contours, and the remaining eight had inflections in their contours (e.g., U-shaped). Nine of the twelve AM sounds had no strong changes in AM frequency, two increased, and one had a complex pattern of modulation. The large single hydrophone AM value of the “highest frequency” (Table II) is the result of measuring all of the side bands for the 12 AM sounds. The measured bandwidth of

TABLE III. Comparison of vocalizations produced by young of large whale species. Age classifications are taken directly from referenced papers and may have been assessed by non-similar standards. Sample size provided when presented in literature. AM=amplitude modulated, FM=frequency modulated, Hz=hertz, SD =standard deviation, s=second, and MSB=mean sound bandwidth.

Species, age classification, sample size	Type: Bandwidth (Hz) MSB, SD, range ^a	Mean duration, SD, range (s) ^a	Source
Humpback whale (<i>Megaptera novaeangliae</i>) calf vocalizations linked with two-element array (2006: <i>n</i> =1 calf, 21 vocalizations)	Pulsed: MSB 2359, (SD 243) FM: MSB 1024, (SD 395) AM: MSB 1305, (SD 182) Overall range: 238–7118	Pulsed: 0.16, (SD 0.07) FM: 0.25, (SD 0.20) AM: 0.47, (SD 0.28) Overall mean: 0.21, (SD 0.15), Range: 0.01–0.66	This study
Humpback calf-attributed vocalizations recorded with single hydrophone (2001–2005: <i>n</i> =28 calves, 60 vocalizations)	Pulsed: MSB 2808, (SD 2136) FM: MSB 531, (SD 677) AM: MSB 3519, (SD 2608) Overall range: 140–4000	Pulsed: 0.38, (SD 0.24) FM: 0.58, (SD 0.50) AM: 0.77, (SD 0.61) Overall mean: 0.56 Range: 0.08–2.5	This study
Humpback calf-attributed vocalizations recorded with single hydrophone (1996–2003: <i>n</i> =8 calves, 49 vocalizations)	Constant rate pulse: MSB 794, Increasing or decreasing rate pulse: MSB 775, Upswept frequency tone: MSB 1297, Sound combination: MSB 1021, Median fundamental frequency 90, Overall range: 30–3000	Mean: 0.38, Range: 0.11–0.71	Pack et al., 2005
Adult humpback groups (<i>n</i> =54)	Social sounds range: 50–10 000, ^b dominant frequencies <2000, mostly FM upsweeps	Range: 0.25–> 5	Silber, 1986
Adult male humpbacks (>100)	Song range: 20–> 24000	Range: 300–1980	Payne and McVay, 1971; Helweg et al., 1992; Au et al., 2000, 2001, 2005, 2006; Fristrup et al., 2003; Potter et al., 2003
Gray whale (<i>Eschrichtius robustus</i>) female calf, 1.5–7 months old (<i>n</i> =1 calf) ^c (240 h of recordings)	Ranges: Type 1a “croak” pulses ^d : 70–4000 Type 1b “pop” pulses ^e : 70–4000 Type 3 “moan” ^d : 80–2120 Type 4 “grunt” ^d : 70–5000	Type 1a: 0.039, SD 0.012 Type 1b: 0.072, SD 0.027 Type 3: 0.44, SD 0.20 Type 4: 0.34, SD 0.090	Wisdom et al., 2001
North Atlantic right whale (<i>Eubalaena glacialis</i>) female calf (<i>n</i> =1 calf, 9 calls)	Warble range: 470–8410	Range: 0.43–4.77	Parks and Tyack, 2005

TABLE III. (Continued.)

Species, age classification, sample size	Type: Bandwidth (Hz) MSB, SD, range ^a	Mean duration, SD, range (s) ^a	Source
Bryde's whale (<i>Balaenoptera edeni</i>) juvenile ($n=1$ calf, 233 vocalizations) ^c	Discrete pulse range: 400–610 Pulsed moan range: 200–900	Discrete pulse range: 0.010, ^g Pulsed moan range: 0.5–51	Edds <i>et al.</i> , 1993
Bryde's whale calf ($n=1$ calf, 36 calls) ^h	Discrete pulse series range: 700–900	Discrete pulse range: 0.025–0.040,	Edds <i>et al.</i> , 1993

^aMean, MSB, median, SD, and/or range are reported if available. Studies did not always report the same units and parameters.

^bMaximum recording equipment frequency was 10 kHz.

^cCaptive animal.

^dProduced by 1.5 months of age.

^eProduced at 7 months of age.

^f1–2 year old animal

^g10 was indicated simply as “duration” in Edds *et al.* (1993) and appears to be a range compared to other numbers presented in the original document table.

^hRecorded with an omnidirectional hydrophone on two occasions when only first-year free-ranging calves were present at the surface, whereas an adult companion was diving. The discrete pulses were loudest when a calf was close to the hydrophone and thus may have been produced by a calf (Edds *et al.*, 1993). Discrete pulses were recorded only near these individual calves during opportunistic studies of free-ranging Bryde's whale vocalizations.

these AM signals is larger than that of the FM signals, partially because only the fundamental was measured and the harmonics were excluded from the measurement.

We recorded unusual behavioral events when calf-attributed vocalizations were recorded that to our knowledge have not been previously reported. A selective representation of these include the following: Repeated grunt series by three separate calves that increased in amplitude followed by the mother joining the calf from depth and “herding” the calf away from the diver, who was less than 5 m from the calf at the time of sound production; this type of directed movement behavior by the mother was not seen when no sounds were recorded. Two of these calves repeatedly produced grunt sounds and simultaneously created underwater bubble streams. One of these calves was recorded for a 3:04-min continuous sequence of grunts, the longest duration of any year and the farthest (>30 m) a calf was away from its mother who was in deeper water and not visible to the diver. The grunts increased in tempo and coincided with repeated bubble streams and an underwater “jaw clap.”

IV. DISCUSSION

Nonsong vocalizations occur in all adult humpback group compositions on the wintering grounds, including those with a calf, as documented previously and herein (Tyack, 1983; Silber, 1986; Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005). For the first time, measured time delays between array bearings provide measurable evidence corroborating that a male humpback calf produced 21 nonsong vocalizations as recorded with a nonstatic two-element array mounted on an underwater video camera. Previously, vocalizations have been attributed to individual humpback calves on the wintering grounds based only on observational evidence and recordings with a single-hydrophone video

camera (including the 60 vocalizations from 28 other calves reported herein) (Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005). Although convincing, the methodology used in these studies cannot unequivocally rule out that the sounds did not come from another source/whale that was nearby or not visible because one omnidirectional hydrophone cannot provide directional bearings spatially linking acoustic data to a source. However, the two-element array calf recordings combined with similarities in sound characteristics between this calf and other calf-attributed vocalizations provide further substantiation that both male and female humpback calves vocalize.

Nonsong vocalizations appear more common among wintering humpback calf pods than previously reported. Herein, nonsong vocalizations were recorded in 65% of 170 calf pods. Silber (1986) recorded nonsong social sounds in only 7% of 14 mother–calf–escort groups and in none of seven lone mother–calf pairs. Pack *et al.* (2005) attributed 49 vocalizations to eight humpback calves off Maui (the number of calf pods that did not vocalize was not reported). In addition, we found nonsong vocalizations more common in lone mother–calf pairs than among mother–calf–escort groups. Similarly, Zoidis and Green (2001) reported a significantly higher vocalization rate (10.9 vocalizations per whale per hour) among 12 mother–calf pairs compared to 50 mother–calf–escort groups (4.4), 25 surface-active groups of three or more adults with no calves (4.2), and seven adult dyads (1.7). In contrast, both Silber (1986) and Pack *et al.* (2005) reported nonsong or calf vocalizations primarily among mother–calf–escorts. Per Pack *et al.* (2005), five of eight calves that vocalized were escorted by a mother and one escort including one singing escort; the remaining three groups with such sounds were a mother–calf pair, one mother–calf with two escorts, and one lone calf (the defini-

tion, i.e., duration of how long a calf was “alone” was not indicated). Five of these calves were males and three were females (Pack *et al.*, 2005). In comparison, we attributed vocalizations to 11 male and 18 female calves.

Calf vocalizations recorded with the two-element array were simple in structure and limited in repertoire with short duration and interpulse interval, and predominantly low frequency and relatively narrow bandwidth. These characteristics were not significantly different from other vocalizations attributed to humpback calves in this study and are similar to acoustic characteristics reported in earlier reports of calf vocalizations (Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005) (Table III). Calves appear to produce sequences of the same sound in some instances. Repeated grunt bouts were made by the two-element-array recorded calf and were also recorded near calves by the single hydrophone. Similarly, Pack *et al.* (2005) reported that four calves produced sound sequences at a mean interval of 4.4 s, the spectral characteristics of which were similar to the grunt sounds we recorded (Fig. 2). In addition, vocalizations were documented simultaneous to bubble emissions from the blowhole for both the two-element array recorded calf as well as calves recorded with the single hydrophone herein and in Pack *et al.* (2005) (Figs. 1 and 2).

Pack *et al.* (2005) found that calf-attributed vocalizations were statistically similar to “noncalf social sounds” (terminology from Pack *et al.* 2005) but were significantly different from adult song units; the former were noted to have a narrower frequency range and shorter duration (Table III). Our results for calf vocalizations based on both the two-element array and single hydrophone recordings generally corroborate these findings, as do earlier reports that song is more complex than nonsong adult and calf vocalizations (Silber, 1986; Zoidis and Green, 2001; Zoidis *et al.*, 2005). In addition, pulsed signals were frequent among calves compared to the known repertoire of pulsed sounds produced by adult humpbacks in Hawaii (e.g., Payne and McVay, 1971; Darling, 1983; Payne, 1983; Silber, 1986; Helweg *et al.*, 1992; Au *et al.*, 2000). However, the most common type of signal recorded by the single hydrophone was FM signals, as found by Silber (1986) for groups of three or more adults off Maui (Table III). Most AM signals we recorded near calves had no strong evidence of changes in AM frequency. In contrast, social sounds of surface-active adult humpback groups typically exhibit considerable modulation in the AM frequency, producing the sensation of a frequency sweep (Silber, 1986).

Underwater video documenting behaviors and surroundings concurrent with two-element array recordings were important in providing empirical real-time evidence that a calf produced vocalizations. This approach allows an animal to be monitored visually and acoustically (i.e., it remains in view) for extended periods, so that underwater behaviors can be continuously recorded concurrently with vocalizations. Previous studies (e.g., Tyack, 1981, 1983; Darling, 1983; Silber, 1986) recorded nonsong sounds among adult humpback whales by deploying a single hydrophone from a small vessel. More recently, Dunlop *et al.* (2005, 2006), and Dunlop and Noad (2007) recorded nonsong vocalizations in Australia

remotely from shore using a stationary array. No directional data linking vocalizations to individuals were presented in these previous studies.

The function and biological significance of calf vocalizations are unknown. Several potential hypotheses are proposed. Some types of calf vocalizations may elicit the mother’s approach. In most cases, a calf closely (<5 to 10 m) approached the diver either silently or with nonsong vocalizations during a surfacing bout, with no reaction from the mother. However, when on three occasions a calf emitted repeated grunt vocalizations, with increasing incidence and amplitude, twice with bubbles and once with an accompanying jaw clap, the mother surfaced quickly, approached, and seemingly intentionally “herded” the calf directly away. Certain sounds (e.g., FM signals, repetitive grunts, particularly those that increase in amplitude) and/or bubble streams may function as either isolation or “alarm” calls by the calf to alert and/or call the mother. Alarm or isolation calls occur among mother-young groups of other mammalian species including dolphins (reviewed in Tyack, 2000), bats (Balcombe, 1990), and primates (Robinson, 1982). The calf may also produce vocalizations when encountering a novel stimulus (i.e., a close encounter with a diver or boat), or as unidirectional contact communication from the calf to the mother [i.e., where only one individual recognizes the call of the other and not *visa versa* (Torjanni *et al.*, 2006)]. Documentation is lacking as to whether humpback mothers or other adults use sound to communicate with calves. To date, the published evidence has not shown this.

A few studies have been able to individually link vocalizations to young of other baleen whale species including gray (Wisdom *et al.*, 2001), northern right (Parks and Tyack, 2005; Parks and Clark, 2007), and Bryde’s whales (Edds *et al.*, 1993); however, some of these studies have involved captive animals and may not be representative of free-ranging animals (Table III). Although the vocalizations themselves are quite different between species and are limited to a few individuals, their overall characteristics are generally similar to humpback calf-attributed vocalizations in terms of simplicity, limited repertoire, short duration, and predominantly low and narrowband frequency, when compared to adults of the same species (Edds *et al.*, 1993; Wisdom *et al.*, 2001; Parks and Tyack, 2005; Parks and Clark, 2007) (Table III). A captive juvenile Bryde’s whale produced primarily pulsed moans with amplitude and frequency modulation, and on two occasions, free-ranging isolated Bryde’s calves were linked with series of 4–11 discrete pulse calls (Edds *et al.*, 1993). Series of pulsed vocalizations (i.e., pulse trains) were also commonly produced by a captive gray whale calf (Wisdom *et al.*, 2001) as well as an entrapped juvenile humpback (Beamish, 1979) and humpback calves reported herein and by Pack *et al.* (2005) (Table III). Published individual sound confirmation of Northern right whale calves is limited to one free-ranging female based on bearing data collected with an acoustic array on the feeding grounds (Parks and Tyack, 2005; Parks and Clark, 2007). This calf produced stuttered “screamlike” calls interrupted by many pauses when alone at the surface as the other adults in the group dove. The calls

were generally of higher pitch and often longer in duration than adult female “screams” used to initiate surface-active adult groups (Parks and Tyack, 2005).

The biological significance of vocalizations produced by humpback calves and how it may change depending on social structure, environmental cues, ontogeny, and behavior, as well as whether mothers vocalize, remains to be further investigated. Circumstances of calf-attributed vocalizations recorded with a single hydrophone provide strong indication that the calf is most likely the sound source rather than the mother, including in lone mother–calf pairs. Compelling observational data include vocalizations recorded coincident with bubble emissions by humpback calves during both two-element and single hydrophone recordings, similar to humpback whale calves and a juvenile reported elsewhere (Beamish, 1979; Zoidis and Green, 2001; Pack *et al.*, 2005; Zoidis *et al.*, 2005). A captive juvenile Bryde’s whale emitted bubbles only when vocalizing, throughout the vocalizations, and only from the right blowhole (Edds *et al.*, 1993). Dolphins sometimes emit bubbles simultaneous to sound production (Dahlheim and Awbrey, 1982; McCowan, 1995; McCowan and Reiss, 1995; Dudzinski, 1996; Herzog, 1996; Killebrew *et al.*, 1996, 2001), although this relationship is not consistent (Caldwell *et al.*, 1990; Fripp, 2005). However, it cannot be ruled out that some sounds recorded by the single hydrophone were produced by the mother without corroboration from directional acoustic data. Northern right whale mothers vocalize to their calves when they become separated, presumably to reunite the two (Parks and Clark, 2007). Similar contact calls may occur between humpback mothers and calves but have not yet been recorded or identified, possibly due to low-amplitude source levels that are difficult to detect except at close range. The relatively low amplitude of calf vocalizations we recorded may be why calves have only recently been reported to vocalize (Zoidis and Green, 2001).

Further analyses of the acoustic characteristics and behavioral context of calf vocalizations are underway, including their role as a potential indicator of stress, with implications for management concerns in areas with elevated anthropogenic activity and underwater noise such as Hawaii.

ACKNOWLEDGMENTS

The authors thank Randy Bates, Charles Bishop, Dan DenDanto, M. Green, Carol Hart, Thea Jenson, Terry McCabe, Don Moses, Dan Shapiro, Ethan Silva, Jessica Sherman, J. Pantukhoff, and Norbert Wu for their assistance and support with field portions of this project. They thank Pete Gehring, Thomas F. Norris, Shannon Rankin, Carol Spencer, P. Stevick, and Jenelle Black for reviewing this manuscript and/or for their editorial or technical input. They thank all our donors and patrons that have funded this work so that this publication was possible. They are also grateful to E. M. Blair, J. Dennis, S. Katona, D. Kearney, P. Tadd, A. Waldron, and A. Wright for their support and encouragement over the years.

Au, W. W. L., Darling, J., and Andrews, K. (2001). “High-frequency harmonics and source level of humpback whale songs,” *J. Acoust. Soc. Am.*

110(5), Part 2, 2770.

- Au, W. W. L., Lammers, M. O., Stimpert, A., and Schotten, M. (2005). “The temporal characteristics of humpback whale songs,” *J. Acoust. Soc. Am.* **118**, 1940.
- Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., and Andrews, K. (2006). “Acoustic properties of humpback whale songs,” *J. Acoust. Soc. Am.* **120**, 1103–1110.
- Au, W. W. L., Popper, A. N., and Fay, R. R., eds. (2000). *Hearing by Whales and Dolphins*, Springer Handbook of Auditory Research Vol. **12** (Springer, New York), 1–485.
- Baker, C. S., and Herman, L. M. (1984). “Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters,” *Can. J. Zool.* **62**, 1922–1937.
- Balcombe, J. P. (1990). “Vocal recognition of pups by Mexican free-tailed bats, *Tadarida brasiliensis mexicana*,” *Anim. Behav.* **39**, 960–966.
- Beamish, P. (1979). “Behavior and significance of entrapped baleen whales,” in *Behavior of Marine Animals*, Vol 3: Cetaceans, edited by H. E. Winn, and B. Olla (Plenum, New York), pp. 291–309.
- Caldwell, M. C., Caldwell, D. K., and Tyack, P. L. (1990). “A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin,” in *The Bottlenose Dolphin*, edited by S. Leatherwood, and R. R. Reeves (Academic, San Diego), pp. 199–234.
- Cartwright, R. (2005). “A comparative study of the behaviour and dynamics of humpback whale (*Megaptera novaeangliae*) mother and calf pairs during their residence in nursery waters,” Ph.D. dissertation, Manchester Metropolitan University, Manchester, U.K., pp. 1–259.
- Cetos (2007). “Calf activity (behavioral and acoustic) during social sound production, as recorded with two-element hydrophone array,” Cetos Research Organization Internet website http://www.cetosresearch.org/research/humpback_findings.htm, last accessed 17 July 2007.
- Charif, R. A., Clark, C. W., and Frstrup, K. M. (2004). *Raven 1.2 User’s Manual* (Cornell Laboratory of Ornithology, Ithaca), pp. 1–205.
- Clapham, P. J., Palsbøll, P. J., Mattila, D. K., and Vasquez, O. (1992). “Composition and dynamics of humpback whale competitive groups in the West Indies,” *Behaviour* **122**, 182–194.
- D’Vincent, C. G., Nilson, R. M., and Hanna, R. E. (1985). “Vocalization and coordinated feeding behaviour of the humpback whale in southeastern Alaska,” *Sci. Rep. Whales Res. Inst.* **36**, 41–47.
- Dahlheim, M. E., and Awbrey, F. (1982). “A classification and comparison of sounds of captive killer whales (*Orcinus orca*),” *J. Acoust. Soc. Am.* **72**, 661–670.
- Darling, J. D. (1983). “Migrations, abundance and behavior of Hawaiian humpback whales (*Megaptera novaeangliae*) (Borowski),” Ph.D. dissertation, University of California at Santa Cruz, Santa Cruz, CA, pp. 1–147.
- Darling, J. D., and Bérubé, M. (2001). “Interactions of singing humpback whales with other males,” *Marine Mammal Sci.* **17**, 570–584.
- Darling, J. D., Jones, M. E., and Nicklin, C. P. (2006). “Humpback whale songs: Do they organize males during the breeding season?” *Behaviour* **143**, 1051–1101.
- Dudzinski, K. M. (1996). “Communication and behavior in the Atlantic spotted dolphins (*Stenella frontalis*): Relationships between vocal and behavioral activities,” Ph.D. dissertation, Texas A&M University, College Station, TX, pp. 1–218.
- Dunlop, R. A., Noad, M. J., Cato, D. H., and Stokes, D. (2007). “The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*),” *J. Acoust. Soc. Am.* **122**, 2893–2905.
- Dunlop, R. A., Noad, M. J., and Cato, D. H. (2005). “Widespread and contextual use of social communication in migrating humpback whales,” *Abstracts, 16th Biennial Conference on the Biology of Marine Mammals*, San Diego, CA, p. 79.
- Edds, P. L., Odell, D. K., and Tershy, B. R. (1993). “Vocalizations of a captive juvenile and free-ranging adult-calf pairs of Bryde’s whales, *Balaenoptera edeni*,” *Marine Mammal Sci.* **9**, 269–284.
- Fripp, D. (2005). “Bubblestream whistles are not representative of a bottlenose dolphin’s vocal repertoire,” *Marine Mammal Sci.* **21**, 29–44.
- Frstrup, K. M., Hatch, L. T., and Clark, C. W. (2003). “Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts,” *J. Acoust. Soc. Am.* **113**, 3411–3424.
- Glockner, D. A. (1983). “Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment,” in *Communication and Behavior of Whales*, edited by R. Payne (Westview Press, Boulder), pp. 447–464.
- Glockner, D. A., and Venus, S. C. (1983). “Identification, growth rate, and behavior of humpback whale (*Megaptera novaeangliae*) cows and calves

- in the waters off Maui, Hawaii, 1977–79,” in *Communication and Behavior of Whales*, edited by R. Payne (Westview Press, Boulder), pp. 223–258.
- Glockner-Ferrari, D. A., and Ferrari, M. J. (1990). “Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975–1988: The life history, reproductive rates and behavior of known individuals identified through surface and underwater photography,” Rep. Int. Whaling Com. Special Issue Vol. **12**, 161–169.
- Helweg, D. A., Frankel, A. S., Mobley, J. R., Jr., and Herman, L. M. (1992). “Humpback whale song: Our current understanding,” in *Marine Mammal Sensory Systems*, edited by J. A. Thomas, R. A. Kastelein, and A. Ya. Supin (Plenum, New York), pp. 459–483.
- Herzing, D. L. (1996). “Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*,” *Aquat. Mamm.* **22**, 61–79.
- Jurasz, J. M., and Jurasz, V. P. (1979). “Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska,” *Sci. Rep. Whales Res. Inst.* **31**, 69–83.
- Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J. S., and Whitehead, H. (1979). “Identification of humpback whales by fluke photographs,” in *Behavior of Marine Animals—Current Perspectives in Research, Vol. 3: Cetaceans*, edited by H. E. Winn, and B. L. Olla (Plenum, New York), pp. 33–44.
- Kibblewhite, A. C., Denham, R. N., and Barnes, D. J. (1966). “Unusual low-frequency signals observed in New Zealand waters,” *J. Acoust. Soc. Am.* **41**, 644–655.
- Killebrew, D. A., Mercado, E. III, Pack, A. A., and Herman, L. M. (1996). “Burst-pulse sounds of a neonate bottlenosed dolphin,” *J. Acoust. Soc. Am.* **100**, 2610.
- Killebrew, D. A., Mercado, E., III, Herman, L. M., and Pack, A. A. (2001). “Sound production of a neonate bottlenosed dolphin,” *Aquat. Mamm.*, **27**, 34–44.
- Mann, J. (1999). “Behavioural sampling methods for cetaceans: A review and critique,” *Marine Mammal Sci.* **15**, 102–122.
- McCowan, B. (1995). “A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Tursiops truncatus*),” *Ethology* **100**, 177–194.
- McCowan, B., and Reiss, D. (1995). “Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae: *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis,” *Ethology* **100**, 193–209.
- Noad, M. J., Dunlop, R., Stokes, D., Miller, P., and Biassoni, N. (2006). “Humpback whale social sounds: Source levels and response to playback,” *J. Acoust. Soc. Am.* **120**, 3012.
- Norris, T. F., McDonald, M., and Barlow, J. (1999). “Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration,” *J. Acoust. Soc. Am.* **106**, 506–514.
- Pack, A. A., Herman, L. M., Deakos, M. H., Hakala, S., Craig, A. S., Olson, J. R., Spitz, S. S., Herman, E., Goetschius, K., and Lammers, M. O. (2005). “First report of sounds recorded from individual humpback whale calves on the Hawaiian wintering grounds,” *Abstracts, 16th Biennial Conference on the Biology of Marine Mammals*, San Diego, CA, p. 216.
- Parks, S. E., and Clark, C. W. (2007). “Acoustic communication: social sounds and the potential impacts of noise,” in *The Urban Whale: North Atlantic Right Whales at the Crossroads*, edited by S. D. Kraus, and R. M. Rolland, (Harvard University Press, Cambridge, MA), pp. 310–332.
- Parks, S. E., and Tyack, P. L. (2005). “Sound production by North Atlantic right whales (*Eubalaena glacialis*) in surface active groups,” *J. Acoust. Soc. Am.* **117**, 3297–3306.
- Payne, R. S. (1978). “Behavior and vocalizations of humpback whales (*Megaptera* sp.),” in *Report on a Workshop on Problems Related to Humpback Whales (*Megaptera novaeangliae*) in Hawaii*, edited by K. S. Norris and R. R. Reeves, Report prepared for the U.S. Marine Mammal Commission, Washington, D.C., NTIS PB-280 794, pp. 56–78.
- Payne, R. S., editor (1983). *Communication and Behavior of Whales* (Westview Press, Boulder).
- Payne, R. S., and McVay, S. (1971). “Songs of humpback whales,” *Science* **173**, 585–597.
- Potter, J. R., Deakos, M. H., Koay, T. B., Durville, C., and Pack, A. A. (2003). “Up close and personal: Recording humpback whale song at close ranges (10–50 m),” *Proceedings, Oceans 2003 MTS/IEEE Conference*, San Diego, CA, p. 472.
- Robinson, J. G. (1982). “Vocal systems regulating within-group spacing,” in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Petersen (Cambridge University Press, Cambridge), pp. 94–116.
- Sharpe, F. A., Dill, L. M., Beaver, V., and Spellman, B. (1998). “Killing me softly: Feeding calls of the Alaskan humpback whale,” *Abstracts, World Marine Mammal Science Conference*, Monaco, pp. 123.
- Silber, G. K. (1986). “The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*),” *Can. J. Zool.* **64**, 2075–2080.
- Spitz, S., Herman, L. M., and Pack, A. A. (2000). “Measuring sizes of humpback whales (*Megaptera novaeangliae*) by underwater videogrammetry,” *Marine Mammal Sci.* **16**, 664–676.
- Thompson, P. O. W., Cummings, W. C., and Kennison, S. J. (1977). “Sound production of humpback whales, *Megaptera novaeangliae*, in Alaskan waters” *J. Acoust. Soc. Am.* **62**, 1–182.
- Torriani, V. G., Vannoni, E., and McElligott, A. G. (2006). “Mother-young recognition in an ungulate hider species: A unidirectional process,” *Am. Nat.* **168**, 412–420.
- True, F. W. (1904). “The whalebone whales of the western North Atlantic compared with those occurring in European waters with some observations on the species of the North Pacific,” *Smith. Contrib. Know.* **33**, 1–332.
- Tyack, P. (1981). “Interactions between singing Hawaiian humpback whales and conspecifics nearby,” *Behav. Ecol. Sociobiol.* **8**, 105–116.
- Tyack, P. (1983). “Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds,” *Behav. Ecol. Sociobiol.* **13**, 49–55.
- Tyack, P., and Whitehead, H. (1983). “Male competition in large groups of wintering humpback whales,” *Behaviour* **83**, 132–154.
- Tyack, P. L. (1982). “Humpback whales respond to sounds of their neighbors” Ph.D. dissertation, Rockefeller University, New York, NY, pp. 1–207.
- Tyack, P. L. (2000). “Functional aspects of cetacean communication,” in *Cetacean Societies: Field Studies of Dolphins and Whales*, edited by J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (University of Chicago Press, Chicago), pp. 270–307.
- Winn, H. E., Bischoff, W. L., and Taruski, A. G. (1973). “Cytological sexing of cetaceans,” *Mar. Biol. (Berlin)* **23**, 343–346.
- Winn, H. E., and Winn, L. K. (1978). “The song of the humpback whale (*Megaptera novaeangliae*) in the West Indies,” *Mar. Biol. (Berlin)* **47**, 97–114.
- Wisdom, S., Bowles, A. E., and Anderson, K. E. (2001). “Development of behavior and sound repertoire of a rehabilitating gray whale calf,” *Aquat. Mamm.* **27**, 239–255.
- Zoidis, A. M., and Green, M. (2001). “Relationship of social vocalizations to pod size, composition and behavior in the Hawaiian humpback whale,” *Abstracts, 15th Biennial Conference of the Biology of Marine Mammals*, Vancouver, B.C., <http://www.cetosresearch.org/main.htm> last accessed 21 September 2007.
- Zoidis, A. M., Smultea, M. A., Fertl, D., Day, A. J., DenDanto, D., Ertl, A. S., Hayes, J., and Whitt, A. D. (2005). “Can you hear me now? Social sounds and underwater behavior of Hawaiian humpback whale (*Megaptera novaeangliae*) calves,” *Abstracts, 16th Biennial Conference of the Biology of Marine Mammals*, San Diego.