A description of sounds recorded from melon-headed whales (Peponocephala electra) off Hawai'i

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Between 2004 and 2006, large groups of melon-headed whales were recorded off the Big Island of Hawai'i. No other odontocete species were sighted in these groups. Recordings contained echolocation clicks, burst-pulse sounds, and whistles. Echolocation clicks typically contained energy beginning at 13 kHz and continued strongly to the frequency cutoff of the recording system, suggesting that the frequency content of the clicks continued well beyond 24 kHz. Burst-pulse sounds were typically short, with a mean duration of 586 ms with a mean inter-pulse interval of 2.47 ms. The distribution of numbers of pulses was skewed toward fewer pulses, with a mean of 46.7 pulses. Overall, whistles were relatively simple frequency-modulated downsweeps, upsweeps, and sinusoidal signals. Fundamental frequencies ranged from 890 Hz to 23.5 kHz. Most whistles had smooth contours, although frequency steps were observed. Whistles were generally short, with a mean duration of 586 ms. The acoustic characteristics of these whistles were similar to those in the only previously published descriptions of melon-headed whale vocalizations [Watkins *et al.* (1997). Caribbean J. Sci. 33, 34–40; Janik and Curran (2007). 17th Biennial Conference on the Biology of Marine Mammals, Capetown, South Africa] and were shown to be distinguishable from whistles of other odontocete species. © *2010 Acoustical Society of America*. [DOI: 10.1121/1.3365259]

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I. INTRODUCTION

Relatively little is known about the biology and life history of melon-headed whales (Peponocephala electra), which are distributed in tropical to warm-temperate waters worldwide (Perryman et al., 1994; Brownell et al., 2009). Large groups of these animals are seen regularly off all the main Hawaiian Islands over a range of water depths (255-4407 m) (Shallenberger, 1981; Baird et al., 2003), but most frequently in depths greater than 2000 m (Huggins et al., 2005). Shallenberger (1981) described melon-headed whales as especially frequent off the Waianae coast of O'ahu, the north Kohala coast of Hawai'i, and the leeward coast of Lana'i. Typically they eat small schooling fish, but also feed on squid (Sekiguchi et al., 1992; Jefferson and Barros, 1997). These medium-sized dolphins are thought to feed deep in the water column because one of their primary prey, mesopelagic squid, are found in waters up to 1500 m deep (Jefferson and Barros, 1997).

Boat-based surveys estimated the median melon-headed whale group size around the main Hawaiian Islands to be 305 individuals, with a range from 17 to 800 animals (Huggins et al., 2005). In Hawai'i, melon-headed whales are known to interact with humpback whales (Megaptera novae-angliae) (HMMC, unpublished), rough-toothed dolphins (Steno bredanensis), pantropical spotted dolphins (Stenella attenuata) (Huggins et al., 2005), and short-finned pilot whales (Globicephala macrorhynchus) (Migura and Meadows, 2002), and have been observed avoiding killer whales (Orcinus orca) (Huggins et al., 2005). Inter-island movements from Kaua'i to Hawai'i have been documented based on photo-identified individuals (Huggins et al., 2005). Little is known about this species elsewhere in its range, and until

recently, most knowledge about its biology comes from mass strandings (Perryman *et al.*, 1994).

Like many delphinids, melon-headed whales produce echolocation click trains, burst-pulse sounds (BPSs), and whistles. Echolocation click trains are a series of individual clicks that are usually broadband signals with a rapid rise time (Caldwell and Caldwell, 1971). Burst-pulses are composed of individual pulses that are perceived as a continuous sound by humans because the inter-pulse interval (IPI) is shorter than the integration time (<5 ms; Murray et al., 1998) and appear in spectrograms as harmonic bands (Watkins, 1967). Whistles are pure-tone, narrow-band frequency-modulated signals (Caldwell et al., 1990). Each of these signal types was examined separately in this study.

Knowledge of melon-headed whale vocalizations is limited to sparse previous recordings from the Caribbean (Watkins *et al.*, 1997) and off Indonesia (Janik and Curran, 2007). Group size estimates from these investigations ranged from 10 to 14 animals for the Caribbean study to greater than 50 in the Indonesian study. We compare our results with these two previous studies and provide the first descriptive report of melon-headed whale vocalizations in the North Pacific Ocean.

II. METHODS

A. Field methods

During the course of our annual humpback photoidentification and boat-based song recording studies, we searched offshore waters near the fish aggregation device (FAD) buoy "XX," located approximately 11 nautical miles west of Kawaihae Harbor along the northwest coast of the island of Hawai'i (i.e., the Kohala coast). Observations and





FIG. 1. (A) shows the pointed tips of the melon-headed whale pectoral fins. (B) shows the white lips, facial mask, and dorsal cape that are diagnostic of melon-headed whales. Photo taken under NFMS Permit No. 774-1714.

recordings were made from a 6-m Boston Whaler, powered by a Honda four-stroke 130 HP engine. Identification photos and underwater acoustic recordings were collected on each occasion. When a group of melon-headed whales was sighted, the research vessel was slowly driven near the animals. Observations were conducted to describe their behavioral state, estimate group size, and determine the presence/absence of calves or other species. In order to ensure that no other odontocete species were associated with the melon-headed whales, the research vessel was slowly driven through the entire group, with experienced observers using both naked eye and handheld binoculars to identify each subgroup as well as to estimate group size. Behavioral sampling

followed an *ad libitum* group-follow protocol. While not ideal, this protocol was used due to unfamiliarity with the behavioral repertoire of this species and the size of the group (Mann, 1999).

Audio recordings were made with a High-Tec HTI-96-MIN hydrophone (frequency response of 2 Hz–30 kHz, sensitivity of -170 dB re 1 V/ μ Pa) lowered to a depth of approximately 8 ms, connected to a Creative Nomad Jukebox 3 that was recording at a 48 kHz sampling rate. The audio was monitored with headphones until vocalizations became too faint to be clearly heard. At this point, the vessel was re-positioned closer to the group and recording resumed.

B. Species identification

Photographs taken during each encounter were later compared to field guides (Stewart et al., 2002) to confirm species identification. While melon-headed whales are similar in appearance to pygmy killer whales (Feresa attenuata), the acutely pointed tips of the pectoral fins and the deep-dipping cape below the dorsal fin are reliable diagnostic characters (Jefferson and Barros, 1997). Figure 1(A) shows the melon-headed whales' characteristic pointed pectoral fin tips and the white lips, facial mask, and dorsal mask are visible in Fig. 1(B).

C. Analysis methods

Melon-headed whales produce three types of sounds: echolocation clicks, burst-pulse, sounds and whistles. Figure 2 shows a sonogram of a sample from the recordings that contains all three types. Each signal type is sufficiently different to warrant different analysis methods. Briefly, echolocation clicks could be detected automatically, whereas burst-pulse sounds and whistles were selected by manually stepping through the recording and visually identifying and saving individual burst-pulses or whistles to individual files for further analysis. Further details on the analysis of each signal type are given below.

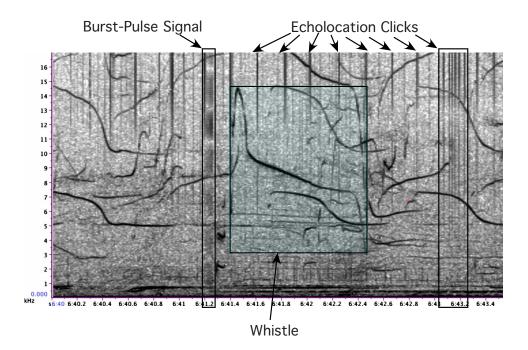


FIG. 2. (Color online) A sample spectrogram that includes all three signal types. These include echolocation clicks, which have a high frequency bias in energy distribution. Burst-pulse sounds have energy throughout the recorded spectrum, and whistles show a typical odontocete frequency-modulated whistle structure.

The 48 kHz sampling rate of the recorder was insufficient to record all the frequencies contained within the echolocation clicks. Therefore, we focused on their temporal characteristics. The XBAT (version 5) template detector (Figueroa, 2007) was used to find and measure the time of occurrence of echolocation clicks. The differences in times of click onset were used as the measure of inter-click intervals (ICIs). A relatively high correlation threshold value of 0.5 was used in the template detector to minimize false detections.

The sampling rate of 48 kHz was again insufficient to capture all the frequencies within the broadband pulses that make up the BPSs. Therefore, there was no attempt to analyze the frequency content of the signals. Rather, the temporal characteristics were examined. All high-quality burst-pulse sounds were selected and exported as individual waveform files. The criterion for "high quality" included no strong overlapping vocalizations and a signal-to-noise ratio (SNR) > 12 dB, where SNR was defined as follows:

SNR = $10 \times \log_{10}(\text{value of the largest sample/}$ modal value of the recording).

All data were reviewed in RAVEN PRO 1.3 (Charif et al., 2007) as spectrograms using the following parameters: fast Fourier transform (FFT) size=1024, Hanning window, and 75% overlap. When a BPS was encountered, it was exported as a single waveform file. These files were analyzed with a custom written MATLAB (Mathworks, 2000) program that measured the IPI, duration, and the number of pulses contained in the signal.

Whistles were examined in RAVEN PRO 1.3 as spectrograms that were calculated using the same parameters listed above. Clear and distinct whistles were marked as "events" within RAVEN and analyzed using most of the metrics described in Oswald et al., 2007. That paper used a semiautomatic measurement system that was not freely distributed, nor does it work well with overlapping signals (Rudd, personal communication). Therefore, the measurements were made manually. Specifically, each whistle was examined to measure maximum, minimum, starting and ending frequencies, signal duration, and the number of inflection points and frequency steps. Inflection points were defined as a change from positive to negative or negative to positive slope, while a step is a sharp break in the signal with a change in frequency. Since group size estimates during the three recording sessions ranged from a few hundred to over 1000 animals, virtually all whistles overlapped with one or more signals. This condition prevented automatic whistle measurement. To obtain reliable measures, only those whistles that were clear and distinct were measured. Whistles from 2004 and 2005 were measured quantitatively while data from 2006 were reviewed to compare signals with those recorded in prior years, as well as to note any previously unrecorded whistle types. Recordings from 2006 did not vary appreciably from those collected in 2004 and 2005. To provide consistency in measurements, only one analyst (Frankel) measured all the whistle parameters.

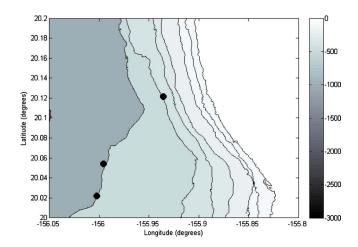


FIG. 3. (Color online) The study site and the locations of the three study encounters with melon-headed whales. Depth contours of 0, 100, 200, 300, 400, and 500 m are shown. The whales were found near the 400 and 500 m isobaths.

III. RESULTS

Melon-headed whales were observed on three occasions between 2004 and 2006 with a total observation time of 408 min. Three recording sessions yielded 87.3 min of acoustic data. Observation conditions were good, with Beaufort sea state ranging between 1 and 3, with a swell of 0.75 to 1.5 m. Group sizes were large, with best estimates of 300, 550, and 600 animals for the three observation occasions, respectively. Water depths at these locations ranged from 397 to 587 m, based on National Geophysical Data Center Coast Relief Model data (3-s resolution). The approximate location of each of the recording sessions is shown in Fig. 3.

Melon-headed whale behavior observed on all three occasions between 2004 and 2006 included slow travel and socializing. The main group was typically composed of numerous subgroups separated from each other by five to ten body lengths. Each subgroup remained at the surface for extended periods of time, often for several minutes. Slow travel was characterized by all observable animals oriented in the same direction, swimming at less than 3 kn (5.56 km/h). Socializing involved animals rolling at the surface, with other types of aerial behavior and body contact. On several instances, groups of animals passed very close to the research vessel, with some individuals swimming underneath the vessel. The mean net speed, calculated from first to last vessel global positioning system (GPS) locations, was 1.19 kn (2.20 km/h).

During two observations, melon-headed whales were associated with humpback whales. The resultant recordings included humpback whale song that was readily differentiated from odontocete vocalizations. Humpback whale song has an easily recognized, stereotypical signal structure, and low frequency emphasis that has been observed in other single-species humpback recordings from this area (Frankel, unpublished). No other odontocete species were present when the melon-headed whale recordings were made, even though great care was made to search the entire area thoroughly for other cetaceans. On two occasions, oceanic white tipped sharks (*Carcharhinus longimanus*) were associated with the

TABLE I. Summary statistics for echolocation and burst-pulse sounds.

	Echolocation click interval (ms)	Burst-pulse duration (ms)	No. of pulses within BPS (<i>n</i>)	Mean inter-pulse intervals (ms)
Mean	80.7	102.9	46.0	2.5
Median	64.0	69.1	39.0	2.3
Mode	26.7	10.8	12.0	2.5
Std. Dev.	66.8	98.6	37.2	1.1
N	29 931	171	171	171

The descriptive statistics for echolocation clicks and burst-pulse sounds are presented.

melon-headed whales. No vessels other than ours were seen in the area during recording sessions nor heard on the recordings. All recordings from these three sightings of melonheaded whales contained echolocation clicks, BPSs, and whistles, and these are illustrated in Fig. 2.

Data analysis detected 29 931 echolocation clicks from 1.5 h of recordings. The distribution of ICIs was skewed toward smaller values, with a mean and median values of 80.7 and 64.0 ms (Table I). Figure 4 shows that 28 788 (96.1%) of the intervals that were less than 500 ms. The large observed group sizes made it possible that two whales were recorded simultaneously, thereby affecting the ICI measure, potentially biasing it toward a lower value. While the unimodal distribution of ICIs (Fig. 4) suggests that overlapping click trains were either rarely or frequently recorded, this could not be resolved without directional recording equipment.

A total of 174 burst-pulse sounds were extracted from the recordings and analyzed to measure duration, IPI, and number of pulses of each signal. The majority of signals (98.3%) were less than 1 s in duration. The three longest signals were 1.1, 1.8, and 2.7 s in duration and were considered outliers. The mean duration of the remaining 171 signals was 102.9 ms with a median value of 69.1 ms. As shown

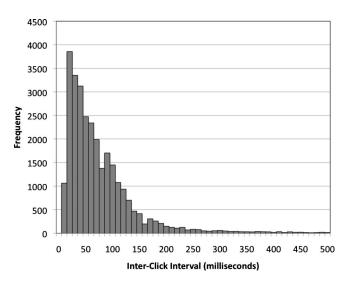


FIG. 4. The distribution of echolocation inter-click intervals is presented. The mean was 80.7 ms and the median value was 64.0 ms. The distribution is clearly non-normal with a pronounced skew toward smaller values.

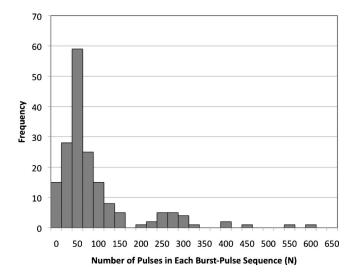


FIG. 5. The distribution of burst-pulse sounds is presented. Most (171 of 174) of these sounds had a duration less than 1 s, and these are shown here. The distribution is strongly skewed toward smaller values and has a mean of 105.1 ms and a median of 69.4 ms.

in Fig. 5, the distribution was skewed toward shorter durations. Burst-pulse IPI summary statistics are presented in Table I.

The mean number of pulses in each BPS was 46, while the median was 39. Again, the distribution of numbers of pulses within each signal also had a skewed distribution. Two signals had counts of 639 and 930 pulses, while the previously mentioned data set of 171 signals ranged from 4 to 231 pulses. The distribution of the numbers of pulses is shown in Fig. 6, and summary statistics are provided in Table I.

Finally, the IPI values were examined. While all IPIs within a signal were measured, only the mean IPI for each signal was reported, to account for the variable number of pulses in each signal. These values ranged from 0.73 to 6.04 ms with a mean of 2.5 and median of 2.3 ms. The distribution of the mean IPIs is shown in Fig. 7, and summary statistics are provided in Table I.

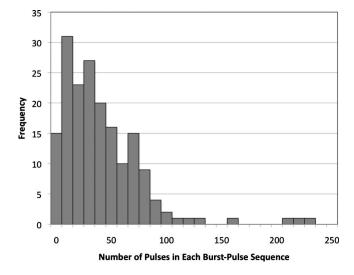


FIG. 6. The distribution of the number of pulses within the 171 burst-pulse sounds analyzed in Fig. 4. The mean was 46 pulses with a median of 39 pulses. Again, the distribution is strongly skewed toward smaller values.

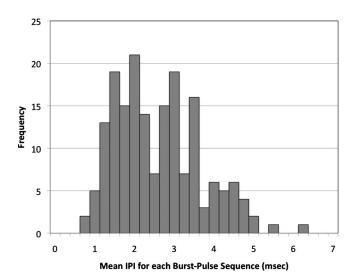


FIG. 7. The distribution of mean IPIs for all 174 burst-pulse sounds are shown. The mean IPI was 2.5 ms with a median value of 2.3 ms. This value did not have the noted skew that was send in the echolocation intervals shown in Fig. 3.

Melon-headed whale whistles typically had a simple structure. The majority (93%) of whistles had three or fewer inflection points. Again, the majority of whistles (68%) had no steps at all, while 88.2% had three or fewer steps. However, a small percentage (4.1%) of the whistles had complex structures including several frequency steps (ten or more), while only one whistle had more than ten inflection points. Overall, the general whistle contours appeared similar to those reported by Watkins et al. (1997). Table II provides a side by side comparison of Caribbean melon-headed whale whistle measurements reported by Watkins et al. (1997) with measurements from the whales recorded off Hawai'i. The Hawaiian sample (this study) shows a wider frequency range but a lower average frequency than the Caribbean sample. Additionally, the Hawaiian whistle samples had lower minimum frequencies (1.2 vs 5.5 kHz), lower dominant frequencies (8.06 vs 12.75 kHz), and a greater range of duration values (1.4 vs 0.9 s) than those from the Caribbean. The 24.5 kHz maximum reported by Watkins et al. (1997) exceeds our equipment-limited measurement of 24 kHz. However, ex-

TABLE II. A comparison of whistle measurements between the Caribbean and Hawai'i.

Whistles	Watkins (n=26)	Frankel and Yin (n=343)
Frequency range (kHz)	5.5-24.5	1.2–24 ^a
Downsweep starting frequency (kHz)	10.5-18	2.6-19.4
Downsweep ending frequency (kHz)	5.5-12.5	0.6-13.4
Upsweep starting frequency (kHz)	10.5-18	1.2-11.6
Upsweep ending frequency (kHz)	12-24.5	$2.6-24^{a}$
Dominant frequency (mode) (kHz)	12.75	8.06
Duration (s)	< 0.1-0.9	< 0.1 - 1.4

The measures reported by Watkins *et al.* (1997) for whistles are reproduced here and compared to the values from the Hawaiian sample. The frequency range of the Hawaiian whistles extend lower in frequency and have a longer maximum duration than those reported from the Caribbean. ^aLimited by sampling rate.

amination of the Hawaiian whistles that reached 24 kHz had significant energy at that frequency, indicating that these whistles probably extended even higher in frequency. In general, the Hawaiian sample had a greater range for all of the whistle metrics than the Caribbean sample. This may be a natural result of differential whistle sample sizes (Caribbean N=26; Hawai'i N=343). However, the lower frequency emphasis of the Hawaiian sample may be due to real biological differences between the two populations. Furthermore, Watkins et al. (1997) reported that whales were most vocal when active. Two of the three observations in Hawai'i were characterized as milling and the third as traveling, yet vocal activity was high in all three observations. Because only the ranges of values were reported for the Watkins et al. (1997) study, statistical comparisons with the Hawaiian sample were not possible.

In addition to a comparison of the whistle descriptive statistics with those from Watkins *et al.* (1997), we also compared values from this study to the whistle measurements of other species from the Pacific Ocean. This comparison used the metrics and values reported by Oswald *et al.* (2007) in their Table II. Mean and standard deviation values for melonheaded whale signals are presented in Table III. The data from both frequency measurements of the same melonheaded whales are graphed relative to the other species in Fig. 8.

This frequency-based comparison found that melonheaded whales use a frequency range similar to that of rough-toothed dolphins although the number of inflection points differs strongly between these two species.

IV. DISCUSSION

Little is known about melon-headed whales, and this paper reports the first description of vocalizations of melon-headed whales from the North Pacific Ocean. Vocalization types included echolocation clicks, burst-pulse sounds, and whistles. Analysis focused on different parameters for each vocalization type. Echolocation clicks appeared to have a typical delphinid structure with very short and broadband signals. Click analysis focused on temporal characteristics since recording equipment limitations prevented analysis of spectral composition.

Echolocation clicks were extracted from the recordings with an automated click detector set at a high threshold value. Therefore, only loud clicks were detected and analyzed. Furthermore, the beam pattern of most echolocating odontocete species is pronounced (Au et al., 1995). These two factors made it likely that the recorded clicks that were analyzed were produced only from animals either near the hydrophone and/or oriented toward it. This rationale, combined with the unimodal distribution of ICIs, suggest that a stable number (i.e., one or two) echolocating whale(s) were recorded at one time. If multiple whales were recorded echolocating at one time, this may have biased the ICI value downward. Recordings of both single wild and captive baiji (Lipotes vexillifer) and bottlenose dolphins (Tursiops truncatus) had unimodal ICI distributions, which supports this assumption (Akamatsu et al., 1998).

TABLE III. Measurements of melon-headed whale whistles.

	Beginning frequency (kHz)	Ending frequency (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Duration (s)	No. of inflection points	No. of steps
Mean	6.08	9.59	5.31	10.77	0.6	1.35	1.36
Std. Dev.	2.36	5.88	1.8	4.35	0.3	1.72	3.05

The mean and standard deviation for the 363 melon-headed whistles measured in this study are presented. Oswald *et al.* (2007) reported these metrics for different species in their Table II. Those data as well as the melon-headed data are presented graphically in Fig. 7.

If melon-headed whales adjust their ICI to allow the echo to return before producing another click, as do many delphinids (Turl and Penner, 1989; Johnson *et al.*, 2008), then the modal ICI value of 26.7 ms indicates a modal distance of \sim 10 m from the echolocating animal to the hydrophone. Again, this estimate is based on an assumption that only one whale was echolocating at one time. Such a range-dependent adjustment of ICIs could explain the skewed distribution of ICIs and the large differences between mean and modal values (80.3 vs 26.7). These data also suggest that the animals may have been using echolocation in a social context and/or they may have been investigating the hydrophone itself, as has been noted in other species (Ritter, 2002; Kuczaj and Yeater, 2007).

Inter-click intervals from the current study were compared with published studies of other species of delphinids and revealed both similarities and differences. Several of these species are found in the same area as melon-headed whales, and have been known to associate with them. Pygmy killer whale ICIs range from 50 to 120 ms (Madsen et al., 2004b). Short click trains of wild false killer whales (Pseudorca crassidens) had stable ICIs of 25 ms and ranged be-

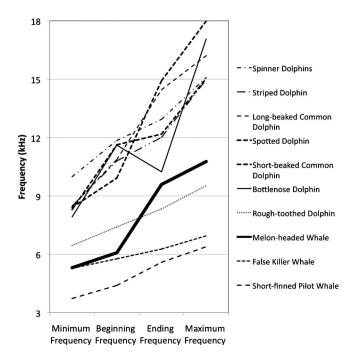


FIG. 8. Frequency measures of melon-headed whales and those of nine other odontocete species are plotted. The melon-headed whale values are plotted as the thick dark line, and can be readily distinguished from the other species.

tween 25 and 200 ms (Madsen *et al.*, 2004a). Free-ranging Risso's dolphins (*Grampus griseus*), which have not been reported to associate with melon-headed whales, have stable ICIs of approximately 20 ms within short click trains and a range 25–200 ms for longer trains (Madsen *et al.*, 2004a). The values reported for melon-headed whales fall within the range reported for other delphinids of similar size. However, the value of the ICIs may be more a function of range to target than species differences, since many species have been shown to adjust their ICI as the distance to target varies (e.g., Madsen *et al.*, 2005).

Melon-headed whale burst-pulse sounds recorded in Hawai'i appeared to be similar to those recorded in the Caribbean. The Caribbean sample typically had 40 or more pulses in a sequence while the Hawaiian sample had a mean of 46. The maximum repetition rate from the Caribbean sample was reported as about 1200 pulses/s while the minimum IPI for the Hawaiian sample was 0.73 ms or 1370 pulses/s, very similar to that from the Caribbean.

There are few studies reporting quantitative descriptions of BPS, and the manner in which they are being reported varies among papers. Nevertheless, a comparison between the results of this study and studies on other odontocete species reveals differences between these studies. The Hawaiian melon-headed whale signals had markedly more BPS per sequence (4-231 vs 6-18) than northern right whale dolphins (Lissodelphis borealis), although the stereotypy seen in Lissodelphis signals suggest a specific communicative function analogous to signature whistles in other dolphins (Rankin et al., 2007). The variable nature of burst-pulse sounds in Peponocephala, as well as the existence of whistles, suggests that they may serve a more general function, as has been suggested for spinner dolphins (Stenella longirostris) (Lammers et al., 2006). The range of the rate of production of burst-pulse sounds was wider than that reported for white-beaked dolphins (Lagenorhynchus albirostris), although the mean production rate was lower in melonheaded whales (493/s vs 719/s) (Simard et al., 2008). Until burst-pulse sounds are better understood, and described for more species, interpreting these differences in signal characteristics remains difficult.

The general characteristics of whistles from Hawaiian melon-headed whales were similar to those recorded in the Caribbean. The measured range of frequencies for whistles was greater in the Hawaiian sample, although this wider range may result from a larger sample size (n=343 vs 26). However, the frequency emphasis of the Hawaiian sample was consistently lower than that of the Caribbean sample,

and may reflect a real biological difference between the two populations. Watkins *et al.* (1997) reported low levels of ambient noise at their recording location, and both sea state and vessel traffic was very low at the Hawaiian recording location. Therefore, it is unlikely that these whistle frequencies were modified in response to environmental conditions, as has been reported elsewhere (May-Collado and Wartzok, 2008).

Watkins et al. (1997) reported that melon-headed whale sound levels were variable, but generally at relatively low levels. These sounds were often partially masked by ambient noise, even at the short distances of the observations and in the comparatively quiet oceanic ambient noise of calm deep water. While we were unable to measure source level, the SNR of our recordings was quite high, often in excess of 50 dB. The spectral ambient noise in this area has been measured between 55 and 75 dB re 1 μ Pa²/Hz for the 1–4 kHz region (Frankel and Clark, 1998). Animals were often observed within 10 m of the hydrophone. Given a nominal 100 Hz bandwidth for whistles, and a transmission loss for 10 m distance, these values suggest a maximum source level of approximately 165 dB re 1 μ Pa at 1 m. This approximate value is greater than the 155 dB re 1 μ Pa at 1 m reported by Watkins et al. (1997) and similar to the source level reported for bottlenose dolphin whistles of 169 dB re 1 μ Pa at 1 m (Janik, 2000). What differs between the two melon-headed whale samples is the continuously high amplitude in the Hawaiian recordings, while the Caribbean animals were reported to be soft and frequently masked by low ambient noise. This difference in amplitude parallels the marked difference in group size. Groups in the Caribbean had 10-14 whales while the Hawaiian groups contained up to approximately 1000 animals. Watkins et al. (1997) observed that "the occurrence and relative level of click bursts and whistles correlated with increased whale activity." Most of the animals we observed were slow-moving with only occasional aerial behaviors, yet these animals still had source levels apparently higher than those from the Caribbean. This suggests that group size as well as activity level may be a correlate of vocalization source level. Furthermore, Watkins et al. (1997) reported that whales were most vocal while active, and slowly traveling whales produced few, if any calls. Our observations were characterized by milling and slow travel, yet vocal production was high. This increase in vocal activity may also be a result of larger group sizes.

Hawaiian whistles were measured using a quantitative technique developed for discrimination and species identification of different odontocete species (Oswald *et al.*, 2007). The mean values from those data and corresponding measures from the current study are presented in Fig. 8. An initial comparison of these measures indicates that a combination of frequency measures and number of inflections makes whistles of melon-headed whales readily distinguishable from the other species examined to date. The frequency measures of the *Stenella* and *Delphinus* species are well above those of the melon-headed whale. The frequency of roughtoothed dolphin whistles overlap somewhat with those of the *Peponocephala*, but the mean number of inflection points is markedly greater in rough-toothed dolphins (2.6 vs 0.6) al-

lowing for discrimination between these two species. Finally, the frequencies of the other large odontocetes are lower than those of the melon-headed whale. These differences could enable researchers to discriminate the signals of melon-headed whales from other odontocetes, especially when visual confirmation (due to observational conditions, or evasive groups of animals) is not possible. However, samples from additional groups and from other geographical areas and behavioral contexts are needed to confirm these distinctions

Future recordings made with hydrophone arrays would allow the calculation of source level and separation of whistles. Use of equipment with higher sampling rates would facilitate a more complete description of the vocalizations, including a more detailed description of what role high frequency vocalizations play in melon-headed whale social behavior. Additional research should also include nocturnal acoustic and behavioral studies to determine if diel (i.e., involving a 24-h period that usually includes a day and the adjoining night) differences in call behavior exist (Stienessen, 1998).

Description of individual species' vocal characteristics and a better understanding odontocete acoustic behavior is essential, not solely for a basic understanding of cetacean behavior. Several stranding or near-stranding events raise the possibility that melon-headed whales may respond strongly to anthropogenic signals (Southall *et al.*, 2006) although these events may have been caused by other factors (Brownell *et al.*, 2009). A more complete knowledge of the vocalizations of species that may be susceptible to manmade disturbance will enable more effective acoustic monitoring which can be used to reduce anthropogenic impact on marine mammals.

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