Discriminating features of echolocation clicks of melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*), and Gray's spinner dolphins (*Stenella longirostris longirostris*)

Simone Baumann-Pickering,[a] Sean M. Wiggins, and John A. Hildebrand
Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0205

Marie A. Roch
Department of Computer Science, San Diego State University, 5500 Campanile Drive, San Diego, California 92182-7720

Hans-Ulrich Schnitzler
Eberhard-Karls-Universität Tübingen, Zool. Institut, Abt. Tierphysiologie, Auf der Morgenstelle 28, 72076 Tübingen, Germany

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Spectral parameters were used to discriminate between echolocation clicks produced by three dolphin species at Palmyra Atoll: melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*) and Gray's spinner dolphins (*Stenella longirostris longirostris*). Single species acoustic behavior during daytime observations was recorded with a towed hydrophone array sampling at 192 and 480 kHz. Additionally, an autonomous, bottom moored High-frequency Acoustic Recording Package (HARP) collected acoustic data with a sampling rate of 200 kHz. Melon-headed whale echolocation clicks had the lowest peak and center frequencies, spinner dolphins had the highest frequencies and bottlenose dolphins were nested in between these two species. Frequency differences were significant. Temporal parameters were not well suited for classification. Feature differences were enhanced by reducing variability within a set of single clicks by calculating mean spectra for groups of clicks. Median peak frequencies of averaged clicks (group size 50) of melon-headed whales ranged between 24.4 and 29.7 kHz, of bottlenose dolphins between 26.7 and 36.7 kHz, and of spinner dolphins between 33.8 and 36.0 kHz. Discriminant function analysis showed the ability to correctly discriminate between 93% of melon-headed whales, 75% of spinner dolphins and 54% of bottlenose dolphins.
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I. INTRODUCTION

Analyzing cetacean sounds to the species level is an important step in processing long-term passive acoustic recordings made in a marine environment. Identification of a variety of mysticete calls has been successful and their signals have been automatically detected in long-term acoustic recordings (e.g., Sirović *et al.*, 2004, Oleson *et al.*, 2007, Munger *et al.*, 2008, Sirović *et al.*, 2009), in addition to a few odontocete calls (e.g., Mellinger *et al.* 2004, Verfuß *et al.*, 2007, Soldevilla *et al.*, 2010), but the discrimination of most odontocete calls remains difficult. Clicks produced by sperm whales, beaked whales and porpoises are distinctly different to those of delphinids due to their temporal and spectral properties (Goold and Jones, 1995, Kamminga *et al.*, 1996, Zimmer *et al.*, 2005, Johnson *et al.*, 2006, McDonald *et al.*, 2009). In this paper we are concerned with the discrimination of dolphin signals. Dolphins produce two types of signals: (1) tonal frequency-modulated signals, called whistles and (2) broadband pulsed signals, called clicks (Herman and Tavolga, 1980). Intermediate sounds with a character between the two basic types can also be produced with click sequences grading into whistles and vice versa (Murray *et al.*, 1998a). Whistles have a fundamental frequency in most cases below 20 kHz with harmonic intervals up to 100 kHz (Lammers *et al.*, 2003). Their durations vary between 50 ms and 3 s (Ding *et al.*, 1995, Bazúa-Durán and Au, 2002) and are used primarily in a social context, to regulate group organization and function (Herman and Tavolga, 1980, Norris *et al.*, 1994, Janik and Slater, 1998). They may carry an individual-specific signature in some species (Caldwell *et al.*, 1990) and may be important in keeping up contact within a group of animals (Janik, 2000; Lammers *et al.*, 2006). Most clicks are used to detect, localize and characterize a target object, e.g., prey or background (Au, 1993). These clicks have a frequency range mostly between 10 and 150 kHz and are temporally spaced to allow processing of

[a]Author to whom correspondence should be addressed. On leave from: Eberhard-Karls-Universität Tübingen, Zoologisches Institut, Abteilung Tierphysiologie, Auf der Morgenstell 28, 72076 Tübingen, Germany. Electronic mail: sbaumann@ucsd.edu

the two-way travel time between the sound source and the object (Au, 1993). Broadband clicks can be further distinguished by their temporal pattern. In the terminal buzz during echolocation, clicks may appear in rapid trains, to give continuous prompt updates on the target location when the animal is approaching a target for prey capture (e.g., Madsen *et al.*, 2005, Verfuß *et al.*, 2009). Rapid trains of clicks are also termed burst pulses (Herman and Tavolga, 1980). The human auditory system perceives them as having a tonal quality where the pitch is related to the inter-click interval (Murray *et al.*, 1998a, 1998b). They are believed to be used in social interactions for short distance communicative purposes (Caldwell and Caldwell, 1967, Dawson, 1991, Norris *et al.*, 1994, Lammers *et al.*, 2006).

Efforts have been made to classify delphinid whistles (e.g., Oswald *et al.*, 2003, 2004, Oswald, 2007, Steiner 1981, Rendell *et al.* 1999, Matthews *et al.* 1999) but recent advances in field and autonomous long-term recordings allow use of higher frequency ranges to classify delphinid echolocation clicks to the species level (e.g., Roch *et al.*, 2007, 2008, Soldevilla *et al.*, 2008 Gillespie and Caillat, 2008, Jarvis *et al.*, 2008). The discrimination of dolphin species by their echolocation signals is important since to date, all dolphin species recorded are known to use click type signals, but some species may not produce whistles (Herman and Tavolga, 1980, Au, 2003). Others may not use whistles under certain behavioral contexts (Benoit-Bird and Au, 2009). Most research on delphinid echolocation has focused on target detection (e.g., Au, 1993; Kastelein *et al.*, 1999) and discrimination (e.g., Au, 1993; Kastelein *et al.*, 1997) and only a few studies have analyzed species-specific aspects of clicks. The click properties duration and peak frequency were the major species discriminating factors despite the difference in species compositions in each study (Kamminga *et al.*, 1996, Akamatsu *et al.*, 1998). Clicks of four different porpoise species were partially separated from each other and fully from bottlenose dolphins (*Tursiops truncatus*) (Kamminga *et al.*, 1996). False killer whale clicks (*Pseudorca crassidens*) were distinguishable from various dolphin and porpoise clicks by these parameters (Nakamura and Akamatsu, 2003). Baiji (*Lipotes vexillifer*) and bottlenose dolphins did not separate entirely but clicks from baiji had a tendency toward lower frequencies than those of bottlenose dolphins (Akamatsu *et al.*, 1998).

Most research has analyzed only clicks that are on-axis of the sonar beam because Au *et al.* (1978) showed a strong distortion of spectral content of off-axis clicks and those clicks appear to be longer in duration. The authors hypothesized that multipaths, due to reflections within the head, from the environment, or both, were causing these off-axis click distortions. Lammers and Castellote (2009) provide evidence that a beluga whale (*Delphinapterus leucas*) uses two signal generators to produce a single click. This click recorded off-axis shows two pulses, each having a different center frequency. In generating two pulses for one echolocation click the beluga might be able to control both energy and frequency distribution. Soldevilla *et al.* (2008) analyzed on- and off-axis clicks together, arguing that because the orientation of the vocalizing animal is unknown during passive acoustic monitoring surveys the spectral information of all recorded clicks should be described and taken into account for species identification. They also agree that on-axis clicks alone may not represent the full variety of received clicks and internal reflections of pulses may reveal the anatomy of the vocalizing animal and therefore carry a species-specific aspect only observed in off-axis clicks. They were able to identify several species-specific peaks in the spectra of Risso's (*Grampus griseus*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), especially in the long duration clicks with reverberations, but not in bottlenose, long-beaked common (*Delphinus capensis*) and short-beaked common dolphin (*Delphinus delphis*) clicks. The authors hypothesized that the spectral peaks were caused by the morphology of the skull and sound producing organs of these dolphin species with peaks in clicks appearing for species with more symmetric head morphology.

Melon-headed whales (*Peponocephala electra*), bottlenose and Gray's spinner dolphins (*Stenella longirostris longirostris)* are regularly observed in the waters surrounding Palmyra Atoll. They all use whistles and clicks as acoustic signals. Melon-headed whales are pelagic dolphins that occur worldwide in tropical and subtropical oceanic waters (40°N–35°S) (Perryman, 2009, Jefferson *et al.*, 2008). Their echolocation clicks have a dominant frequency between 20 and 40 kHz (Watkins *et al.*, 1997). They are mostly observed offshore over deep waters unless the deep water is close to shore. They are a highly social species with 100–500 animals (maximum up to 2000) in one pod (Jefferson *et al.*, 2008). They can grow up to 2.78 m in body length with males being slightly larger than females (Perryman, 2009). Bottlenose dolphins and Gray's spinner dolphins occur worldwide in coastal and oceanic waters (Norris *et al.*, 1994, Jefferson *et al.*, 2008). Bottlenose dolphins are widely distributed in tropical and temperate waters mostly between 45°N and 45°S with some exceptions at higher latitudes. The on-axis echolocation signals of wild bottlenose dolphins have bimodal peak frequencies with a 60–90 and 110–140 kHz range and 10–20 μs duration (Akamatsu *et al.*, 1998). Their pods rarely exceed 20 animals but group sizes can be up to several hundred, especially in offshore waters. They can reach between 1.9–3.8 m in body length as adults with males in some populations being somewhat larger (Jefferson *et al.*, 2008). Gray's spinner dolphins are the most typical form of spinner dolphins. They are found pantropically, in all tropical and most subtropical waters (40°N–40°S) (Jefferson *et al.*, 2008). For free ranging spinner dolphins the peak frequency in their echolocation clicks is reported to be 70 ± 23 kHz, the center frequency is 80 ± 12 kHz and click durations are 9 ± 3 μs (Schotten *et al.*, 2003). Spinner dolphin group sizes range from less than 50 up to several thousands. Adult females reach 1.4–2.0 m in length; adult males are 1.6–2.1 m (Jefferson *et al.*, 2008). Melon-headed whales and spinner dolphins use daytime hours for resting and socializing and feed during the night on mesopelagic prey (Brownell *et al.*, 2009, Norris *et al.*, 1994). Bottlenose dolphins rest, socialize, and feed during day and night time hours (Wells and Scott, 2002).

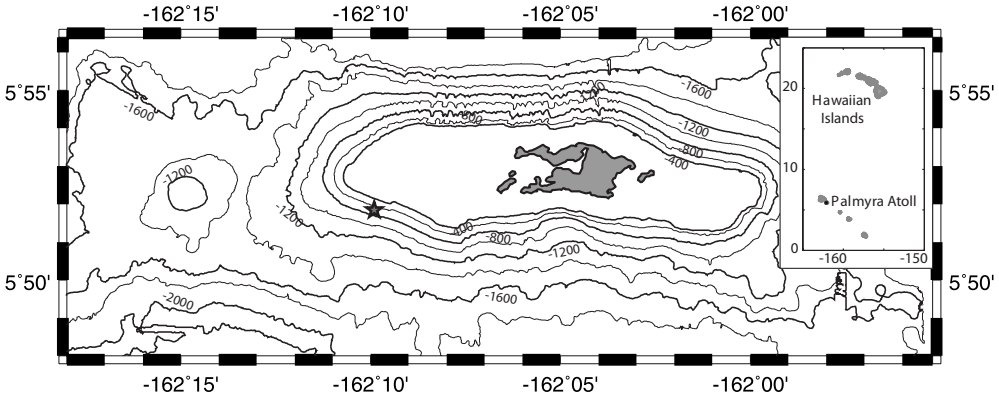

FIG. 1. Bathymetric map of Palmyra Atoll and position of HARP indicated with a star. Top right insert shows approximate location of Palmyra Atoll. Bathymetry data courtesy of NOAA Coral Reef Ecosystem Division, Pacific Islands Fisheries Science Center and the Pacific Islands Benthic Habitat Mapping Center, SOEST, University of Hawaii. Coastline data courtesy of National Geophysical Data Center, NOAA Satellite and Information Service, WVS Coastline Database. Plotted with GMT by Paul Wessel and Walter H. F. Smith.

This paper describes the spectral and temporal characteristics of melon-headed whale, bottlenose and Gray's spinner dolphin echolocation clicks recorded during daytime observations. We show that these three species can be distinguished by their median peak and center frequencies and that the feature differences can be improved by pooling groups of clicks to reduce variability. We discuss these results in relation to other click descriptions and classification studies, as well as the recording instrumentation and the animals' morphological features.

II. MATERIALS AND METHODS

A. Data collection

Our study area was off-reef of Palmyra Atoll, extending from 162°15′W to 161°57′W and from 5°57.6′N to 5°49.2′N (Fig. 1). Visual and acoustic surveys were conducted off the 26 ft Davis boat, *Zenobia*, during two field seasons from October 16 to November 7, 2006 and September 18 to October 13, 2007. During our daytime surveys we kept a constant visual and acoustic watch with two to three observers and circumnavigated the atoll choosing a route dependant on sea conditions, mostly within 0.5 to 4 km of the reef edge. The small boat and heavy swell largely precluded use of binoculars for searching. In an average sea state 3 condition, we had a detection limitation of about 1 km. When we visually or acoustically detected animals we approached them for identification, school size estimation, photography and acoustic recordings. Recordings were only made when no other cetacean group was detected within a radius of 1 km. Published studies indicate that echolocation clicks are not detectable beyond about 1 km (Richardson *et al.*, 1995; Philpott *et al.*, 2007). If clicks had been nevertheless detectable then the elimination of clicks with low signal-to-noise ratio (see below) likely removed possible clicks of other echolocating dolphins in distances larger 1 km, assuring single species recordings.

For the acoustic survey, we used a four-channel hydrophone array streamed on 80 m of cable. Depending on the animals' behavior, the array was either towed with speeds between 2 and 8 kn at a water depth of 10–15 m, or deployed as a stationary array with a maximum depth of 80 m. The array was equipped with HS150 hydrophones (Sonar Research & Development Ltd., Beverley, U.K.), which had a sensitivity of −205 dB re V/μPa and a flat frequency response of ±1 dB over the analysis range of 8 to 85 kHz. The hydrophones were connected to custom-built preamplifiers and band-pass filter electronic circuit boards (Wiggins and Hildebrand, 2007). The circuit boards were designed to flatten the ambient ocean noise (i.e., pre-whiten), which resulted in a nonlinear frequency response that provided greater gain at higher frequencies where ambient noise levels are lower and sound attenuation is higher. Data from 2006 was digitally sampled with a MOTU Traveler (Mark of the Unicorn, Cambridge, MA) at a sampling frequency of 192 kHz and recorded directly to a computer hard-disk drive with the software Ishmael (Mellinger, 2001). In 2007, audio recordings were made with PCTape (custom made hardware and software, Department of Animal Physiology, University of Tübingen and Menne BioMed). The sampling frequency was set to 480 kHz and audio data were also directly recorded to a hard-disk drive.

Parallel to this effort, an autonomous High-frequency Acoustic Recording Package (HARP) was placed on the steep slope off Palmyra Atoll's western terrace (Fig. 1). The HARP design differed from what was described in Wiggins and Hildebrand (2007) as it was in a mooring configuration with the hydrophone floating at 20 m above the seafloor. It recorded from October 19, 2006 until March 23, 2007. The HARP was located at 5°51.85′N 162°09.91′W in 650 m water depth. The recorder was set to a sampling frequency of 200 kHz and scheduled with a recording duration of 5 min every 20 min. On the HARP, we used an omni-directional transducer (ITC-1042, www.itc-transducers.com), which had an approximately flat (±2 dB) frequency response from 10 Hz to 100 kHz with a hydrophone sensitivity of −200 dB re V/μPa. As in the arrays, it was connected to a custom-built preamplifier board with band-pass filter and also was designed to follow the reciprocal of ocean ambient noise in order to maximize the dynamic range of the recorder. The

differing frequency responses of the various preamplifier boards and hydrophones were compensated for during analysis.

During these two field seasons, a total of 32 boat-based visual encounters with melon-headed whales (*Peponocephala electra*), 100 with bottlenose dolphins (*Tursiops truncatus*), and 15 with Gray's spinner dolphins (*Stenella longirostris longirostris*) took place in the waters surrounding Palmyra Atoll. Acoustic recordings were made during some of these encounters and subsets of these were used for the acoustic analysis. We observed melon-headed whales during one and bottlenose dolphins during two of these single species boat-based visual encounters swimming very close to the HARP location while the HARP was recording, but Gray's spinner dolphins were not. No successful acoustic array recordings were made simultaneously to visual encounters above the HARP.

B. Signal processing

Signal processing was performed using custom software routines in MATLAB (Mathworks, Natick, MA). Recording sequences were selected out of all array recordings that had only a few animals vocalizing at a time and showed high signal to noise ratios with sound pressure levels that infrequently clipped the recorder. All HARP data collected during the visual encounters above the HARP were used.

Clicks were automatically located within the sequences using a two-step approach as described in detail in Soldevilla *et al.* (2008). During the first step, clicks were detected automatically in the spectral domain taken from 10 ms segments. When 12.5% or more of the frequency bins between 15–85 kHz had signal-to-noise ratios exceeding 10 dB, the segment was hypothesized to contain clicks. These automatically selected clicks in the array and HARP data were then verified by an analyst and false detections were removed. Click detections on array recordings of 2007 had a large number of false detections of echo sounder pings from the research vessel. The data for spinner dolphins were manually inspected and false detections were removed. This was not possible for click detections of melon-headed whales and bottlenose dolphins due to the very large number of detections. All detections with peaks in the main frequency and sideband frequencies of the echo sounder were therefore removed from the analysis. The second automatic selection step determined the exact start and end point of the roughly defined clicks. The finer resolution time domain click detection algorithm described in Soldevilla *et al.* (2008), using a Teager energy operator (Kaiser, 1990, Kandia and Stylaniou, 2006), was applied.

The click sequences were digitally filtered with a 10-pole Butterworth band-pass filter. The low cutoff frequency was at 8 kHz to minimize the influence of low frequency noise. The high cutoff frequency was set to 85 kHz (for 192, 200 kHz samples) or 200 kHz (for 480 kHz samples) to avoid aliasing effects. To calculate signal-to-noise ratios, a 5 ms window was picked preceding every click. Spectra of each signal and preceding noise were calculated using 1.33 or 1.28 ms of data for samples with 192 or 200 kHz sampling rate, respectively, and a 256-point Hann window centered around the click and in the beginning of the noise sample. A Hann window of 1024-points and resulting 2.13 ms of click and noise data were used for signals sampled at 480 kHz. The frequency-related signal parameters peak and center frequency, −3 and −10 dB bandwidth were processed using methods from Au (1993). Signal-to-noise ratio was calculated with the RMS level of each click and its preceding noise. To use only good quality pulses and clicks for the signal description, potentially clipped signals were eliminated by allowing only signals with amplitudes up to 80% of the maximum system capability. Not all clipped clicks were removed with this procedure. A notable effect of clipping was a visible distortion of the signal in the time series within the first few cycles resulting in peak frequencies below 20 kHz. Therefore, only clicks with peak frequencies of at least 20 kHz were subsequently analyzed. Furthermore, all FM pulses with a signal-to-noise ratio of less than 10 dB were discarded. Signal parameters are influenced by the distance and orientation of the vocalizing animal to the recording hydrophone. Lower frequencies are less attenuated over distance than higher frequencies. The orientation of the whale to the recording device changes the signal properties as well, as higher overall amplitudes and more high frequency energy is expected when the whale's vocal beam is on axis with the recorder (Au, 1993). No efforts were undertaken to minimize these influences.

For statistical analysis, the data were reduced as detailed below to avoid over-representation of an individual's clicks and acquire independence of the clicks analyzed, since a click train is produced by one individual and this individual might have made several click trains. The reduction was also used to generate comparably sized data sets. Ten clicks in array recordings 2006, twenty clicks in HARP recordings 2006 and one click in array recordings 2007 were randomly picked per minute of recording (Table I). Mean spectra were calculated from the reduced set of single clicks. To compare mean spectra of the different species with each other, the

TABLE I. Overview of data used in the spectral and temporal click analysis for melon-headed whales (pe), bottlenose dolphins (tt) and Gray's spinner dolphins (sl) with three different recording systems;[1] single-species, separate encounters,[2] used to calculate averaged clicks,[3] used for statistical analysis.

		pe	tt	sl
Array 2006, 192 kHz	Number of encounters[1]	5	5	4
	Recording duration (min)	23	20	21
	Automatic click detections[2]	2216	2348	1557
	Averaged clicks (group size 50)[3]	44	46	31
	Constrained random samples[3]	230	200	210
HARP 2006, 200 kHz	Number of encounters[1]	1	2	–
	Recording duration (min)	15	30	–
	Automatic click detections[2]	2241	3576	–
	Averaged clicks (group size 50)[3]	44	71	–
	Constrained random samples[3]	300	300	–
Array 2007, 480 kHz	Number of encounters[1]	4	22	3
	Recording duration (min)	280	180	90
	Automatic click detections[2]	18,702	13,542	1810
	Averaged clicks (group size 50)[3]	37	40	36
	Constrained random samples[3]	280	180	180

TABLE II. Spectral and temporal click parameters of melon-headed whale, bottlenose dolphin and Gray's spinner dolphin clicks, calculated for each recording situation. Values are given as medians with first and third quartiles in squared brackets. n: number of clicks in analysis.

	Peak frequency (kHz)	Center frequency (kHz)	Duration (ms)	Inter-click interval (ms)	Lower −10 dB frequency (kHz)	Bandwidth −10 dB (kHz)	Lower −3 dB frequency (kHz)	Bandwidth −3 dB (kHz)
				Melon-headed whales				
2006 array 192 kHz (n=230)	27.0	31.1	0.45	150	19.5	18.0	24.0	5.3
	[24.8 30.9]	[28.5 34.7]	[0.31 0.74]	[64 319]	[15.8 24.0]	[10.5 30.0]	[21.0 27.8]	[4.3 8.3]
2006 HARP 200 kHz (n=300)	28.5	28.4	0.29	86	21.0	18.0	24.8	6.8
	[26.3 29.3]	[26.4 31.0]	[0.24 0.38]	[40 173]	[19.5 22.5]	[12.0 24.0]	[23.3 26.3]	[4.5 8.3]
2007 array 480 kHz (n=280)	25.3	32.2	0.25	86	16.8	20.2	21.6	5.6
	[23.0 28.6]	[28.2 37.9]	[0.17 0.42]	[29 193]	[14.1 20.5]	[12.2 28.6]	[19.7 25.3]	[3.8 10.3]
				Bottlenose dolphins				
2006 array 192 kHz (n=200)	30.8	34.0	0.44	68	21.4	18.8	27.0	6.8
	[26.3 35.3]	[29.6 38.2]	[0.34 0.71]	[40 145]	[18.0 25.5]	[11.3 25.5]	[23.3 30.0]	[4.5 9.0]
2006 HARP 200 kHz (n=300)	35.6	37.0	0.42	80	24.0	24.0	32.3	6.0
	[29.3 48.0]	[32.2 43.8]	[0.29 0.69]	[45 120]	[21.8 36.0]	[17.3 30.6]	[25.5 44.3]	[4.5 8.3]
2007 array 480 kHz (n=180)	27.2	39.8	0.31	97	20.2	15.5	24.4	5.2
	[24.8 32.3]	[31.2 51.8]	[0.22 0.56]	[46 297]	[16.9 25.2]	[8.9 22.9]	[21.1 29.1]	[3.3 7.5]
				Spinner dolphins				
2006 array 192 kHz (n=210)	35.6	36.6	0.37	121	24.0	21.0	32.3	5.3
	[30.8 40.5]	[33.6 40.6]	[0.21 0.62]	[67 318]	[19.5 29.5]	[11.3 35.3]	[27.8 37.7]	[4.5 7.5]
2006 HARP 200 kHz	–	–	–		–	–	–	–
2007 array 480 kHz (n=180)	33.8	43.1	0.21	235	23.0	22.0	30.0	6.6
	[27.2 40.1]	[34.1 58.3]	[0.14 0.33]	[96 1555]	[18.8 29.4]	[12.4 34.7]	[23.9 36.1]	[3.9 9.3]

spectra were normalized to 0 dB at 8 kHz, the lower cutoff frequency of the band-pass filter. The click parameters were skewed in their distribution and therefore non-parametric statistical tests were calculated. MATLAB was used to compute Kruskal-Wallis one-way analysis of variance tests for species discrimination by click parameters. A post-hoc test with Bonferroni correction was run to single out non-significant results among pairs of species. The influence of the different recording systems was tested with a nested ANOVA. The results were optimized in their variability by grouping clicks, using the entire automatically selected data set. For this procedure a certain number of clicks were grouped consecutively within the recorded sequence. Mean spectra were calculated for all groups, and spectral click parameters were determined from the mean spectra. Median values were calculated for the temporal parameters. For statistical comparison the large sample size of melon-headed whale and bottlenose dolphin click averages of array recordings 2007 were randomly reduced by factor 10 and 5, respectively. A discriminant function analysis was run with the program JMP (SAS Institute Inc., Cary, NC) for both single as well as averaged click parameters to separate species through these values. The entire data set was used and the results are not indicative of a classification system that would provide separate training and test sets.

III. RESULTS

A. Analysis of individual echolocation clicks

The echolocation clicks of melon-headed whales, bottlenose and Gray's spinner dolphins are similar, yet they are significantly different in several parameters. The temporal parameters, duration and inter-click interval, are all weak parameters for species discrimination (Table II, Table III, Table IV). When tested for significance with an ANOVA for each recording situation (array 2006, 2007 and HARP 2006), they showed significant differences between species except for inter-click intervals on HARP recordings (Table III). A post-hoc test clarifies that the inter-click interval in all recording situations was not significant between melon-headed whale clicks and either spinner or bottlenose dolphin clicks depending on recording instrumentation. Duration was not significantly different for melon-headed whale and spinner dolphin clicks in the array 2006 recordings (Table III). Additionally, there was a significant influence of the recording instrumentation on all parameters, accounting for an especially large part of the variance in the temporal parameters (Table IV, nested ANOVA).

Spectral parameters of clicks showed highly significant differences between species in all recording situations (Table II, Table III, ANOVA). The exception was for the −3dB bandwidth of all species, and the −10dB bandwidth for melon-headed whale and either spinner or bottlenose dolphin clicks in two out of three recording situations (Table III, post-hoc test). These bandwidth parameters all showed no significant differences, therefore, bandwidth was considered a weak parameter for species discrimination. All other spectral parameters were more robust. The lower −10dB frequency was least important among the spectral parameters with the lowest significance level and the highest influence of recording instrumentation (Table III, Table IV). Melon-headed whales had the lowest peak and center frequencies

TABLE III. Discrimination of spectral click parameters of melon-headed whale, bottlenose dolphin and Gray's spinner dolphin single clicks by Kruskal-Wallis one-way analysis of variance calculated for each recording situation. Values are given as Chi^2 test results and their p values.*: $p<0.05$, n.s.: not significant.

	Peak frequency (kHz)	Center frequency (kHz)	Duration (ms)	Inter-click interval (ms)	Lower −10 dB frequency (kHz)	Bandwidth −10 dB (kHz)	Lower −3 dB frequency (kHz)	Bandwidth −3 dB (kHz)
Array 2006	128.3/*	110.7/*	23.6/*	38.1/*	42.9/*	6.3/*	123.5/*	12.5/*.
HARP 2006	168.1/*	269.6/*	53.2/*	1.6/n.s.	98.1/*	34.5/*	146.8/*	0/n.s.
Array 2007	103.6/*	87.0/*	40.6/*	50.5/*	103.1/*	18.6/*	116.5/*	8.3/n.s.
Post-hoc test with Bonferroni correction: all pairs significant unless otherwise reported. Melon-headed whales (pe), bottlenose dolphins (tt), Gray's spinner dolphins (sl)								
Array 2006	*	*	n.s. pe/sl	n.s. pe/sl	*	n.s. pe/tt	*	n.s. pe/sl
HARP 2006	*	*	*	n.s. pe/tt	*	*	*	n.s. pe/tt
Array 2007	*	n.s. sl/tt	*	n.s. pe/tt	*	n.s. pe/sl	*	n.s. pe/sl

and the lowest −3 and −10dB frequencies in all recording situations. Spinner dolphins had the highest frequencies in their clicks and bottlenose dolphins were nested in between these two species (Table II, Fig. 2). Median peak frequencies of melon-headed whales ranged between 25.3 and 28.5 kHz for the three different recording systems used. Median peak frequencies of bottlenose dolphins were in between 27.2 and 35.6 kHz. Spinner dolphins had median peak frequencies between 33.8 and 35.6 kHz. Median center frequencies were distributed similarly. Melon-headed whale center frequencies ranged from 28.4 to 32.2 kHz. Median center frequencies of bottlenose dolphins were in between 34.0 and 39.8 kHz. Spinner dolphins had median center frequencies between 36.6 and 43.1 kHz. Melon-headed whales showed variability with 3–6 kHz quartile widths for peak frequencies and 5–10 kHz for center frequencies. Both bottlenose dolphins and spinner dolphins had much larger variability between 8–19 and 9–24 kHz for peak and center frequencies, respectively. There was a significant difference between recording instrumentation (Table IV, nested ANOVA). The variability of peak and center frequencies seemed especially low for HARP recordings of melon-headed whales (3–5 kHz), for all species in array recordings of 2006 (6–10 kHz) and particularly high for HARP recordings of bottlenose dolphins (12–19 kHz) and for 2007 array recordings of spinner dolphins (13–24 kHz). The center frequency of 2007 array recordings with 480 kHz sampling rate was 4 to 7 kHz higher than in recordings with lower sampling rates due to a larger bandwidth and considerable energy above the 96 or 100 kHz recording limit of the other systems.

B. Analysis of averaged echolocation clicks

To optimize species discrimination through their click parameters, calculating an average click from several single clicks reduced the variability. Therefore, consecutive clicks of a sequence were grouped together with a given number of averaged clicks (group size), mean spectra were calculated

TABLE IV. Examination of the effect of instrumentation on the significant separation of clicks of melon-headed whales, bottlenose and Gray's spinner dolphins. Results of nested ANOVAs with species nested in instrumentation, $p<0.0001$ unless otherwise reported. DF=degrees of freedom. SSQ=sum of squares.

		Fit of model		Species (DF 2)	Species nested in instrumentation (DF 5)
Peak frequency	R^2	0.12	F	100.4	8.0
	$F_{7,1872}$	37.0	SSQ	27,273.3	5424.8
Center frequency	R^2	0.23	F	164.2	49.4
	$F_{7,1872}$	79.7	SSQ	36,216.8	27,220.2
Duration	R^2	0.05	F	23.7	9.7
	$F_{7,1872}$	14.3	SSQ	7.0×10^{-6}	7.1×10^{-6}
Inter-click interval	R^2	0.05	F	16.4	13.0
	$F_{7,1872}$	13.4	SSQ	123.4	243.0
Lower −10 dB frequency	R^2	0.08	F	59.7	7.8
	$F_{7,1872}$	24.4	SSQ	16,291.7	5348.3
Bandwidth −10 dB	R^2	0.04	F	19.0	7.1
	$F_{7,1872}$	10.1	SSQ	7785.9	7266.0
Lower −3 dB frequency	R^2	0.12	F	96.2	8.4
	$F_{7,1872}$	36.1	SSQ	25,815	5649.6
Bandwidth −3 dB	R^2	0.01	F	1.1	4.0
	$F_{7,1872}$	3.1	SSQ	33.2	309.5
	p	0.003	p	0.34	0.001

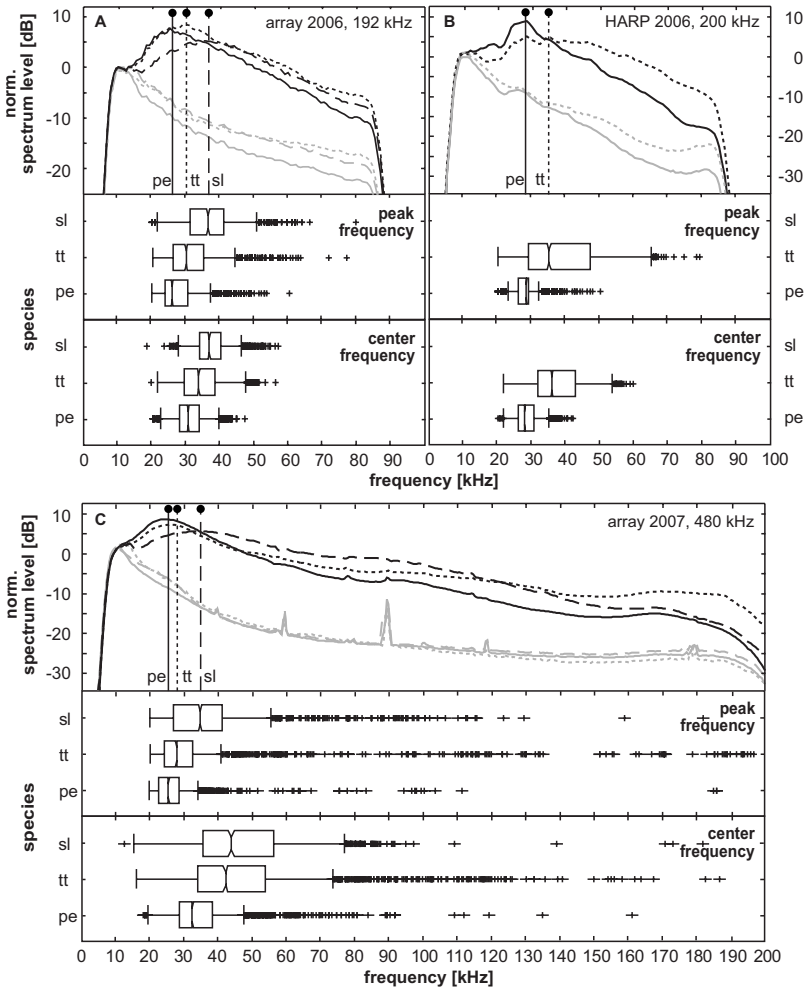

FIG. 2. Spectral patterns of echolocation clicks of melon-headed whales (pe—*Peponocephala electra*), bottlenose dolphins (tt—*Tursiops truncatus*) and Gray's spinner dolphins (sl—*Stenella longirostris longirostris*). Top plot of A, B and C) Mean click spectra (black lines) and mean noise spectra (gray lines) of melon-headed whales (solid line), bottlenose dolphins (dotted line) and spinner dolphins (dashed line). Vertical lines indicate median peak frequency. Center and bottom graphs show box plot distributions of peak and center frequency, respectively.

and spectral and temporal parameters were extracted. The resulting quartiles of grouped clicks were progressively smaller, the larger the group size [Fig. 3(A)]. The quartiles with group sizes larger than 50 clicks varied only minimally. This trend was noticeable for all species and all recording situations. The variability, calculated in distance between first and third quartile, was on average reduced by 3 kHz. Only the variability of peak frequencies from HARP data did not improve. Melon-headed whales had an especially small variability in their frequency values after grouping. As a result of the reduced variability, peak frequency quartiles of grouped bottlenose dolphin clicks were separated from those of grouped spinner dolphin clicks; however, most center frequency quartiles of bottlenose dolphins overlapped with both melon-headed whales and spinner dolphins [Fig. 3(B), Table V].

Mean spectra have a smoother curve than single clicks. Therefore, the median −10 and −3dB bandwidths became considerably larger and the values for lower −10 and −3dB frequencies were lower. All click parameters, except interclick interval on HARP recordings, showed significant values for species separation (Table VI). Post-hoc pair-wise comparison revealed though that only peak and center frequency, as well as the corresponding lower −3dB frequency, were robust. Peak frequency and lower −3 dB frequency had all but one pairs of species significantly different from each other in that value. Center frequency had all pairs of species significantly different.

C. Discriminant function analysis of single and averaged echolocation clicks

Analysis of single clicks by discriminant function analysis showed high levels of false detection with an average of 42.7% using all click parameters and 48.9% using only the most robust parameters (peak, center, lower −3 dB frequency) over all recording instrumentation (Table VII). The discrimination result improved with averaged clicks to 28.4% and 37.3%, respectively. Especially in averaged click results, it is evident that false detections increased when data from all recording instrumentation were pooled. Bottlenose dolphin clicks had the largest number of false classifications, which was almost at random for single clicks and more often confused with melon-headed whale than spinner dolphin clicks. Averaged melon-headed whale clicks were correctly classified in 93% of all cases (Table VIII). The misclassifications were more likely with bottlenose dolphins. The discrimination rate for bottlenose dolphin increased to 54% correct classification.

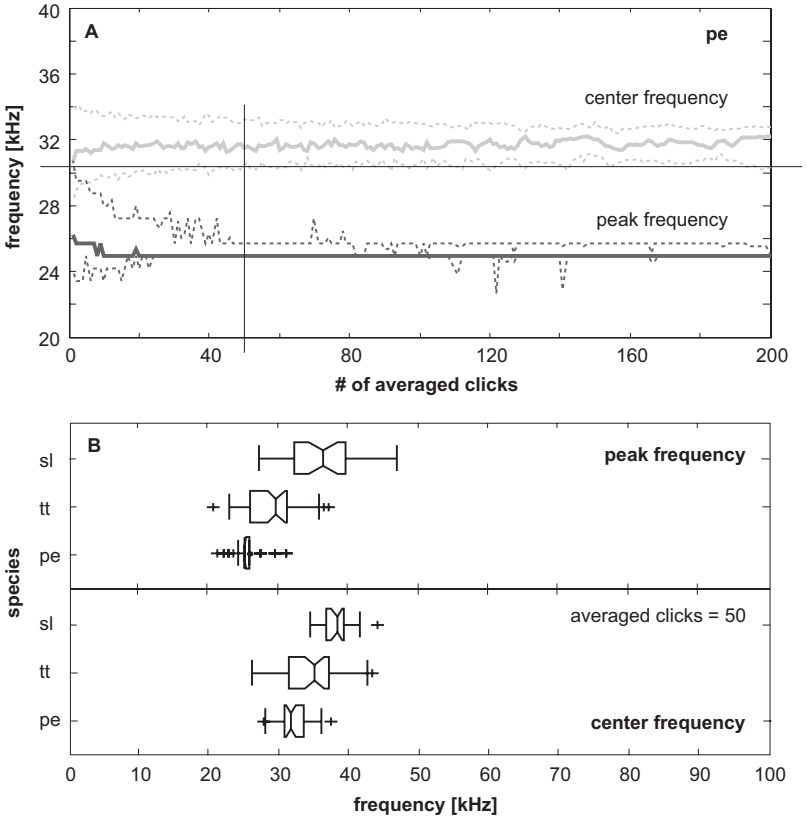

FIG. 3. Median peak and center frequencies of grouped echolocation clicks in array data of 2006 which had the lowest overlap in quartiles (Table IV). (A) Center frequency (light gray) and peak frequency (dark gray) versus number of averaged clicks for melon-headed whale clicks (pe—*Peponocephala electra*); median frequency as solid gray lines, quartiles as dashed gray lines; black crossed lines indicate 50 averaged clicks where quartiles started to vary minimally. (B) Box plot distributions of peak and center frequency of all species with 50 averaged clicks (melon-headed whales, *Peponocephala electra*—pe; bottlenose dolphins, *Tursiops truncates*—tt; Gray's spinner dolphins, *Stenella longirostris longirostris*—sl).

IV. DISCUSSION

The temporal parameters, duration and inter-click interval, were significantly different between species, yet these differences were not robust. For example, click durations of melon-headed whales were significantly longer than click durations of bottlenose dolphins on array recordings of 2006, but array recordings of 2007 and recordings from the HARP in 2006 showed click durations of bottlenose dolphins to be

TABLE V. Spectral and temporal click parameters of melon-headed whale, bottlenose dolphin and Gray's spinner dolphin averaged clicks (group size 50), calculated for each recording situation. Values are given as medians with first and third quartiles in squared brackets. n: number of clicks in analysis.

	Peak frequency (kHz)	Center frequency (kHz)	Duration (ms)	Inter-click interval (ms)	Lower −10 dB frequency (kHz)	Bandwidth −10 dB (kHz)	Lower −3 dB frequency (kHz)	Bandwidth −3 dB (kHz)
				Melon-headed whales				
2006 array 192 kHz (n=44)	25.5	30.8	0.46	138	12	40.9	19.5	14.3
	[25.5 27.6]	[29.7 33.0]	[0.34 0.67]	[104 191]	[8.3 13.5]	[35.4 47.8]	[18.8 21.0]	[10.7 19.3]
2006 HARP 200 kHz (n=44)	29.7	29.7	0.29	78	14.1	30.1	24.2	9.8
	[26.6 30.5]	[28.9 30.9]	[0.27 0.31]	[63 107]	[9.4 21.1]	[23.6 38.1]	[23.4 25.0]	[9.4 10.2]
2007 array 480 kHz (n=37)	24.4	32.6	0.27	124	10.8	39.8	18.8	14.5
	[23.2 26.7]	[29.9 35.3]	[0.20 0.33]	[62 155]	[8.4 13.4]	[32.8 45.0]	[17.8 19.9]	[11.7 17.6]
				Bottlenose dolphins				
2006 array 192 kHz (n=46)	30.0	33.5	0.44	67	16.5	40.1	22.9	11.3
	[26.3 31.3]	[30.7 36.8]	[0.37 0.62]	[48 101]	[11.6 17.3]	[30.2 48.2]	[20.1 24.9]	[9.6 16.5]
2006 HARP 200 kHz (n=71)	36.7	38.3	0.38	80	21.1	41.4	28.1	14.1
	[30.5 47.7]	[34.7 43.9]	[0.32 0.64]	[63 98]	[8.6 24.2]	[31.3 53.1]	[24.2 41.4]	[10.2 18.0]
2007 array 480 kHz (n=40)	26.7	37.3	0.29	107	8.7	43.1	19.5	13.6
	[24.8 28.1]	[31.0 47.1]	[0.24 0.41]	[63 181]	[8.0 12.9]	[32.6 52.1]	[18.8 22.9]	[10.1 16.3]
				Spinner dolphins				
2006 array 192 kHz (n=31)	36.0	37.1	0.37	140	7.5	54.0	27.0	18.8
	[33.8 39.8]	[36.0 38.3]	[0.21 0.44]	[108 200]	[7.5 14.3]	[44.3 60.0]	[24.8 29.3]	[16.5 24.0]
2006 HARP 200 kHz	–	–	–		–	–	–	–
2007 array 480 kHz (n=36)	33.8	47.9	0.21	284	8.4	68.9	24.1	20.9
	[27.9 39.4]	[37.0 50.9]	[0.17 0.25]	[132 809]	[8.0 9.3]	[55.0 93.0]	[21.2 28.0]	[16.4 24.6]

TABLE VI. Discrimination of spectral click parameters of melon-headed whale, bottlenose dolphin and Gray's spinner dolphin averaged clicks (group size 50) by Kruskal-Wallis one-way analysis of variance calculated for each recording situation. Values are given as Chi^2 test results and their p values.*: $p<0.05$, n.s.: not significant.

	Peak frequency (kHz)	Center frequency (kHz)	Duration (ms)	Inter-click interval (ms)	Lower −10 dB frequency (kHz)	Bandwidth −10 dB (kHz)	Lower −3 dB frequency (kHz)	Bandwidth −3 dB (kHz)
Array 2006	67.4/*	49.7/*	9.93/*	37.0/*	21.5/*	25.4/*	53.0/*	22.5/*.
HARP 2006	45.4/*	78.4/*	29.7/*	0.1/n.s.	9.0/*	23.1/*	20.6/*	29.7/*
Array 2007	37.5/*	30.2/*	29.5/*	21.2/*	7.4/*	41.0/*	27.9/*	23.2/*
Post-hoc test with Bonferroni correction: all pairs significantly different unless otherwise reported. Melon-headed whales—pe;bottlenose dolphins—tt; Gray's spinner dolphins—sl								
Array 2006	*	*	n.s. pe/tt	n.s. pe/sl	n.s. pe/sl	n.s. pe/tt	*	n.s. pe/tt
HARP 2006	*	*	*	n.s. pe/tt	*	*	*	*
Array 2007	n.s. pe/tt	*	n.s. pe/tt	n.s. pe/tt	n.s. pe/tt, tt/sl	n.s. pe/tt	n.s. pe/tt	n.s. pe/tt

longest. This was statistically underlined by a significant influence of recording instrumentation, especially in these parameters. Both click duration and inter-click interval were dependent on the random click selection during analysis and most likely also the behavioral situation of the recorded animals. Clicks recorded off-axis tend to have longer durations than on-axis and the angle of the vocalizing animals to the recording instrument was unknown. Furthermore, inter-click interval is changed depending on the distance of the echolocating animal to a target. This variability in echolocation did not prove to have species-specific characters but was task and location dependent. Therefore, temporal parameters were not well suited for species classification.

The spectra of melon-headed whales, bottlenose and spinner dolphin clicks showed species-specific frequencies. The peak and center frequency relationships between species showed melon-headed whales having the lowest, bottlenose dolphins the middle and spinner dolphins the highest frequencies. These peak and center frequencies were lower than previously given in the published literature. Bottlenose dolphin clicks have been described with bimodal peak frequencies at 60–90 and 110–140 kHz (Akamatsu *et al.*, 1998, Au, 1993). The peak frequency of spinner dolphin clicks was given at 50–90 kHz and the center frequency at 70–90 kHz (Schotten *et al.*, 2003). These parameters were derived from presumably on-axis clicks of free ranging animals. Our data set comprised not only on-axis but all clicks independent of the animals' angle to the recording instrument. The farther a click is recorded off the axis of the animals' sonar beam, both horizontally and vertically, the lower in frequency is the strongest peak of the spectra (Au, 1980). Field recordings of dolphins should have many more off-axis than on-axis clicks and these dominate the mean spectra and median frequency values even though the on-axis clicks are expected to have a higher apparent source level. Additionally, Cranford (2000) suggests that there are two components of sound generation, one tissue-born and one airborne. The tissue-born component is higher in frequency, more directional and stronger in amplitude. The airborne component is a by-product of the sound generation, being omni-directional and lower in frequency and amplitude. Possibly the latter component plays an important role in the frequency composition of off-axis clicks and might account largely for the low frequency reported here. Melon-headed whales had the least variability of all species in the click frequency parameters. This might indicate that their on-axis clicks do not have frequency peaks as high as those published for bottlenose or spinner dolphins. Interestingly, recordings made with a restricted 192 or 200 kHz compared to 480 kHz sampling rate had a similar distribution of peak frequencies for each of the three species. The higher sampling rate did not reveal significant peaks in higher frequencies, which could have shifted median peak frequencies upwards. Center frequencies tended to be higher in the 480 kHz data, which can be attributed to energy above the Nyquist rate of data sampled at 192 or 200 kHz [Fig. 2(C)].

There may be a bias due to recording instrumentation which had significant impact on all parameters (Table IV, nested ANOVA). A bias could be due to differences in sea states, locations around the atoll and animal behavior during times of recording, but this is considered less likely. Samples of data were used ensuring variability of locations (except for HARP), days, and behavior for each recording instru-

TABLE VII. Classification of single clicks and averaged clicks (group size 50) of melon-headed whales, bottlenose dolphins and Gray's spinner dolphins by discriminant function analysis. PF: peak frequency, CF: center frequency, L-3dBF: lower −3 dB frequency.

	Percent misclassified			
	All parameters		PF, CF, L-3dBF	
	Single clicks	Averaged clicks	Single clicks	Averaged clicks
2006 array 192 kHz	44.8	11.6	48	31.4
2006 HARP 200 kHz	20.3	4.3	21.2	6.1
2007 array 480 kHz	42.7	25.7	50.6	33.6
All instrumentation	42.7	28.4	48.9	37.3

TABLE VIII. Confusion matrix of discriminant function analysis. Results of classification of melon-headed whales (pe), bottlenose dolphins (tt) and Gray's spinner dolphins (sl), all recording instrumentation, all classification parameters. Actual rows by predicted columns.

	Single clicks					Averaged clicks				
	pe	sl	tt	Total count	% correct	pe	sl	tt	Total count	% correct
pe	632	80	98	810	87	116	2	7	125	93
tt	278	169	233	680	34	50	23	84	157	54
sl	92	212	86	390	54	8	50	9	67	75

ment. The shapes of spectra of different species within one recording instrument follow the same general pattern (Fig. 2). This suggests that the bias is an effect from the recording instrumentation itself. As only the preamplifier with band-pass filter boards and hydrophones were calibrated, other components of the instrument are not accounted for in the transfer function that was applied. This could have caused a shift of the peaks slightly to lower or higher frequencies with a few dB offset. Furthermore, the PC Tape system used in the 2007 array recordings had a better signal-to-noise ratio than the MOTU or HARP used in 2006, which changes detectability of clicks and the start of each click might be masked. This small loss in the beginning of a signal with few hundreds of μs duration and its major signal content in the beginning could affect the spectral content. The location with respect to water depth of the recording hydrophone may also influence the properties of the data. The array recordings were made in surface water where wind and wave noise are more dominant in the 10–20 kHz range than for recordings made at the seafloor. Seafloor recordings by the HARP in 500–600 m water depth may lose a portion of the higher frequencies due to attenuation and frequencies might cancel each other out due to interference of multiple paths. Also, the animals might have had a different vertical angle to the HARP hydrophone than the array hydrophones due to different depths. This means that even though species-specific characteristics were detected for the different recording instrumentations, these characteristic differences are very slight, but it is important for classification purposes to have exact calibrations or recordings with the exact same instrumentation.

Grouping of clicks and calculating a mean grouped click optimized the discrimination possibilities by reducing variability within the clicks of one species. Following the argument of Soldevilla *et al.* (2008) and Roch *et al.* (2008) that off-axis clicks with their reverberations carry species-specific information due to propagation within the head of the vocalizing animal, grouping clicks and calculating their mean should enhance these species-specific qualities. The results of the discriminant function analysis (Table VII, Table VIII) showed a distinctly higher correct discrimination rate of all species with averaged clicks. In a next step, with the knowledge of the differences shown within our results, both the single and grouped clicks of each recording set could be tested with more sophisticated classification techniques to further enhance the results (Au *et al.*, 2010).

Morphology, particularly of the sound producing organs, may be a relevant factor for acoustic species discrimination. Overall body size does not correlate with click frequencies. While melon-headed whales had the lowest frequencies, they were not the largest animals. Adult males have a mean body length of 2.52 m (Perryman, 2009). Yet bottlenose dolphins can grow up to 3.8 m (Jefferson *et al.*, 2008) and those observed at Palmyra Atoll were similar in size or larger than the melon-headed whales. Several possible mechanisms within the head could have an influence on the spectral and temporal structure of the emitted click. The sound producing organs are a structural group in the upper nasal region called the monkey lips dorsal bursae (MLDB) (Cranford *et al.*, 1996). Within the MLDB exist two independent sets of phonic lips which are shown in bottlenose dolphins to both simultaneously produce echolocation clicks while only one produces whistles (Cranford *et al.*, 2000). These two sound generators probably work together to produce a single, strong amplitude broadband click (Cranford and Amundin, 2003). One click produced on two sound sources simultaneously leads to a single click on-axis of the sonar beam but has two successive pulses in off-axis clicks due to different distances from the receiver to each phonic lip. This could lead to interferences between these two pulses (Lammers and Castellote, 2009). Species-specific spectral click structures could emerge as a result of the interference. Another explanation could be that the sound produced with these two sources has a direct path on-axis but is reflected on different materials within the head generating a multi-path set of pulses off-axis with the species-specific spectral properties (Soldevilla *et al.*, 2008). And lastly, as mentioned above, the airborne component as a by-product of the sound generation could add low frequency content, especially for off-axis clicks. Either one of these cases or any combination could be the reason for species-specific clicks. Anatomical head structures are a key factor as Soldevilla *et al.* (2008) hypothesized that species with near symmetrical head morphology show several very distinct species-specific peaks in their click spectra, while species with asymmetrical head anatomy tend to not have clear peaks. Melon-headed whales, bottlenose and spinner dolphins are all species with asymmetrical skulls (Fig. 4). Following the above argument, we can confirm that though the spectral properties of clicks of these three species were different from each other, none of them showed a distinct set of peaks in their spectra. A model of the exact sound pathways such as Cranford *et al.* (2008) have described for Cuvier's beaked whales could help answer this question.

V. CONCLUSIONS

Melon-headed whales, bottlenose dolphins and spinner dolphins recorded during daytime at Palmyra Atoll showed

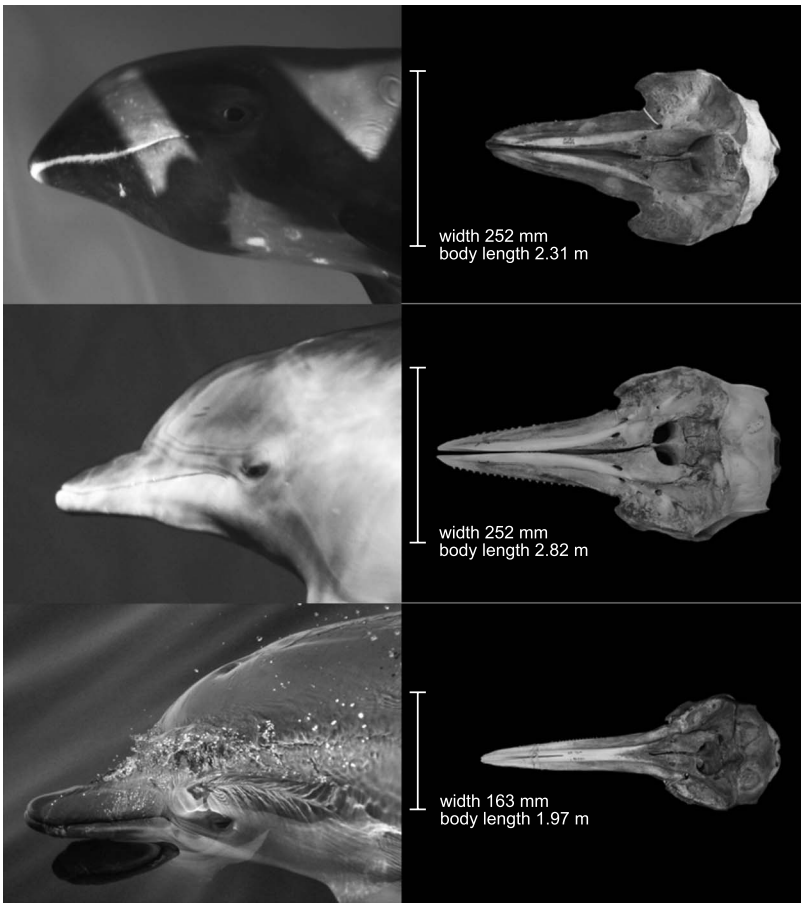

FIG. 4. Skull comparisons. Underwater image at Palmyra Atoll (left) and example skull dorsal view (right) of melon-headed whale (top), bottlenose dolphin (middle) and spinner dolphin (bottom). All three species have asymmetric skulls with left side larger than the right.

species-specific spectral properties of their echolocation clicks. The differences were small, so that different recording systems had an impact on species discrimination results. In future work, it should be further investigated if the described results are amenable to more sophisticated automatic classification techniques. Furthermore, precise knowledge of the sound pathways within the animal could lead to an understanding of the generation of species-specific spectral parameters. Investigations of more species and comparisons among geographic regions of the same species might reveal phylogenetic and evolutionary patterns.

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