Species Identification and Measurement of Activity in Odontocete Species of Palmyra Atoll by Acoustic Monitoring

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GENERAL INTRODUCTION

The study of cetaceans is often difficult because of their broad but patchy distribution and our limited access to their environment. Ship-based and aerial surveys are costly methods that are restricted in their overall duration. They need good weather conditions and daytime hours for visual confirmation (Barlow, 2006).

Autonomous long-term passive acoustic monitoring is a viable method to study cetacean abundance, distribution, behavior and movement patterns independent of weather or time of the day over long periods of time and at remote locations. Autonomous passive acoustic monitoring, however, has to overcome its own difficulties. The recorder has limited recording range and is therefore a point source of information. Cetacean vocalizations need to be matched with the vocalizing species. Cetaceans might be present yet not vocalizing and therefore behavioral patterns of vocalization need to be understood. Source levels of different species should be known to interpret detection range and detection probability of certain species. Advances have been made to classify some cetacean sounds to species level. Identification of many mysticete calls has been successful and their signals have been automatically detected on long-term data (e.g. Munger et al. 2008, Sirovic et al. 2004, 2009, Oleson et al. 2007) but the discrimination of most odontocete calls remains difficult. Signals 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; Johnson et al., 2006; Zimmer et al., 2005, McDonald et al. 2009). Whistles from several dolphin species have proven to be classifiable (Oswald et al., 2006). Echolocation clicks from two delphinid species, Risso's dolphins and Pacific white-sided dolphins, show species-specific spectral peaks (Soldevilla et al., 2008). More work will be necessary to further classify other delphinid species by their signals.

Our study area Palmyra Atoll (Fig. 1.2) is one of the most isolated atolls worldwide, has never sustained a permanent human population, is far from major shipping lanes, and has as a result an almost pristine coral reef structure (Brainard et al., 2005). It is part of the northern Line Islands located in the central Pacific, about 1700 km south of Hawaii. Since 2001 Palmyra Atoll is protected as part of the United States Pacific Islands National Wildlife Refuge Complex and since January 2009 it became part of the new Pacific Remote Islands Marine National Monument. Palmyra's coral reef biodiversity has its roots in its location within the Inter-tropical Convergence Zone through which it receives larvae and nutrients from either the Pacific Equatorial Current or the Pacific Equatorial Countercurrent. Large numbers of pelagic and migratory fish stocks, seabirds, marine mammals, and sea turtles are found in conjunction with these currents to the atoll (Gulko et al, 2000). The climate around Palmyra is dominated by El Niño-Southern Oscillation (ENSO) events. The convergence zone has warm, less saline waters to the west (warm pool) and cold, more saline waters to the east (cold tongue). Large-scale oceanographic fluctuations occur during ENSO which shift the convergence zone eastwards of Palmyra Atoll during El Niño (warm) and westwards during La Niña (cold) events (Picaut et al., 1996). Palmyra Atoll consists of a circular string of about 50 forested islands that sustain a large seabird population. Nutrient outflow from the terrestrial ecosystem probably contributes to the high productivity at the atoll. Palmyra waters have a dense sound scattering layer (SSL) around the entire atoll which rises to shallow waters at night and has a substantial offshore extent (Brainard et al., 2005). Nighttime foraging cetaceans, such as the regularly at Palmyra Atoll observed species of melon-headed whales and spinner dolphins (Brainard et al., 2005, trip reports Baumann-Pickering, Pitman and Ballance, Roth), forage on fish and squid of this mesopelagic boundary community.

Little is known about the role that cetaceans have within an ecosystem such as Palmyra Atoll. Their high metabolic needs as mammals, however, should not be underestimated (Brainard et al., 2005). To judge their influence a more detailed assessment of abundance, composition and behavior is necessary.

The goal of this thesis has been to gather baseline data on cetacean species present at Palmyra Atoll, to describe and classify their acoustic signals, and to analyze their diel patterns. Ultimately seasonal rhythms, correlations of abundance with ecological factors, and habitat preference will be accessible for future work through the information gathered within this thesis.

Publication of the results and contributions from others

All three chapters of the dissertation are currently being prepared for submission to scientific journals for publication of the material. The dissertation author was the primary investigator and author. Co-authors for these chapters will be Prof. Dr. J. A. Hildebrand, Prof. Dr. H.-U. Schnitzler, and Dr. S. M. Wiggins who supplied the technical equipment, supervised this thesis and provided valuable comments on the manuscripts for each chapter.

Chapter 1 will have Dr. M. A. McDonald as co-author who helped with his expertise in beaked whale signal detection and classification and who provided valuable comments on the manuscripts for all chapters.

Chapter 2 will have Prof. Dr. M. A. Roch as co-author who helped with her expertise in dolphin signal detection and classification and who provided valuable comments on the manuscripts for all chapters.

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Chapter 1

Echolocation Signals of a Poorly Known Beaked Whale at Palmyra Atoll, Probably *Mesoplodon hotaula*

ABSTRACT

Long-term acoustic recordings from Palmyra Atoll, northern Line Islands in the central Pacific, showed beaked whale like upsweep FM pulses produced by an unknown species. From October 2006 to September 2007 an autonomous High-frequency Acoustic Recording Package (HARP), was mounted on the seafloor in water of about 600 m depth, southwest of the atoll, and was programmed to record with 100 kHz bandwidth for 5 minutes every 20 minutes. The peak frequency of the detected beaked whale pulses was at 48 kHz and the signal swept from 34 to 65 kHz (-10 dB bandwidth). Pulse duration was 430 μs and inter-pulse interval was 225 ms. The inter-pulse interval had a bimodal distribution. Besides the vast majority (74%) of single inter-pulse intervals there were double inter-pulse intervals of 450 ms. Two buzz sequences, probably prey capture attempts, were detected when the inter-pulse intervals went below 20 ms and the spectral structure of the pulses changed to not frequency modulated, transient clicks. Buzz clicks were about 20 dB lower in amplitude than prior FM pulses. These clicks had a 39 kHz bandwidth and a peak frequency at 37 kHz. Pulse duration was 160 μs and inter-click interval was between 4 and 10 ms. Signals from the Palmyra beaked whales had higher frequencies, broader bandwidths, longer pulse durations and shorter inter-pulse intervals than previously described FM pulses of Blainville's and Cuvier's beaked whales (Zimmer et al., 2005, Johnson et al., 2006). They were distinctly different temporally and spectrally from the unknown beaked whale at Cross Seamount, Hawaii (McDonald et al., 2009). It is very likely that these beaked whales are of the genus *Mesoplodon*, according to several recent sightings at the atoll. They are probably *M. hotaula*, consistent with genetic analysis of stranded skulls from Palmyra Atoll (Dalebout, unpublished results).

INTRODUCTION

Beaked whales are among the least known large mammals on the planet as they are infrequently encountered in the field and difficult to identify (e.g. Pitman, 2008). They are pelagic, deep foraging divers with rather short surface intervals between dives (e.g. Tyack et al., 2006). Many of the more than 20 species of beaked whales are known only from strandings and the study of skeletal material (Jefferson et al., 2008). The *Mesoplodon* beaked whales are rarely seen alive although they are the most speciose cetacean genus (Pitman, 2008). The number of mesoplodont species is still increasing with two new species described as recently as 1991 and 2002 (Reyes and Van Waerebeek, 1991, Dalebout et al., 2002). Based on preliminary analysis of skull features of two stranded specimens from Palmyra Atoll and molecular genetics of a tissue sample from a stranding at Kirabati Island, Dalebout et al. (2007) suggested that these animals may represent yet another undescribed species of mesoplodont beaked whale. However, recent findings (Dalebout, unpublished data) showed that these animals are genetically identical with one stranded specimen found in Sri Lanka, the beaked whale species *Mesoplodon hotaula*, initially described by Deraniyagala (1963a and 1963b). The species *M. hotaula* was considered synonomous with *M. gingkodens* (Moore and Gilmore, 1965) and because of the similar cranial osteology, has probably been mistaken for *M. ginkodens* numerous times. No other records since 1963 showed the presence of *M. hotaula*, either stranded or alive. During our field trips in fall 2007 and 2008 an unknown species of mesoplodont beaked whale was repeatedly seen (trip reports Baumann-Pickering, Pitman and Ballance, Roth). There has been no confirmed beaked whale sighting of another species at this location. This was most likely a living example of *M. hotaula* at Palmyra Atoll (Fig. 1.1). The head shape was unlike *M. densirostris* and the dorsal fin shape unlike *M. peruvians* (Jefferson

et al., 2008). These two species are the most likely to occur at Palmyra Atoll based on the known geographical distribution of mesoplodonts (MacLeod et al., 2006, Jefferson et al., 2008). Cookiecutter shark (*Isistius brasiliensis*) bites did not heal with characteristic white scars in this species which makes them distinguishable in the field, at least from *M. densirostris* (trip report Pitman and Ballance). To distinguish *M. hotaula* from *M. gingkodens* a biopsy sample would probably be necessary. In order to be certain about the precise species at Palmyra Atoll, more photos, particularly of adult males with their distinct tooth patterns on each side of the lower jaw, and biopsy samples would be crucial.

Fig. 1.1: Surfacing sequence of mother-calf pair, *Mesoplodon hotaula* at Palmyra Atoll, photo taken October 2007.

Until a few years ago, the acoustic behavior of beaked whales was barely known, with descriptions being incomplete due to restrictions in recording bandwidths (e.g. Caldwell and Caldwell, 1971, Lynn and Reiss, 1992, Dawson et al., 1998). There has been an increased investigation effort after several mass strandings of beaked whales which may have been linked to anthropogenic noise during military sonar exercises (Simmonds and Lopez-Jurado, 1991, Frantzis, 1998, Jepson et al., 2003). New acoustic technologies, recording a larger frequency range in the field, have made it possible to find the ultrasonic echolocation signals of beaked whales. Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales are the more commonly encountered and best studied among this family of cetaceans. They use upsweep frequency modulated (FM) pulses for echolocation which are species and activity specific (Johnson et al., 2004, Madsen et al., 2005, Zimmer et al., 2005, Johnson et al., 2006, Johnson et al., 2008). Johnston et al. (2008) and McDonald et al. (2009) report an FM ultrasonic sound of unknown origin with beaked whale characteristics, discovered on a yearlong broad-band acoustic recording from Cross Seamount, Hawaii. Other beaked whales within the genus *Hyperoodon* and *Berardius* use short duration, broadband clicks without frequency sweep (Dawson et al., 1998, Rogers and Brown, 1999, Hooker and Whitehead, 2002), like most other echolocating cetaceans (Au, 1993). So far we know Baird's, Arnoux's and Blainville's beaked whales also produce whistles (Dawson et al., 1998, Rogers and Brown, 1999, Rankin and Barlow, 2007), while whistles from unidentified small beaked whales have been recorded in the Antarctic, but not published, in part because of the species identification difficulty (Hildebrand 2009 pers. comm.).

The echolocation signals of Blainville's and Cuvier's beaked whales are very similar linear upsweep FM pulses of about 270 and 200 μs duration, sweeping from 26 to 51 kHz and 31 to

54 kHz with center frequencies of 38 and 42 kHz, and inter-pulse intervals of 370 and 380 ms, respectively (Zimmer et al., 2005, Johnson et al., 2006). Source levels of up to 214 dB re 1 µPa at 1 m peak-to-peak (pp) have been reported for Cuvier's beaked whales (Zimmer et al., 2005). The directivity index is a value for the width of a beam or major lobe of a receiving or transmitting system. It compares a directional with an omnidirectional receiver or source. The larger the directivity index value becomes, the more directional is the system. Head scan rates are a measure of how quickly an animal moves the head or body and with it its beam from one side to the other while ensonifying a target. Zimmer et al. (2005) measured a narrow beamwidth with directivity index of 30 dB and head scan rates of 25 degrees per second for these whales. The beaked whales from Cross Seamount (Johnston et al., 2008, McDonalds et al., 2009) had a very different FM pulse with a sweep from 35 to near 100 kHz (the bandwidth of the recording), very long pulse durations of 987 µs, and short dominant inter-pulse intervals of 110 ms.

Most work on toothed whale echolocation has been with captive animals and has focused on target detection (e.g. Au, 1993, Kastelein et al., 1999) and discrimination (e.g. Au, 1993, Kastelein et al., 1997) while little is known about prey capture, particularly in the wild. A few recent studies show that the phases of prey capture in odontocetes (e.g. Miller et al., 1995, Madsen et al., 2002, Johnson et al., 2004, Miller et al., 2004, Akamatsu et al., 2005, Madsen et al., 2005, Johnson et al., 2006, Johnson et al., 2008, Jones et al., 2008, Verfuss et al., 2009) are very similar to those of prey capture in bats (e.g. Griffin et al., 1960, Kalko and Schnitzler, 1989, Surlykke et al., 1993, Schnitzler and Kalko, 1998, Miller and Surlykke, 2001, Schnitzler et al., 2003, Melcon et al., 2007). Vocalizing with long intervals is used to search for prey items while a group of signals with very short intervals, the buzz, indicate prey capture

attempts. Blainville's beaked whales (*Mesoplodon densirostris*) use FM echolocation pulses at 0.2–0.6 s inter-pulse intervals to detect and approach prey. At a distance to prey of about 3–4 m, they switch to a buzz, using lower energy unmodulated clicks for prey capture (Madsen et al. 2005; Johnson et al. 2006, 2008).

This chapter describes the spectral and temporal characteristics of beaked whale signals found on a yearlong seafloor acoustic survey at Palmyra Atoll, most likely produced by *Mesoplodon hotaula*. We show that echolocation behavior of this species is similar to that of other whales in this genus, with echolocation signal types and signal timing changing dependent on context. We discuss their echolocation behavior in relation to echolocating dolphins and bats.

MATERIALS AND METHODS

Data collection

An autonomous High-Frequency Acoustic Recording Package (HARP) was placed on a steep slope off Palmyra Atoll's western terrace (Fig. 1.2). 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 (see Appendix I). The instrument recorded from October 19, 2006 until March 23, 2007 and from April 9, 2007 until September 18, 2007. The recording gap of 16 days between the two deployments corresponded to servicing of batteries and disk drives. During the first deployment the HARP was located at 05° 51.85' N 162° 09.91' W in 650 m water depth. It was then deployed about 1 km east of the initial location at 05° 51.88' N 162° 09.36' W in 550 m depth. The recorder was set to a sampling frequency of 200 kHz and a duty cycle with an on duration of 5 minutes every 20 minutes. The frequency response of the hydrophone was designed to follow the reciprocal of ocean ambient

noise in order to maximize the dynamic range of the recorder (Wiggins and Hildebrand, 2007). Low frequencies with high ambient noise and little attenuation over distance were amplified less than high frequencies with low ambient noise and strong attenuation. At the U.S. Navy's TRANSDEC facility in San Diego the HARP hydrophone was calibrated with a reference hydrophone and projector (transfer function for HARP see Appendix IIIB).

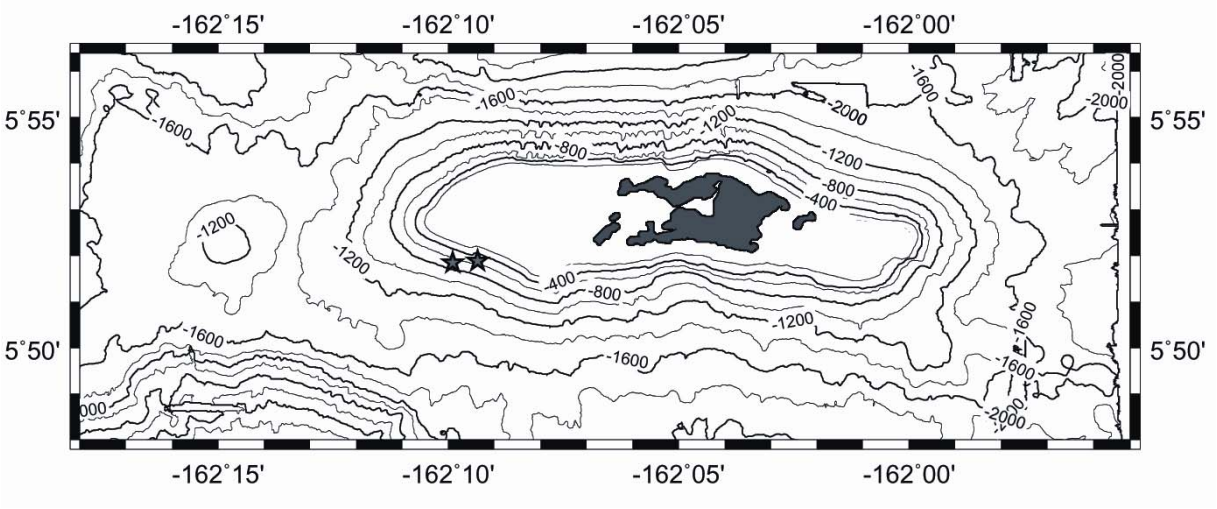

Fig. 1.2: Bathymetry map of Palmyra Atoll and positions of HARPs indicated with stars. Bathymetry data courtesy of NOAA Coral Reef Ecosystem Division, Pacific Islands Fisheries Science Center and the Pacific Islands Benthic Habitat Mapping Center, SOEST, University of Hawaii. Coastline data courtesy of National Geophysical Data Center, NOAA Satellite and Information Service, WVS Coastline Database. Plotting with GMT by Paul Wessel and Walter H. F. Smith.

Signal processing

Signal processing was performed using custom-made routines in MATLAB (Mathworks, Natick, MA). Beaked whale type sweep signals were found on the long-term recordings throughout the year. These signals had, in comparison to delphinid clicks, longer durations of at least 200 μs and a frequency sweep. Sixty-five sequences with good quality signals were randomly selected for describing the frequency modulated (FM) pulse. Within all sequences of the year there were only two calling bouts with differing signal pattern and signal structure categorized as buzz clicks, based upon their faster repetition rate and spectral properties. The sequences were digitally filtered with a 10-pole Butterworth band-pass filter. The low cutoff frequency was at 8 kHz for FM pulse sequences. Buzz clicks had a much lower sound pressure level and therefore the low cutoff frequency was raised to 16 kHz in these sequences to improve the signal-to-noise ratio. The high cutoff frequency was at 85 kHz for both signal types to prevent analysis of possibly aliased parts of the recorded signal.

FM pulses and buzz clicks were automatically selected using a two step approach. The first step used cross-correlation as a matched filter to detect signals. Cross-correlation gave the degree of linear relationship between an example pulse as the model and the data set to be analyzed. The threshold for cross-correlation was set very low with about 2% missed pulses and missed pulses were below -8 dB signal-to-noise ratio. There was accordingly a high false alarm rate. These automatic selections were manually scanned and false detections were deleted. A 2.5 ms time series window was roughly defined around the detected FM pulses, a 2 ms window around the detected buzz clicks. The second automatic selection step determined the exact start and end point of the roughly defined FM pulses und buzz clicks. The finer resolution click detection algorithm (Soldevilla et al., 2008) using the Teager energy operator

(Kaiser, 1990, Kandia and Stylaniou, 2006) was applied. In order to calculate signal-to-noise ratios, a 5 ms time series window was roughly picked preceding every FM pulse and a 2.5 ms window preceding every buzz click. Spectra of each signal and preceding noise were calculated using 1.28 ms of data and a 256-point Hann window centered around the click and in the beginning of the noise sample. For the calculation of received levels the spectra were corrected for 1 Hz bins and the system transfer function was added. This resulted in an overall system response flat to within ±2 dB from 8 and 16 to 85 kHz for pulses and buzz clicks, respectively. Click received levels are given over a band encompassing the click energy. The -10 dB bandwidth of pulses in this study has a median of about 15 kHz and the -10 dB bandwidth of buzz clicks has a median of 4 kHz (Table 1.1). Therefore 27 dB and 14 dB (10 log (bandwidth)) were added to pulses and buzz clicks, respectively, to approximately represent click sound pressure levels on a plot of ambient noise levels. Signal-to-noise ratio was calculated at peak-to-peak level of each FM pulse or buzz click.

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 dynamic range of the recording system. Furthermore all FM pulses with a signal-to-noise ratio of less than 10 dB and buzz clicks less than 6 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 following equation (Richardson et al., 1995) was used to approximate the influence of attenuation: $a = 0.036 f^{1.5}$ dB/km with f being frequency in kHz. At a distance of 100 m the 25-85 kHz band was attenuated 0.5-2.8 dB. Thus for short ranges the recorded spectra is similar in shape to the source spectra. At 1 km the attenuation will be 5-28 dB in the

signal range and therefore distort the spectral characteristics especially in the high frequencies. The orientation of the whale to the recording device changes the signal properties 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). To minimize these biases for the calculation of median signal parameters, only highest amplitude signals were used. FM pulse parameters were calculated with signals having received levels higher than 145 dB re 1uPa at 1 m (pp) leaving 2853 pulses for analysis. All buzz clicks were included in the median calculation. The frequency-related signal parameters peak and center frequency, -3 and -10 dB bandwidth were processed using methods from Au (1993). A histogram of the inter-pulse interval was computed using a 10 ms bin width from which several peaks in distribution appeared. The group of the nearest minimum was defined between every peak and it was excluded for further analysis. All inter-pulse intervals of one peak between two minima were taken to calculate its median and the 10% and 90% confidence borders. Inter-pulse intervals, smaller than 70 ms, were discarded for the calculation of median inter-pulse intervals because they showed either the approach to a target or background, or indicated the presence of two animals vocalizing at the same time. Inter-pulse intervals longer than 550 ms were discarded as they did not show any further peak structure and appeared due to larger gaps between FM pulse bouts.

RESULTS

FM pulse echolocation signals

The data analysis of the long-term data showed upsweep FM pulses similar to beaked whales but produced by an unknown species. A total of 11,794 FM pulses were used for the signal description. The median lower -10 dB frequency was at 34 kHz and the signals had an average -10 dB bandwidth of 31 kHz. The lower -3 dB frequency was at 40 kHz with a 15 kHz bandwidth at -3 dB. The center frequency was at 46 kHz and the peak frequency at 48 kHz (Fig. 1.3). The median pulse duration was 430 µs and a single inter-pulse interval had a median value of 225 ms (Table 1.1).

FM pulse frequency values and received levels had a distinct relationship (Fig. 1.4A). The lower and upper values of the -3 dB frequency were lowest at around 135 dB re 1 µPa at 1 m (pp) received level with 41 and 51 kHz, respectively. Both values rose quickly to higher frequencies, up to 62 and 68 kHz, when the received level was lower. There was only a slight increase in frequency for the lower -3 dB value up to 43 kHz and a stronger increase for the upper -3 dB value to 59 kHz when the received level was 161 dB re 1 µPa at 1 m (pp). Standard deviations were fairly narrow in the range of 135 to 161 dB re 1 µPa at 1 m (pp) received level with ±5-7 kHz in the lower and ±6-8 kHz in the upper -3 dB frequency. Pulse duration (Fig. 1.4B) was shortest with 320 µs at a received level of around 135 dB re 1 µPa at 1 m (pp) and was longer with higher received levels up to 161 dB re 1 µPa at 1 m (pp) and 700 µs. This was the result of a better signal-to-noise ratio at higher signal levels. The signal duration also became slightly longer below 135 dB re 1 µPa at 1 m (pp) up to 400 µs. Standard deviation for durations between 135 and 161 dB re 1 µPa at 1 m (pp) received level was ±80-170µs. The maximum received level, which the instrumentation allowed before clipping

occurred, was about 165 dB re 1 μPa at 1 m (pp) near the peak frequencies. At received levels of above 161 dB re 1 μPa at 1 m (pp), standard deviations of frequencies and duration grew quickly which was an artifact of the limitation of the recording system as the automatic pulse selection procedure may not have eliminated all clipped clicks.

The inter-pulse interval had a bimodal distribution (Fig. 1.4C and D). The vast majority (74%) of inter-pulse intervals were in the range of 80 and 380 ms with a median of 225 ms, and 90% confidence intervals at 140 and 270 ms. There were also sequences with double inter-pulse intervals with a median of 450 ms, and 90% confidence intervals at 420 and 480 ms (Fig. 1.5).

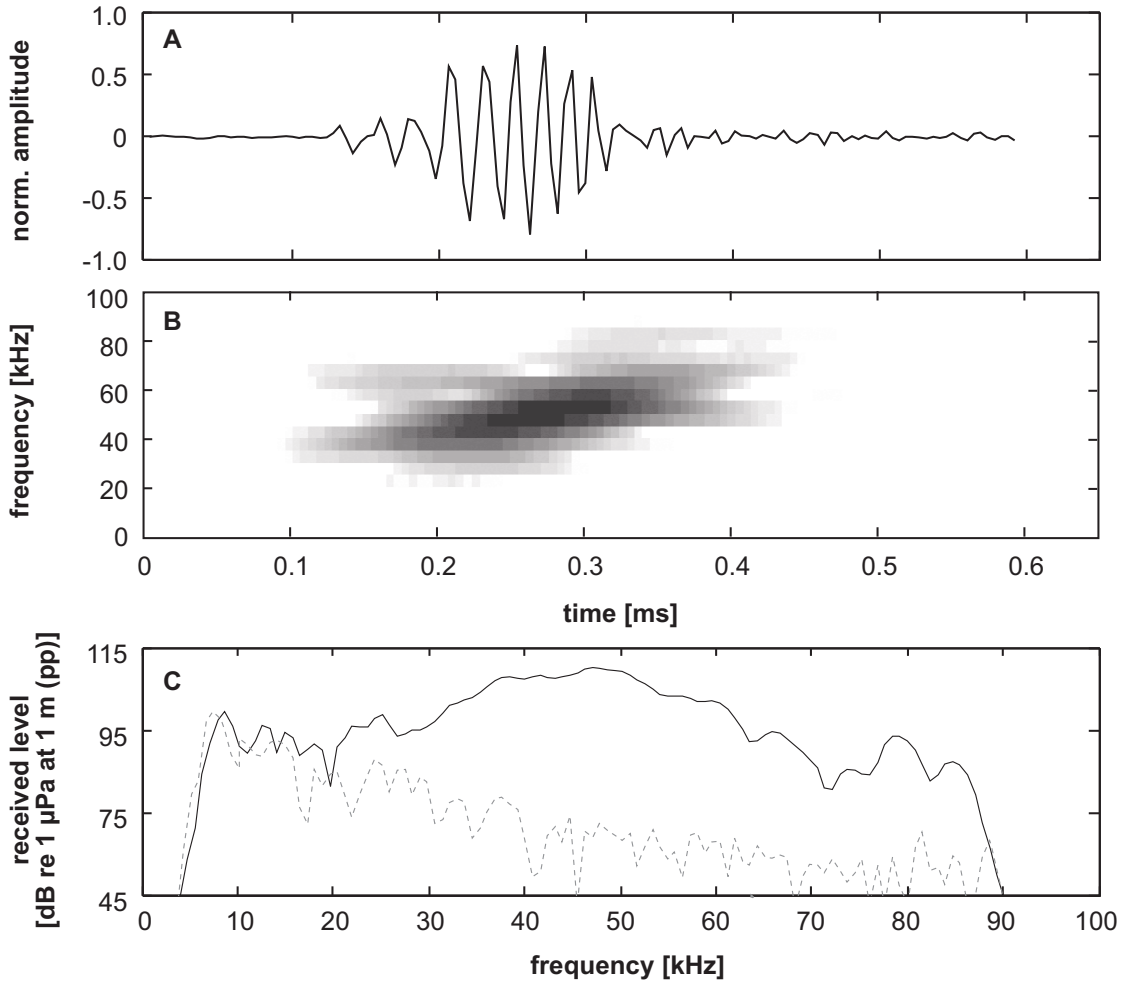

Fig. 1.3: Typical upsweep FM pulse recorded at Palmyra Atoll. It represents the sum of 303 pulses; all with a signal-to-noise ratio between 25 and 26 dB. A) Waveform with normalized amplitude versus time, B) spectrogram (Hann window, 40-point FFT, 98% overlap) with frequency versus time, and C) spectra (Hann window, 256-point FFT) with received level versus frequency. The continuous line represents the FM pulse while the dashed line shows the preceding noise floor.

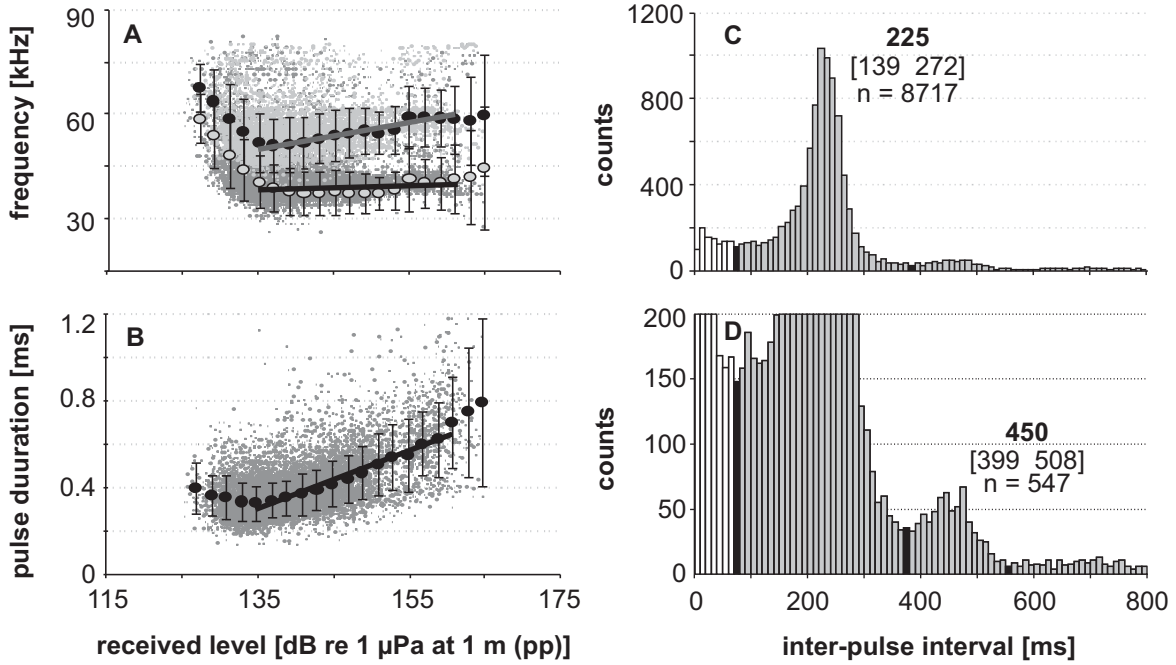

Fig. 1.4: FM pulse echolocation signals recorded at Palmyra Atoll. A) Lower -3 dB frequency (dark grey) and upper -3 dB frequency (light grey) versus received level with mean value and standard deviation of groups with 2 dB bin width, line of best fit from 135 to 161 dB re 1 µPa at 1 m (pp) (lower -3 dB frequency: $y = 0.09x + 31.1$, $R^2 = 0.2$; upper -3dB frequency: $y = 0.3x + 13.3$, $R^2 = 0.9$). B) Pulse duration versus received level with mean value and standard deviation of groups with 2 dB bin width, line of best fit from 135 to 161 dB re 1 µPa at 1 m (pp) ($y = 0.01x - 1.2$, $R^2 = 0.97$). Data basis (n) for A) and B) were 11,794 pulses. C and D) Histogram of bimodally distributed inter-pulse interval (n=9264) with C showing the dominant first peak and D the smaller second peak. Black bars indicate excluded group minima, bold numbers show median value of each peak, values in brackets give 10% and 90% confidence borders and n indicates number of inter-pulse intervals per peak.

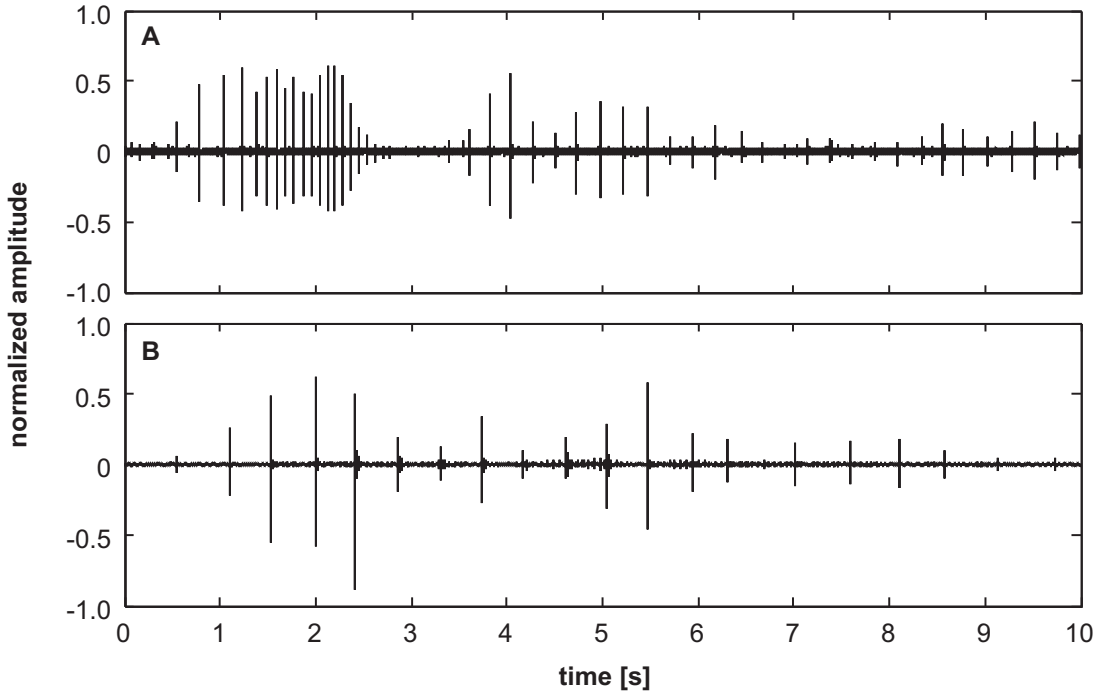

Fig. 1.5: FM pulse echolocation sequences with A) single and shorter inter-pulse intervals (median 225 ms) and B) double inter-pulse intervals (median 450 ms).

Buzz sequences

Two buzz sequences with a total of 291 buzz clicks were detected and 252 of these were used for the signal description. The sequences were categorized as a buzz if a regularly spaced echolocation pulse sequence with inter-pulse intervals larger than 70 ms was followed by a sequence with clicks of less than 20 ms inter-click intervals. Buzz clicks were about 20 dB lower in amplitude than prior FM pulses. These clicks were not frequency modulated, transient signals with a median lower -10 dB frequency of 32 kHz and a 39 kHz bandwidth. The median lower -3 dB frequency was at 35 kHz with a 4 kHz bandwidth. They had a center frequency of 35 kHz and a peak frequency of 37 kHz (Fig. 1.6). The median duration was 160 µs and the inter-click interval was between 4 and 10 ms (Table 1.1). The two recorded buzz sequences

differed from each other temporally (Fig. 1.7). They both had a series of regularly spaced FM pulses and then one shorter inter-pulse interval with FM pulse before changing the signal structure to buzz clicks and shortening the inter-click interval drastically. One buzz sequence had continuously decreasing inter-click intervals starting at 9 ms and reducing it to a minimum of 3.5 ms. There was a long gap of about 700 ms before regular FM pulses were continued. The other buzz sequence started out with very short inter-click intervals around 4-5 ms, then varied between 7 and 10 ms. The sequence ended with a 500 ms gap before regularly spaced FM pulses were taken up again.

Table 1.1: Signal parameters of FM pulses with a received level larger than 120 dB re 1 µPa at 1 m (pp) (N=65, pulse n=2,853, inter-pulse interval n=11,729) and buzz clicks (N=2, buzz click n=252, inter-click interval n=291); N = number of sequences, n= number of signals.

		FM pulses		Buzz clicks	
Parameter	Unit	Median	(10-90%)	Median	(10-90%)
Peak frequency	kHz	47.7	(41.4-54.1)	36.7	(31.3-43.8)
Center frequency	kHz	45.7	(35.7-53.6)	34.6	(30.6-39.0)
Lower -3 dB frequency	kHz	39.8	(36.7-47.7)	35.2	(28.9-41.4)
-3 dB bandwidth	kHz	14.8	(9.4-20.3)	3.9	(3.1-5.5)
Lower -10 dB frequency	kHz	34.4	(31.3-39.8)	32.0	(25.0-38.3)
-10 dB bandwidth	kHz	31.3	(22.7-53.1)	39.1	(33.6-45.3)
Duration	µs	430	(290-700)	160	(120-260)
1st Inter-pulse interval	ms	225	(139-272)	5.3	(3.8-8.6)
2nd Inter-pulse interval	ms	450	(399-508)	-	-

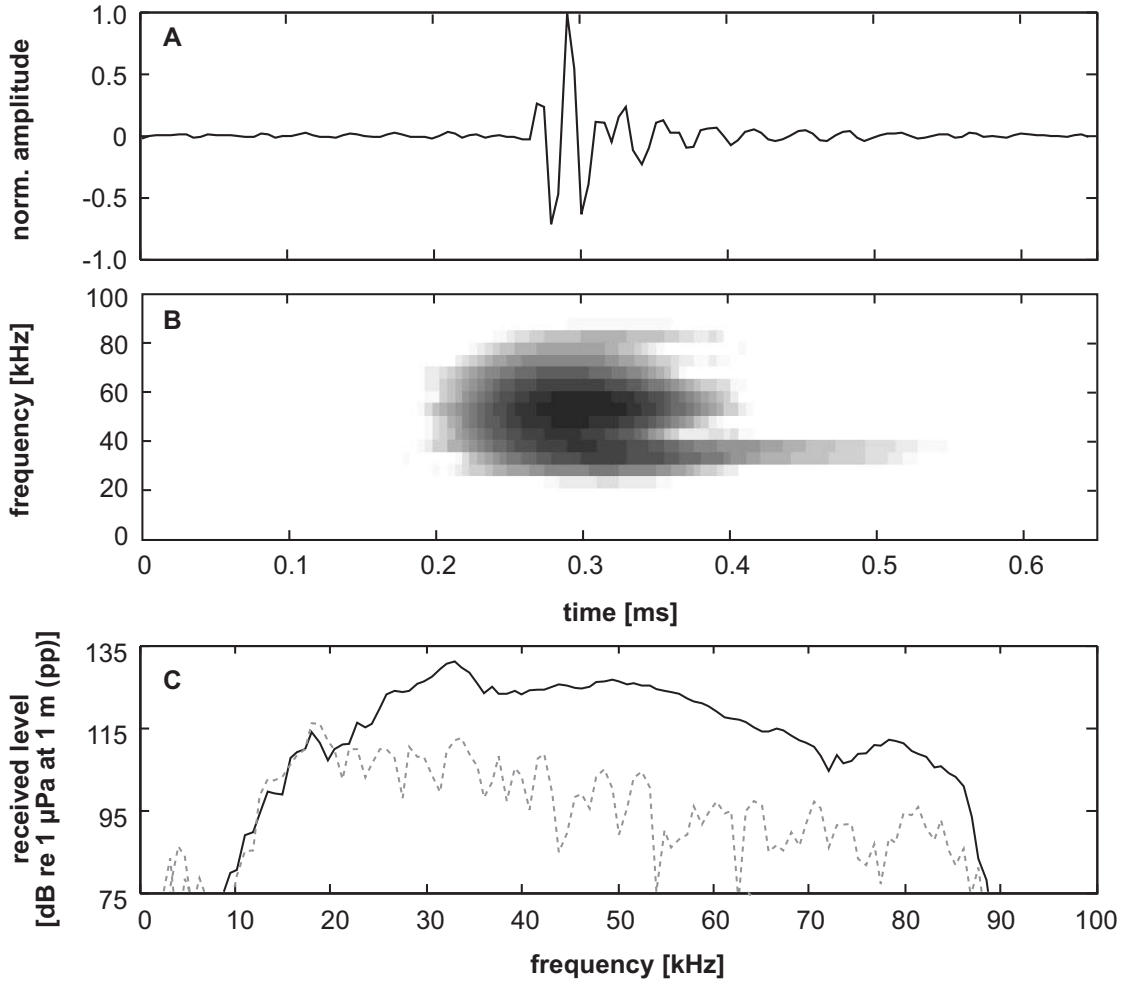

Fig. 1.6: Typical buzz click recorded at Palmyra Atoll. It represents the sum of 48 clicks; all with a signal-to-noise ratio larger than 16 dB. A) Waveform with normalized amplitude versus time, B) spectrogram (Hann window, 40-point FFT, 98% overlap) with frequency versus time, and C) spectra (Hann window, 256-point FFT) with received level over frequency. The continuous line represents the buzz click while the dashed line shows the preceding noise floor.

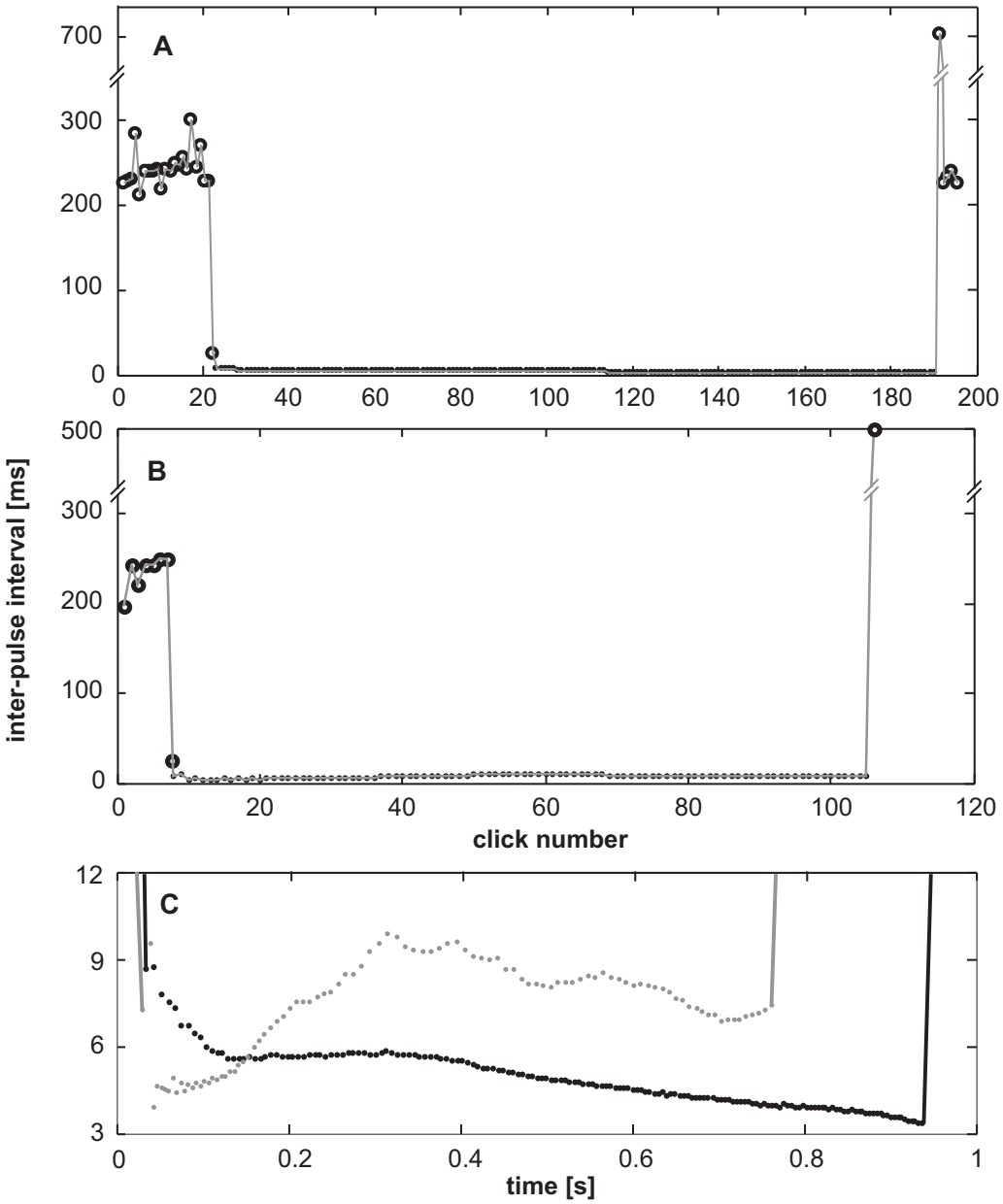

Fig. 1.7: A and B) Change from regular pulses to clicks of buzzes in two sequences with shortening of inter-pulse intervals (open circles) before the buzz clicks to a minimum of 26 ms (A) and 24 ms (B) followed by inter-click intervals (points) between 4 and 10 ms. After the buzz there was a pause of 708 ms (A) and 499 ms (B) before echolocation pulses were resumed. C) Detail of buzz inter-click intervals (points) versus time of sequence A (black) and B (grey). Lines in the beginning and end indicate long inter-pulse intervals.

DISCUSSION

Species correlation

Not all beaked whales use upward FM pulse echolocation signals but it is likely that echolocation signals with such sweeps originate from beaked whales because they are the only odontocetes that have been reported to produce swept signals. The beaked whale signals described here are unlike previously published FM pulse descriptions in their temporal and spectral properties. They are different in most aspects to those found at Cross Seamount (Johnston et al., 2008, McDonald et al., 2009). They are more similar to those of Cuvier's and Blainville's beaked whales in comparison, with a broader bandwidth, their sweep at higher frequencies, higher peak and center frequencies, distinctly longer durations and much shorter inter-pulse intervals (Table 1.2).

It is very likely that the recorded sounds on the long-term dataset were produced by the unknown mesoplodont whale regularly encountered at Palmyra Atoll, presumably *Mesoplodon hotaula*. It has been the only confirmed species of beaked whale observed around the atoll. And on the long-term recording only two incidences with other swept signals with differing signal properties have been found throughout the entire year of observation. These two sequences had signal properties that were most similar spectrally and temporally to those described for *M. densirostris*.

Table 1.2: Comparison of FM pulse parameters of beaked whales. Time bandwidth product was calculated with -10 dB bandwidth and duration.

	lower -10 dB frequency [kHz]	-10 dB bandwidth [kHz]	center frequency [kHz]	duration [µs]	inter-pulse interval [ms]	time bandwidth product
Blainville's beaked whale[1]	26	25	38	270	370	0.68
Cuvier's beaked whale[2]	31	23	42	200	380	0.46
"Cross Seamount" beaked whale[3]	~50	>50	>70	987	110	4.94
"Palmyra" beaked whale (*M. hotaula*?)	34	31	46	430	225	1.33

On-axis echolocation signals

Beaked whale echolocation signals are very directional. Zimmer et al. (2005) reported for Cuvier's beaked whales a directivity index of 30 dB and head scan rates of 25 degrees per second. With these beam characteristics only a few seconds of a continuous signal sequence with mostly on axis pulses would be detectable on a stationary recorder. Looking at the relationship of the spectral properties of FM pulse echolocation signals and received levels

[1] Johnson et al., 2006

[2] Zimmer et al., 2005

[3] McDonald et al., 2009, personal communication

described within this paper, one can see that starting at around 135 dB re 1 µPa at 1 m (pp) received level and higher (Fig. 1.4A) only near on-axis signals were recorded. The lower -3 dB frequency was almost unaffected and altered only between 41 and 43 kHz in that amplitude range while the upper -3 dB frequency changed within 51 to 59 kHz. This frequency shift was most likely due to different distances of the vocalizing animal to the recorder, which attenuated higher frequencies more. A similar trend can be seen in the relationship of duration and received level (Fig. 1.4B). With a received level above 135 dB re 1 µPa at 1 m (pp) the duration was getting longer due to a better signal-to-noise ratio. At received levels of above 161 dB re 1 µPa at 1 m (pp) standard deviations of frequencies and duration grew quickly which was an artifact of the limitation of the recording system since probably not all clipped clicks were eliminated through the automated process. About 78% of all recorded pulses were therefore likely near on-axis FM-pulses. Frequencies were higher and durations became slightly longer below 135 dB re 1 µPa at 1 m (pp) received levels, indicating a distortion of the signal and the start of off-axis signals.

Inter-pulse interval

Mesoplodon hotaula had single inter-pulse intervals around a median of 225 ms, with quartiles of 190 to 250 ms (Fig. 1.4C). Despite the automatic detection that also counted sequences with several animals vocalizing, which would result in shorter inter-pulse intervals, or dropped occasional low amplitude signals within a sequence, favoring longer intervals, the majority (74%) of inter-pulse intervals were within the distribution peak of the single inter-pulse interval. The inter-pulse interval should approximately reflect the two-way transit time to the target that the whale is detecting, or the maximum detection range for searching (Au, 1993).

The maximum detection range for 225 ms inter-pulse intervals would be 170 m (c_{water} = 1500 m/s), possible lag time not taken into account. This inter-pulse interval has a distinctly shorter range than what is known for Blainville's and Cuvier's beaked whales (Table 1.2) as well as northern bottlenose whales (Hooker, 1999) which all have an inter-pulse interval of about 400 ms and a range of about 300 m.

There was a second peak in the distribution of inter-pulse intervals produced by *M. hotaula* (Fig. 1.4D) at 450 ms, which was exactly double the value of the first and dominant peak. A methodological error due to dropped signals in the detection algorithm can be ruled out as the example echolocation sequence in Fig. 1.5B illustrates. Inter-pulse intervals, signals and breathing are coupled with wing beats in bats (e.g. Schnitzler, 1971, Suthers et al., 1972). In search flight usually one pulse is emitted per wing beat and breath (e.g. Schnitzler et al., 1987, Britton et al., 1997, Wong and Waters, 2001). Kalko (1994) showed in the field that the common pippistrelle bat occasionally has wing beats without sound emission and therefore inter-pulse intervals that are longer. This leads to a multimodal distribution of shorter and longer inter-pulse intervals. (e.g. Ahlén, 1981, Schnitzler et al., 1987, Zingg, 1988, 1990, Holderied, 2001). For beaked whales there does not seem to be a connection between the locomotor system and sound emission as fluke rates during swimming are lower. We do not have a hypothesis for the use of a certain single or double inter-pulse interval. Yet the preference for a species-specific single and double inter-pulse interval indicates a specialized way of interpreting the auditory scene.

Several species of beaked whales seem to have a species-specific inter-pulse interval (Zimmer et al., 2005, Johnson et al., 2006, McDonald et al., 2009) while other delphinids do not show a species-specific inter-click interval but adapt it to their echolocation task (e.g. Verfuß et al.,

2005, Verfuß et al., 2009). Generally, all echolocating odontocetes probably adjust their vocal behavior to environmental conditions and optimize their echolocation temporally to a certain habitat and prey, similar to what is known for insectivorous bats. Bats hunting in open space, away from vegetation and ground, use long echolocation signals with long inter-pulse intervals during search phase. This allows for long distance detection of prey or background structures. When bats hunt in more narrow and cluttered environment near vegetation or over the ground they use shorter signals and shorter inter-pulse intervals during search phase (Neuweiler, 1983, Kalko and Schnitzler, 1993, Jensen and Miller, 1999, Schnitzler et al., 2003, Schaub and Schnitzler, 2007). According to this knowledge we propose that the double inter-pulse interval of *M. hotaula* is probably used in larger distances to the background when a broader view is of interest. Since our recorder is stationary at the seafloor, most likely the largest part of a dive when vocalizing is spent at depth while hunting (e.g. Johnson et al., 2006, Tyack et al., 2006), double inter-pulse intervals are being emitted when swimming higher in the water column, and the sound beam being very directional, chances are low for recording this kind of vocal behavior very often.

Prey capture

There have been two sequences in the yearlong acoustic data recorded by the bottom-moored recorder that had a terminal buzz after a series of regularly spaced FM pulses which originated undoubtedly from this species of beaked whale. The low number could be either due to the strong directionality of the click with sound pressure levels 20 dB lower than FM pulses, or because the main foraging depth of the whales were at a different depth than the stationary recorder.

Clicks with short inter-click intervals are either terminal buzzes during prey capture (e.g. Madsen et al., 2005, Verfuß et al., 2009) or burst pulses used in a social context (e.g. Lammers et al., 2006). Burst pulses tend to be singular events independent of other echolocation signals. The sequences with short inter-click intervals described had a structure as expected for foraging namely with search and approach phase and therefore prey capture attempts are more likely than social calls. The echolocation behavior of foraging odontocetes is similar to those of bats although these two animal groups use different echolocation signal structures. Regardless of the different types of echolocation pulses in bats, prey capture sequences can be divided into a search phase and an approach phase (Griffin et al., 1960). During the search phase the animals emit signals with long pulse durations and intervals which both decrease during the approach phase. An initial and a terminal part can be distinguished during the approach phase (Melcon et al., 2007). The terminal part of a prey capture sequence, often called a buzz, consists of the last group of signals which is emitted before the contact with the prey.

In several studies with beaked whales the emitted pulse and the returning echo during search and approach phase were described through recordings obtained with a system attached to a diving and vocalizing animal. The inter-pulse intervals during search and approach phase were much longer than the two-way travel time to the apparent target and inter-pulse intervals were in most cases not reduced when the animals started to approach the prey after detection (Madsen et al., 2005, Johnson et al., 2008). There were no obvious differences in inter-pulse intervals of search and initial approach phase. Only at the terminal part of the approach the animals emitted a buzz which was characterized by inter-click intervals around 10 ms. The use of stable inter-pulse intervals in beaked whales during search and the initial approach was interpreted to be used for maintaining a broad view in a multi-target environment and low click

rates would be beneficial for strong signals (Madsen et al., 2005). The strong preference of *M. hotaula* for a certain inter-pulse interval supports this theory for another beaked whale species. Verfuß et al. (2009) show for harbor porpoise that the approach phase can be divided into two parts. The first part is an initial part with more or less constant click intervals and the second part is a terminal part or buzz which starts out with a sharp reduction in inter-click interval and ends with the shortest inter-click intervals. The two approach sequences presented in this paper suggest a different behavior for *M. hotaula*, which switches from a search and initial approach phase with long inter-pulse intervals directly with only one transition pulse to a terminal part with very short inter-click intervals (4-10 ms), the buzz. The signal parameters changed from a longer duration FM pulse during search and initial approach phase to broadband, short duration clicks during the buzz. Distinct click types for the different phases of prey capture have previously been described similarly for Blainville's beaked whales (Johnson et al., 2006).

The two buzz sequences illustrated within this paper (Fig. 1.7) were probably one successful prey catch and one unsuccessful attempt. One sequence had continuously shorter inter-click intervals starting at around 9 ms and reducing it to 3.5 ms towards the end of the buzz. This seems very similar to buzz sequences shown for Blainville's beaked whales (Johnson et al., 2006). The second sequence started out with very short inter-click intervals around 4-5 ms and then varied between 7 and 10 ms. The buzz was also shorter in overall duration. This could indicate a prey target that was lost in the pursuit of capture or identification of the potential prey as an undesirable species or size.

Beaked whales are known to hunt for squid and fish in deep waters. MacLeod et al. (2003) review that *Mesoplodon* species seem to prefer fish while the genera *Ziphius* and *Hyperoodon* favor squid. The stomach contents of all genera contained a wide variety of cephalopod species and families with no clear preference for bioluminescent prey species, vertical migrating prey

species or prey species with specific body compositions. Mesoplodont whales had a preference for smaller prey items under 500 g while *Hyperoodon* and *Ziphius* would hunt for larger cephalopods of over 1000 g. The authors concluded that *Mesoplodon* occupies a different dietary niche than *Hyperoodon* and *Ziphius*, yet the latter two are geographically separated. The structure of the echolocation sequences emitted by a foraging beaked whale determines the detection range and therefore the kind of prey it is best suited to capture. The detection range of *M. hotaula* is shorter due to shorter inter-pulse intervals than the range of Blainville's and Cuvier's beaked whales. This could indicate that this species forages closer to the seafloor.

CONCLUSION

The echolocation signals of the unknown beaked whale at Palmyra Atoll were spectrally and temporally different to previously published FM pulse beaked whale signals. The use of FM pulses during the search and initial approach phase and the switch to broadband clicks for the buzz, and with it probably prey capture, is a signal structural strategy already known for another beaked whale, *Mesoplodon densirostris*. The "Palmyra Atoll" beaked whale most likely also belongs to the genus *Mesoplodon* and might be *M. hotaula*. Further investigations should include acoustic recordings of the animals with visual confirmation, photographs of adult males and biopsy samples to be certain about the species producing these signals. The signal description of this chapter is the basis for an analysis of diel and seasonal patterns of this species. It will give us insight into the natural behavior of a beaked whale species in a pristine coral reef environment with very little human impact.

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Chapter 2

Classification of Echolocation Signals of Melon-headed Whales (*Peponocephala electra*), Bottlenose Dolphins (*Tursiops truncatus*), and Gray's Spinner Dolphins (*Stenella longirostris longirostris*) at Palmyra Atoll

ABSTRACT

Classification of three dolphin species through spectral parameters of their signals is presented. Melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*) and Gray's spinner dolphins (*Stenella longirostris longirostris*) have been visually observed and acoustically monitored at Palmyra Atoll. We recorded their acoustic behavior during daytime observations with a towed hydrophone array sampling at rates of 192 and 480 kHz. Additionally, from October 2006 to September 2007, an autonomous High-frequency Acoustic Recording Package (HARP) was mounted on the seafloor in water of about 600 m depth and was programmed to sample with 200 kHz for 5 minutes every 20 minutes. Melon-headed whales had the lowest peak and center frequencies, spinner dolphins had the highest frequencies and bottlenose dolphins were nested in between these two species. -3 and -10 dB bandwidths were similar for all species. Temporal parameters were not suited for classification. Frequency differences were significant within but not across recording systems. Classification results were optimized by reducing variability within a set of single clicks by calculating mean spectra for groups of clicks. Peak frequency was the strongest classification parameter. Median peak frequencies of grouped clicks (group size 50) of melon-headed whales ranged between 24.9 and 28.0 kHz, of bottlenose dolphins between 26.3 and 34.8 kHz and of spinner dolphins between 35.0 and 37.0 kHz. The species-specific frequencies might be due to morphological structures within the head of the different species.

INTRODUCTION

Passive acoustic monitoring has become a powerful tool for the study of cetacean abundance and behavior during towed hydrophone surveys (e.g. Barlow and Taylor, 2005) and remote, long-term monitoring with autonomous systems (e.g. Mellinger et al., 2004, Sirovic et al., 2004, Oleson et al., 2007, Verfuß et al., 2007, Lammers et al., 2008, Munger et al., 2008). To analyze the recorded cetacean sounds to the species level, discrimination and classification of the signals is necessary. Identification of many mysticete calls has been successful and their signals were automatically detected on long-term data (e.g. Sirovic et al., 2004, Oleson et al., 2007, Munger et al., 2008, Sirovic et al., 2009) but the discrimination of most odontocete calls remains difficult. Signals 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 about 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. 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 0.05 and 3.2 s (Wang et al., 1995, Bazúa-Durán and Au, 2002). They are thought to be used primarily in a social context, used 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 have a function in echolocation to detect, characterize and

localize a target object, being prey, predator or environment (Au, 1993). These clicks have a frequency range mostly between 10 and 150 kHz and are temporally spaced to allow the two-way travel time from the sound source to the object, back to the receiver and be processed (Au, 1993). Broadband clicks can be further distinguished by their temporal pattern. Clicks may appear in rapid trains during echolocation, in the terminal buzz, when the animal is approaching a target during prey capture to give continuous prompt updates on the target location (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., 1998, Rossing, 2007). 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, 2006) 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). The discrimination of dolphin species by their echolocation signals becomes relevant 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) and others may not use whistles under certain behavioural 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 very few studies analyzed species-specific aspects of clicks. The click properties duration and peak frequency were discriminating factors in the studies of Kamminga et al. (1996), Akamatsu et al. (1998), and Nakamura and Akamatsu (2003). Clicks of different porpoise species were separated

from each other and from delphinids. False killer whale clicks (*Pseudorca crassidens*) were distinguishable from dolphin clicks by these parameters. Akamatsu et al. (1998) showed that baiji (*Lipotes vexillifer*), and bottlenose dolphins (*Tursiops truncatus*) did not separate entirely but clicks from baiji had a tendency toward lower frequencies than those of bottlenose dolphins. Most research has been conducted analyzing only clicks that are on-axis of the sonar beam since 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 effects. 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 together and taken into account for species identification. Also on-axis clicks alone may not represent the full spectrum of clicks and internal reflections of pulses may reveal the anatomy of the vocalizing animal and therefore carry a species-specific aspect. They were able to identify several species-specific peaks in the spectra of Risso's and Pacific white-sided dolphins, especially in the long duration clicks with reverberations, but not in bottlenose, long-beaked common and short-beaked common dolphin clicks. They hypothesize that this was due to more symmetric versus asymmetric 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 (*Tursiops truncatus*) 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 20-40 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 reach up to 2.78 m 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). Captive bottlenose dolphins show peak frequencies between 110-130 kHz and 50-80 µs duration in their on-axis clicks (Au, 1993). Their pods rarely exceed 20 animals but, especially in offshore waters, group sizes can be up to several hundreds. 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). 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; 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).

This chapter 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 discrimination can be improved by pooling groups of clicks to reduce variability. We discuss these results in relation to prior click descriptions and discrimination studies, as well as the recording instrumentation and the animals' morphological features.

MATERIALS AND METHODS

Data collection

Our study area consisted of the off-reef of Palmyra Atoll, extending in longitude west to east from 162° 15' W to 161° 57' W and in latitude north to south from 5°57.6' N to 5°49.2' N (Fig. 1.2). Recordings were obtained using a towed hydrophone array 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.

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 at a water depth of 10-15 m or deployed as a stationary array with a maximum depth of 80m. The array was equipped with HS150 hydrophones (Sonar Research & Development Ltd., Beverley, UK). These hydrophones exhibited a flat frequency response (±3 dB) from 1 to 150 kHz. The hydrophones were connected to custom-built preamplifiers and bandpass filter electronic circuit boards: R100 in

2006 and R400 in 2007 (custom design, Scripps Institution of Oceanography, Appendix II). The circuit boards were designed to flatten the ambient ocean noise, 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. Two different analog-to-digital conversion systems were used in 2006 and 2007 to convert and record the acoustic signals. 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 hard- and software, Department of Animal Physiology, University of Tübingen and Menne BioMed). The sampling frequency was set to 480 kHz and audio data was also directly recorded to a hard-disk drive.

Parallel to this effort an autonomous High-frequency Acoustic Recording Package (HARP) was placed on a steep slope off Palmyra Atoll's western terrace. 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 (Appendix I). It recorded from October 19, 2006 until March 23, 2007 and from April 9, 2007 until September 18, 2007. The recording gap of 16 days between the two deployments corresponded to servicing of batteries and hard drives. During the first deployment the HARP was located at 05° 51.85' N 162° 09.91' W in 650 m water depth. It was then deployed about 1 km east of the initial location at 05° 51.88' N 162° 09.36' W in 550 m depth. The recorder was set to a sampling frequency of 200 kHz and duty cycled with an on duration of 5 minutes every 20 minutes. On the HARP we used an omni-directional transducer (ITC-1042, www.itc-transducers.com) which has an approximately flat (±2 dB) frequency response. It was, as in the arrays, connected to a custom-built preamplifier

board with bandpass filter (series R300, Appendix II) and also was designed to follow the reciprocal of ocean ambient noise in order to maximize the dynamic range of the recorder. The HARPs were calibrated with a reference hydrophone and projector at the U.S. Navy's TRANSDEC facility in San Diego. The differing frequency responses of the various systems were compensated for during analysis.

During these two field seasons a total of 32 encounters with melon-headed whales (*Peponocephala electra*), 100 encounters with bottlenose dolphins (*Tursiops truncatus*), and 15 encounters with Gray's spinner dolphins (*Stenella longirostris longirostris*) took place in the waters surrounding Palmyra Atoll. During several encounters both melon-headed whales and bottlenose dolphins were observed swimming and vocalizing very close to the HARP location while the HARP was recording.

Signal processing

Signal processing was performed using custom routines in MATLAB (Mathworks, Natick, MA). Good quality recordings were selected out of the array recordings of 2006. The selected sequences 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 data collected during the encounters above the HARP were used. The array recordings in 2007 were not so restricted to high quality to better judge the overall usability of the passive monitoring methods.

Clicks were automatically located within the sequences using a two-step approach as described in Soldevilla et al. (2008). During the first step clicks were detected automatically in the spectral domain within a rough start and end point defined by when 12.5% of the frequency bins were larger than a 10 dB threshold within a defined click bandwidth of 15–85 kHz. These

automatically selected clicks in the array and HARP data of 2006 were then verified manually and false detections were removed. Click detections on array recordings of 2007 had a large amount of false detections of echo sounder pings of the research vessel. The data for spinner dolphins was 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. 90% of detections with peaks in the main frequency and sideband frequencies of the echo sounder were removed from the analysis. The second automatic selection step determined the exact start and end point of the roughly defined clicks. The finer resolution click detection algorithm (Soldevilla et al., 2008) using a Teager energy operator (Kaiser, 1990, Kandia and Stylaniou, 2006) was applied.

The 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 at 85 kHz for data sampled with 192 or 200 kHz and at 200 kHz for data collected with 480 kHz sampling rate to prevent analysis of possibly aliased parts of the recorded signal. To calculate signal-to-noise ratios, a 5 ms time series 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-point and resulting 2.13 ms of click and noise data were used for signals sampled at 480 kHz. For the calculation of received levels the spectra were corrected for 1 Hz bins and the system transfer function was added (Appendix II). This resulted in an overall system response flat to within ±2 dB from 8 to 85 kHz or 200 kHz for clicks of sampling rates 192 and 200 kHz or 480 kHz, respectively. Click received levels are given over a band encompassing the click energy. The

-10 dB bandwidth of clicks of all species compared in this study has a median of about 20 kHz (Table 2.2). Therefore about 30 dB (10 log (bandwidth)) was added in order to approximately represent click sound pressure levels on a plot of ambient noise levels. 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 at peak-to-peak level of each click. 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 waves resulting in peak frequencies below 20 kHz (Appendix III). 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.

Mean spectra were calculated with normalized data. Spectra of all individual clicks were set to 0 dB at peak frequency. The corresponding noise spectra were adjusted according to the signal value. To compare mean spectra of the different species with each other the spectra were normalized to 0 dB at 8 kHz, the lower cutoff frequency of the bandpass filter. For statistical analysis the data was reduced 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. One or two clicks were randomly picked per minute of recording (Table 2.1). The reduction was also used to generate comparably sized data sets. The mean spectra of Fig. 2.1 were generated using all detected clicks before data reduction. The statistical values in Table 2.2 and Table 2.3 as well as the resulting box plot distributions in Fig. 2.1 were the outcome of the reduced data set. The program JMP (SAS Institute Inc.) was used to calculate Kruskal-Wallis one-way analysis of variance tests for species discrimination by click parameters. The results were optimized in their variability by grouping clicks of data using the entire automatically selected data set. For this procedure a certain amount of clicks were grouped consecutively within the recorded sequence. Normalized mean spectra were calculated for all groups as described above and peak and center frequencies were determined from the mean spectra.

Table 2.1: 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. A) Number of encounters, B) Recording duration [min.], C) Automatic click detections, used for mean spectra and group analysis, D) Reduced number of clicks for statistical analysis.

	Array 2006, 192 kHz				**HARP 2006, 200 kHz**				**Array 2007, 480 kHz**			
	A	B	C	D	A	B	C	D	A	B	C	D
pe	5	23	2216	230	1	15	2241	300	4	280	18,702	280
tt	5	20	2348	200	2	30	3576	300	22	180	13,542	180
sl	4	21	1557	210	-	-	-	-	3	90	1810	180

RESULTS

Echolocation click parameters

The echolocation clicks of melon-headed whales, bottlenose and Gray's spinner dolphins are similar and difficult, yet possible, to discriminate. The temporal parameters, duration and inter-click interval, tested for each recording situation (array 2006, 2007 and HARP 2006), showed significant differences between species; however, when comparing recording situations these differences were not stable (Table 2.2). For example, click durations of melon-headed whales were distinctly longer than click durations of the other two species 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 longest. Both click duration and inter-click interval were probably 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 not controlled for. Furthermore inter-click interval is changed depending on the distance of the echolocating animal to a target.

Spectral parameters of clicks, except for bandwidth, showed highly significant differences between species in all recording situations and therefore seem to be species-specific (Table 2.3, ANOVA). The -3dB and -10dB bandwidths of all species were not significantly different (Table 2.3, ANOVA). Melon-headed whales had the lowest peak and center frequencies and accordingly also 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 2.2, Fig. 2.1). Median peak frequencies of melon-headed whales ranged between 25.8 and 28.5 kHz for the three different recording systems used. Median

peak frequencies of bottlenose dolphins were in between 28.1 and 35.3 kHz. Spinner dolphins had median peak frequencies between 34.5 and 36.8 kHz. Median center frequencies were distributed similarly. Melon-headed whale center frequencies ranged from 28.1 to 32.1 kHz. Median center frequencies of bottlenose dolphins were in between 33.5 and 35.6 kHz. Spinner dolphins had median center frequencies between 37.3 and 42.2 kHz. Melon-headed whales showed a smaller variability with only 3-7 kHz quartile widths for peak frequencies and 5-11 kHz for center frequencies. Both bottlenose dolphins and spinner dolphins had much larger variability between 8-18 and 7-21 kHz for peak and center frequencies, respectively. There seemed to be a bias between recording situations, probably due to either the instrumentation or the recording environment. The variability of peak and center frequencies seemed especially low for all species in array recordings of 2006 (6-10 kHz) and particularly high for HARP recordings of bottlenose dolphins and for 2007 array recordings of spinner dolphins. The center frequency of 2007 array recordings with 480 kHz sampling rate was 6 to 12 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.

Table 2.2: 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 -10dB frequency [kHz]**	**Bandwidth -10dB [kHz]**	**Lower -3dB frequency [kHz]**	**Bandwidth -3dB [kHz]**
Melon-headed whales								
2006 array 192 kHz	26.3	30.3	0.51	112	17.3	20.6	23.3	6.0
(n=230)	[24.0 30.8]	[28.0 33.7]	[0.31 0.74]	[54 254]	[14.8 21.2]	[11.1 30.9]	[19.5 27.0]	[4.5 9.8]
2006 HARP 200 kHz	28.5	28.1	0.30	78	21.0	18.0	24.0	6.8
(n=300)	[26.3 29.3]	[26.1 30.8]	[0.24 0.40]	[36 169]	[18.9 22.5]	[12.8 24.6]	[23.3 26.3]	[4.5 8.8]
2007 array 480 kHz	25.8	32.1	0.25	83	17.6	19.5	22.5	6.1
(n=280)	[23.1 29.1]	[28.0 38.9]	[0.18 0.37]	[34 181]	[14.5 20.2]	[13.1 27.5]	[19.7 25.8]	[3.8 9.8]
Bottlenose dolphins								
2006 array 192 kHz	30.0	33.5	0.42	70	20.3	19.9	26.3	6.8
(n=200)	[26.3 34.5]	[29.3 38.1]	[0.34 0.66]	[38 110]	[17.3 24.8]	[12.0 27.0]	[22.5 30.0]	[5.3 9.0]
2006 HARP 200 kHz	35.3	35.6	0.40	81	24.0	24.0	32.3	6.0
(n=300)	[29.3 47.3]	[31.8 43.1]	[0.29 0.66]	[47 127]	[21.0 34.3]	[15.8 30.8]	[25.5 43.5]	[4.5 9.0]
2007 array 480 kHz	28.1	40.5	0.34	138	19.2	17.6	24.4	5.2
(n=180)	[24.2 32.8]	[31.0 52.3]	[0.23 0.56]	[64 282]	[16.4 26.6]	[10.9 24.4]	[21.1 30.5]	[3.8 7.9]
Spinner dolphins								
2006 array 192 kHz	36.8	37.3	0.36	136	24.8	22.5	33.8	5.3
(n=210)	[31.5 41.4]	[34.3 40.8]	[0.22 0.62]	[70 232]	[20.1 30.8]	[11.8 34.5]	[28.5 37.5]	[4.3 7.5]
2006 HARP 200 kHz	-	-	-		-	-	-	-
2007 array 480 kHz	34.5	42.2	0.22	233	22.7	22.7	30.5	5.2
(n=180)	[26.7 42.1]	[35.6 56.2]	[0.14 0.31]	[69 1135]	[18.8 30.5]	[9.8 36.6]	[23.9 38.4]	[3.3 8.9]

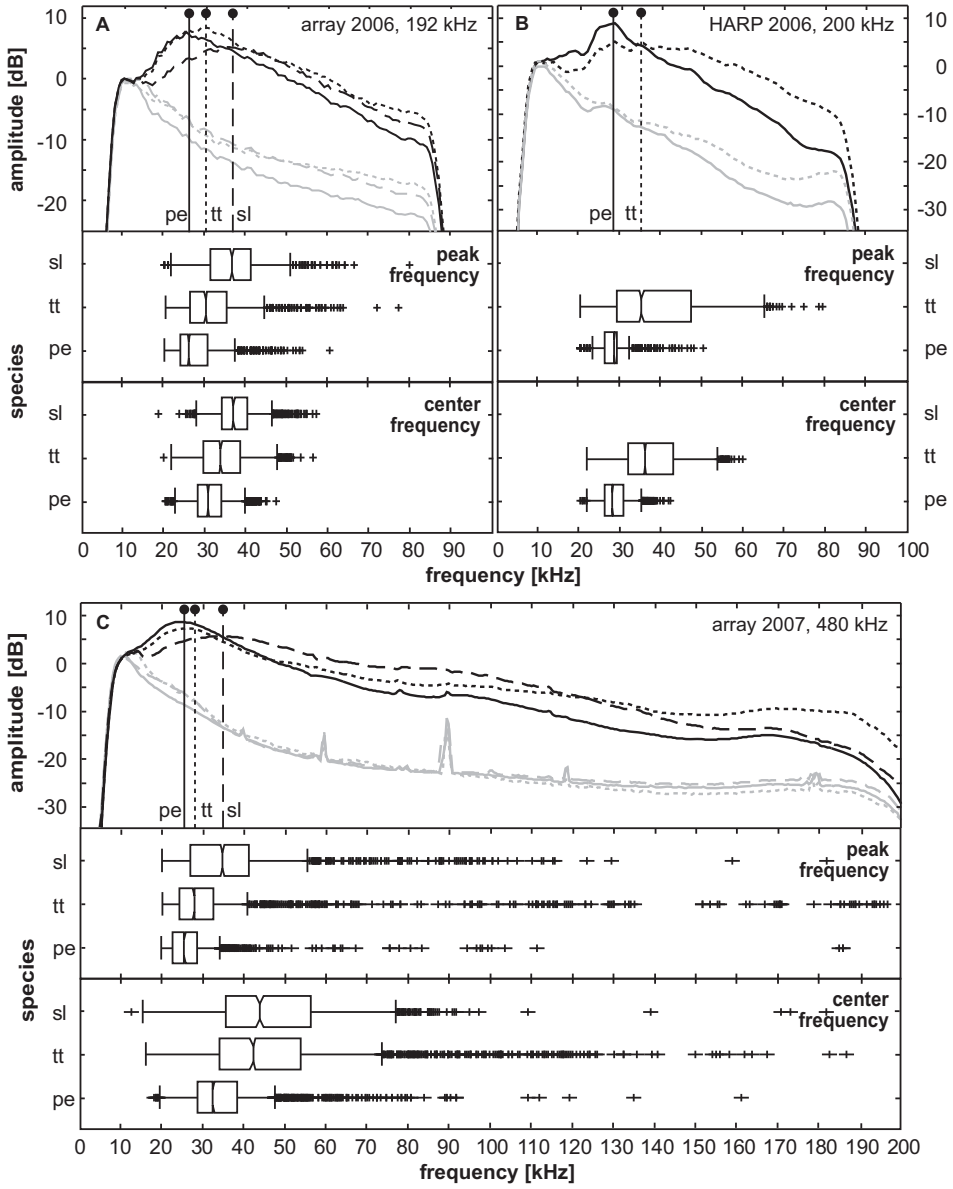

Fig. 2.1: Spectral patterns of echolocation clicks of melon-headed whales (pe – *Peponocephala electra*), bottlenose dolphins (tt – *Tursiops truncatus*) and Gray's spinner dolphins (sl – *Stenella longirostris longirostris*). Top plot of A, B and C) Mean click spectra (black lines) and mean noise spectra (grey 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.

Table 2.3: 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. ***: p<0.0001, *: p<0.05, n.s.: not significant.

	Peak frequency [kHz]	**Center frequency [kHz]**	**Lower -10dB frequency [kHz]**	**Bandwidth -10dB [kHz]**	**Lower -3dB frequency [kHz]**	**Bandwidth -3dB [kHz]**
Array 2006: p	***	***	***	n.s.	***	n.s.
Chi² (2)	160.2	153.2	93.2	3.9	177.8	13.1
HARP 2006: p	***	***	***	*	***	n.s.
Chi² (1)	173.1	254.6	101.3	28.0	150.3	0
Array 2007: p	***	***	***	n.s.	***	n.s.
Chi² (2)	80.5	84.4	79.1	7.5	102.1	5.0

Effects on frequencies by grouping of consecutive clicks

To optimize species discrimination through their spectral click values the variability was reduced by calculating a mean click out of several single clicks. Therefore consecutive clicks of a sequence were grouped together with a given group size, mean spectra were calculated and the resulting peak and center frequencies were extracted. Fig. 2.2A shows as an example, melon-headed whale clicks from array recordings of 2006 with click groups of sizes 2 to 200 clicks. The resulting quartiles of grouped clicks were progressively smaller the larger the group size. The quartiles with group sizes larger than 50 clicks varied only minimally. This trend was noticeable for all species and all recording situations.

Median peak frequencies of grouped clicks, which in the following refers to group size 50, summarized in Table 2.4, was between 0.5 and 2 kHz lower than those of single clicks for melon-headed whales and bottlenose dolphins. Median peak frequencies of spinner dolphin click

groups however were 0.2 and 0.5 kHz higher. All median center frequencies of grouped clicks were between 0.5 and 3 kHz higher, except the median center frequency in the case of spinner dolphin array recordings of 2007 which was 9 kHz higher. The variability, calculated in distance between first and third quartile, was reduced between 2 and 7 kHz, on average 4 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, the frequency quartiles of grouped melon-headed whale clicks were entirely separated from those of grouped spinner dolphin clicks. Peak frequency quartiles also did not overlap with those of bottlenose dolphin clicks from array and HARP recordings of 2006 but did overlap with those from array recordings of 2007. 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. 2.2B, Table 2.4).

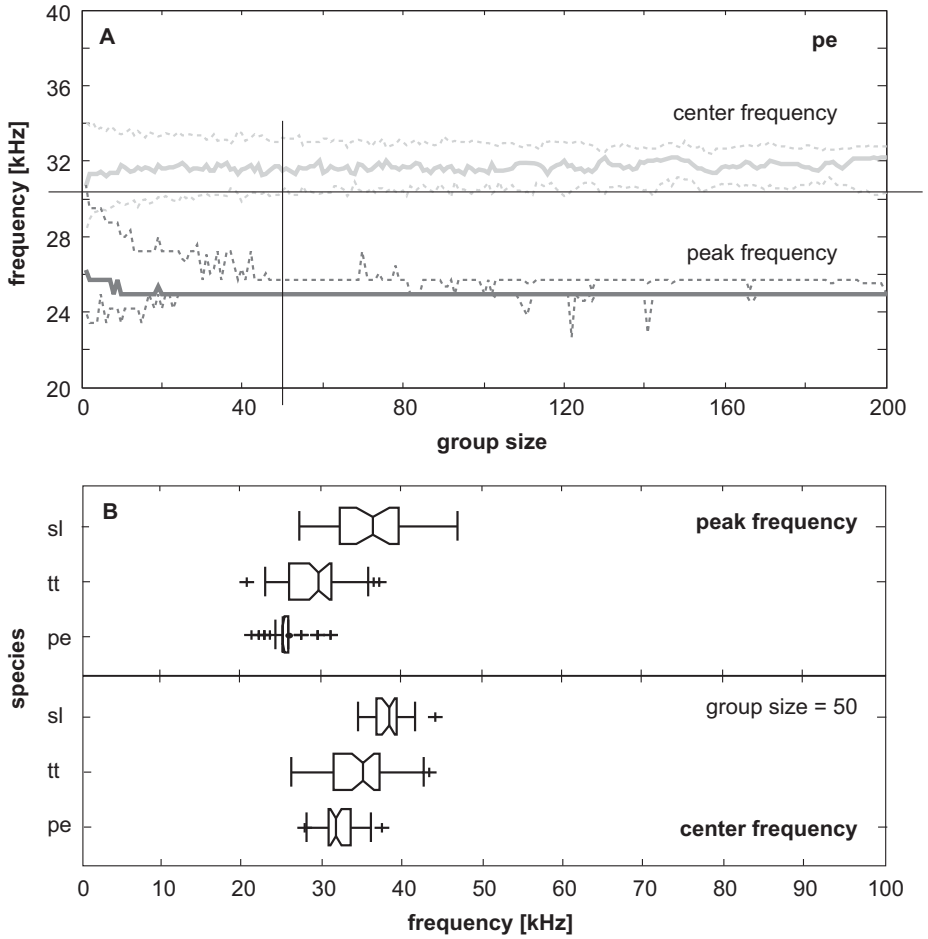

Fig. 2.2: Median peak and center frequencies of grouped echolocation clicks in array data of 2006 which had the lowest overlap in quartiles (Table 2.4). A) Center frequency (light grey) and peak frequency (dark grey) versus group size of melon-headed whale clicks (pe – *Peponocephala electra*); median frequency as solid grey lines, quartiles as dashed grey lines; black crossed lines indicate group size 50 where quartiles started to vary minimally. B) Box plot distributions of peak and center frequency of all species (pe; bottlenose dolphins, *Tursiops truncatus* – tt; Gray's spinner dolphins, *Stenella longirostris longirostris* – sl).

Table 2.4: Median peak and center frequencies of echolocation clicks with group size 50 of melon-headed whale, bottlenose 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 mean grouped clicks in analysis.

	Peak frequency [kHz]	**Center frequency [kHz]**
Melon-headed whales		
2006 array 192 kHz	24.9	31.7
(n=44)	[24.9 25.7]	[30.2 33.0]
2006 HARP 200 kHz	28.0	28.9
(n=44)	[25.5 28.7]	[27.9 30.1]
2007 array 480 kHz	24.9	34.0
(n=374)	[23.0 26.3]	[31.2 37.3]
Bottlenose dolphins		
2006 array 192 kHz	28.7	35.0
(n=46)	[25.7 31.0]	[31.5 37.5]
2006 HARP 200 kHz	34.8	37.5
(n=71)	[28.7 46.1]	[33.8 42.3]
2007 array 480 kHz	26.3	43.6
(n=204)	[23.8 28.2]	[36.4 51.1]
Gray's spinner dolphins		
2006 array 192 kHz	37.0	37.8
(n=31)	[32.3 39.9]	[36.2 39.1]
2006 HARP 200 kHz	-	-
2007 array 480 kHz	35.0	51.2
(n=36)	[28.9 39.2]	[39.6 54.7]

DISCUSSION

The mean spectra of melon-headed whales, bottlenose and spinner dolphins showed species-specific frequencies. Resulting median 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). Our dataset comprised not only on-axis but all clicks independent of the animals' angle to the recording instrument. The further 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). A recording of dolphins in the field 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. 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. The higher sampling rate did not reveal significant peaks in higher frequencies which could have shifted median peak frequencies upwards. It did cause a shift to 6-12 kHz higher center frequencies though which can be explained by the integration of energy over a larger frequency bandwidth for data sampled with the 480 kHz which did not have its peak but did have considerable energy above 100 kHz (Fig. 2.1C).

There may be a bias due to recording instrumentation. Species could be discriminated within a set of recordings but not as clearly across different recording systems. The peak and center

frequency relationships between species showed melon-headed whales having the lowest, bottlenose dolphins the middle and spinner dolphins the highest peak and center frequencies and were stable over all recording systems. There could be a bias due to differences in sea states, locations and animal behavior, but this is considered unlikely. Several encounters on different days at different locations, with different behaviors were randomly included in each data set for each recording instrument. More likely is an effect from the recording instrumentation itself. We may not have applied perfect transfer functions which could shift the peaks slightly to lower or higher frequencies with a few dB offset. Furthermore, PC Tape 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 spectra after fast Fourier transformation. 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 loose 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 characters were detected for the different recording instrumentations, these characters are very slight and 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 reflections within the head of the vocalizing animal, grouping clicks and calculating their mean should enhance these species-specific qualities. Automated classification techniques like Gaussian mixture models or support vector machines applied on all recorded clicks and including data from all recording instrumentations with the method developed by Roch et al. (2007, 2008) did not show convincing results (authors unpublished data). 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 automated classification techniques and may show interesting results.

Morphology and particularly morphology of the sound producing organs may be a relevant factor for acoustic species discrimination. Overall body size does not correlate with 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, one animal reached 2.78 m in length (Perryman, 2009). Yet bottlenose dolphins can grow up to 3.8 m (Jefferson et al., 2008) and those observed at Palmyra were large animals. Two 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 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 click (Cranford et al., 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 off-axis due to runtime differences which then 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-pulse click off-axis with the species-specific spectral properties (Soldevilla et al., 2008). Either one of these cases or both combined could be the reason for species-specific clicks. Anatomical head structures are a key factor in both cases. Species with near symmetrical head morphology show several very distinct species-specific peaks in their click spectra while species with asymmetrical head anatomy do not have clear peaks (Soldevilla et al., 2008). Melon-headed whales, bottlenose and spinner dolphins are all species with asymmetrical skulls (Fig. 2.3). 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 distinct 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 solve this question.

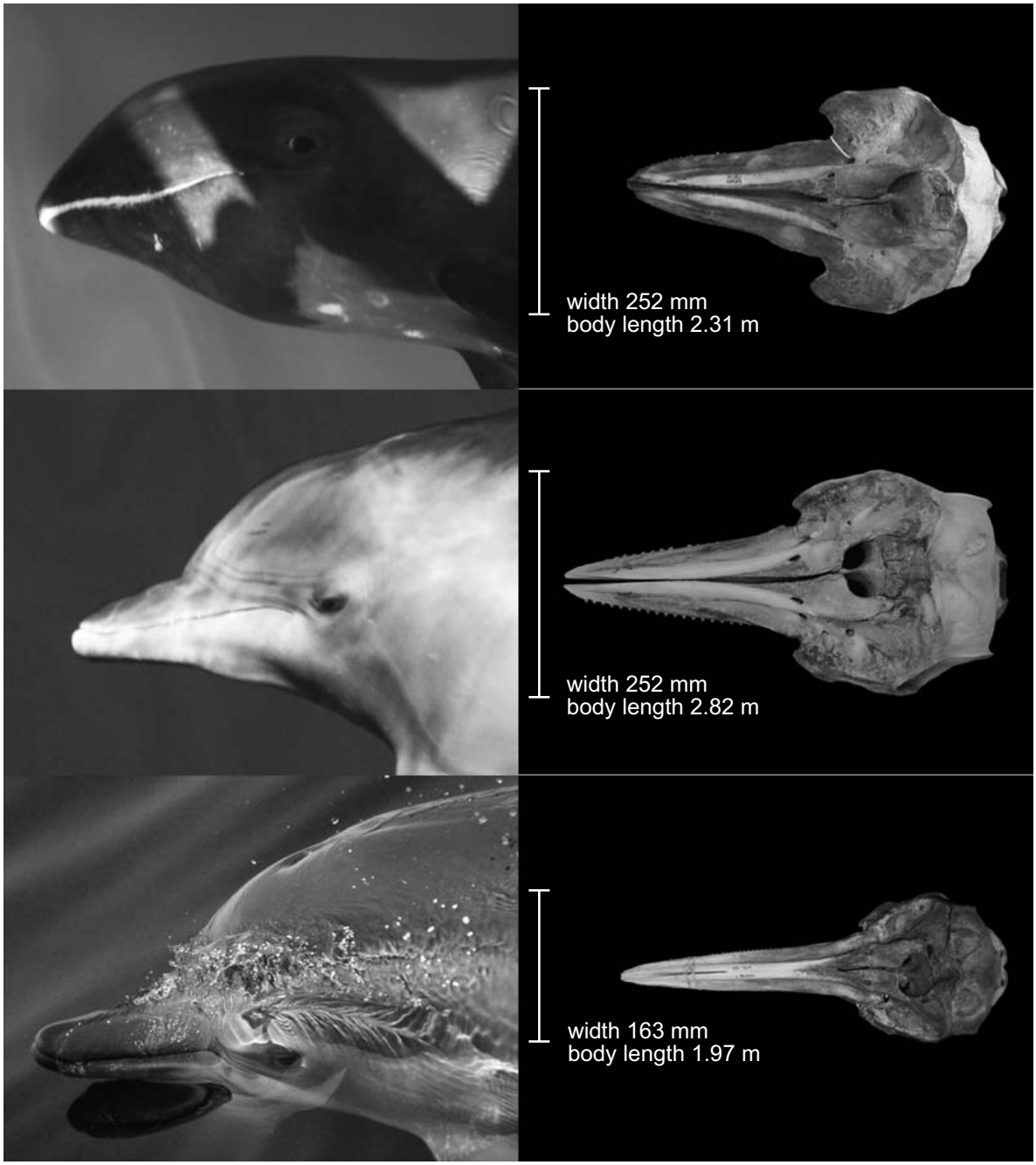

Fig. 2.3: Skull comparisons. Underwater picture at Palmyra Atoll (left) and example skull dorsal view (right) of melon-headed whale (top), bottlenose dolphin (middle) and spinner dolphin (bottom).

CONCLUSION

Melon-headed whales, bottlenose dolphins and spinner dolphins recorded during daytime at Palmyra Atoll showed species-specific spectral properties of their echolocation clicks. The differences were only slight so that different recording systems had an impact on classification results. In a further step it should be investigated if the described results also hold up in automatic classification techniques such as support vector machines or Gaussian mixture models. Furthermore, precise knowledge of the sound pathways 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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Chapter 3

Melon-headed Whale (*Peponocephala electra*)

Diel Acoustic Behavior near Palmyra Atoll

ABSTRACT

Little is known about the behavior of wild melon-headed whales, which occur in tropical offshore waters at relatively low densities. We visually observed and acoustically monitored this species during several field seasons at Palmyra Atoll (Chapter 2). From October 2006 to September 2007 an autonomous High-frequency Acoustic Recording Package (HARP), was mounted on the seafloor in water of about 600 m depth, southwest of the atoll, and was programmed to record with 100 kHz bandwidth for 5 minutes every 20 minutes. We observed the animals resting close to the atoll during the day and moving towards the HARP location in the late afternoon hours, presumably to feed during the night (Brownell et al., 2009). The melon-headed whales' whistles recorded on the HARP were distinctly different from whistles of other delphinid species regularly observed at the atoll. Whistles were used as a discrimination parameter for the long-term data analysis. Melon-headed whales whistled most frequently in the afternoon with a peak before sunset. The peak melon headed whale echolocation period occurred during the night, probably when hunting. Spectral features of echolocation clicks of melon-headed whales at Palmyra Atoll changed from day to night. The median peak frequency of the clicks during the day was at 29.7 kHz (quartiles of 27.3 & 33.9 kHz). At night the median peak frequency shifted upwards to 36.0 kHz (quartiles of 33.6 & 38.3 kHz). This frequency shift might be to avoid acoustic masking due to increased background noise over a wide frequency band from unknown acoustic sources during the night, or it could indicate deliberate change of echolocation beamwidth and therefore frequency during two different behavioral stages. Daytime resting, slow traveling and socializing might require a wider beam than nighttime feeding when the whales are likely focusing on small prey targets.

INTRODUCTION

Remote and autonomous long-term acoustic monitoring provides the possibility to study dolphin behaviors such as movement patterns, foraging or mating (e.g. Mellinger et al., 2004, Sirovic et al., 2004, Oleson et al., 2007, Verfuß et al., 2007, Lammers et al., 2008, Munger et al., 2008, Sirovic et al., 2009). These behaviors are otherwise difficult to investigate with more traditional methods such as visual line-transect studies, especially over long periods of time, because of restraints due to costs, weather conditions, remoteness of a location and the invisible behavior of the animals when submerged or at night. Descriptions of diel behavior were until recently restricted to daylight observations and nighttime foraging of many dolphin species was inferred from evening foraging activity or stomach content analysis during different times of the day (e.g. Würsig and Würsig, 1979; Norris and Dohl, 1980; Amano et al., 1998). Dolphin foraging behavior in relation to diel vertical and horizontal movements of the Deep-Scattering Layer (DSL) was lately successfully studied using active acoustics (Benoit-Bird and Au, 2003, 2009a, 2009b, Benoit-Bird et al., 2004). Spinner dolphins (*Stenella longirostris*) and dusky dolphins (*Lagenorhynchus obscurus*) followed the DSL horizontally for foraging while its prey came into more shallow water depths during the course of the night. Spinner dolphins in Hawaii also tracked prey abundance in the mesopelagic boundary community vertically, following their prey migration towards the shore instead of feeding exclusively offshore the entire night. Active acoustic techniques were capable of revealing complex cooperative foraging strategies in spinner dolphins. Boat based studies using active acoustics cannot provide long-term information to assess changes over time however, and the acoustic signal transmitted may influence the animals' behavior.

Many vocal animals, both terrestrial and marine, are known to undergo diel cycles in their vocal activity. Diel calling patterns have been reported for several baleen whale species (Au et al., 2000, Stafford et al., 2005, Wiggins et al., 2005, Munger et al., 2008). Common dolphins (*Delphinus delphis*) have been shown to whistle more often at night although the study's recording bandwidth was not great enough to comparatively describe echolocation activity (Goold, 2000). Striped dolphins (*Stenella coeruleoalba*), harbor porpoises (*Phocoena phocoena*) and an unknown species of beaked whales produce more echolocation clicks at night which may indicate an increase in feeding activity (Notarbartolo di Sciara and Gordon, 1997, Carlström, 2005, Johnston et al., 2008, Todd et al., 2009). Dolphin signals were detected on autonomous long-term recordings at Makua Beach, Hawaii, where spinner dolphins are known to rest during the day, with their highest acoustic activity in the morning and mid afternoon (Lammers et al., 2008).

Melon-headed whales (*Peponocephala electra*), bottlenose (*Tursiops truncatus*) and Gray's spinner dolphins (*Stenella longirostris longirostris)* are regularly observed around Palmyra Atoll. 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). 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 reach up to 2.78 m 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 further polewards. Their pods rarely exceed 20 animals but especially in offshore waters, group sizes can be up to

several hundreds. 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). Spinner dolphin group sizes range from less than 50 up to several thousands. Adult females reach 1.4-2.0 m; 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).

All three species use whistles and clicks as acoustic signals. Whistles are tonal frequency-modulated sounds while clicks are broadband pulsed signals (Herman and Tavolga, 1980). They also make intermediate sounds where click sequences grade into whistles and vice versa. Whistles probably serve a communicative purpose in a social context and might be used to regulate group organization and function (Herman and Tavolga, 1980, Norris et al., 1994, Janik and Slater, 1998, Janik, 2000; Lammers et al., 2006b). Clicks generally have their purpose in echolocation to detect, characterize and localize a target for spatial orientation or feeding (Au, 1993). They are thought to also have an important communicative role within a group (Lammers et al., 2003, Götz et al., 2006, Benoit-Bird and Au, 2009b). Several studies have analyzed and compared the whistle structure of bottlenose dolphins and spinner dolphins. Species-specific whistle characteristics have been found for these and other species (Steiner, 1981, Wang et al., 1995, Oswald et al., 2003, 2007). Bottlenose dolphin whistles have stereotyped loop structures with great frequency modulation while spinner dolphins in comparison have fewer loops (Steiner, 1981, Wang et al., 1995). The frequency range of bottlenose dolphins is lower than the

range of spinner dolphins (Wang et al., 1995). Body length correlates with mean maximum frequency of whistles with larger species having lower frequencies (Wang et al., 1995). Hawaiian spinner dolphins emit whistles with frequencies between 2 and 22 kHz (94%) and an average maximum frequency of 15.9 kHz which is consistent with Wang et al.'s (1995) body size theorem. Whistles are most often upsweeps (47%) (Bazua-Duran and Au, 2002). Oswald et al. (2007) show a higher mean number of inflection points (2.9 vs. 1.9), longer duration whistles (1.1 s vs. 0.6 s), and a larger number of steps (2.2 vs. 0.8) for bottlenose dolphins than spinner dolphins. The mean maximum frequency for spinner dolphins is 15.1 kHz and is therefore comparable to other literature results. Yet bottlenose dolphins in that study have a mean maximum frequency of 17.1 kHz and are very much higher in frequency than Wang et al.'s (1995) 11.3 kHz. Spinner dolphins have higher frequencies than bottlenose dolphins in all other frequency measures (Oswald et al. 2007). Melon-headed whale whistles have not previously been compared with other species and literature values are overall rare. The whistle frequency ranges from 1 to 24 kHz (Frankel and Yin, 2007, Watkins et al., 1997) with dominant frequencies at 8 to 12 kHz (Watkins et al., 1997) and durations of less than 0.1 s to 2.3 s (Frankel and Yin, 2007). They are described to be relatively simple up and down sweeps, as well as sinusoidal signals (Frankel and Yin, 2007). Janik and Curran (2007) showed chorusing in whistling melon-headed whales where 82% of whistles overlapped and 11% of these were of the same type.

Echolocation click structures are species-specific when comparing these three dolphin species (Chapter 2). The most distinct parameter is the median peak frequency. Melon-headed whales recorded during daytime hours have median peak frequencies below 29 kHz (upper quartile

value for grouped clicks of melon-headed whales, Table 2.4) while the other two species have higher values (lower quartile value for grouped clicks of bottlenose dolphins, Table 2.4).

This study uses long-term passive acoustic monitoring to investigate diel behavior of cetaceans, particularly melon-headed whales at Palmyra Atoll on a yearlong autonomous acoustic survey. Considering the nighttime foraging activity of melon-headed whales, it is hypothesized that the greatest count of clicks with median peak frequency below 29 kHz occurs at night when this species is presumably foraging. It is shown that melon-headed whales whistle most actively during the afternoon hours and echolocate most intensively at night, shifting their echolocation peak frequency to higher values at night. The diel acoustic pattern is discussed with implications for resting, socializing and foraging.

MATERIALS AND METHODS

Data collection

An autonomous High-frequency Acoustic Recording Package (HARP) was placed on a steep slope off Palmyra Atoll's western terrace. 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 (see Appendix I). It recorded from October 19, 2006 until March 23, 2007 and from April 9, 2007 until September 18, 2007. The recording gap of 16 days between the two deployments corresponded to servicing of batteries and hard drives. During the first deployment the HARP was located at 05° 51.85' N 162° 09.91' W in 650 m water depth. . It was then deployed about 1 km east of the initial location at 05° 51.88' N 162° 09.36' W in 550 m depth. The recorder was set to a sampling frequency of 200 kHz and duty cycled with an on duration of 5 minutes every 20 minutes. From January 1 until January 11, 2007, the

instrument recorded 5 minutes approximately every 6 minutes. The HARP used an omni-directional transducer (ITC-1042, www.itc-transducers.com) which has a flat (±2 dB) frequency response. It was connected to a custom-built preamplifier board and bandpass filter (series R300, Scripps Institution of Oceanography, transfer function Appendix II B). The circuit boards were designed to flatten the ambient ocean noise, 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. The HARP's were calibrated with a reference hydrophone and projector at the U.S. Navy's TRANSDEC facility in San Diego. The system response was compensated for during analysis.

During the two field seasons a total of 32 encounters with melon-headed whales (*Peponocephala electra*), 100 encounters with bottlenose dolphins (*Tursiops truncatus*), and 15 encounters with Gray's spinner dolphins (*Stenella longirostris longirostris*) took place in the waters surrounding Palmyra Atoll. During several encounters both melon-headed whales and bottlenose dolphins were observed swimming and vocalizing very close to the HARP location while the HARP was recording.

Signal processing

Signal processing was performed using the MATLAB (Mathworks, Natick, MA) based custom program Triton and other MATLAB custom routines. Raw HARP data was converted to a wav similar format, called xwav, which had additional meta-information on recording start and stop times. The timing data was needed when analyzing the duty-cycled xwav-files, especially at times when there were gaps or irregularities in the recording schedule.

Clicks were automatically located within the sequences using a two-step approach as described in Soldevilla et al. (2008). During the first step clicks were detected automatically in the spectral domain using a 1024-point FFT with 50% overlap and a Hann window. The rough start and end point was defined by when 12.5% of the frequency bins were larger than a 10 dB threshold within a defined click bandwidth of 15–85 kHz. The second automatic selection step determined the exact start and end point of the roughly defined clicks. The finer resolution click detection algorithm (Soldevilla et al., 2008) using a Teager energy operator (Kaiser, 1990, Kandia and Stylaniou, 2006) was applied. The algorithm detected all dolphin transient signals independent of species and detections were used for temporal analysis. The sequences with detections 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 at 85 kHz to prevent analysis of possibly aliased parts of the recorded signal. To calculate signal-to-noise ratios, a 5 ms time series window was picked preceding every click. Spectra of each signal and preceding noise were calculated using 1.28 ms of data and a 256-point Hann window centered around the click and in the beginning of the noise sample. For the calculation of received levels the spectra were corrected for 1 Hz bins and the system transfer function was added. This resulted in an overall system response flat to within ±2 dB from 8 to 85 kHz. Click received levels are given over a band encompassing the click energy. The -10 dB bandwidth of clicks of all species compared in this study has a median of about 20 kHz (Table 2.2). Therefore about 30 dB (10 log (bandwidth)) was added in order to approximately represent click sound pressure levels on a plot of ambient noise levels. Peak frequency was extracted as the frequency with the highest amplitude within each spectrum. Signal-to-noise ratio was measured at peak-to-peak level of each click. To ensure quality of the clicks analyzed, 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 waves resulting in peak frequencies below 20 kHz (Appendix III). 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. The HARP data format used 75 s segments, making this a convenient analysis length. To reduce variability in click data and to find species-specific peak frequency click values (see chapter 2), the median peak frequency of all clicks of each 75 s segment was computed.

Melon-headed whale vocalizations were identified in a further step. Long-term spectral averages (LTSAs, Wiggins and Hildebrand, 2007) were calculated for easier visual access to the long-term recordings. Each spectrum was an average of 4000 spectra which were created using the Welch algorithm (Welch, 1967) with 1000-point fast Fourier transforms (FFTs), Hann windows and no overlap. The averaged spectra were then aligned over time resulting in long-term spectrograms with a resolution of 100 Hz in frequency and 5 seconds in time. The year's data was manually inspected through LTSAs. When whistles were notable in the LTSA, the sequence was inspected more closely with spectrograms of 5 s lengths, 3000-point FFTs, 80% overlap, Hann window and a frequency range of 0 to 30 kHz. Start and end times of these sequences were noted with start and end of a full segment if the whistles were classified to be of the origin of melon-headed whales. These decisions were based on literature values (Watkins et al., 1997, Frankel and Yin, 2007) and compared to recordings made with a towed hydrophone array described in chapter 2. Mixed species recordings within the picks cannot be ruled out.

Diel Analysis

Data about sunrise and sunset at Palmyra Atoll was acquired from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Sunrise occurred between 06:33 and 07:06 hours, sunset between 18:29 and 19:01 hours. There was a maximum time shift in sunset and sunrise of 33 minutes over the winter and 12 minutes over the summer. Since full hours of the day were pooled in the diel analysis these differences in sunrise and sunset were not further considered. Hours between 07:00 and 19:00 were defined as daytime. Presence and absence data were calculated for 75 s HARP recording segments. Zero or ones were assigned if clicks were absent or present, respectively, to process diel variation. Numbers of clicks per hour were counted resulting in hourly click rates. Recording time per hour was calculated from recording start times and durations. Hourly click rates were divided by recording time per hour resulting in click rates per minute to eliminate occasional scheduling errors and to account for duty-cycled data. Daily click rate per minute was subtracted from hourly click rate per minute to reduce the influence of variability between days giving an adjusted click rate per minute. To test the diel pattern of absence-presence data, the count of segments with detections per hour for day and night time was statistically compared with t-tests. Adjusted click rates per minute and median peak frequencies of each hour of detections grouped for day and night time were also statistically compared with t-tests.

RESULTS

Acoustic activity of all species

Clicks were detected in 66% of all segments over the course of monitoring. Vocalizations of odontocetes were present every day, both during day and night. There was a very distinct pattern of day and night acoustic activity originating from odontocete signals as well as from an unknown biological source (Fig. 3.1). Signals from the unknown biological source were undeterminable but there was an increase in background noise in the range of 3 to 90 kHz starting around sunset and lasting until sunrise. Additionally between about 20:00 and 22:00 hours local time there was a distinct recurring noise with a peak at around 5 kHz. During that time the maximum day-night amplitude difference was 12 dB at 5 kHz. Otherwise up to about 30 kHz there was a doubling of the background amplitude at night (Fig. 3.2) which continuously decreased at higher frequencies. Odontocete clicks were more frequently detected during the night than during the day (Fig. 3.3A, $t_{18}=9.4$, $p<0.00001$). The mean number of clicks per minute was likewise higher during the night than during the day (Fig. 3.3B, $t_{7619}=2.4$, $p<0.01$). Highest click rates were found in the beginning of the night and were continuously decreasing during the night.

Median peak frequency was used for the spectral analysis of clicks as it has proven to be a species-specific parameter during daytime observations (see Chapter 2). All peak frequencies of clicks detected within segments of 75 s recordings were pooled and the median peak frequency was calculated. Melon-headed whales recorded during the day had median peak frequencies in the HARP data below 29 kHz (upper quartile value for grouped clicks of melon-headed whales, Table 2.4, Chapter 2) while the other two delphinids regularly present at the atoll had median peak frequencies above 29 kHz (lower quartile value for grouped clicks of bottlenose dolphins,

Table 2.4, Chapter 2). When looking at the distribution of median peak frequencies of click segments below and above 29 kHz in relation to the time of the day (Fig. 3.4A), the majority of segments with median peak frequencies below 29 kHz, presumably produced by echolocating melon-headed whales, were detected during the day and especially in the afternoon hours until sunset (t_{15}=5.3, p<0.0001). Median peak frequencies of above 29 kHz made up the vast majority, 88%, of all segments calculated and seemed to dominate during the night (t_{20}=10.7, p<0.00001) with a clear increase just after sunset and a decrease within one hour after sunrise (Fig. 3.4B).

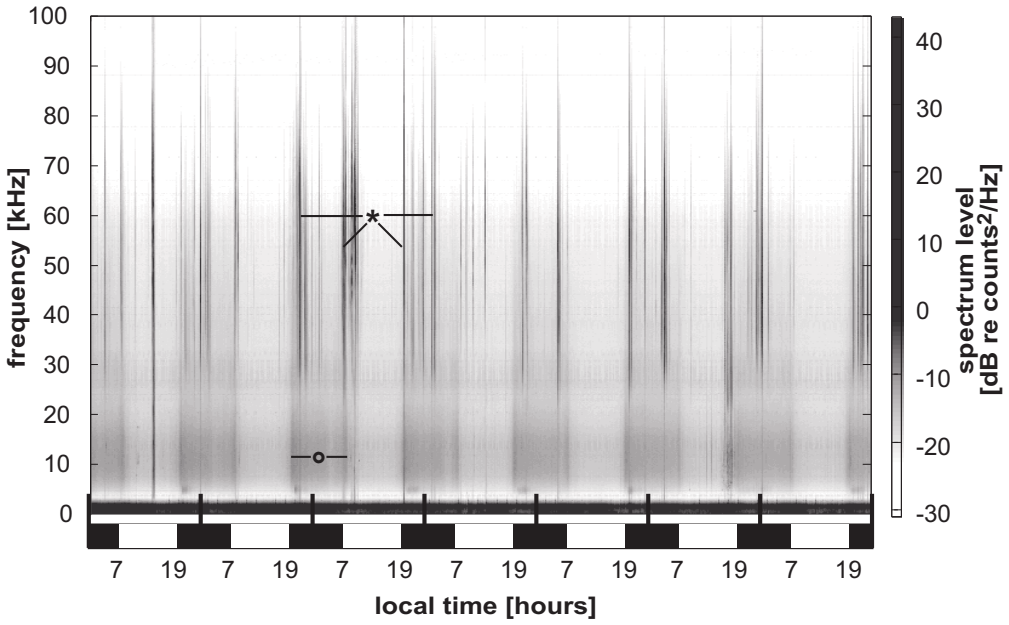

Fig. 3.1: Diel acoustic changes on long-term recording at Palmyra Atoll with strong background noise (°) and higher odontocete click activity (*) at night. Long-term spectral average (LTSA) with frequency versus time, showing one week of recordings, starting on January 26, 2007 at midnight until February 1, 2007 at midnight local time. Pattern at bottom indicates daytime (white) and nighttime (black) with vertical bars at midnight.

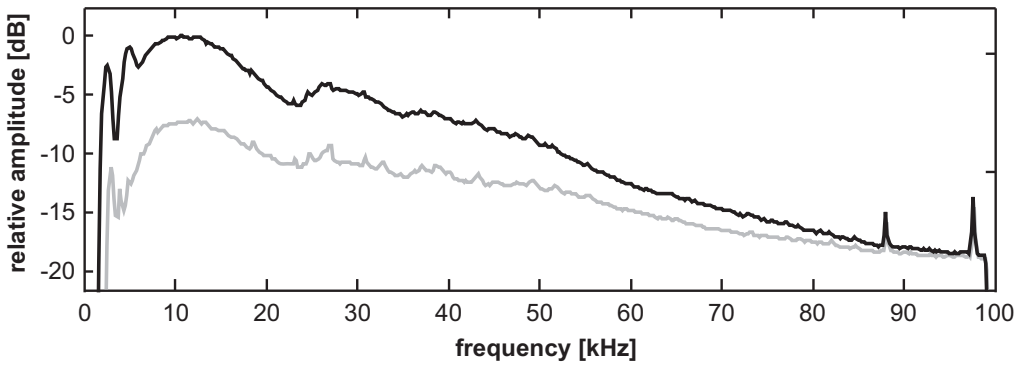

Fig. 3.2: Background noise (not corrected for system response) on HARP at Palmyra Atoll on June 6, 2007 at 20:00 hours (nighttime noise, black) and June 7, 2007 at 13:20 hours (daytime noise, grey). 1000 FFT over 30 s with 0% overlap. Bandpass filter over 3 to 99 kHz. Especially strong nighttime noise increase at 5 kHz (+12 dB) between 20:00 and 22:00 hours, doubling of amplitude (+6 dB) up to about 30 kHz.

Discrimination of melon-headed whale signals from other delphinids

Whistles from melon-headed whales can be distinguished from whistles made by other delphinids. Melon-headed whale whistles were mostly short upsweeps or downsweeps, some were almost constant in frequency and occasionally some were very strongly modulated. The whistle frequencies ranged between 5 and 20 kHz, with the most energy around 12 kHz (Fig. 3.5, Fig. 3.6). During the afternoon hours melon-headed whales were observed with a low rate of echolocation but were very actively whistling with lots of overlaying signals (Fig. 3.5), described as chorusing (Janik and Curran 2007). In contrast, during the night there were a lot of echolocation clicks and only a few single whistles (Fig. 3.6). Energy of echolocation clicks in Fig. 3.5A and Fig. 3.6A started at around 23 and 26 kHz, respectively. As a comparison, bottlenose dolphin whistle recordings, made in the presence of the animals, show strongly modulated whistles (Fig. 3.7). The whistle frequencies for bottlenose dolphins were generally

higher than for melon-headed whales and ranged between 8 and 23 kHz (Fig. 3.7B). Energy of echolocation clicks in Fig. 3.7A also started at around 23 kHz.

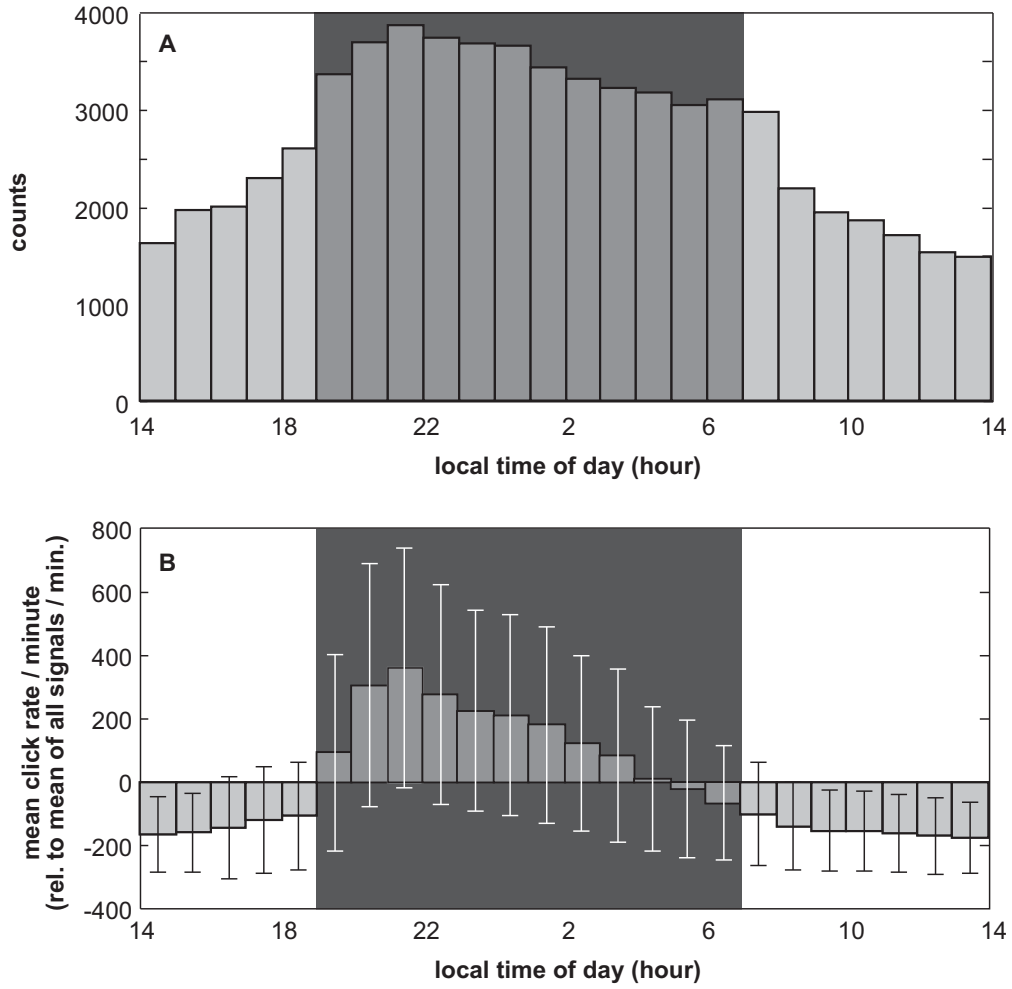

Fig. 3.3: Odontocete clicks versus local time of day. A) Distribution of detections of clicks in 75 s segments. B) Mean click rate relative to the mean of all signals per minute with standard deviation. Nighttime is shown with grey background.

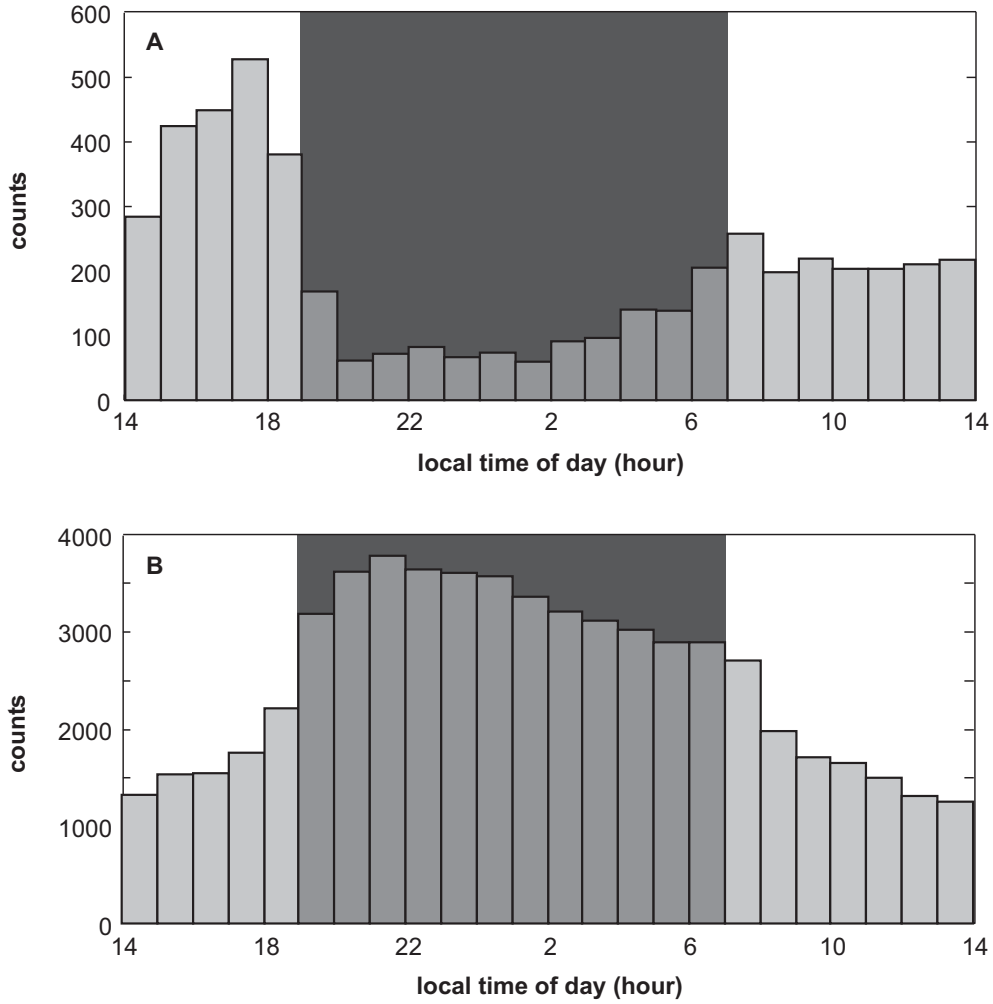

Fig. 3.4: Histogram of median peak frequency of all clicks per 75s segment in relation to hour of the day. A) Hours of the day when median peak frequency was <29 kHz (n=7484). B) Hours of the day when median peak frequency was ≥29 kHz (n=57472). Periods of nighttime are shown with grey background; n = number of 75 s segments with click detections.

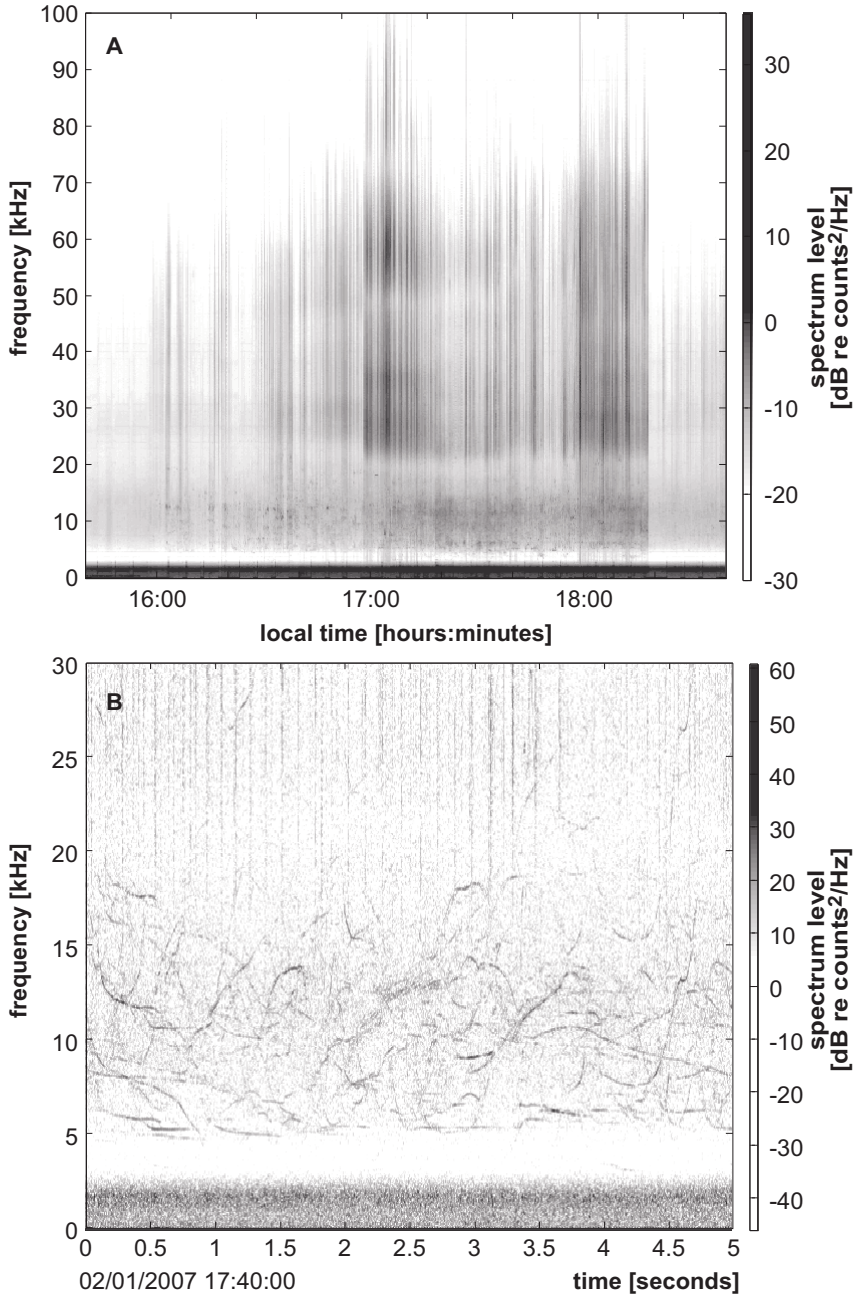

Fig. 3.5: Melon-headed whale whistles and clicks in the afternoon on long-term recording at Palmyra Atoll from February 1, 2007. A) Long-term spectral average (LTSA) showing 3 hours of recording, starting at 15:40 local time. 2000 FFT, 5s, 0% overlap. B) Spectrogram showing 5 s of recording, starting at 17:40 local time. 3000 FFT, 80% overlap.

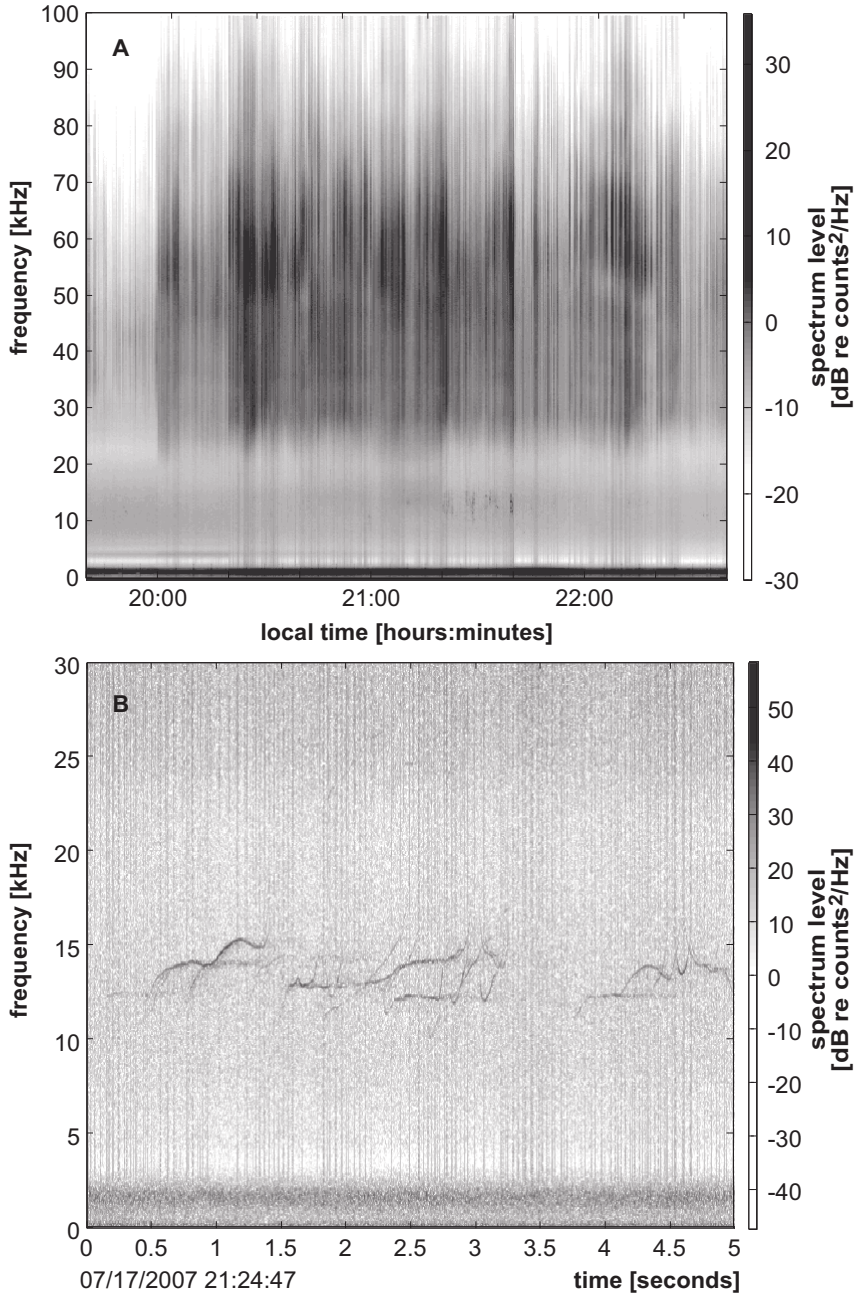

Fig. 3.6: Melon-headed whale whistles and clicks at night on long-term recording at Palmyra Atoll from July 17, 2007. A) LTSA showing 3 hours of recording, starting at 19:40 local time. 2000 FFT, 5 s, 0% overlap. B) Spectrogram showing 5 s of recording, starting at 21:24:47 local time. 3000 FFT, 80% overlap.

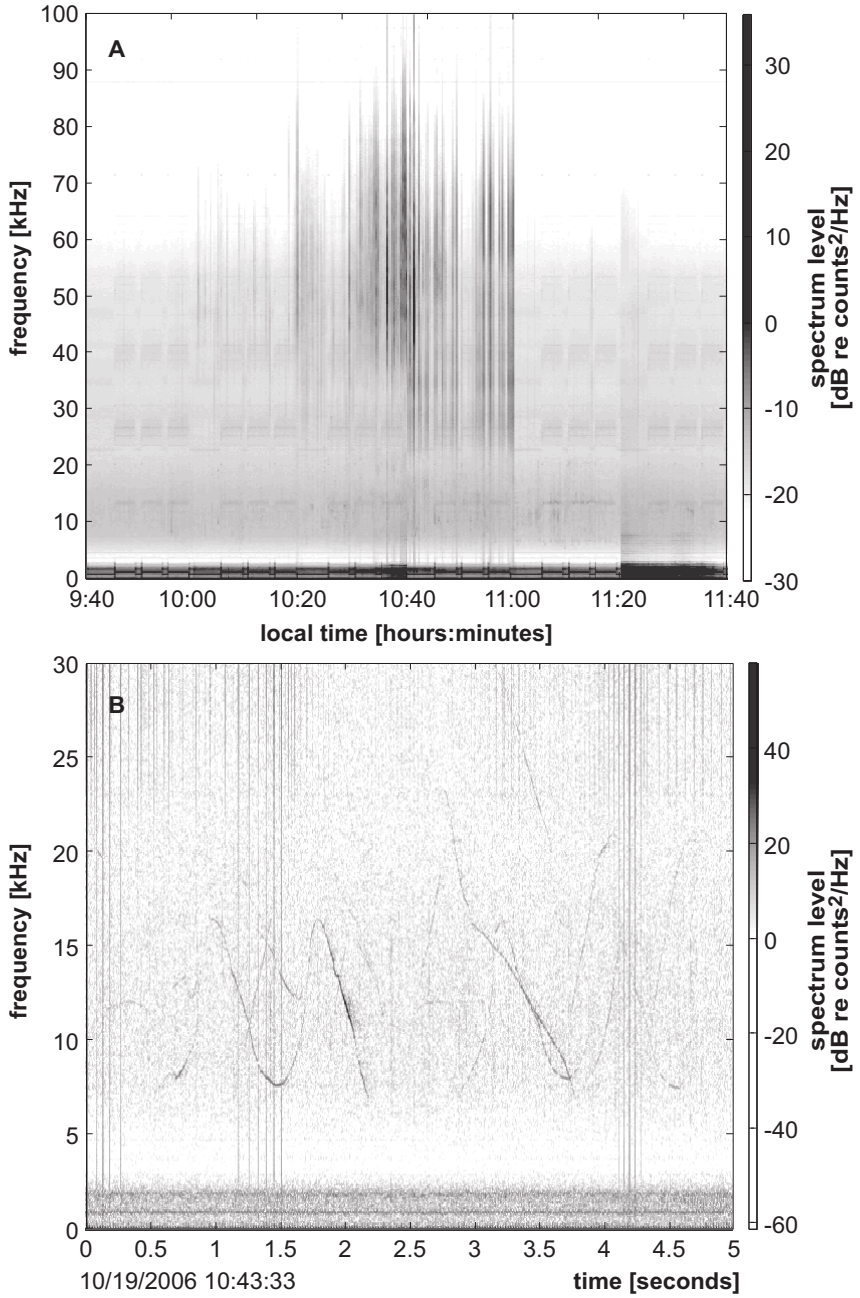

Fig. 3.7: Bottlenose dolphin whistles and clicks in the morning on long-term recording at Palmyra Atoll from October 19, 2006. A) LTSA showing 2 hours of recording, starting at 9:40 local time. 2000 FFT, 5 s, 0% overlap. B) Spectrogram showing 5 s of recording, starting at 10:43:33 local time. 3000 FFT, 80% overlap.

Shift in spectral features of melon-headed whales' echolocation clicks

Most segments with MHW whistles were detected in the late afternoon (Fig. 3.8A). During that time echolocation click activity was low but increasing towards sunset (Fig. 3.8B). Fewer segments with MHW whistles (Fig. 3.8A, $t_{13}=2.34$, $p<0.05$) and lower whistling activity in those segments (Fig. 3.6) were found during the night. Echolocation click rates were higher throughout the night than during the day ($t_{228}=22.5$, $p<0.00001$) with a strong decrease towards sunrise. Median peak frequencies of MHW echolocation clicks shifted from the expected frequencies below 29 kHz during the day, as described in Chapter 2, to higher frequencies at night (Fig. 3.9, $t_{1975}=26.9$, $p<0.00001$). The shift was so significant that median peak frequencies of only 3% of the nighttime segments in comparison to 46% of the daytime segments were below 29 kHz. The median of the median peak frequencies during the day was 29.7 kHz (27.3 kHz, 33.9 kHz quartiles) while it was 36.0 kHz at night (33.6 kHz, 38.3 kHz quartiles).

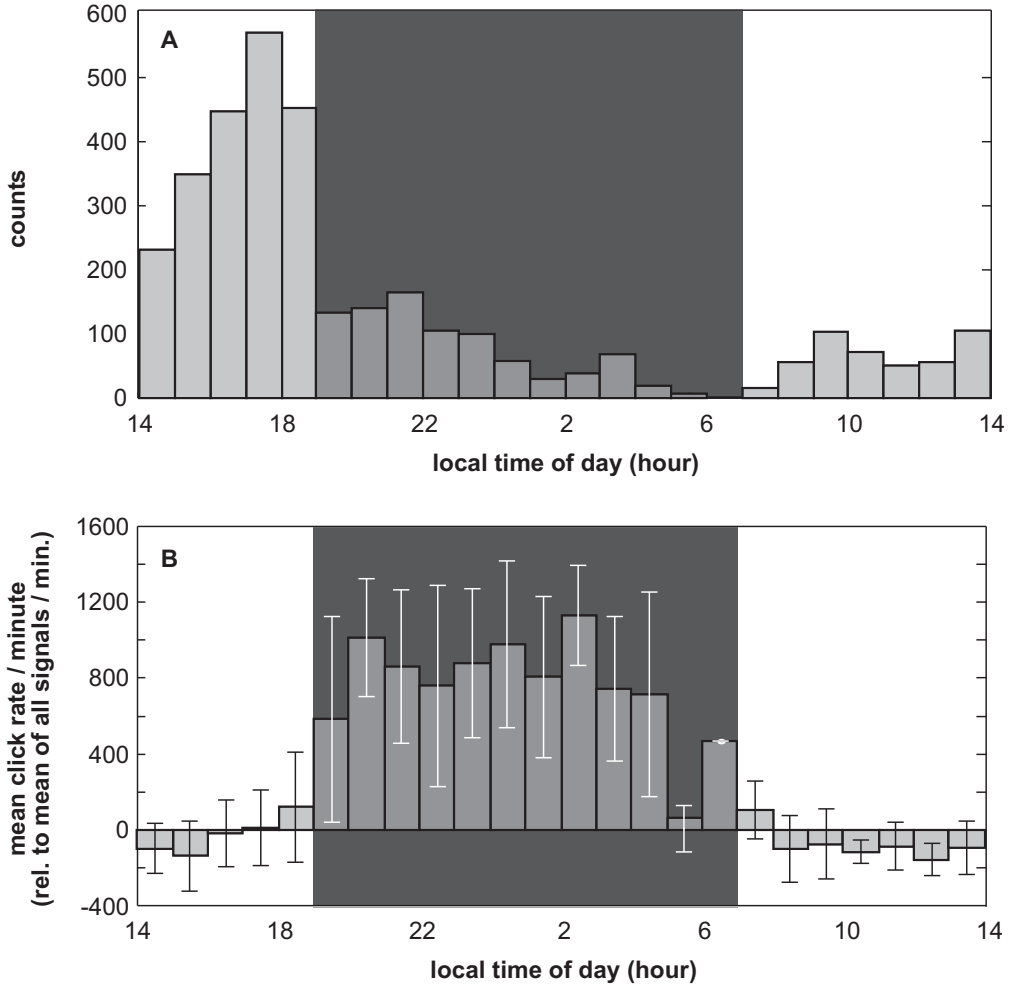

Fig. 3.8: A) Number of 75 s segments with MHW whistles detected versus time of day. B) Mean click rate relative to the mean of all signals per minute with standard deviation versus time of day. Nighttime is shown with grey background.

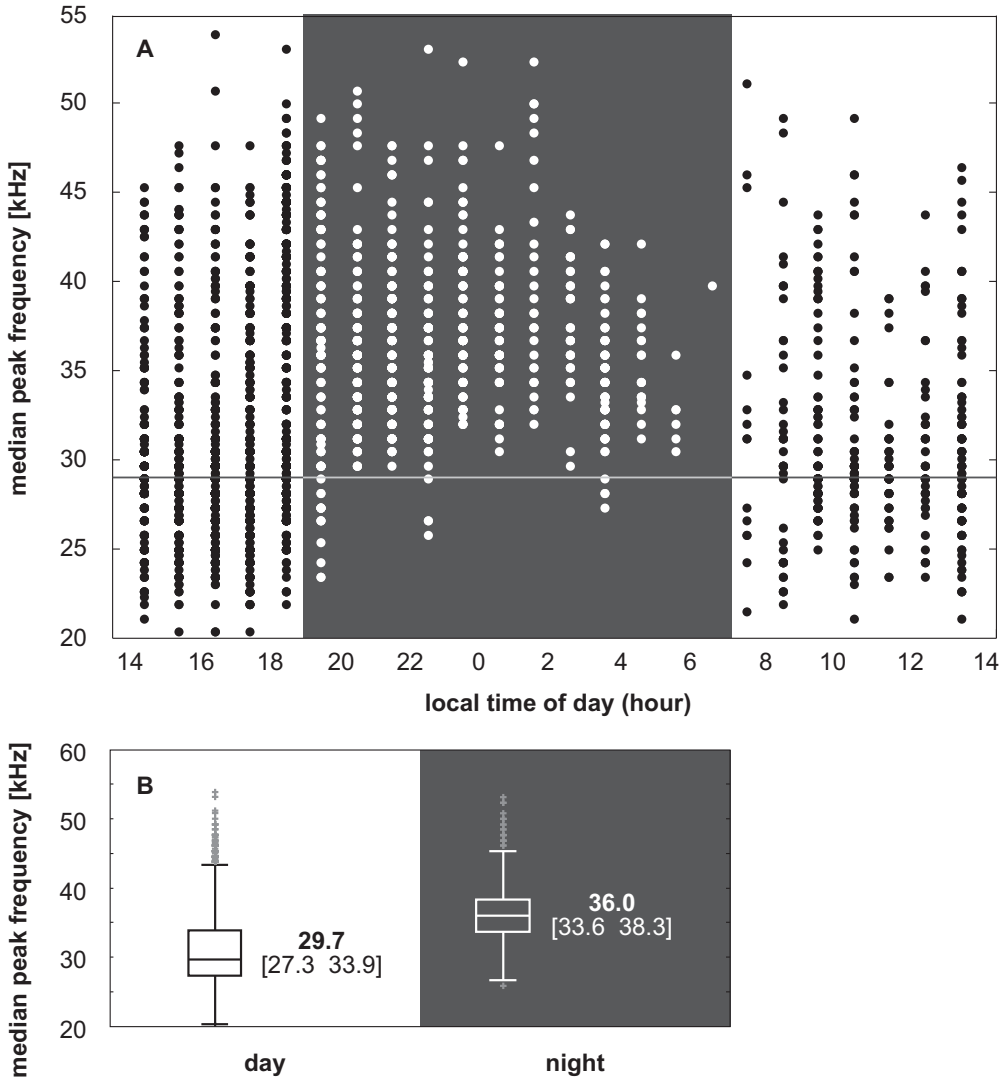

Fig. 3.9: A) Median peak frequency of 75s segments with MHW whistles versus time of day, number of segments n=3357. Horizontal line indicates 29 kHz. B) Boxplot distribution of median peak frequency; daytime, n=2632; nighttime, n=725; bold values indicate median of median peak frequency in kHz, 25 and 75 percentiles are given in brackets. Nighttime is shown with grey background.

DISCUSSION

Long-term passive acoustic monitoring made detailed diel acoustic echolocation behavior of odontocetes at Palmyra Atoll accessible. There was a strong diel pattern with high acoustic activity throughout the night, highest click rates directly after sunset, and low activity during the day. Spinner dolphins and melon-headed whales are both known to feed on mesopelagic prey during the night (Brownell et al., 2009, Norris et al., 1994) while bottlenose dolphins do not have a preferred feeding time during the day (Wells and Scott, 2002). Additionally, observations around the atoll show that in proximity to the reef a probably resident group of up to 1000 melon-headed whales, up to 400 spinner dolphins and several smaller groups of up to 70 bottlenose dolphins were regularly encountered (trip reports Baumann-Pickering, Pitman and Balance, Roth). Melon-headed whales and bottlenose dolphins were commonly observed in the vicinity of the HARP, spinner dolphins only occasionally. Melon-headed whales have a daily migratory and behavioral pattern at Palmyra Atoll (Brownell et al., 2009). They are resting and socializing along the reef edge near the atoll over more shallow water in the morning and early afternoon and move westwards to deeper water towards the HARP in the early evening. No nighttime observations have been reported. The strong increase in click activity during the night is therefore probably primarily due to melon-headed whales but also to spinner dolphins. Detections of segments with odontocete clicks show a different distribution than detections of segments with melon-headed whale whistles. Odontocete click detections increase in the later afternoon, are continuously high during the night and decrease about one hour after sunrise and have their lowest values around noon and in the early afternoon. Detections of segments with melon-headed whale whistles have a strong peak in the afternoon until shortly before sunset, a steep drop off at the beginning of the night and lowest detections before sunrise. This

comparison shows that whistles and clicks are used selectively during different phases of the day. Whistles have been shown to be important for socializing and might be used to regulate group organization (Herman and Tavolga, 1980, Norris et al., 1994, Janik and Slater, 1998, Janik, 2000, Lammers et al., 2006b) while clicks are generally used to echolocate (Au, 1993). Melon-headed whales travel slowly while socializing to their feeding grounds in the afternoon (Brownell et al., 2009). This is accompanied with active whistling and low click rates. Spinner dolphins do not emit whistles during group foraging and only emit very few whistles during surfacing at night (Benoit-Bird and Au, 2009b). If melon-headed whales have a similar behavior then it is not surprising that hardly any whistles were recorded during the nights monitored and that detected numbers of segments with whistles were correspondingly low.

Odontocete click rates were much higher at night than during the day yet the highest rates occur shortly after sunset and continuously decreasing towards sunrise. Melon-headed whale click rates in comparison were high and fairly stable in density throughout the night while click rates during the day were consistently low, slightly increasing before sunset and sharply decreasing after sunrise. Studies of several odontocete species, where behavioral and acoustical patterns were observed simultaneously, found high click rates during foraging, intermediate click rates during traveling and socializing, and low click rates during resting (Norris et al., 1994, Barrett-Lennard et al., 1996, Van Parijs and Corkeron, 2001, Nowacek, 2005, Verfuß et al., 2005, Soldevilla et al., 2008, Benoit-Bird and Au, 2009b, Verfuß et al., 2009). The diel click rate pattern at Palmyra Atoll for all odontocetes as well as the pattern of melon-headed whales alone supports the hypothesis of nighttime foraging and daytime resting and socializing for most of the vocal individuals present at the atoll. The difference in click rate pattern between the entire data set where click rates decreased throughout the night, and only melon-headed whales whose click

rates were more stable at night, might be due to the selective process of analyzing only segments when melon-headed whale whistles were present. These segments with whistles might have periods of particularly high activity at night or it could indicate that melon-headed whales are active throughout the night but forage outside the acoustic range of the recorder during the second part of the night such that their signals do not dominate then.

High rates of nighttime echolocation for spinner dolphins and melon-headed whales are related to diel patterns in prey migration (Lammers et al., 2006a, Benoit-Bird and Au, 2003, Benoit-Bird et al., 2004). Mesopelagic biomass communities undergo a vertical and horizontal migration from deep waters during the day to surface waters at night, with a peak density in shallow water around midnight. At Palmyra Atoll the densest aggregations would be expected at the edges of the slopes around the atoll. Because the slopes of the atoll are very steep, night foraging would happen in very close proximity to the HARP despite its considerable depth. The background noise diel pattern might be related to this movement of the deep scattering layer. Another origin for the noise could be snapping shrimp activity if the signal were to originate from much shallower reef areas and travel to deep water (Au, 1998, Watanabe et al., 2002, Lammers et al., 2008).

Median peak frequencies of melon-headed whales shifted from a median 29.7 kHz to 36.0 kHz during the noisy and food rich nighttime period. Melon-headed whale echolocation clicks had proven to be stable below 29 kHz during daytime array recordings (see Chapter 2). This was also true for echolocation clicks on daytime HARP recordings of segments with melon-headed whale whistles. At night however, median peak frequencies below 29 kHz were very rare. This shift in frequency could be explained through either one or both of the following adaptive processes. 1) Spectral changes of the signals to higher frequencies could be due to differences in the

echolocation tasks during day versus night. 2) Signals with higher frequencies are less likely to be masked by the increased noise level at night. Different behavioral stages between day and night might ask for echolocation signals with different detection ranges and resolution. During daytime resting, socializing and slow traveling a broader view and therefore a larger beamwidth with lower frequency would be preferential than during nighttime foraging where a small target could be better resolved with a narrow beamwidth and higher frequency. A broad bandwidth of the emitted click is beneficial for localization and characterization of a target (Au 1993) yet the detection of targets in broad band noise are difficult with a large bandwidth (Madsen and Wahlberg, 2007). Shifting the signal to a higher frequency with a given transmitting aperture also improves directionality which is helpful in a cluttered environment (Au, 1993). Also the higher frequency allows for a better resolution of a small target like prey fish or squid. A negative point for the higher in comparison to lower frequencies is the stronger attenuation of sound energy over distance which decreases the detection range (Richardson et al. 1995). The higher directionality, smaller resolution and lower detection range which come with the higher frequency might not be desired for a broader view of the spatial constellation of background and conspecifics but could be well suited for nighttime foraging when the frequency shift occurs. However, the rather small frequency change between day and night would have only a small effect on the localization accuracy which makes it not very likely that this is the driving force for the observed difference. More likely would be that signals shifted to higher frequencies are less vulnerable to be masked by increased nighttime background noise levels. Au (1993) reported a strong frequency shift in clicks to higher peak frequencies for a false killer whale (*Pseudorca crassidens*) in captivity which was moved from the quieter San Diego Bay to Kaneohe Bay, Oahu. Background noise in Kaneohe Bay is dominated by strong broadband snapping shrimp

activity. An increase in frequency was observed for echolocation clicks and probably also for whistles produced at night by melon-headed whales at Palmyra Atoll. Background noise was doubled during the night up to about 30 kHz and was continuously less increased up to 90 kHz. Therefore, the increased nighttime background noise could have a masking effect particularly on the lower frequency parts of the signals and a shift to higher frequencies for both echolocation signals and social calls could reduce this effect.

CONCLUSION

Diel acoustic patterns were revealed for odontocete species, in particular melon-headed whales at Palmyra Atoll through long-term passive acoustic monitoring and support the nighttime forager hypothesis. The strong diel difference though between use of whistles and use of clicks shows the need for automatic species classification by their echolocation clicks as well as their whistles to attribute so far unknown times of very vocal periods, especially at night, to specific species. The diel shift of median peak frequencies of echolocating melon-headed whales, depending on masking avoidance or echolocation task or both indicates that the spectral structure of a click is not a rigid entity but can be intentionally modulated. This makes automation of species classification an even more difficult challenge. The findings on the behavioral ecology of, especially, foraging melon-headed whales will help to assess the relevance of cetacean species within the ecosystem and energy flow of a healthy coral reef like Palmyra Atoll. To judge the impact of these high trophic level predators on the reef, more insights into their actual prey species and the function of that prey within the ecosystem would be important.

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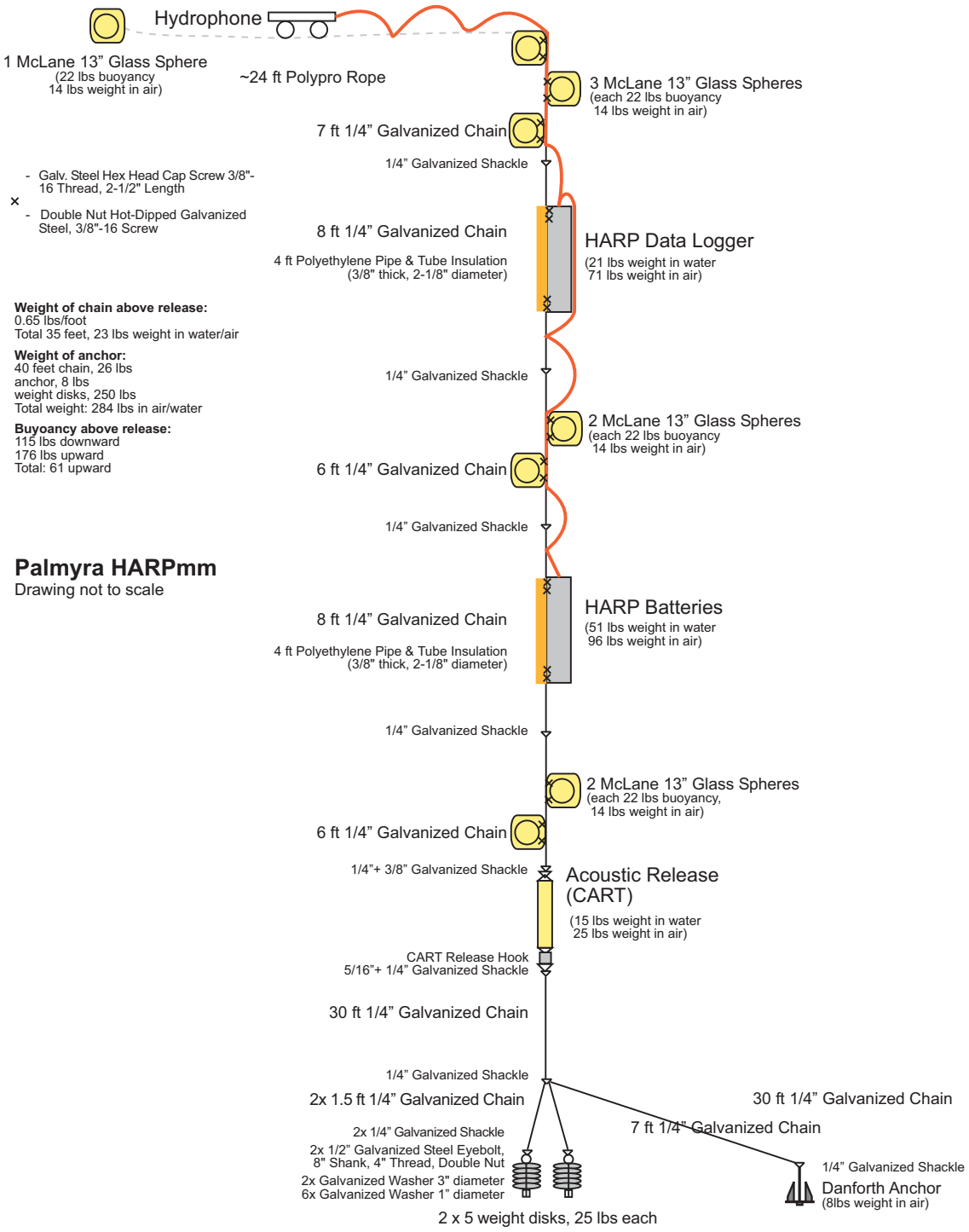
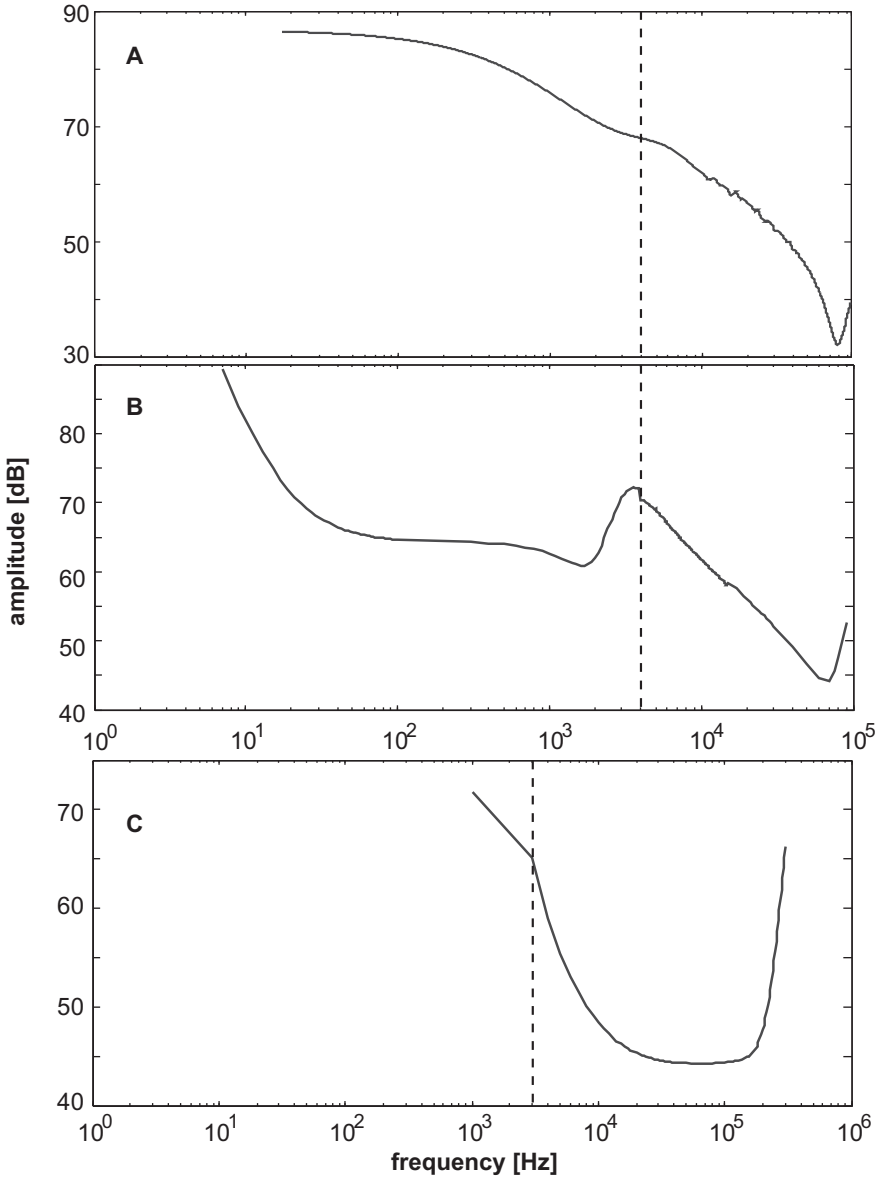
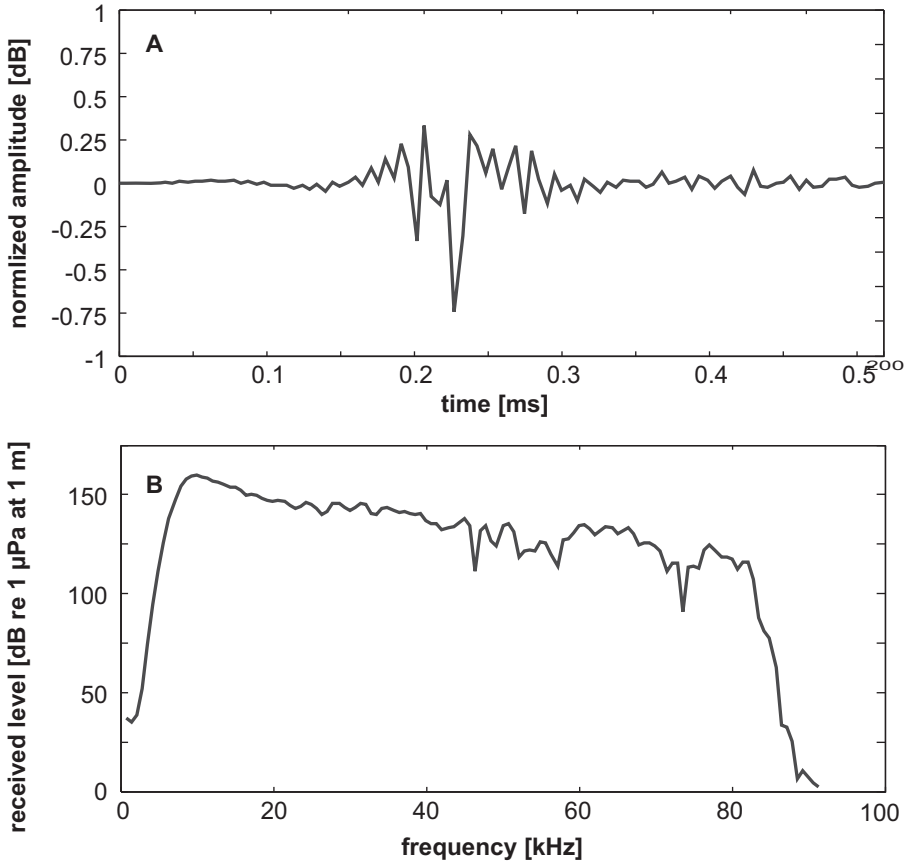
Appendix I: Sketch of Palmyra Atoll High Frequency Acoustic Recording Package mini mooring (HARPmm)



Appendix II: Transfer functions for hydrophone boards with low and high frequency (HF) channel. A) 100 series, board HT110, HF 3-100 kHz, used in array recordings 2006; B) 300 series, board HT323, HF 3-100 kHz, used in HARP; C) 400 series, board HT417, HF 2-200 kHz, used in array recording 2007. Dashed vertical line indicates transition between channels.



Appendix III: Example for a clipped click recording with distortion of signal and maximum amplitude below 80% of the maximum system capability resulting in peak frequencies below 20 kHz. Recording of melon-headed whales from October 24, 2006 at 21:03:41.27 hours (GMT). A) Timeseries of click with amplitude normalized to +/-1 as the maximum amplitude range of the system. B) Spectrum of distorted click with peak frequency at 10.5 kHz.



SUMMARY

Acoustic recordings of four cetacean species from Palmyra Atoll, northern Line Islands in the central Pacific, were used to describe and classify their acoustic signals and to analyze their diel patterns at the atoll. Melon-headed whales (*Peponocephala electra*), bottlenose dolphins (*Tursiops truncatus*), Gray's spinner dolphins (*Stenella longirostris longirostris*), and a poorly known beaked whale (probably *Mesoplodon hotaula*) have been visually observed and acoustically monitored at Palmyra Atoll. We recorded their acoustic behavior during daytime observations with a towed hydrophone array sampling at rates of 192 and 480 kHz. Additionally, from October 2006 to September 2007, an autonomous High-frequency Acoustic Recording Package (HARP) was mounted on the seafloor in water of about 600 m depth and was programmed to sample with 200 kHz for 5 minutes every 20 minutes.

Long-term acoustic recordings showed beaked whale like upsweep FM pulses produced by an unknown species. The peak frequency of the detected beaked whale pulses was at 48 kHz and the signal swept from 34 to 65 kHz (-10 dB bandwidth). Pulse duration was 430 μs and inter-pulse interval was 225 ms. Besides the vast majority (74%) of single inter-pulse intervals there were double inter-pulse intervals of 450 ms. Two buzz sequences, probably prey capture attempts, were detected when the inter-pulse intervals went below 20 ms and the spectral structure of the pulses changed to not frequency modulated, transient clicks. Buzz clicks were about 20 dB lower in amplitude than prior FM pulses. These clicks had a 39 kHz bandwidth and a peak frequency at 37 kHz. Pulse duration was 160 μs and inter-click interval was between 4 and 10 ms. Signals from the Palmyra beaked whales had higher frequencies, broader bandwidths, longer pulse durations and shorter inter-pulse intervals than previously described FM pulses of Blainville's and Cuvier's beaked whales (Zimmer et al., 2005, Johnson et al. 2006). They were

distinctly different temporally and spectrally from the unknown beaked whale at Cross Seamount, Hawaii (McDonald et al., 2009). It is very likely that these beaked whales are of the genus *Mesoplodon*, according to several recent sightings at the atoll. They are probably *M. hotaula*, consistent with genetic analysis of stranded skulls from Palmyra Atoll (Dalebout, unpublished results).

Classification of three dolphin species through spectral parameters of their signals is presented. Melon-headed whales had the lowest peak and center frequencies, spinner dolphins had the highest frequencies and bottlenose dolphins were nested in between these two species. -3 and -10 dB bandwidths were similar for all species. Temporal parameters were not suited for classification. Classification results were optimized by reducing variability within a set of single clicks by calculating mean spectra for groups of clicks. Peak frequency was the strongest classification parameter. Median peak frequencies of grouped clicks (group size 50) of melon-headed whales ranged between 24.9 and 28.0 kHz, of bottlenose dolphins between 26.3 and 34.8 kHz and of spinner dolphins between 35.0 and 37.0 kHz. The species-specific frequencies might be due to morphological structures within the head of the different species.

Little is known about the behavior of wild melon-headed whales, which occur in tropical offshore waters at relatively low densities. The melon-headed whales' whistles recorded on the HARP were distinctly different from whistles of other delphinid species regularly observed at the atoll. Melon-headed whales whistled most frequently in the afternoon with a peak before sunset. The peak melon headed whale echolocation period occurred during the night, probably when hunting. Spectral features of echolocation clicks of melon-headed whales at Palmyra Atoll changed from day to night time. The median peak frequency of the clicks during the day was at 29.7 kHz. At night the median peak frequency shifted upwards to 36.0 kHz. This frequency shift

might be to avoid acoustic masking due to increased background noise over a wide frequency band from unknown acoustic sources during the night, or it could indicate deliberate change of echolocation beamwidth and therefore frequency during two different behavioral stages. Daytime resting, slow traveling and socializing might require a wider beam than nighttime feeding when the whales are likely focusing on small prey targets.

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05-09/2007	Development of methodologies, National University of Singapore, Marine Mammal Research Lab, Dr. Elizabeth Taylor

Second university degree

10/2000-02/2006	Diplom Biology, Eberhard-Karls-Universität Tübingen; Biological major: animal physiology; minors: zoology, pharmacology; Master's thesis: "Inter- and intraspecific comparison of the echolocation behavior of serotine (*Eptesicus serotinus*) and northern bats (*Eptesicus nilssonii*)"

First university degree

1994-1999	Diplom Ingenieur (FH) Audiovisual Media Stuttgart Media University
1993-1994	Exchange student in Grenoble, France, Université Stendhal Grenoble

High school graduation

1983-1993	Illertal-Gymnasium Vöhringen, Germany, Abitur
1989-1990	Exchange student in Arcata, CA, USA, High school diploma

Professional Career

04-07/2005	Teaching assistant in basics of animal physiology – colloquium, lab
09/2003-02/2004	Internship Whale Museum, Madeira – field and laboratory work
04-07/2003	Teaching assistant in zoology – tutorial, lab course
04/2002-07/2003	Research assistant in the lab of Prof. Schnitzler, Universität Tübingen
2001-2005	CEO of the multimedia agency *e-xentric GmbH*, Stuttgart
1999-2001	Management position *jangled nerves GmbH*, Stuttgart
1997-1999	CEO of the multimedia agency *Medienmacher GmbH*, Ludwigsburg