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Different modes of acoustic communication in deep-diving short-finned pilot whales (*Globicephala macrorhynchus*)

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ABSTRACT

Toothed whales use a pneumatic sound generator to produce echolocation and communication sounds. Increasing hydrostatic pressure at depth influences the amplitude and duration of calls but not of echolocation clicks. Here we test the hypothesis that information transfer at depth might be facilitated by click-based communication signals. Wild short-finned pilot whales (27) instrumented with multisensor DTAGs produced four main types of communication signals: low- and medium-frequency calls (median fundamental frequency: 1.7 and 2.9 kHz), two-component calls (median frequency of the low and high frequency components: 2 and 9 kHz), and rasps (burst-pulses with median interclick interval of 21 ms). Rasps can be confused with foraging buzzes, but rasps are shorter and slower, and are not associated with fast changes in body acceleration nor reduced acoustic output of buzzes, characteristic of prey capture attempts. Contrary to calls, the energy flux density of rasps was not significantly affected by depth. This, and a different information content, may explain the observed increase in the relative occurrence of rasps with respect to calls at depth, and supports the hypothesis that click-based communication signals may facilitate communication under high hydrostatic pressure. However, calls are produced at depth also, indicating that they may carry additional information relevant for deep-diving animals, including potential communication among whales diving at the same time in this highly social deep-diving species.

Key words: information transfer, communication, acoustic physiology, animal behavior, acoustic tags.

Delphinids produce a wide variety of vocalizations, ranging from widely spaced pulses to continuous tonal, near-sinusoidal signals (*e.g.,* Murray *et al.* 1998). Categorizing signals and building up acoustic repertoires have traditionally been based on

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structural differences perceived by humans (Caldwell and Caldwell 1968, Ford 1989, Herzing 1996). However, a true understanding of how vocal signals are parsed must be derived by considering both the structural and functional features of the vocalizations.

In the case of frequency-modulated signals, such as whistles (Caldwell and Caldwell 1965), it is known that bottlenose dolphins are able to recognize known signatures based on their fundamental frequency contour (Sayigh *et al.* 1999, Janik *et al.* 2006). Thus, a common method to categorize whistles is quantifying contour similarities using either multiple observers (Sayigh *et al.* 1999, 2013), crowdsourcing (Sayigh *et al.* 2013), or computer-based comparisons (Deecke and Janik 2006, Brown and Miller 2007, DeRuiter *et al.* 2013). The classification of click-based signals is more problematic. Toothed whales produce sequences of echolocation clicks when exploring their surroundings, interspersed by short click series with a dramatic increase in the click repetition rate, named buzzes, associated with prey capture attempts (Miller *et al.* 2004, Johnson *et al.* 2004, Madsen *et al.* 2005*a*, Aguilar de Soto *et al.* 2008). However, some click-based signals, often described as burst-pulsed sounds, are used for short-range social communication (Herzing *et al.* 1996). Some burst-pulse signals, such as rasps, are apparently used for communication in beaked whales but may be confused with echolocation buzzes if not examined with caution (Aguilar de Soto *et al.* 2012). This underlines the importance of developing objective methods to classify click-based signals, in order to avoid bias in the quantification of acoustic events related with foraging and communication.

Sound production in toothed whales is a pneumatic process driven by pressurizing air in the nasal passages (Ridgway 1980, Ridgway and Carder 1988) and exciting vibrations of the phonic lips (Ridgway and Carder 1988, Cranford *et al.* 1996, Madsen *et al.* 2011). The nasal system is normally closed during sound production and air is recycled using a series of air sacs connected to the phonic lips (Dormer 1979), enabling continued sound production throughout prolonged dives (Wahlberg *et al.* 2001, Madsen *et al.* 2005*b*). It has been suggested that pulse repetition rate and whistle fundamental frequency are determined by a combination of nasal air pressure and phonic lip tension (Cranford *et al.* 1996, Madsen *et al.* 2011). Both echolocation clicks and tonal signals are produced pneumatically by passing air through the phonic lips, but tonal signals such as whistles require a higher nasal air pressure for sound production (Ridgway and Carder 1988). Therefore, whistles likely require a greater total air volume than a click series of equivalent duration (Ridgway and Carder 1988, Jensen *et al.* 2011). Two studies have found evidence that tonal sounds are more susceptible to changes in the air volume available for pneumatic sound production. Ridgway *et al*. (2001) reported that one of two trained belugas performing auditory tests emitted lower intensity response whistles at depth than near the surface, while the other whale did not whistle at depth at all. Jensen *et al.* (2011) found that the energy content of tonal calls produced by wild short-finned pilot whales decreased as a function of depth, indicating that biophysical limitations in the air-driven sound generator affect the tonal sound production of toothed whales. These findings suggest that click-based communication might be especially relevant at depth, where the production of whistles or calls is limited by the reduced air-volume available for sound production.

This paper investigates how communication signals are affected by hydrostatic pressure and how social, deep-diving species deal with biophysical restrictions on sound generation at depth. We describe the main communication signals used by free-ranging short-finned pilot whales (*Globicephala macrorhynchus*), test how different signals used by this species are affected by changes in depth, and quantify the depth-dependent occurrence of communication signals. We discuss how short-finned pilot whales use several types of signals throughout foraging dives to fulfill their communication requirements in spite of the challenges of vocalizing at depth with a pneumatic sound generator.

Methods

Study Area, Data Collection, and Tagging Protocol

Short-finned pilot whales can be found year-round in the lee area off the southwest coast of Tenerife (Canary Islands), where a resident community of some 380 individuals coexists with an unknown number of transients (Heimlich-Boran 1993). The vocal behavior of these whales was studied using motion and acoustic recording DTAGs (Johnson and Tyack 2003) attached with suction cups to the whales. Version 2 DTAGs are equipped with two hydrophones separated by 2.5 cm to record sound with a 96 or 192 kHz sampling rate, 16-bit resolution, and 90 dB of dynamic range. Tags also include a depth sensor and a set of triaxial accelerometers and magnetometers sampling at 50 Hz. Tags were deployed on pilot whales using a 5 m hand-held carbon fiber pole (more information in Aguilar de Soto *et al.* 2008). Mother-calf pairs were not approached for tagging but young animals occasionally joined with previously tagged adults. Short-term behavioral reactions, such as flinches or tail slaps, were observed in some whales due to the close approach of the boat and the initial contact of the suction cups with the skin. However, these reactions lasted only a few seconds after tagging.

Pictures of tagged whales were taken for individual photo-identification, but not all the individuals were recognizable. Thus, we cannot exclude that some animals may have been retagged in different years. Given the relatively large population size, *ca.* 380 (Heimlich-Boran 1993), we expect a relatively low number of potentially retagged individuals.

Identification and Quantification of Tagged Whale Vocalizations

Multisensor acoustic recording tags are useful tools to study the ecological context of sound production of individual whales thanks to the simultaneous recording of sound and movement. However, it is still challenging to recognize unambiguously the vocalizations produced by the tagged whale when whales swim in cohesive social groups (Johnson *et al.* 2009). Pilot whales often form tight aggregations at the surface where the tag can record sounds produced by nearby untagged whales. Here, acoustic recordings were initially inspected using custom-written Matlab 6.5 (Mathworks, Nantick, MA) scripts to identify recorded vocalizations. Rolling spectrograms (512 point Hanning window, 50% overlap) and amplitude envelopes of 15 s long sections were examined visually by analysts who listened to each segment and marked individual sounds of interest. Each sound was filtered with a 6-pole Butterworth high-pass filter with a cut-off frequency of 500 Hz. The received level (RL) was then calculated as the root-mean-squared (RMS) sound pressure values over a 95% energy window (Madsen and Wahlberg 2007) and corrected for the nominal tag sensitivity to obtain the apparent output ($AO_{r.m.s}$) of the signals (Madsen *et al.* 2005*a*). The time delay between the stereo hydrophones was estimated as the peak of the cross-correlation function and improved to subsample accuracy by interpolating between digital samples using linear quadratic regression. The AOA (angle of arrival to the tag) of each sound was estimated from the time delay, τ, as: AOA = $\sin^{-1}(\tau c/d)$, where c is the speed of sound in seawater and d is the hydrophone separation (Johnson *et al.* 2006). For each tagged whale, signals with a high RL and a consistent AOA were tentatively classified as produced by that whale.

Prevalence of Signals at Depth

To investigate patterns of signaling as a function of depth, we used all pilot whale data sets that contained 50 or more manually classified communication signals (rasps and calls) for a total of 18 data sets. First, we calculated probability density functions for calls and rasps as a function of depth using a 50 m Gaussian kernel. We then quantified how the use of rasps changed by depth as the ratio of rasps to the total number of communication signals. We divided depth into five bins, with the first (surface) bin containing signals from 0 to 50 m (roughly close to depth of lung collapse), and each of the four subsequent bins containing approximately 25% of the remaining signals to balance the data set at different depth bins for the analysis. We then used a Kruskal-Wallis test followed by a Dunn's test (Benjamini-Yekutieli correction) for pairwise comparisons to test if signal use changed between depth layers. It cannot be excluded the possibility that some signals produced near the tagged whale by untagged conspecifics may have been erroneous classified as produced by tagged whales. However, this analysis is robust to this source of bias because it compares overall signal occurrence for different depth bins, so the probability of mismatch is the same for rasps and calls.

Selection Criteria for Signals from Tagged Individual

Untagged animals near the tagged whale can sometimes produce signals that may be received at the tag with higher RL and similar AOA than signals produced by the tagged whale. Some analyses are not robust to this source of bias and require high certainly about the origin of the vocalizations. So, to identify a subset of the vocalizations that could be attributed to the tagged whales with high certainty (named "focal signals" hereafter), we developed an automatic method. This method selected objectively signals recorded with a high RL and an AOA consistent with the orientation of the tag on the body of the animal. To add a further layer of information, signals were considered focal only if they were produced within a stereotypical vocal pattern that was first identified during deep dives. In these dives, whales tend to disperse (Aguilar de Soto 2006), resulting in a lower ambiguity about the identity of the vocalizing animal. The combination of the high RL, AOA and this vocal pattern was used to classify signals automatically with the following analytical steps:

(1) High quality signals—All signals received with sufficient quality throughout the vocalization to either detect all clicks (in the case of click-based signals) or to trace the fundamental frequency contour (in the case of calls) were considered high quality signals potentially produced by the tagged whales. The signal-to-noise ratio (SNR) of these signals was calculated as the difference between the RL (RMS) of the signal (95% energy window) and the RL of 0.2 s before them. The SNR of the high quality signals ranged from 1 to 56 dB.

(2) Signals produced during pauses in clicking—Clicks from tagged whales were located using a supervised click detector programmed in Matlab 6.5, based on typical

click characteristics of short-finned pilot whales studied in the same area (Aguilar de Soto 2006). Focal clicks contain energy at low frequencies (Johnson *et al.* 2006, 2009; Hansen *et al.* 2008; Fig. S1). This is presumably caused by tissue conduction or off-axis effects and provides a cue to discriminate clicks produced by the tagged whale from clicks produced by conspecifics. This enabled us to observe that tagged whales click regularly both in the descent and the ascent of the dives (Aguilar de Soto 2006; Fig. S1), while other types of vocalizations (buzzes, rasps, calls and other sounds types, called indeterminate sounds) are often produced during pauses between consecutive click series (Fig. 1). This repetitive vocal pattern was broadly distributed in most dives and occurred also at the surface, albeit less frequently. Thus, to decrease the risk of including nonfocal signals, we selected only high quality signals produced within this pattern, *i.e.,* occurring within 1 s of the end of a click sequence. This threshold was determined by the change in slope of a survival plot representing the time-lag between the start of the signals and the end of the previous click series.

(3) Consistency of the angle of arrival(AOA) of the signals to the tag—The short duration of typical delphinid clicks results in accurate AOA estimates from the two tag hydrophones. Here, we defined a range of focal AOA for the calls, rasps, and buzzes, based on the observed variation in AOA from clicks immediately preceding these signals. Out of all signals fulfilling the filters described in (1) and (2), we considered signals with an AOA within ±10° of the mean AOA of the clicks in the previous click series or within the AOA range of these clicks to be focal.

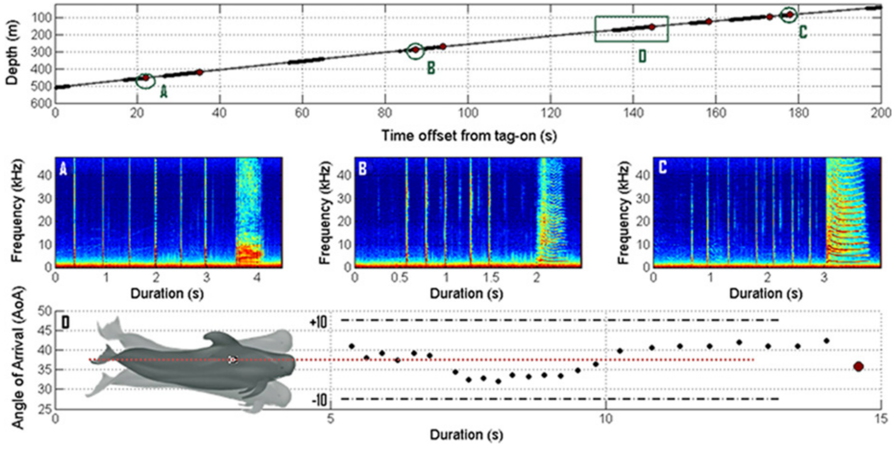

Figure 1. Upper panel: section of the ascent phase of a deep foraging dive, marking the occurrence of echolocation clicks (black dots) and high quality vocalizations (red circles). Notice the repetitive vocal pattern of click series followed by high quality signals. Examples of this pattern (marked with green circles and a square) are shown in (A)–(C) with spectrogram views (Hamming, 1024 NFFT, 50% overlap) of click series followed by a rasp (A), a low frequency call (B) and a medium frequency call (C). (D) represents a detailed view of the variation in the angle of arrival (AOA) of clicks produced by the tagged whale (black dots). The plot also shows the mean AOA (red dotted line) of the click series preceding a vocalization (red circle), and the ±10° of the mean AOA range (dot-dash line) used to classify the vocalizations as produced by the tagged whale (for a detailed explanation see text).

Analysis of Click-based Signals

In Blainville's beaked whales (*Mesoplodon densirostris*), echolocation buzzes can be distinguished from similar burst-pulse sounds, named rasps, because rasps are formed by long and frequency modulated clicks, whereas buzzes are formed by short and broadband clicks (Aguilar de Soto *et al.* 2012). Additionally, rasps and buzzes are produced in different behavioral contexts, *e.g.*, buzzes are associated with a significant increase in acceleration rate (jerk) consistent with hunting events, while rasps are not (Aguilar de Soto *et al.* 2012). While beaked whales produce frequency modulated clicks as well as buzz clicks (Zimmer *et al.* 2005, Johnson *et al.* 2006), short-finned pilot whales only produce broadband unmodulated clicks (Aguilar de Soto 2006), thus rasps and buzzes cannot be distinguished by the click properties of these two signal types. Here, rasps and buzzes were tentatively separated based on aural cues and apparent differences in the spectrograms (Fig. 2). Clicks from each rasp and buzz were then located using a supervised click detector and the mean interclick interval (ICI) was calculated as the mean of the time between clicks. The signal duration was defined as the length of a window containing 95% of the total signal energy after subtracting the noise intensity of a 0.2 s segment immediately preceding the onset of the vocalizations. Differences in ICI, AO, and duration between focal rasps and focal buzzes were analyzed using linear mixed-effects models. Models with ICI, AO, or duration as response variables and including signal type as an explanatory variable were compared to null models without this variable by means of likelihood ratio tests.

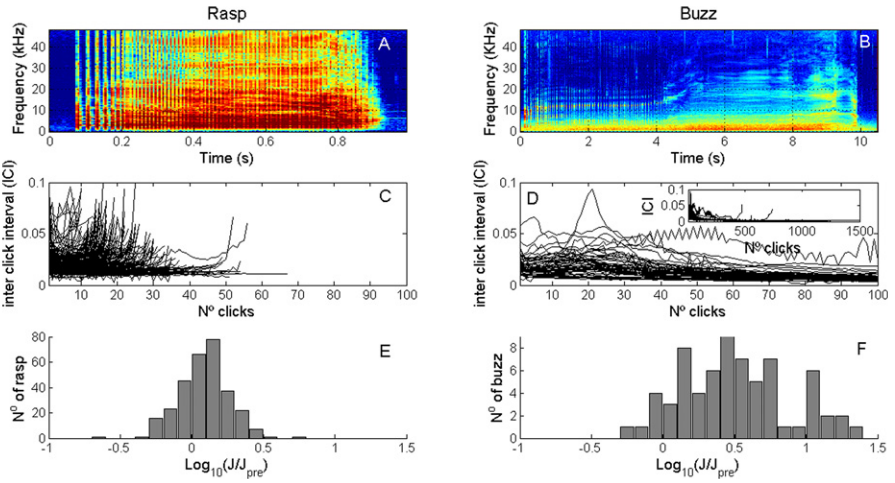

Figure 2. Two types of click-based vocalizations produced by tagged short-finned pilot whales. The upper panels show the spectrograms (Hamming, 1,024 NFFT, 50% overlap) of examples of a rasp (A) and a buzz (B). Note that the *x*-axes of both spectrograms are different. Medium panels show the interclick interval (ICI) distribution throughout 251 focal rasps (C) and 44 focal buzzes (D) recorded with high signal-to-noise ratio in 19 and 7 different whales, respectively. The box in D shows the complete duration of buzzes, while the *x*-axis of the main panel is adjusted to allow comparison with rasps. The lower panels show histograms of the log transformed ratio of the acceleration rate or jerk (J) during rasps (E) and buzzes (F) with respect to periods of equal duration immediately before the production of each signal (J_{pre}).

Analysis of Calls

Calls were analyzed individually using an interactive custom-written Matlab tool. For each call, a spectrogram was calculated and displayed (Hamming window, FFT size and frame length 4,096, 50% overlap for a spectral resolution of 200 Hz and a temporal resolution of 2.5 ms). The fundamental frequency contour was traced manually in the spectrogram and a dynamic 6-pole high-pass filter was adjusted so that the cut-off frequency was below the minimum visible fundamental frequency. The call duration was then calculated as the length of a window containing 95% of the total filtered signal energy. The subsequent analysis of the fundamental frequency showed that the distribution of the mean of the fundamental frequency was bimodal with the lowest point between modes at 2,300 Hz (Fig. 3). We used this point as a frequency threshold to separate calls into low frequency calls (LFC) and medium frequency calls (MFC). In addition, some calls had two independent time-frequency contours and these biphonic calls were termed two component calls (TCC) (Fig. 3).

Analysis of Acceleration Rate (Jerk)

To test for differences in the behavioral context of the signals, we computed the jerk signature within the 95% energy duration of the signal, given by the root-mean-square value of the differentiated three-axis acceleration of the whale, after decimating the accelerometer data to 25 Hz (Ydesen *et al.* 2014). We tested for differences in the jerk during signal production and within a period of equal duration immediately before the signal using a Wilcoxon signed-rank test. This was done for calls, rasps and buzzes separately. Then, we tested for differences in the magnitude of the jerk

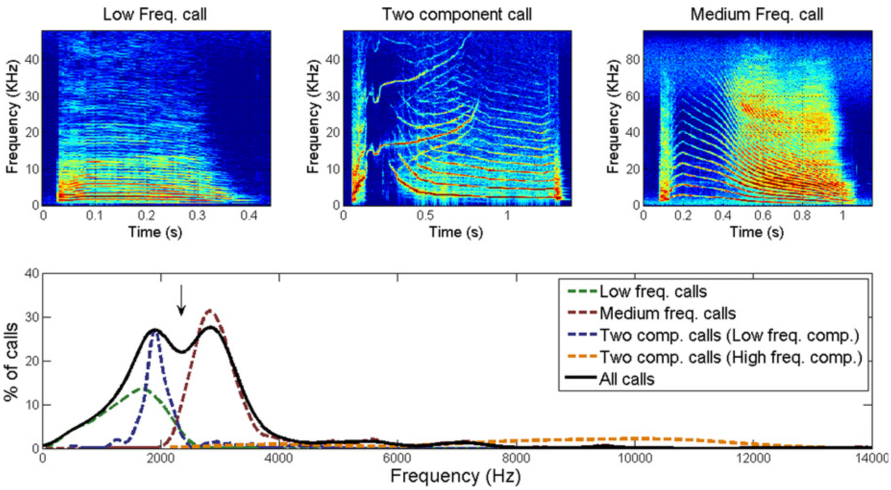

Figure 3. Types of calls produced by tagged short-finned pilot whales. The upper panels show the spectrogram (Hamming, 1,024 NFFT, 50% overlap) of a low frequency call, a two components call, and a medium frequency call. The lower panel shows the mean frequency of the fundamental of all calls grouped together (continuous black line) and divided by call type. The change in slope at 2,300 Hz (indicated with an arrow) was used to discriminate between low and medium frequency calls.

change among signal types using a Kruskal-Wallis test followed by a pairwise Dunn's test for comparisons between pairs of signals (rasps, buzzes, and calls) using the Benjamini-Yekutieli correction.

Effects of Depth

Differences in the mean depth of occurrence of rasps and calls were examined using a linear mixed-effects model with depth as an outcome and type of call as an explanatory variable. A second linear mixed-effects model was also created, adding an explanatory variable indicating whether the signals were calls or rasps. Each of these models was compared with a null model using a likelihood ratio test.

To investigate the effect of depth on the output level of both calls and rasps, we first estimated the energy flux density (EFD) as [AO + 10log(duration)] (Jensen *et al.* 2011) as a measure of the total energy in the signal. Then a linear mixed-effects model was constructed with EFD as response variable and the logarithm of depth, the signal type, and the interaction between these two as explanatory covariables. Linear mixed-effects models were adjusted for the random effect of individual and day in order to account for the potential dependence of the observations.

All statistical analyses were performed using R statistical software version 3.1.0 (http://www.R-project.org) using a level of significance at 5%. The results are expressed with 95% confidence interval (CI).

Results

Two pilot whale tagging cruises were conducted in autumn 2004 and spring 2008 totaling 8 d of effort. Each day, we tagged whales observed in close association at the surface (*i.e.*, less than some five body lengths among them), but we have no information about their long-term association. We tagged 27 whales (128 h of tag recordings), with an average of five tagged whales per day (2–6 whales per day) and an average of 3.6 h of tag recording duration. Out of 3,306 high quality signals recorded (excluding echolocation clicks), a total of 2,024 were manually classified as produced by the tagged whales, while 936 signals were classified as "focal" with the automatic method. Results for each tag deployment using both selection methods are summarized in Table 1. The number of vocalizations identified as produced by the tagged whales using the automatic method is on average 46% of those classified manually (Table 1). Figure 4 shows the depth distribution of the signals of all whales selected manually and with the automated method.

Tagged short-finned pilot whales produced a variety of vocalizations. Table 2 summarizes the main parameters of the signal types analyzed, including 94.4% of all signals classified as focal with the automatic method. These were calls with a rich harmonic content, rasps, and buzzes. The remaining 5.6% were classified as indeterminate sounds and not analyzed. Indeterminate vocalizations were those that did not fit in any of the main categories considered here.

The occurrence of the different signal types in each tag recording is shown in Table 1. Pooling all data, medium frequency calls (MFC) were the most abundant focal signal (34.4%), followed by rasps (28.1%), low frequency calls (LFC) (13.8%), and two components calls (TCC) (13.1%). Buzzes were relatively rare (5% of all focal signals), in part because most of them were associated with high-speed sprinting that increased the flow noise over the tag, reducing the SNR and thus preventing the

Table 1. Results summary for all tagged pilot whales analyzed ($n = 27$). The number of signals classified as produced by the tagged whale manually and using the automatic method (marked with an asterisk) is shown for each type of vocalization. “All nearby signals” indicates the total number of high quality vocalizations recorded in each tag, *i.e.*, with sufficient SNR to characterize the fundamental frequency or identify all clicks in the case of buzzes and rasps (see text).

Tag code	Duration (h)	# deep dives >500 m	# Medium freq. calls (MFC)	# Low frequency calls (LFC)	# Two component calls (TCC)	# Rasps	#Indeterminate sounds	# Buzzes	All nearby signals
pw04_295b	7.56	10	78/50*	2/0*	0/0*	66/21*	9/2*	14/3*	213
pw04_295f	3	5	35/34*	0/0*	4/3*	17/12*	3/0*	6/6*	73
pw04_296a	5.64	9	40/31*	46/31*	9/0*	39/14*	11/8*	12/7*	162
pw04_296b	2.32	2	2/2*	22/1*	0/0*	7/4*	3/0*	2/0*	51
pw04_296c	0.43	0	1/1*	0/0*	0/0*	1/0*	0/0*	0/0*	2
pw04_296d	5.07	12	24/11*	23/9*	4/0*	52/24*	4/0*	12/3*	160
pw04_297a	1.73	2	2/2*	4/1*	2/0*	7/3*	1/0*	1/1*	21
pw04_297b	1	1	1/1*	3/1*	0/0*	11/5*	1/0*	0/0*	22
pw04_297d	0.9	0	0/0*	0/0*	0/0*	2/2*	0/0*	0/0*	3
pw04_297f	16.2	12	43/15*	16/15*	0/0*	8/3*	27/2*	10/6*	107
pw04_297h	10.1	6	8/5*	14/5*	1/0*	29/5*	10/3*	47/15*	148
pw04_297i	5.4	2	31/27*	9/3*	2/0*	18/1*	21/9*	3/2*	92
pw04_297j	3.8	0	2/0*	0/0*	0/0*	2/1*	4/0*	0/0*	19
pw08_108d	8	8	19/18*	9/2*	0/0*	30/20*	9/1*	2/0*	130
pw08_110a	10	5	4/2*	12/1*	37/4*	9/2*	19/3*	18/0*	412
pw08_110b	4.26	4	82/41*	28/15*	1/0*	39/13*	11/3*	4/0*	191
pw08_110c	9.74	4	5/3*	3/2*	0/0*	8/1*	6/3*	0/0*	64

(Continued)

Table 1. *(Continued)*

Tag code	Duration (h)	# deep dives >500 m	# Medium freq. calls (MFC)	# Low frequency calls (LFC)	# Two component calls (TCC)	# Rasps	#Indeterminate sounds	# Buzzes	All nearby signals
pw08_110d	7.5	8	37/16*	35/19*	4/1*	40/28*	7/3*	4/0*	197
pw08_112a	0.74	1	1/1*	0/0*	0/0*	10/3*	0/0*	1/0*	19
pw08_112b	2.8	5	41/27*	3/2*	1/0*	25/15*	1/0*	1/0*	78
pw08_112e	1.12	2	16/9*	0/0*	0/0*	34/21*	2/1*	1/0*	57
pw08_113a	2.23	0	5/2*	0/0*	15/4*	4/1*	4/0*	0/0*	65
pw08_113b	2.58	1	11/5*	24/13*	34/8*	5/5*	12/4*	0/0*	187
pw08_113c	12.76	14	10/12*	3/2*	137/90*	114/56*	27/2*	7/3*	655
pw08_113d	1.48	0	1/1*	0/0*	0/0*	2/1*	1/1*	0/0*	9
pw08_115a	0.62	0	1/3*	12/7*	15/12*	8/2*	35/6*	0/0*	91
pw08_115c	1.78	0	5/2*	5/1*	1/0*	5/0*	13/2*	1/0*	78
Total	128.76	113	505/322*	273/130*	267/122*	592/263*	241/53*	146/46*	3,306

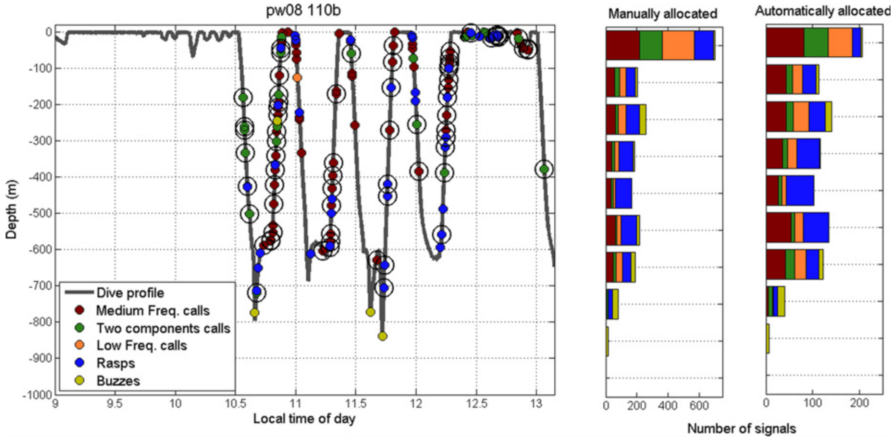

Figure 4. Example dive profile of a tagged short-finned pilot whale. The occurrence of vocalizations classified manually as produced by the tagged whale is represented by circles colored according to the signal type in the legend. Signals classified as focal using the automatic method are marked by a black circle. The histograms show the depth distribution of all signals classified as produced by the tagged whale manually and using the automatic approach (note the different scale in the x-axis), pooling the data from all tagged whales analyzed here ($n = 27$).

classification of many buzzes as focal with the automatic method. This effect of flow noise over the tag masks substantial parts of the buzzes affecting the characterization of their acoustic parameters.

For click-based signals, rasps were 2.51s (95% CI 2.28–2.75) shorter than buzzes ($P < 0.0001$). Buzz clicks were produced at a faster rate than rasps, with an average increase in ICI of 0.0181 s (95% CI 0.0143–0.0219; $P < 0.0001$) (Table 2, Fig. 2), resulting in a larger number of clicks per signal in buzzes (an average of 55 clicks more for every second of duration). Results also showed that the RMS output of buzzes were on average 5 dB (95% CI 2–8) lower than rasps ($P = 0.0005$).

The jerk changed significantly during the production of rasps, buzzes, and calls, and during periods preceding each signal, for the three signal types. However, the jerk difference was considerably higher during buzzes (pseudomedian of differences in jerk signature of 21.70, 95% CI 16.47–27.53, $P < 0.0001$; Fig. 2) than during rasps (pseudomedian of differences 0.65, 95% CI 0.28–1.03, $P = 0.0003$; Fig. 2) or during calls (pseudomedian of differences −0.16, 95% CI −0.26—0.06, $P = 0.0009$). When comparing the jerk difference among buzzes, rasps, and calls, results denoted significant differences between the change in jerk of all pairwise comparisons (Kruskal-Wallis test: $P < 0.0001$, Dunn's test: $P < 0.0001$ for all pairwise comparisons), with the jerk changing most during buzzes.

Calls were produced on average 105 m (95% CI 74–136) shallower than rasps ($P < 0.0001$), while there were no significant differences in the mean depth among the three call types ($P = 0.2067$). Out of the 27 whales, the 18 that produced 50 or more communication signals (rasps + calls) exhibited some variation in the use of rasps and calls with depth (Fig. 5). Nine whales, including almost all those with the greatest number of signals (mean of 180 signals per whale), showed a general decrease in calls with a concurrent increase in rasps with depth (Fig. 5A). Five individuals (mean of

Table 2. Main parameters of medium frequency calls (MFC), low frequency calls (LFC), two components calls (TCC), rasps (RS), and buzzes (BZ) identified as produced by the tagged whale with the automated method.

		MFC		LFC		TCC				RS		BZ	
Parameters	Unit	Median	(5%–95%)	Median	(5%–95%)	Median		(5%–95%)		Median	(5%–95%)	Median	(5%–95%)
Duration	s	0.2	(0.08–0.74)	0.35	(0.13–0.7)	0.54		(0.14–1.16)		0.37	(0.18–0.63)	2.7	(0.7–6.8)
Apparent output	dB re 1mPa	131	(114–149)	133	(116–147)	134		(116–158)		131	(118–148)	124	(106–139)
Interclick interval	ms	—	—	—	—	—		—		21	(11–50)	6	(4–10)
Depth	m	284	(3–635)	220	(2–632)	236		(4–706)		415	(69–682)	679	(154–839)
						Low freq. comp.	High freq. comp.	Low freq. comp.	High freq. comp.				
Fundamental frequency	kHz	2.9	(2.4–6.7)	1.7	(1.1–2.2)	2	9	(1.6–3.0)	(3.8–14.8)	—	—	—	—
n/no. tagged whales		322/25		130/18		122/7				263/25		46/9	

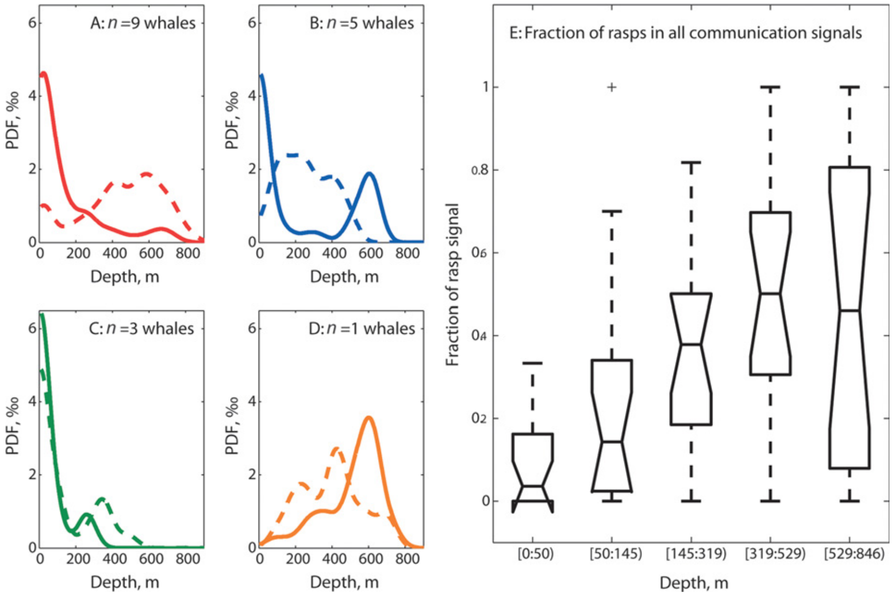

Figure 5. Patterns of vocal signaling as a function of depth for 18 free-ranging pilot whales producing 50 or more communication signals. (A)–(D) shows the probability density plots calculated using a 50 m Gaussian kernel for calls (continuous line) and rasps (dash line). (A) Nine whales, including almost all individuals with highest total number of signals (mean 180 signals/whale), exhibit a general decrease in call rate and a concurrent increase in rasp rate as a function of depth. (B) Five whales (mean 84 signals/whale) show a similar pattern, but with a secondary increase in the proportion of calls at greater depth (note that this does not take into account time spent at depth). (C) Three whales (mean 53 signals per whale) show an overall decrease in both the number of calls and rasps with depth, with very little emphasis on rasps. (D) A single animal (producing 62 signals) shows a general increase in both calls and rasps at depth. (E) Shows the fraction of rasps compared to the total number of rasps and calls for surface (0–50m) and for increasing depths, for all whales analyzed (*n*=18), with each depth bin containing *ca*. 25% of the total number of calls and rasps (note the general tendency to increase the use of rasps with increasing depth).

84 signals per whale) break this pattern due to a subsequent increase in call rate towards the deeper part of their dives (Fig. 5B). Three individuals (mean of 53 signals per whale) show a general decrease in both call and rasp use with depth, with very little emphasis on rasps (Fig. 5C); and one individual (62 signals) did not call near the surface and showed a general increase in both calls and rasps with depth (Fig. 5E). An analysis of how the ratio of rasps to total signals change with increasing depth indicates that the use of rasps change (Kruskal-Wallis test: $P = 0.0012$), with fewer rasps produced at the surface (Fig. 5E, bin 1) than at depth (4 bin 4 and 5 bin) (Dunn's test with Benjamini-Yekutieli adjustment: $P = 0.0005$ for bin 1 and bin 4 and $P = 0.0048$ for bin 1 and bin 5).

The relationship between the logarithm of depth and EFD for all signal types seemed to be approximately linear with two different slopes depending on the depth of the animal. Particularly, it exhibited a point of inflexion around 20 m and the models included therefore an interaction coefficient depending on whether the animal was above or below this point (Fig. 6). Results showed that above 20 m, the EFD for all signal types were highly variable in relation to depth. Below 20 m, rasps were longer and had a higher EFD (Fig. 6), although the EFD was not significantly related to increasing depth below 20m ($P = 0.4995$). In contrast to rasps, EFD significantly decreased with increasing depth for all call types. The average decrease in EFD per each 10% increase in depth was 1 dB (95% CI 1.0–1.5) for MCF, 2 dB (95% CI 1.3–2.2) for TCC and 1 dB (95% CI 0.6–1.4) for LFC (all $P < 0.0001$). The rate of change in EFD below 20 m was the same for MFC and LFC ($P = 0.3229$), whereas the rate of change in EFD was significantly faster for TCC compared to MFC ($P = 0.0245$, Fig. 6).

DISCUSSION

Short-finned pilot whales are deep-diving toothed whales (Aguilar de Soto *et al.* 2008) that produce tonal calls at depths of up to 800 m (Jensen *et al.* 2011). It has been shown that increasing hydrostatic pressure as a function of depth imposes an environmental constraint on sound production by limiting the duration and amplitude of tonal calls (Jensen *et al.* 2011). In contrast, the amplitude of echolocation clicks of other toothed whales does not seem to be affected by depth (Madsen *et al.* 2002, Johnson *et al.* 2004). It remains unclear whether burst-pulsed communication signals are affected by depth, and whether free-ranging toothed whales may be

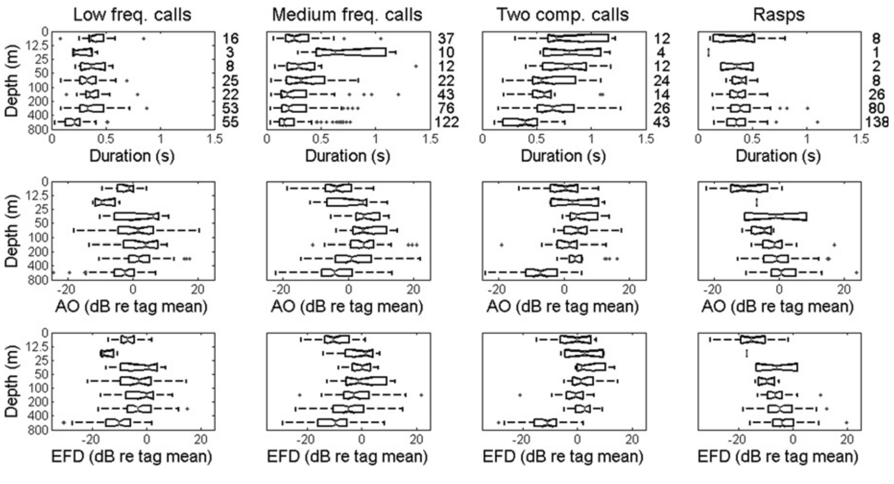

Figure 6. Duration, apparent output (AO), and energy flux density (EFD) of all focal calls types and rasps ($n = 130$ low freq. calls, 318 medium frequency calls, 122 two comp. calls, and 263 rasps) as a function of depth. The numbers on the right of the upper figures show the number of vocalization at each depth layer. AO and EFD were corrected for the potential effect of different tag placements by subtracting from each value the mean for all signals of the same type produced by that tagged whale. The box plots show the pooled data from all tagged whales grouped into geometrically increasing depth bins showing the 25th, 50th (median), and 75th percentile (left, middle, and right lines in the box) of the signals within each depth bin. Whiskers mark the lowest and highest data within 1.5 interquartile range (IQR). Values more than 1.5 IQR away from the median are represented as gray points.

influenced by depth effects in their choice of different types of acoustic signals during dives. Here we show that the energy content of rasps tends to increase, albeit not significantly, with increasing hydrostatic pressure. In the light of these results, we discuss how the effects of hydrostatic pressure in a pneumatic sound production system could contribute to explain the increase in the relative occurrence of rasps with respect to calls at depth. However, we see that rasps do not completely replace calls at depth, suggesting that the information encoded in calls is essential for some aspects of pilot whale social communication and that rasps may have different communicative functions than calls. Although other explanations are possible, we propose the hypothesis that short-finned pilot whales may be transmitting information to other diving members of their social unit with the deep low-output calls, which might be more detectable by members of a social group diving at the same time than by conspecifics at the surface.

Identification of Signals from Tagged Whales

The use of multisensor acoustic tags has increased significantly our knowledge about the foraging behavior and ecology of cetaceans (*e.g.*, Johnson *et al.* 2004, Aguilar de Soto *et al.* 2008, Arranz *et al.* 2011, Madsen *et al.* 2013). This is because echolocation signals produced by the tagged whales can be reliably identified and linked with their behavioral context, inferred from depth and accelerometers in the tag. However, the use of tags in vocal communication studies has been limited by the difficulties in distinguishing the vocalizations emitted by the tagged animal from those produced by nearby conspecifics (Johnson *et al.* 2009, Jensen *et al.* 2011). Most studies have circumvented the problem by pooling communication sounds from tagged whales and nearby conspecifics (Matthews *et al.* 2001, DeRuiter *et al.* 2013, Sayigh *et al.* 2013, Risch *et al.* 2014). In studies where knowing the identity of the caller is important, researchers have implemented criteria based on a combination of cues, for example call received level (RL) and visual estimations of the proximity of conspecifics (Parks *et al.* 2010). Other studies are robust to some bias and have used call RL, angle of arrival (AOA), and vertical separation between the tagged whale and the social group (Jensen *et al.* 2011). Although these cues have proven to be relatively effective when animals are isolated, they may fail in social situations with multiple interacting animals, leading to a potential overestimation of the number of vocalizations being produced by the tagged individual in these contexts.

In contrast to calls, broadband high-frequency echolocation clicks produced by deep-diving toothed whales are, in most cases, clearly distinguishable from those produced by untagged conspecifics. These clicks provide a measure of the expected AOA for focal sounds (see Fig. S1), however, the estimated AOA of focal clicks oscillates as a result of head movements (Wisniewska *et al.* 2012) or potential beam steering (Moore *et al.* 2008). More dramatic changes to the AOA occur when suction-cup attached tags slide along the body of the animal. This change of position can be abrupt (Fig. S1) or the tag may slide progressively throughout a deployment. To reliably identify focal signals, we need to incorporate a dynamic AOA criterion to capture potential changes in tag position throughout a deployment. This was achieved here by defining the threshold of AOA expected for a focal vocalization according to the AOA range of the previous click series. To further reduce the risk of including vocalizations from untagged whales in the analysis, we added a further filter in the classification of focal signals, based on the identification of a stereotyped vocal pattern (signals emitted in the first second of pauses in clicking) (Fig. 1). We cannot dismiss the possibility that an untagged whale follows a tagged whale in tight formation, vocalizing with a RL and AOA consistent with the signals of the tagged whale. However, it seems improbable that an untagged whale dives without producing usual clicks, and then synchronizes its vocal output to emit communication signals within 1 s of the end of a click series produced by the tagged whale. This scenario would not be consistent with the behavior observed in tagged pilot whales producing usual clicks both in the descent and ascent phase of dives (Aguilar de Soto *et al.* 2008).

It is unavoidable that methods using a given vocal pattern as cue for sound source will result in a nonhomogeneous time distribution of false negatives in signal allocation. Particularly, the estimated difference in the number of vocalizations identified in this study as produced by the tagged whales manually and using the automatic method averaged 46%. While the automatic method is clearly underestimating signal production near the surface, where click sequences are scarce, an unknown number of false positives are expected when allocating signals manually. Here, identifying a subset of the recorded vocalizations that can be attributed to tagged whales with high certainty allowed us to quantify signal parameters from the focal animal and relate the occurrence of signals with the movements of the animal on which to base interpretation of the functionality of the signals.

Characteristics of Acoustic Vocalizations

Most characterizations of delphinid vocalizations have been based on aural impressions and visual inspections of spectrograms, assuming that repertoires consist of acoustically discrete signal types (Tyack 1986; Ford 1989, 1991; Herzing 1996). Here, we parsed rasps and buzzes using aural differences which were subsequently supported by differences in duration, ICI and behavioral context. Distinguishing between call types according to their pulsed/tonal structure is more challenging. Human aural discrimination is probably not meaningful for odontocetes with faster auditory temporal processing abilities (<1 ms) than other mammals, probably as a result of the short processing time and high temporal resolution required for echolocation (*e.g.*, Au *et al.* 1988, Au 1993, Mooney *et al.* 2009). Here, we classified calls using an observed threshold separating two modes in the mean fundamental frequency of the call (Fig. 3). A large percentage of MFC (39%) showed gradations from high-repetition pulsed trains (frequently at the beginning of the call) to a continuous, near-sinusoidal signal, which is consistent with the findings of Sayigh *et al.* (2013) in short-finned pilot whale calls from Bahamas as well as in some other delphinids (Murray *et al.* 1998). This gradation from pulsed to tonal sounds supports the hypothesis that the fundamental frequency contour is formed by pneumatically induced tissue vibrations as shown for bottlenose dolphin whistles (Madsen *et al.* 2011).

The structural features of calls may have important implications for acoustic communication at depth. Air volumes required to produce a continuing vibration of the phonic lips in a tonal sound are presumably higher than those required to produce a pulsed vocalization of the same total duration. Here, all calls showed a significant decrease in energy content with increasing depth, as observed previously for tonal signals (Jensen *et al.* 2011). Interestingly, two-component calls were more affected by depth than single-component calls (Fig. 6). This might be a natural consequence of pneumatic limitations at depth since calls with two simultaneous frequency contours inevitably require activation of (and air flow through) both pairs of phonic lips. However, most TCC were produced by one animal (pw08_113c), so it cannot be excluded that the steeper decrease in EFD with depth observed here may be a consequence of some individual characteristic, such as body size.

Rasps May Offer a Click-based Mode of Communication

Rasps are discrete high repetition rate click series that superficially resemble foraging buzzes. However, rasps are significantly shorter and the clicks within them are produced at a slower rate than buzzes. Also, rasps lack the dramatic changes in output level and acceleration rate that are related to buzzes, prey-capture attempts, in other species (Miller *et al.* 2004, Madsen *et al.* 2005*a*, Johnson *et al.* 2006, Aguilar Soto *et al.* 2012). Here, we observed significant and large increases in jerk during buzzes but very little changes in jerk during rasps and calls, suggesting that rasps, as well as calls, are not related to prey capture events. It is unclear whether the small jerk changes found in rasps and calls are related to air movement or other byproducts of vocalization. Furthermore, short-finned pilot whales tend to produce rasps in a similar pattern as calls, *i.e.*, preceded by a pause breaking the continuum with the previous series of echolocation clicks, and be more abundant during the ascent phase of the dives (Fig. 4). In addition, pilot whales reduce the apparent output of their buzz clicks, this is consistent with animals targeting one prey and reducing clutter for the final prey capture attempt, as proposed for other species (Madsen *et al.* 2005*a*, Johnson *et al.* 2006). In contrast, the higher output of rasps than buzzes in all tagged whales is consistent with rasps being used for communication and thus maintaining a high detection range. These differences in the behavioral context of rasps and buzzes lead us to hypothesize that rasps may be related to a form of social communication in short-finned pilot whales.

The increased occurrence of rasps at depth (Fig. 5E) suggests that these signals may play an important role for information transfer by short-finned pilot whales performing routinely deep dives. In contrast to the reduction in duration and output level with depth observed in tonal calls (Jensen *et al.* 2011), and all call types studied here (Fig. 6), the EFD of rasps is not reduced at depth but has a tendency to increase (Table 2, Fig. 6). This supports the hypothesis that rasps are not limited by hydrostatic pressure and may explain the increasing use of rasps in short-finned pilot whales that hunt prey at mesopelagic depths. Click-based communication signals such as rasps may have different communicative functions than calls, and may also help whales to exchange information at depths where tonal sound production is challenged by hydrostatic pressure, since less air volume is required to produce pulsed sounds (Ridgway and Carder 1988). Switching partly from calls to rasps has implications for the potential audience, since the higher frequency content of rasp clicks makes them more directional than calls. This may result in rasps having a better signal to noise ratio (SNR) than calls at any given distance for conspecifics located in front of the source animal, and a lower SNR for conspecifics located elsewhere, decreasing the risk of signal interception by nonintended receivers (Klump and Shalter 1984, Brumm and Todt 2003). It is unknown if whales may purposely take advantage of the higher directionality of high frequency click-signals, or just endure the loss of omnidirectionality as a pay-off for being able to produce high output signals at depth.

Maintaining Social Structure Using Different Communication Modes

Pilot whales produce rasps and different call types during their deep foraging dives, with some calls produced in the deepest part of the dives (Jensen *et al.* 2011, this paper). While the EFD of rasps is not limited by depth, it is difficult to evaluate the potential audience of calls and rasps without measuring background noise and sound propagation in the area. Here we see that pilot whales keep using calls at depths of at least 700 m (Table 2, Fig. 4), but the low level of these deep calls makes it likely that they are better detected by diving conspecifics than by whales at the sea surface. Aguilar de Soto (2006) showed that short-finned pilot whales in the same study area had a variable diving coordination. Many whales tagged while in close vicinity at the surface dived asynchronously, while one trio dived at the same time but separated some 300 m during the deeper part of dives 600–1,000 m deep (Aguilar de Soto 2006). Whales diving simultaneously would thus have higher probability of detecting low output deep calls than more distant whales at the surface.

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SUPPORTING INFORMATION

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Figure S1. Example of the difference in variations of angle of arrival (AOA) of clicks recorded in tags attached to the whale in different body positions, and how AOA can change abruptly during a tag deployment. (A) and (C) show example profiles of deep dives performed by two whales with tags attached to different parts of the body: (A) pw08_110c with the tag attached low and by the side of the dorsal fin; (C) pw08_110d with the tag located on top of the body and in front of the dorsal fin. The occurrence of clicks produced by the tagged whales is shown as black dots in the dive profile. (B) and (D) show the variations in the AOA of the clicks for each dive. The colors represent the fit quality of the AOA cross-correlation estimate (1 = good, 0 = bad), showing that most clicks are high quality. A shift of the pw08_110d tag position, coincident with a sprint performed by the whale in the deepest point of this dive, is shown in the AOA and marked by a black arrow. Note the differences in the variability of the AOA between the two tagged whales, and for pw08_110d before and after the tag shift. (E) shows the average power spectrum of 10 focal and 10 presumably on-axis nonfocal clicks, randomly chosen from different tags sampling at 192 kHz. Note that focal clicks have more energy at low frequencies (here 1–8 kHz) than nonfocal clicks, due to the effect of the sound body transmission from the head to the tag located on the back of the whale, off-axis (Johnson *et al.* 2009).