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Recordings from acoustic tags show that five Blainville's beaked whales produced mid-frequency broadband sounds on all of their deep dives, with each sex producing two different sound types. These broadband sounds are atypical of the regular echolocation sounds previously described for this species. One male produced a total of 75 sounds over four dives, between the depths of 109 and 524 m, and four females produced a total of 71 sounds over 18 dives, between the depths of 305 and 1289 m. Ninety-six per cent of the male sounds and 42% of the female sounds were produced before the onset of foraging echolocation sounds, and all were produced before the deepest point of the dives. Apparent source levels of the sounds ranged from 124 to 132 dB re 1 μPa (RMS) @1 m. These sounds may be candidate communication signals, with their production timed to mitigate the risk of both predation and hypoxia.

Keywords: beaked whales; communication; acoustic; sonar signals; broadband

Introduction

Blainville's beaked whales (*Mesoplodon densirostris*) spend large amounts of time submerged at depths where visibility is very limited (Johnson et al. 2006a; Baird et al. 2008). They dive in small groups [mean group size = 4.1, standard deviation (SD) = 1.9; Claridge 2006] and have an unusual social structure in which individuals associate as a group for months at a time (Claridge 2006; McSweeney et al. 2007). Some cetacean species, such as killer (*Orcinus orca*) and sperm (*Physeter macrocephalus*) whales have a stable matrilineal social structure, preserving associations for decades (Whitehead 2003). In contrast, smaller dolphins have a fission–fusion social structure (Connor et al. 2001), where associations can change minute by minute. Both types of social structures are apparently mediated by acoustic communication signals that vary in conjunction with that social environment, namely group dialects and individual signatures for these two cases (Tyack and Sayigh 1997). Maintaining group cohesion over timescales of months as Blainville's beaked whales are capable of doing likely requires some mechanism for remaining in contact outside visual range. The most likely candidate for maintaining group cohesion is some form of acoustic communication, given its ubiquitous occurrence in other odontocetes.

All odontocetes make echolocation sounds, but non-echolocation sounds have only been described for Blainville's beaked whales twice (Caldwell and Caldwell 1971; Aguilar de Soto et al. 2011; for similar reports of Baird's beaked whales, see Dawson et al. 1998). Most recently, Aguilar de Soto et al. (2011) reported rasps, a series of frequency-

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modulated clicks with short inter-click intervals (ICIs) occurring twice on average twice per dive, and two whistles from a sample of 102 h of acoustic data recorded from the digital recording tags placed on seven Blainville's beaked whales in the Canary Islands, Spain.

This study identifies sounds produced by Blainville's beaked whales that are plausible candidates for communication signals, as they are used by all individuals studied and on all their deep dives, unlike rasps (Aguillar et al. 2011), which are not ubiquitous to all deep dives and therefore may be used for a more specific function.

Materials and methods

Acoustic recording tags (DTags; Johnson and Tyack 2003) sampling at a rate of 192 kHz were attached using suction cups to five free-ranging Blainville's beaked whales during five separate encounters between 2006 and 2007, at the Atlantic Undersea Testing and Evaluation Centre (AUTEC) test range in the Tongue of the Ocean off Andros Island in the Bahamas. The five encounters consisted of three different group compositions; one encounter comprised two adult females, a juvenile and a calf, another encounter consisted of a single adult female and the third encounter involved two adult females and an adult male, resulting in four tags on adult females and one tag on an adult male (Table 1). The five tags recorded 89.46 h of acoustic data that were visually and aurally processed by two independent observers using Adobe Audition and Matlab 6.5 (Mathworks, Cambridge). Sounds were identified from spectrogram visualizations of the acoustic records and their times of occurrence used to extract the corresponding depth data from the tag records. All sounds with the exception of regular echolocation sounds, buzz clicks (a series of clicks with extremely short ICIs and little frequency modulation) and rasps (Aguilar de Soto et al. 2011) were noted. As the DTags had two hydrophones, the time difference of arrival of sounds at the two receivers can be used to calculate the angle of arrival of acoustic signals at the tag (Johnson et al. 2009; Jensen et al. 2011). Consistency in the direction a sound is arriving from helps determine whether the sounds are coming from the tagged animal. The angle of arrival was measured for each sound where possible. Overlapping sounds (conspecific echolocation sounds or flow noise) or a poor signal-to-noise ratio (SNR) meant that it was not possible to obtain this measurement for every sound of interest. In addition, we accessed archive data recorded during the dive times of the tagged whale groups from 82 bottom-mounted hydrophones on the AUTEC tracking range (Moretti et al. 2006) to search for detections of other cetacean species within an approximate 6 nautical mile radius (three hydrophone range) of the tagged whale group. We used the software Raven (version 1.4, Cornell Lab of Ornithology, 2005), with spectrogram settings of 1024-point fast Fourier transform (FFT), Hamming window and a 512-point overlap, to measure

Table 1.   Details of tag deployments.

Tagged animal	Others in group	Date	Recording duration (h:min:s)	Number of dives >100 m
Md539 (AM)	AF + AF	5 September 2007	17:36:41	4
Md518 (AF)	AF + juvenile + calf	23 October 2006	19:23:20	4
Md524 (AF)	None	15 August 2007	17:23:18	4
Md515 (AF)	AF + AM	2 September 2007	17:28:32	4
Md527 (AF)	AF + AM	5 September 2007	17:35:31	6

Notes: The catalogue number of the tagged animal is provided, with age/sex class in parentheses (AM, adult male; AF, adult female).

the features of sounds recorded by the tags directly from the spectrograms. The highest frequency with significant energy ("high frequency" in Raven, henceforth called maximum frequency, in kHz), duration in seconds and the ICI from the start of one click to the start of the next click, where clicks could be clearly identified in the signal waveform, were measured for each sound. Tag flow noise at low frequencies (Johnson et al. 2009) overlapped the lower end of the signals' bandwidth, which prevented us from making sensible bandwidth, mean and minimum frequency measurements of the signals. Finally, we measured the root mean square (RMS) for the received levels of the sounds in Matlab. Apparent source levels of the sounds were calculated following the method of Aguilar de Soto et al. (2011), where "apparent source levels were back-calculated from the signal at the tag assuming spherical spreading over the 2 m separation between the tag and the sound source" (p. 10). This method only measures apparent levels in one direction from the sound source, and we were therefore unable to assess whether the production of the sounds was omnidirectional or otherwise.

Results

We identified four different types of sounds in the recordings that are not previously described as echolocation sounds, buzzes or rasps, comprising 146 sounds in total. Two types, A and B, were produced by the adult male (Figure 1), and two others, C and D, by the adult females (Figure 2). Type A sounds are broadband signals with strong amplitude modulation and a sharp onset, with most energy below 15 kHz (Figure 1(i)). Type B sounds have an increasing bandwidth and are a set of clicks, on average nine, with a large ICI (0.17 s) relative to buzzes (0.012 s; Johnson et al. 2008). Type C sounds are broadband with amplitude modulation, with the pulses having apparent energy peaks at approximately 5, 20 and 45 kHz. Finally, type D sounds are similar to type A sounds, but with approximately a third of the bandwidth and with almost all energy during the first half of the sound, and below 30 kHz. The pulses that make up these sounds show very different frequency content, with little or no frequency modulation, compared to regular echolocation pulses as recorded on the tags (Figure 3), and are also an order of magnitude lower in amplitude than the regular echolocation pulses.

Evidence that the tagged animals were the source of these sounds was derived from both the angle-of-arrival results and the fixed AUTEC hydrophone records from the area. The angles of arrival for all the sounds that were measured were highly consistent with each other and with other sounds from the tagged animal. Eighty per cent of type A and 100% of type B sounds had an angle of arrival within 15° of the mean for each of these types. Eighty per cent of type A and 83% of type B sounds also fell within 15° of the mean of the tagged animals' echolocation sounds, of which five were selected from the first bout of echolocation recorded during each dive. The sounds were therefore consistently arriving from the same direction throughout. The mean angle of arrival for both type A and type B sounds also fell within 1° of the mean angle of arrival for a random selection of echolocation buzzes and rasps from the tagged animal. One of the female tags had only one working hydrophone channel, therefore making it impossible to analyse the angle of arrival of sounds from that tag. However, 75% of all type C sounds where the angle of arrival could be measured arrived within 15° of the mean of those sounds, and the angle-of-arrival measurements of all type C sounds were within 2° of the closest measurable tagged animal sounds. Type D sounds had too low an SNR to measure the angle of arrival accurately. Interestingly, 77% of type D sounds were followed by type C sounds with an average delay of only 1.2 s, suggesting some relationship between these two sounds.
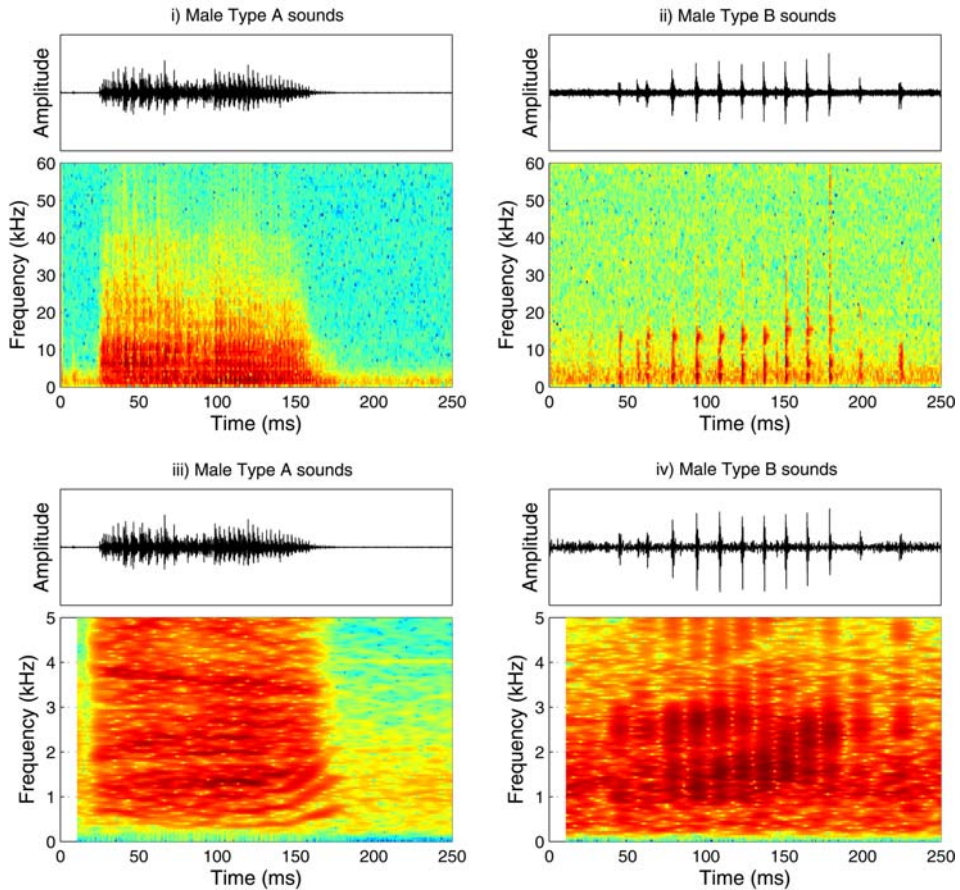
Figure 1.   Waveforms and spectrograms for both the male sounds, A and B, showing both the full frequency bandwidth with a high-pass filter of 1 kHz for each of the sounds; (i) male type A sound and (ii) male type B sound (Hamming 256 FFT, 64 overlap, 192 kHz sample rate), and only the frequency bandwidth between 1 and 4 kHz; (iii) male type A sound and (iv) male type B sound (Hamming 4096 FFT, 4000 overlap, 192 kHz sample rate).

On three of the four tagged male dives, delphinids were detected within an approximate 6 nautical mile range on the AUTEC hydrophones (see Supplementary Material, available online). These detections were purely acoustic, and no species confirmation was obtained visually, so it was not possible to accurately locate or identify the source groups. No characteristic delphinid signals (tonal whistles or broadband echolocation clicks) were detected either aurally or visually on any of the tag recordings analysed. Furthermore, on one of the male dives, there were no delphinids detected within 6 nautical miles, but both type A and type B calls were recorded on this dive at the same amplitude as the other dives. During 13 of the 18 tagged female dives, there were no other species detected within 6 nautical miles of the tagged group on the AUTEC hydrophones. On the remaining five dives, delphinids were detected within an approximate six nautical mile range on the AUTEC hydrophones (see Supplementary Material, available online), but sounds of type C and type D were recorded at similar amplitudes on dives with and
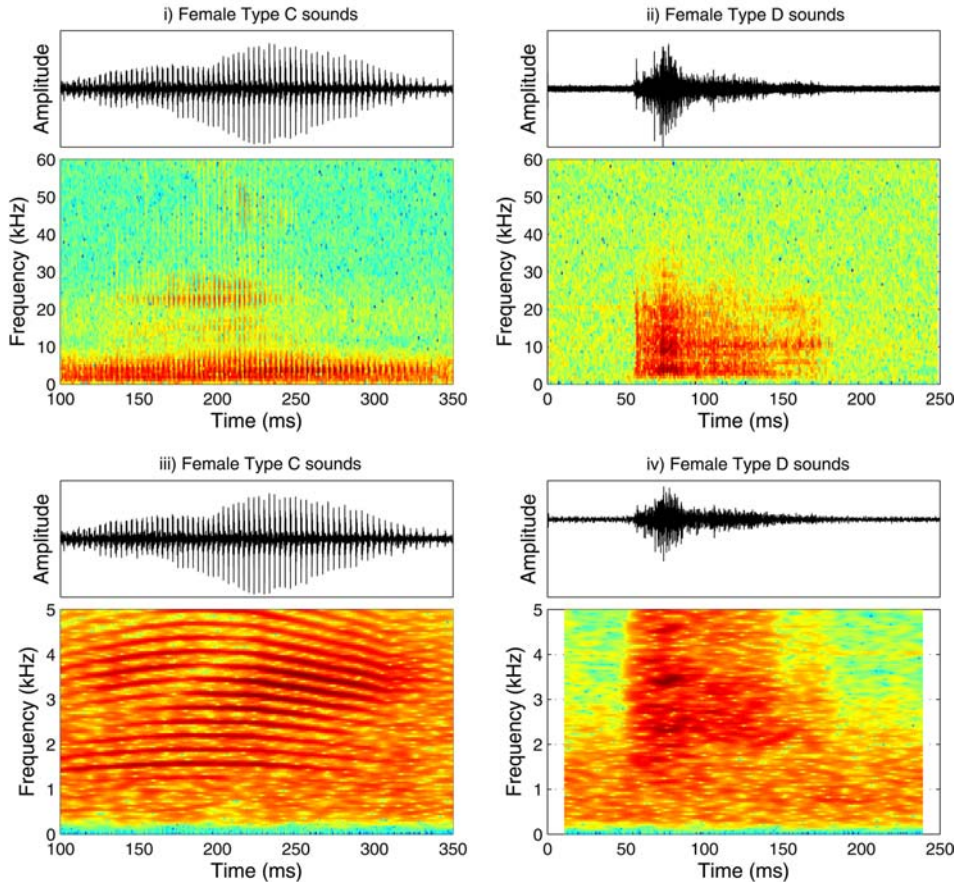
Figure 2.   Waveforms and spectrograms for both the female sounds, C and D, showing both the full frequency bandwidth with a high-pass filter of 1 kHz for each of the sounds; (i) female type C sound and (ii) female type D sound (Hamming 256 FFT, 64 overlap, 192 kHz sample rate), and only the frequency bandwidth between 1 and 4 kHz; (iii) female type C sound and (iv) female type D sound (Hamming 4096 FFT, 4000 overlap, 192 kHz sample rate).

without overlapping delphinids, so there was no pattern of heterospecific presence consistent with them being the source of the sounds we describe.

A further possibility is that the sounds represent flow noise associated with the animal making sharp manoeuvres in the water. The tags have an accelerometer that records the animal's movement on three orthogonal scales, pitch, roll and heading (Johnson et al. 2006a). Inspection of the dive time–depth profiles of each animal during production of these sounds, however, showed no relationship between occurrence of the sounds and strong variation in the animal's pitch, roll or heading (Figure 4(iii), (iv)).

Of the sounds recorded, 96% of those from the male and 42% of those from the females were recorded before the onset of regular echolocation, and the remainder were made between series of echolocation sounds during the foraging phase of the dives (Table 2). The sounds we report occurred between 109 and 1289 m of depth, and always on the descent phase before the deepest point of the tagged animal's dives. The male produced 66 type A sounds and 9 type B sounds over four dives. The four females
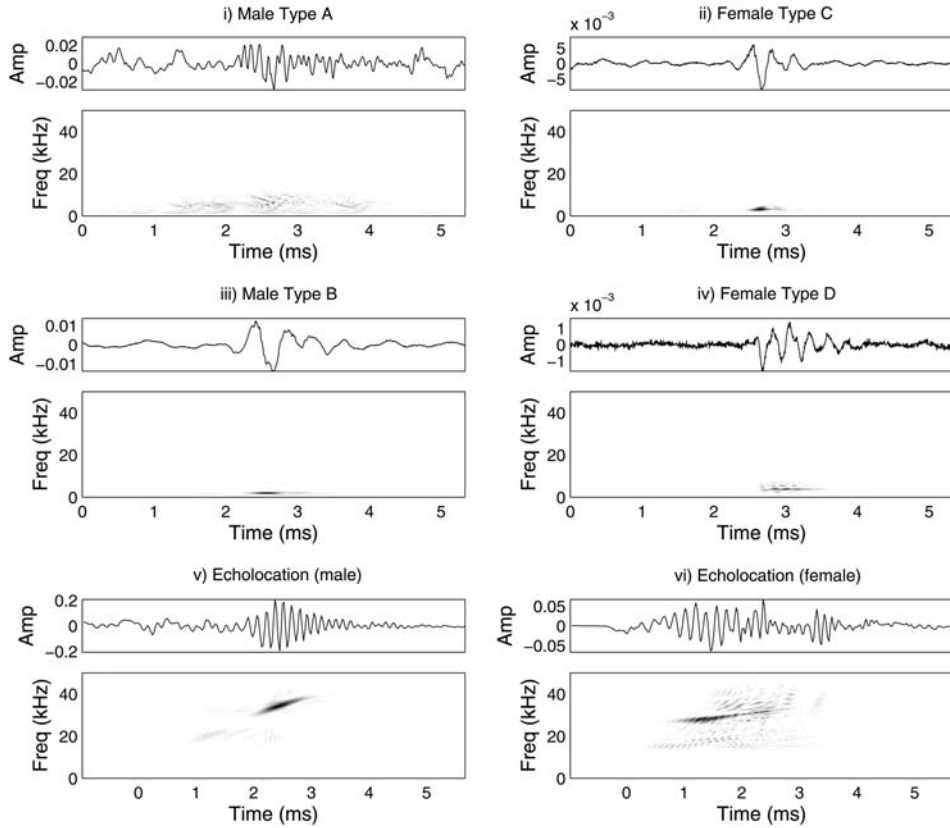
Figure 3.   Waveforms and wigner plots for all four sound types, A–D, showing a single pulse from each sound, and a single click from a male and female, with a high-pass filter of 1 kHz for each of the sounds; (i) male single pulse from type A sound, (ii) female single pulse from type C sound, (iii) male single pulse from type B sound, (iv) female single pulse from type D sound, (v) male single echolocation pulse and (vi) female single echolocation pulse.

produced a total of 38 type C and 33 type D sounds over 18 dives (Table 3). The highest broadband RMS apparent source level for type A sounds, the loudest of the four types recorded, was 132 dB re 1 μPa @ 1 m, and 130 dB for sound type B. The broadband RMS apparent source level for type C sound was 124 dB and for type D sound was 125 dB. These levels should be regarded as indicative only, as there is no information available on signal directionality, and low-frequency water flow noise from the tag itself (Johnson et al. 2009) overlaps the frequency bandwidth of the signals. These sounds do not correspond with the rasps or whistles described by Aguilar de Soto et al. (2011), as they are much shorter in duration (mean duration 0.23 s vs. rasp mean duration of 0.6 s), and have distinctive frequency content, although they are similar in being broadband and amplitude modulated. We did not detect any whistles in our recordings.

Discussion

We have described four distinct types of sounds recorded from tags placed on free-swimming Blainville's beaked whales. The first question to address is whether these
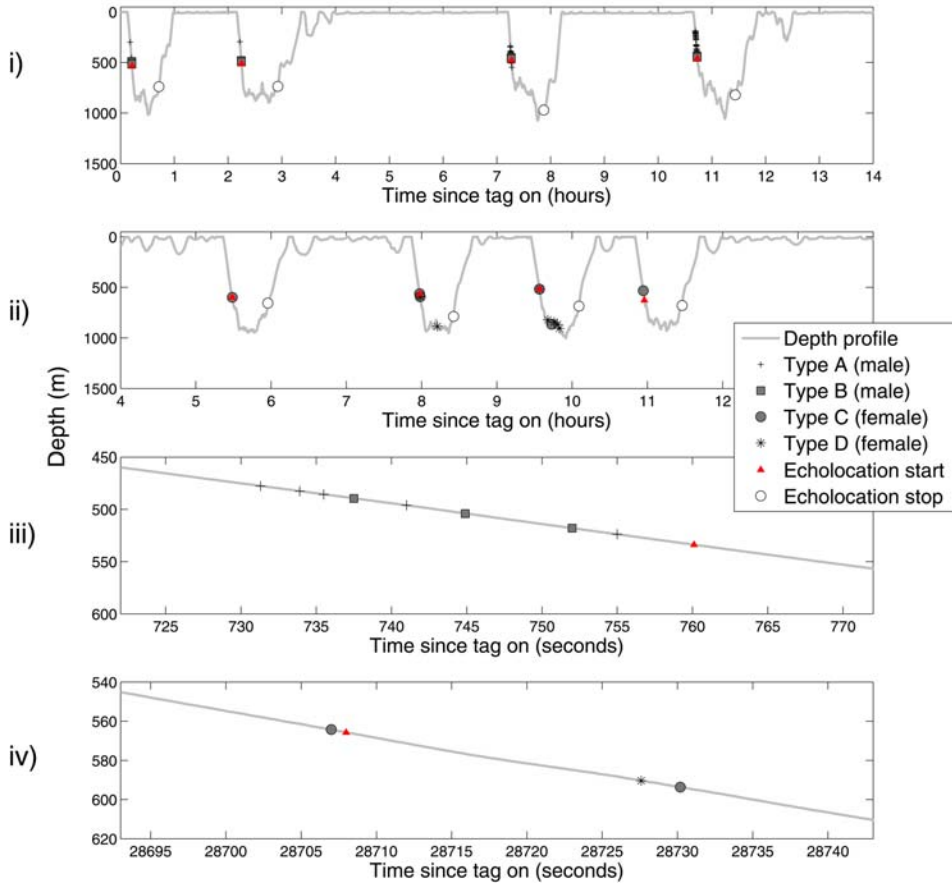
Figure 4. Time–depth profile plots showing the distribution of sound production for (i) the adult male (Md539, tag attachment at 14:31:23 local time), (ii) one of the adult females (Md527, tag attachment at 09:55:17 local time) and (iii, iv) fine-scale plots of the first dives by the (i) male and (ii) female, respectively.

Table 2. Number of each sound type produced, by animal, relative to the commencement of regular echolocation clicking.

Tagged animal	Sound type	No. before clicking commences	No. after clicking commences	Total
Md539 (AM)	A	63	3	66
	B	9	0	9
Md518 (AF)	C	3	0	3
	D	1	0	1
Md524 (AF)	C	6	12	18
	D	8	11	19
Md515 (AF)	C	4	7	11
	D	3	3	6
Md527 (AF)	C	4	2	6
	D	1	6	7
Total		102	44	146

Table 3.   Summary of call parameters and production depth by animal and sound type, showing SD for each in the same units.

Tagged animal	Sound type	Maximum frequency (kHz)/(SD)	Duration (s)/(SD)	Mean ICI (s)/(SD	Mean depth (m)/(SD)
Md539 (AM)	A	60.3/(17.4)	0.14/(0.05)	–	298/(118)
	B	53.2/(20.4)	0.16/(0.03)	0.017(9)/(0.002)	417/(99)
Md518 (AF)	C	74.0/(8.9)	0.33/(0.05)	–	475/(121)
	D	40.3/(NA)[a]	0.14/(NA)	–	533/(NA)
Md524 (AF)	C	54.9/(17.4)	0.47/(0.12)	–	522/(99)
	D	30.2/(7.5)	0.16/(0.04)	–	509/(107)
Md515 (AF)	C	37.8/(20.7)	0.27/(0.06)	–	751/(224)
	D	21.9/(6.8)	0.18/(0.06)	–	803/(296)
Md527 (AF)	C	63.4/(16.1)	0.36/(0.10)	–	612/(129)
	D	25.8/(12.9)	0.09/(0.03)	–	776/(156)

[a] Only one type D sound was recorded from this animal.

sounds were produced by the tagged animal, by other beaked whales or by heterospecifics. Our angle-of-arrival analysis shows that the sound sources were at a consistent angle relative to the axis of the two fixed-tag hydrophones, which was also consistent with other tagged animal sounds (identifiable because echolocation calls from tagged animals typically contain low-frequency energy from tissue transmission that is not present in calls received from non-tagged animals; Johnson et al. 2006). Although some of the recordings were made when delphinids were detected in the same area by other hydrophones, the pattern of their presence in relation to the occurrence of the sounds is incompatible with the notion that the sounds came from the delphinids, and we did not detect any other characteristic delphinid sounds on the recordings. We are therefore confident that these sounds were made by the Blainville's beaked whales that carried the recording tags.

It is unlikely that these sounds are related to foraging, which is known to rely on echolocation sonar signals, as the majority of the male sounds and almost half of the female sounds fell outside of the regular echolocation period, and none of the sounds resemble any known biological echolocation signal. The functions of all beaked whale sounds are subject to speculation to some extent. However, for previously described beaked whale vocalizations, which are regular and buzz clicks, echolocation is highly likely to be the function. The recording of echoes from presumed prey items and a temporal production pattern homologous with echolocation in captive dolphins and bats (Griffin 1958; Au 1993), where direct observation of foraging is possible, provide a high level of confidence that echolocation to find prey is the primary function of most beaked whale signals studied to date (Johnson et al. 2004). The function, if any, of the sounds we report is unknown. It is possible that they are purely physiological rather than communicative in nature and may be related to pressure changes experienced as the animal dives, or the movement of air within the nasal passages in preparation for producing echolocation signals. This seems plausible for the female type D sounds that have a low SNR, occur just prior to type C sounds and aurally sound like recycling of air similar to that observed in sperm whales (Norris and Harvey 1972). We consider this unlikely, however, for the other three sound types because production begins beyond the region of the water column where pressure changes are greatest, and because there is no reason, under this hypothesis, to predict the differences between the male and females that we observed. Therefore, we argue it is most likely that these sounds have a communicative function, although the data we present here cannot prove this. Of course, sounds with a physiological origin can still have a communicative

function, serving as cues and raw material for signal evolution. These hypotheses need not be mutually exclusive either, as the sounds could have multiple functions: physiological and communicative (Gould and Lewontin 1979). As previously referred to, Blainville's beaked whales maintain stable small groups for months at a time, they also forage together, diving and surfacing in synchrony. They may, however, display some special separation during actual foraging, and it may be that regular foraging echolocation sounds hold enough information to maintain group cohesion once foraging has commenced, and therefore additional communication would happen largely outside the foraging period. The female with a calf produced far fewer calls per dive (on average one per dive compared to an average of five per dive for the other tagged females), possibly because any separation between her and her calf during a dive would be limited, and therefore the need to produce communicative sounds reduced.

Much of the behaviour of beaked whales suggests that they minimize, to the extent possible in an air-breathing mammal, the amount of time they spend close to the surface. Neither do they appear to forage in the top 200 m (Johnson et al. 2004). This can be understood by considering beaked whale diving behaviour as an optimization across a three-way trade-off between the risks of oxygen starvation, predation and nutritional starvation. The temporal patterns of occurrence of signalling in birds exemplified by the dawn chorus have been similarly attributed to higher energy levels in individuals at dawn (Whitten 1982), optimal sound propagation circumstances due to lower temperatures at dawn (Brown and Handford 2003) and taking advantage of a time when it is too dark to forage or to be located by predators (Catchpole and Slater 1995). Overall therefore, dawn may be a good time to sing because it simultaneously minimizes risk of predation and lost foraging opportunities while taking advantage of the behavioural flexibility offered by relatively high energy levels. Where in space and time would it make sense for beaked whales to produce communicative sounds? It is reasonable to expect beaked whales to organize signal production according to similar principles: when energy or oxygen levels are high, outside of a foraging period, and at depths that are sufficient to avoid predation. Blainville's beaked whales only produce regular echolocation signals at depths below 200 m (Johnson et al. 2004), possibly because this is the only region in which these animals can forage successfully, but also as an anti-predation precaution, because the signals are potential cues for killer whales and sharks in the upper water column (Madsen et al. 2005; Morisaka and Connor 2007).

The sounds observed in this study occurred at a point within the dive cycle when all of these risks were likely to be minimized simultaneously. The whales showed little evidence of deviation in the dive profile associated with signal production (Figure 4(iii), (iv)), and they were produced at depths where the animals were too deep for their sounds to be a useful cue for predators at the surface. They also occurred in the descent phase of their deep foraging dives, when these animals have greater surplus oxygen reserves than at the equivalent depth on the ascent, and thus the largest margin for behavioural flexibility, even if sound production itself is not demanding on oxygen supplies. During the ascent, animals were likely not vocalizing due to trade-offs between the risks of predation and hypoxia. Ascending to replenish oxygen would not be a time to alert a predator to their presence, given the response options for avoiding the predators are more limited because of the risk of hypoxia. Consequently, we suggest that if vocal communication was to occur among beaked whales, then it would most likely happen between the depth that is likely to represent a limit for surface dwelling predators and the depth at which there is greatest prey density, that is during the descent phase of foraging dives. The sounds observed in this study fit this prediction.

Finally, although we sampled one male only, it is clear that this animal made many more sounds than the females, and the sounds made by the male in our study were louder, particularly type A, than those made by the females. Aguilar de Soto et al. (2011) also reported whistles only made by a male. Future work could attempt to ascertain whether this is a genuinely sexually dimorphic pattern, and try to document these sounds in a broader range of group contexts, in order to work towards testable hypotheses for their function.

Acknowledgements

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