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Insights into Blainville's beaked whale (*Mesoplodon densirostris*) echolocation ontogeny from recordings of mother-calf pairs

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Studying the ontogeny of vocal behavior is crucial to understanding the roles that various factors, such as social influence or acoustic environment, play in the development of normal adult vocal repertoires. The literature on vocal development during ontogeny in marine mammals is scant and largely restricted to captive studies, most likely due to the difficulty of definitively identifying vocalizations from young animals that are often closely associated with their mothers or other adults. However, we do know that dolphins can whistle at birth (Caldwell and Caldwell 1979), and that beluga whales (*Delphinapterus leucas*) vocalize with pulsed trains within an hour after birth (Vergara and Barrett-Lennard 2008). We also know that a neonatal male Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*) was first recorded echolocating 22 d postnatal (Li *et al.* 2007), and two male bottlenose dolphins were recorded echolocating in their fourth postnatal week (Reiss 1988). In one study on bottlenose dolphins, adult females increased their rates of signature whistle production by a factor of ten following the birth of a calf, possibly facilitating the imprinting of the mother's vocal characteristics (Fripp and Tyack 2008). Mother-offspring recognition is likely important in such species where there is either offspring mobility (Sayigh *et al.* 1990, Smolker *et al.* 1993), or separation of mother and calf due to foraging requirements. Subantarctic fur seals (*Arctocephalus tropicalis*), for example,

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learn their mother's call by the time they are 5 d old, allowing them to find the mother again after her foraging trips (Charrier *et al.* 2001).

We might expect vocal development to be similarly important and rapid in deep diving odontocetes that use echolocation to forage outside the photic zone. However, the ontogeny of odontocete echolocation is poorly studied, even in deep diving species that rely solely on acoustic abilities within their foraging habitat. Currently only two recordings of neonate sperm whales (*Physeter macrocephalus*) exist (Watkins *et al.* 1988, Madsen *et al.* 2003), and both came from stranded animals in poor health who ultimately died in captivity. Nonetheless, there was a clear pattern in that the clicks produced from both neonates were lower in frequency when compared to adults, a finding which mirrors studies of echolocation in bats (Moss *et al.* 1997). This contrasts with the general pattern where call frequency decreases as body size increases across mammalian species (Matthews *et al.* 1999, May-Collado *et al.* 2007), possibly because it takes time to develop motor control for high frequency echolocation such as that used by both bats and odontocetes. Across adult beaked whales (family Ziphiidae), smaller species do produce higher frequency signals, although this has been suggested to be an adaptation for detecting smaller prey as much as a function of their body size (Baumann-Pickering *et al.* 2013). However, there is no information to compare echolocation characteristics or behavior in young beaked whales, of any species, as they develop.

Here we investigated the ontogeny of beaked whale foraging search clicks using recordings from mother-calf pairs where the calves were different ages, to discover (1) when calves begin clicking, (2) if there is any change in the production of clicks by the mother, and (3) if calves' clicks are different in structure from their mothers. We focus on the regular FM upsweep search clicks (Johnson *et al.* 2006), but note that this species also makes mid-frequency broadband sounds (Aguilar de Soto *et al.* 2011, Dunn *et al.* 2013) because although the latter may be a form of social communication, they are produced very rarely compared to search clicks. Young Blainville's beaked whales (*Mesoplodon densirostris*) appear to remain with their mothers at all times, diving and surfacing in synchrony for the same duration of time as their mother, and have never been observed at the surface alone in our study area in 155 encounters with calves present, over 25 yr.

All data for this study were collected at the Atlantic Undersea Test and Evaluation Center (AUTEC) in the Bahamas. Groups of beaked whales were detected and tracked acoustically using a fixed hydrophone array (Jarvis *et al.* 2014), which consists of 82 sensors spaced roughly 4 km apart (Ward *et al.* 2008) with a mean depth of 1,630 m (Ward *et al.* 2011). These hydrophones cover an area of approximately 1,500 km^2, and are single channel, with a sampling rate when digitized of 96 kHz. Sixty-eight of the hydrophones have a usable bandwidth from approximately 50 Hz to 48 kHz, and the remaining 14 hydrophones have a smaller bandwidth from 8 kHz to around 50 kHz (Ward *et al.* 2008). Jarvis *et al.* (2014) used an energy detector to identify beaked whale clicks on one or more of the array hydrophones. The detector uses a 2,048 point fast Fourier transform (FFT) with 50% overlap, giving a frequency resolution per bin of 46.875 Hz and a time resolution of 10.67 ms. The magnitude of each bin of the FFT is compared to a "bin specific" noise varying threshold, and a detection is reported if the magnitude is greater than the threshold (Ward *et al.* 2008). A shore team used this system to track whales in real time and convey locations of groups of whales *via* VHF radio to the field research team who then carried out visual observations from a small (6.5 m) rigid hull inflatable boat.

Acoustic recordings were made from the hydrophones that detected clicks from the group of whales that the observers on the boat encountered. Recordings were attributed to the whales that were sighted based on the spatial and temporal correlations between recorded clicking and observed surfacing of the whales. Blainville's beaked whales typically surface approximately 10 min after the cessation of clicking, and only begin clicking within approximately 10 min of commencing the next foraging dive (Tyack *et al.* 2006). Between these foraging dives, they undertake a series of shallow, nonforaging dives (Arranz *et al.* 2011), which terminate with a characteristically long surface interval before they begin their foraging dive by exhibiting a noticeably stronger exhalation, and leave the surface with their body arching high out of the water. This behavior allowed the boat observers to inform the shore team when and where foraging dives commenced, prompting them to monitor nearby hydrophones for the start of clicking. Recordings for this analysis were from all hydrophones with sounds detected during long foraging dives.

The acoustic recordings analyzed for this paper were processed through the default beaked whale click detector in the PAMGUARD software (http://www.-pamguard.org; Gillespie *et al.* 2009), which works by assigning a threshold trigger that selected transient sounds with >10 dB signal-to-noise ratio (SNR). Triggered events are then passed to a frequency based bandwidth classifier that selects clicks with energy concentrated in the 25–40 kHz band. A detection was registered when the SNR in this band exceeded the threshold parameter. For all the clicks that were detected by PAMGUARD, several parameters were measured automatically using a custom Matlab R2014a (8.3.0.532) script: the −3 dB and −10 dB bandwidths, duration, peak frequency, sweep rate, and the starting frequency of the click. The −3 dB and −10 dB bandwidths were calculated with respect to the peak frequency of the signal. The duration of the signal was calculated as the duration in microseconds between the −10 dB points relative to the peak of the envelope of the waveform (the D duration, recommended by Madsen and Wahlberg 2007). Since the signal is digitally sampled, the precise point at which the envelope drops to −10 dB almost always falls between samples. Therefore, we used linear interpolation between sample points to estimate the time at which the envelope passed through the −10 dB level.

Beaked whale clicks used in the search mode of echolocation are frequency modulated (FM) upsweeps (Johnson *et al.* 2004). The sweep rate of FM clicks was calculated by fitting a linear model through the maximum frequency points from the start of the −10 dB duration period to the time of highest energy in the spectrogram of a click, producing a 1 kHz/ms rate. Due to the low sampling rate relative to the frequency of the clicks, the spectrogram had to have a small window size (24 samples) in order to achieve enough resolution to measure the clicks' sweep. Signals identified as clicks with negative sweep rates were discarded from the data set because the FM clicks of beaked whales are upsweeps (Johnson *et al.* 2004). Finally, to ascertain the starting frequency of each click, a spectrogram was created with a 50% overlap and Hamming window. Assuming an upsweep, the first frequency from all frequency values for a click was used as the starting frequency.

These measurements were combined using principal components analysis (PCA) to provide a visual representation of the variation in click characteristics. Standardized variables were used because of the different scales of measurement of the different click parameters. PCA analysis was performed using the statistical software R (R Core Development Team 2010). Recordings were audited manually to check for all sounds incase calf clicks fell outside the detector parameters, and none were present. Due to the directional nature of the search clicks, the automatic detector was used to ensure consistency in the clicks used in the PCA analysis.

Only recordings with groups consisting solely of a mother-calf pair were used in this analysis. Blainville's beaked whale calves typically separate from their mothers between the age of 3 and 4 yr old in the Bahamas (Claridge 2013). Calf age was estimated here using visual estimates of its length relative to its accompanying adult, which we assumed to be the mother, sighting history of the mother, and presence of fetal folds, pigmentation and scarring on the calf: individuals <1 yr old were approximately ½ the mother's length, 1–2-yr-olds were ½–¾ the mother's length, and 3–4-yr-olds were >¾ the mother's length (Claridge 2013). For all the recordings we also ensured there were no acoustic detections of marine mammals located within two hydrophones of the grid of the hydrophones detecting our focal beaked whales to ensure no other adjacent animals were vocalizing at the recording time.

Thus in these recording contexts, if more than one animal was vocalizing, it meant that the calf was vocalizing. To determine whether multiple animals were vocalizing, each acoustic file was visually inspected, examining waveform and spectrogram views in Adobe Audition CS6 (4,096 point FFT with a 75% overlap and Hamming window). Times were noted for the start and end of periods of silence, periods when only one animal was clicking, and periods when there were overlapping click trains, indicating more than one animal was clicking. To enhance the detection of overlapping clicks, each file was amplified by 10 dB. Amplification was required because often one animal's clicks had less energy than the other. Generally, overlapping clicks from two different animals can be visually identified, as the interclick intervals (ICIs) between each click are irregular, and usually there is a discernible difference in amplitude. These differences arise because one animal is either closer to the hydrophone, is at a different aspect angle relative to the hydrophone, or is producing louder clicks. The animals produce their clicks in a narrow 13° wide beam centered on the main anterior-posterior axis of the animal, in which the majority of the click energy is concentrated. Typically, such "on-axis" sound levels are 23 dB greater than levels recorded outside the main beam (Ward Shaffer *et al.* 2013), and the animals also move their head and therefore this beam, −10° to +10° throughout their foraging dives (Ward Shaffer *et al.* 2013). In contrast, single animal clicks tend to have regular ICIs and similar amplitude, or amplitude that changes gradually over a few successive clicks, suggesting that the animal is moving its head in a sweeping motion towards and away from the hydrophone that is recording its clicks (Johnson *et al.* 2006, Ward Shaffer *et al.* 2013).

There were three encounters in which a mother-calf pair was recorded alone (Table 1). In the first, the calf was a neonate, indicated by the presence of fetal folds. There was never more than one animal clicking at any time in the recordings from this encounter (Fig. 1). In contrast, during the second encounter, in which the calf was around 3 mo old, the recordings contained some overlapping clicks, indicating that both animals were clicking some of the time. The recordings from the third encounter, with a calf between 18 mo and 2 yr of age contained the largest percentage of overlapping clicks (Fig. 1). The age estimates of the calves are necessarily imprecise and drawn from inference based on knowledge of calf development in this population (Claridge 2013). The age of the 3-mo-old calf was estimated using characteristics seen in calves known to be this age. The 18-mo–2-yr-old calf was estimated to be this age as it was seen with its mother 14 mo previously and was between ½ and ⅔ of her length at that time. Based on other animals in the photo-identification catalog of this size and known ages, the calf was estimated to be between 6 mo and 1 yr of age at the

Table 1. The data set used for analysis, detailing three encounters, each with a different mother-calf pair, and ordered by the estimated age of the calf, the date of the encounter, the duration of the visual encounters and recordings, the number of clicks detected by the PAMGUARD detector, and the number of hydrophones that recorded vocalizations during each encounter.

Reference	Age of calf	Date	Duration of visual encounter (minutes)	Duration of recordings (minutes)	# Clicks	# Hydrophones
1	~1 wk	1 October 2008	41	45	117	4
2	2–3 mo	25 July 2012	62	11	61	2
3	18 mo–2 yr	1 October 2008	28	37	2,259	5

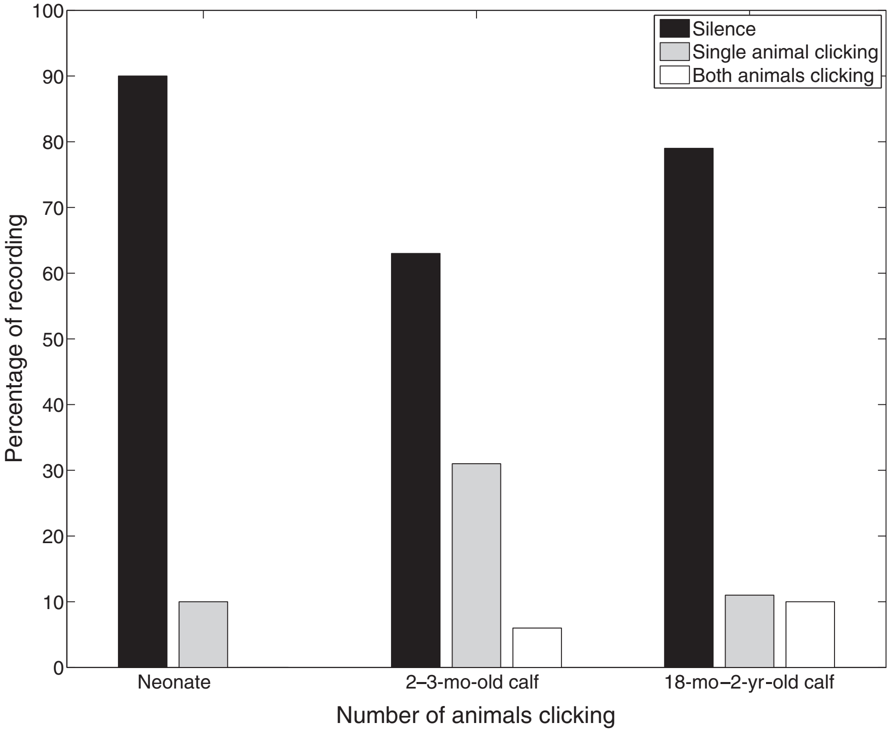

Figure 1. Percentage of time during recordings of three mother-calf pairs with calves of different ages, detailing no clicking, one animal clicking, or both animals clicking.

time of the earlier sighting and hence 18 mo–2 yr when recorded for this study. The encounter with the greatest percentage of silence (*i.e.*, neither mother nor calf clicking) was when the calf was a neonate, followed by the encounter with the oldest calf, and the least amount of silence was from the encounter where the calf was around 3 mo old (Table 1). Although the encounters had recordings of different durations, with the second encounter not having recordings from the entire dive period, there

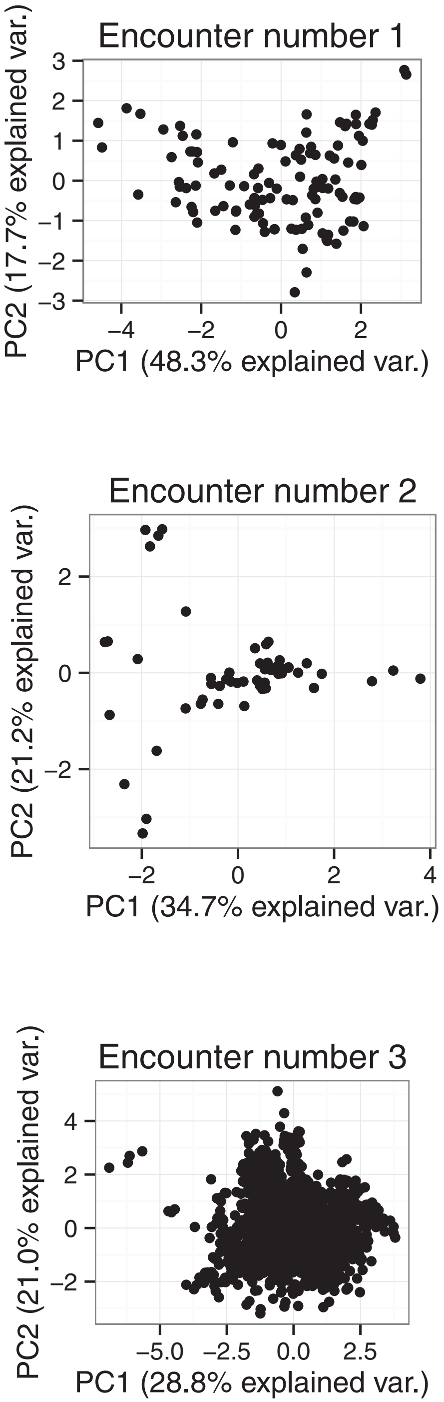

Figure 2. PCA scatterplots of click variables from the three mother-calf pairs.

still does not appear to be any evidence to suggest Blainville's beaked whales increase call production postpartum as has been illustrated in other species.

The removal of negative sweep rate clicks for the PCA analysis required dropping a single click from the first data set, six from the second, and none from the third. The PCA of the click parameters in each of these encounters showed no distinct clusters in the data (Fig. 2) that might correspond to two distinctive populations of clicks, such as would be expected if calf clicks were very different to adult clicks. We assume the single animal clicking from the first data set is the mother and not the calf, due to her need to forage. Therefore if Blainville's beaked whales are not vocalizing immediately after birth, it appears that when they do begin to vocalize their anatomy is adequately developed to produce echolocation clicks that are similar to adults. These results are similar to those reported for both dolphin and porpoise calves, where dolphin calf echolocation was indistinguishable from adults at postnatal day 40, as was a neonate finless porpoise's first recorded click train (Reiss 1988, Li *et al.* 2007).

The first two principal components explained between 50% and 66% of the variation for the three groups, with the −10 dB bandwidth variable being the dominant loading for PC1 in two of the data sets, and sweep rate in the other one (Table 2).

Our recordings provide the first insight into the vocal behavior of female beaked whales with accompanying calves. Our results suggest that Blainville's beaked whales may not be producing upswept search clicks as neonates, presumably because they are entirely dependent on nursing, although we cannot rule out the possibility of a false negative result due to the small sample size. Nonetheless, we did confirm calf vocalizations by around 3 mo of age. These results match other studies on the ontogeny of echolocation, where two dolphin calves and a finless porpoise calf were not recorded echolocating in captivity, presumably an environment with a better chance of detecting vocalizations, for their first 3 wk postnatal (Reiss 1988, Li *et al.* 2007). Blainville's beaked whale calves are proportionally larger at birth relative to their mothers than sperm whale calves (Huang *et al.* 2011), which presumably helps make them more capable of diving with their mothers immediately after birth. Our observations suggest that they dive in synchrony with their mothers, even as neonates, and recent data on diving behavior from satellite transmitter tags also indicates that the mother of a dependent calf dove with similar frequency and to similar depths as females without calves (JD, unpublished data). As neonates are not vocalizing immediately after birth, they may be eavesdropping on their mothers' clicks and therefore the vocal behavior of both mothers and calves may allow the calves to follow their mothers during foraging dives shortly after birth to minimize the time that the calf is alone at the surface and vulnerable to predation.

Table 2. The proportion of variance and loadings from PCA for three mother-calf pairs' click parameters.

Group	PC	Proportion of variance	−3 dB	−10 dB	Duration	Peak frequency	Sweep rate	Starting frequency
1	1	0.48	−0.22	0.55	0.47	0.36	0.49	0.26
1	2	0.18	−0.66	−0.16	−0.06	0.48	−0.11	−0.54
2	1	0.35	0.50	0.64	0.02	0.21	0.47	−0.27
2	2	0.21	−0.07	−0.03	−0.34	−0.69	0.59	0.24
3	1	0.29	−0.25	0.43	0.41	0.46	0.58	0.20
3	2	0.21	0.70	0.53	0.10	−0.38	0.20	−0.18

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