1    # Insights into Blainville's beaked whale (*Mesoplodon*

2    *densirostris*) echolocation ontogeny from recordings of mother-

3    calf pairs

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5    **Charlotte Dunn**[1] and **Diane Claridge**, Bahamas Marine Mammal Research

6    Organisation, P.O. Box AB-20714, Marsh Harbour, Abaco, Bahamas and Sea Mammal

7    Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife

8    KY16 8LB, Scotland; **John Durban**, Southwest Fisheries Science Center, National

9    Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La

10   Jolla Shores Drive, La Jolla, CA 92037, California, USA; **Jessica Shaffer** and **David**

11   **Moretti**, Naval Undersea Warfare Center Division Newport, Code 74, 1176 Howell

12   Street, Newport, Rhode Island 02841-1708; **Peter Tyack** and **Luke Rendell**, Sea

13   Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St

14   Andrews, Fife KY16 8LB, Scotland.

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[1]Corresponding author (e-mail: cdunn@bahamaswhales.org)

17    Studying the ontogeny of vocal behavior is crucial to understanding the roles that various

18    factors, such as social influence or acoustic environment, play in the development of

19    normal adult vocal repertoires. The literature on vocal development during ontogeny in

20    marine mammals is scant and largely restricted to captive studies, most likely due to the

21    difficulty of definitively identifying vocalizations from young animals that are often

22    closely associated with their mothers or other adults. However, we do know that dolphins

23    can whistle at birth (Caldwell and Caldwell 1979), and that beluga whales

24    (*Delphinapterus leucas*) vocalize with pulsed trains within an hour after birth (Vergara

25    and Barrett-Lennard 2008). We also know that a neonatal male Yangtze finless porpoise

26    (*Neophocaena phocaenoides asiaeorientalis*) was first recorded echolocating 22 d

27    postnatal (Li *et al.* 2007), and two male bottlenose dolphins were recorded echolocating

28    in their fourth postnatal week (Reiss 1988). In one study on bottlenose dolphins, adult

29    females increased their rates of signature whistle production by a factor of ten following

30    the birth of a calf, possibly facilitating the imprinting of the mother's vocal

31    characteristics (Fripp and Tyack, 2008). Mother-offspring recognition is likely important

32    in such species where there is either offspring mobility (Sayigh *et al.* 1990, Smolker *et*

33    *al.* 1993), or separation of mother and calf due to foraging requirements. Subantarctic fur

34    seals (*Arctocephalus tropicalis*), for example, learn their mother's call by the time they

35    are five days old, allowing them to re-find the mother after her foraging trips (Charrier *et*

36    *al.* 2001).

37          We might expect vocal development to be similarly important and rapid in deep

38    diving odontocetes that use echolocation to forage outside the photic zone. However, the

39    ontogeny of odontocete echolocation is poorly studied, even in deep diving species that

40    rely solely on acoustic abilities within their foraging habitat. Currently only two

41    recordings of neonate sperm whales (*Physeter macrocephalus*) exist (Watkins *et al.* 1988,

42   Madsen *et al.* 2003), and both came from stranded animals in poor health who ultimately

43   died in captivity. Nonetheless, there was a clear pattern in that the clicks produced from

44   both neonates were lower in frequency when compared to adults, a finding which mirrors

45   studies of echolocation in bats (Moss *et al.* 1997). This contrasts with the general pattern

46   where call frequency decreases as body size increases across mammalian species

47   (Matthews *et al.* 1999, May-Collado *et al.* 2007), possibly because it takes time to

48   develop motor control for high frequency echolocation such as that used by both bats and

49   odontocetes. Across adult beaked whales (family Ziphiidae), smaller species do produce

50   higher frequency signals, although this has been suggested to be an adaptation for

51   detecting smaller prey as much as a function of their body size (Baumann-Pickering *et al.*

52   2013). However, there is no information to compare echolocation characteristics or

53   behavior in young beaked whales, of any species, as they develop.

54        Here we investigated the ontogeny of beaked whale foraging search clicks using

55   recordings from mother-calf pairs where the calves were different ages, to discover (a)

56   when calves begin clicking, (b) if there is any change in the production of clicks by the

57   mother, and (c) if calves' clicks are different in structure from their mothers. We focus

58   on the regular FM upsweep search clicks (Johnson *et al.* 2006), but note that this species

59   also makes mid-frequency broadband sounds (Aguilar de Soto *et al.* 2011, Dunn *et al.*

60   2013) because although the latter may be a form of social communication, they are

61   produced very rarely compared to search clicks. Young Blainville's beaked whales

62   (*Mesoplodon densirostris*) appear to remain with their mothers at all times, diving and

63   surfacing in synchrony for the same duration of time as their mother, and have never

64   been observed at the surface alone in our study area in 155 encounters with calves

65   present, over 25 yr (pers. obs.).

66       All data for this study were collected at the Atlantic Undersea Test and Evaluation

67   Center (AUTEC) in the Bahamas. Groups of beaked whales were detected and tracked

68   acoustically using a fixed hydrophone array (Jarvis *et al.* 2014), which consists of 82

69   sensors spaced roughly 4 km apart (Ward *et al.* 2008) with a mean depth of 1,630 m

70   (Ward *et al.* 2011). These hydrophones cover an area of approximately 1,500 km$^2$, and

71   are single channel, with a sampling rate when digitized of 96 kHz. Sixty-eight of the

72   hydrophones have a usable bandwidth from approximately 50 Hz to 48 kHz, and the

73   remaining 14 hydrophones have a smaller bandwidth from 8 kHz to around 50 kHz

74   (Ward *et al.* 2008). (Jarvis *et al.* 2014) used an energy detector to identify beaked whale

75   clicks on one or more of the array hydrophones. The detector uses a 2048 point fast

76   Fourier transform (FFT) with 50% overlap, giving a frequency resolution per bin of

77   46.875 Hz and a time resolution of 10.67 ms. The magnitude of each bin of the FFT is

78   compared to a "bin specific" noise varying threshold, and a detection is reported if the

79   magnitude is greater than the threshold (Ward *et al.* 2008). A shore team used this system

80   to track whales in real time and convey locations of groups of whales via VHF radio to

81   the field research team who were on a small (6.5 m) rigid hull inflatable boat who then

82   carried out visual observations.

83       Acoustic recordings were made from the hydrophones that detected clicks from

84   the group of whales that the observers on the boat encountered. Recordings were

85   attributed to the whales that were sighted based on the spatial and temporal correlations

86   between recorded clicking and observed surfacing of the whales. Blainville's beaked

87   whales typically surface approximately ten minutes after the cessation of clicking, and

88   only begin clicking within approximately ten minutes of commencing the next foraging

89   dive (Tyack *et al.* 2006). Between these foraging dives, they undertake a series of

90   shallow, nonforaging dives (Arranz *et al.* 2011), which terminate with a characteristically

91  long surface interval before they begin their foraging dive by exhibiting a noticeably

92  stronger exhalation, and leave the surface with their body arching high out of the water

93  (pers. obs.). This behavior allowed the boat observers to inform the shore team when and

94  where foraging dives commenced, prompting them to monitor nearby hydrophones for

95  the start of clicking. Recordings for this analysis were from all hydrophones with sounds

96  detected during long foraging dives.

97      The acoustic recordings analyzed for this paper were processed through the

98  default beaked whale click detector in the PAMGUARD software ([www.pamguard.org](www.pamguard.org),

99  Gillespie *et al.* 2008), which works by assigning a threshold trigger that selected transient

100  sounds with >10 dB signal-to-noise ratio (SNR). Triggered events are then passed to a

101  frequency based bandwidth classifier that selects clicks with energy concentrated in the

102  25-40 kHz band. A detection was registered when the SNR in this band exceeded the

103  threshold parameter. For all the clicks that were detected by PAMGUARD, several

104  parameters were measured automatically using a custom Matlab R2014a (8.3.0.532)

105  script: the -3 dB and -10 dB bandwidths, duration, peak frequency, sweep rate, and the

106  starting frequency of the click. The -3 and -10 dB bandwidths were calculated with

107  respect to the peak frequency of the signal. The duration of the signal was calculated as

108  the duration in $\mu$s between the -10 dB points relative to the peak of the envelope of the

109  waveform (the D duration, recommended by Madsen and Wahlberg 2007). Since the

110  signal is digitally sampled, the precise point at which the envelope drops to -10 dB

111  almost always falls between samples. Therefore, we used linear interpolation between

112  sample points to estimate the time at which the envelope passed through the -10 dB level.

113      Beaked whale clicks used in the search mode of echolocation are frequency

114  modulated (FM) upsweeps (Johnson *et al.* 2004). The sweep rate of FM clicks was

115  calculated by fitting a linear model through the maximum frequency points from the start

116  of the -10 dB duration period to the time of highest energy in the spectrogram of a click,

117  producing a 1 kHz/ms rate. Due to the low sampling rate relative to the frequency of the

118  clicks, the spectrogram had to have a small window size (24 samples) in order to achieve

119  enough resolution to measure the clicks' sweep. Signals identified as clicks with negative

120  sweep rates were discarded from the data set because the FM clicks of beaked whales are

121  upsweeps (Johnson *et al.* 2004). Finally, to ascertain the starting frequency of each click,

122  a spectrogram was created with a 50% overlap and Hamming window. Assuming an

123  upsweep, the first frequency from all frequency values for a click was used as the starting

124  frequency.

125      These measurements were combined using principal components analysis (PCA)

126  to provide a visual representation of the variation in click characteristics. Standardized

127  variables were used because of the different scales of measurement of the different click

128  parameters. PCA analysis was performed using the statistical software R (R Core

129  Development Team 2010). Recordings were audited manually to check for all sounds

130  incase calf clicks fell outside the detector parameters, and none were present. Due to the

131  directional nature of the search clicks, the automatic detector was used to ensure

132  consistency in the clicks used in the PCA analysis.

133      Only recordings with groups consisting solely of a mother-calf pair were used in

134  this analysis. Blainville's beaked whale calves typically separate from their mothers

135  between the age of 3 and 4 years old in the Bahamas (Claridge 2013). Calf age was

136  estimated here using visual estimates of its length relative to its accompanying adult,

137  which we assumed to be the mother, sighting history of the mother, and presence of fetal

138  folds, pigmentation and scarring on the calf: individuals less than 1 yr old were

139  approximately 1/2 the mother's length, 1-2 yr olds were 1/2 to 3/4 the mother's length,

140  and 3-4 yr olds were greater than 3/4 the mother's length (Claridge 2013).  For all the

141 recordings we also ensured there were no acoustic detections of marine mammals located

142 within two hydrophones of the grid of the hydrophones detecting our focal beaked whales

143 to ensure no other adjacent animals were vocalizing at the recording time.

144       Thus in these recording contexts, if more than one animal was vocalizing, it meant

145 that the calf was vocalising. To determine whether multiple animals were vocalizing,

146 each acoustic file was visually inspected, examining waveform and spectrogram views in

147 Adobe Audition CS6 (4096 point FFT with a 75% overlap and Hamming window). Times

148 were noted for the start and end of periods of silence, periods when only one animal was

149 clicking, and periods when there were overlapping click trains, indicating more than one

150 animal was clicking. To enhance the detection of overlapping clicks, each file was

151 amplified by 10dB. Amplification was required because often one animal's clicks had

152 less energy than the other. Generally, overlapping clicks from two different animals can

153 be visually identified, as the inter click intervals (ICIs) between each click are irregular,

154 and usually there is a discernible difference in amplitude. These differences arise because

155 one animal is either closer to the hydrophone, is at a different aspect angle relative to the

156 hydrophone, or is producing louder clicks. The animals produce their clicks in a narrow

157 13° wide beam centred on the main anterior-posterior axis of the animal, in which the

158 majority of the click energy is concentrated. Typically, such 'on-axis' sound levels are 23

159 dB greater than levels recorded outside the main beam (Shaffer *et al.* 2013), and the

160 animals also move their head and therefore this beam, -10° to + 10° throughout their

161 foraging dives (Shaffer *et al.* 2013). In contrast, single animal clicks tend to have regular

162 ICIs and similar amplitude, or amplitude that changes gradually over a few successive

163 clicks, suggesting that the animal is moving its head in a sweeping motion towards and

164 away from the hydrophone that is recording its clicks (Johnson *et al.* 2006, Ward Shaffer

165 *et al.* 2013).

166　　　　There were three encounters in which a mother-calf pair was recorded alone

167　　(Table 1). In the first, the calf was a neonate, indicated by the presence of fetal folds.

168　　There was never more than one animal clicking at any time in the recordings from this

169　　encounter (Fig. 1). In contrast, during the second encounter, in which the calf was around

170　　3 mo old, the recordings contained some overlapping clicks, indicating that both animals

171　　were clicking some of the time. The recordings from the third encounter, with a calf

172　　between 18 mo and 2 yr of age contained the largest percentage of overlapping clicks

173　　(Fig. 1). The age estimates of the calves are necessarily imprecise and drawn from

174　　inference based on knowledge of calf development in this population (Claridge 2013).

175　　The age of the 3 mo calf was estimated using characteristics seen in calves known to be

176　　this age. The 18 mo-2 yr old calf was estimated to be this age as it was seen with its

177　　mother 14 months previously and was between 1/2 to 2/3 of her length at that time.

178　　Based on other animals in the photo-identification catalogue of this size and known ages,

179　　the calf was estimated to be between 6 mo and 1 yr of age at the time of the earlier

180　　sighting and hence 18 mo-2 yrs when recorded for this study. The encounter with the

181　　greatest percentage of silence (i.e. neither mother nor calf clicking) was when the calf

182　　was a neonate, followed by the encounter with the oldest calf, and the least amount of

183　　silence was from the encounter where the calf was around 3 mo old (Table 1). Although

184　　the encounters had recordings of different durations, with the second encounter not

185　　having recordings from the entire dive period, there still does not appear to be any

186　　evidence to suggest Blainville's beaked whales increase call production post partum as

187　　has been illustrated in other species.

188

189　　*Table 1*. The data set used for analysis, detailing three encounters, each with a different

190　　mother-calf pair, and ordered by the estimated age of the calf, the date of the encounter,

191    the duration of the visual encounters and recordings, the number of clicks detected by the

192    PAMGUARD detector, and the number of hydrophones that recorded vocalizations

193    during each encounter.

194

| Ref. | Age of calf | Date | Duration of visual encounter min | Duration of recordings min | # Clicks | # Hyd. |
|------|-------------|------|-----------------------------------|-----------------------------|----------|--------|
| 1 | ~ 1 wk | 1-Oct-2008 | 41 | 45 | 117 | 4 |
| 2 | 2 – 3 mo | 25-Jul-2012 | 62 | 11 | 61 | 2 |
| 3 | 18 mo – 2 yr | 1-Oct-2008 | 28 | 37 | 2,259 | 5 |

195

196
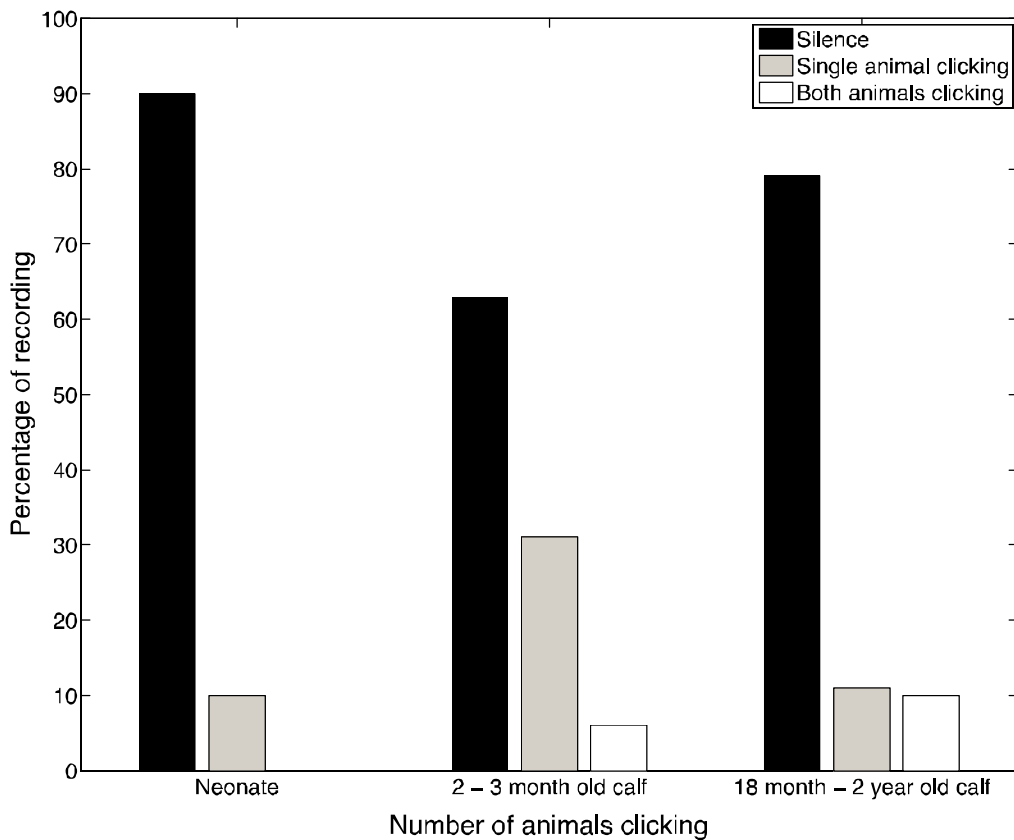


197

198    *Figure 1*. Percentage of time during recordings of three mother-calf pairs with calves of

199    different ages, detailing no clicking, one animal clicking, or both animals clicking.

200

201        The removal of negative sweep rate clicks for the PCA analysis required dropping

202    a single click from the first data set, six from the second, and none from the third. The

203    PCA of the click parameters in each of these encounters showed no distinct clusters in

204    the data (Fig. 2) that might correspond to two distinctive populations of clicks, such as

205    would be expected if calf clicks were very different to adult clicks. We assume the single

206    animal clicking from the first data set is the mother and not the calf, due to her need to

207    forage. Therefore if Blainville's beaked whales are not vocalizing immediately after

208    birth, it appears that when they do begin to vocalize their anatomy is adequately

209    developed to produce echolocation clicks that are similar to adults. These results are

210    similar to those reported for both dolphin and porpoise calves, where dolphin calf

211    echolocation was indistinguishable from adults at postnatal day 40, as was a neonate

212    finless porpoise's first recorded click train (Reiss 1988, Li *et al.*,2007).

213

**Encounter number 1**



**Encounter number 2**



**Encounter number 3**
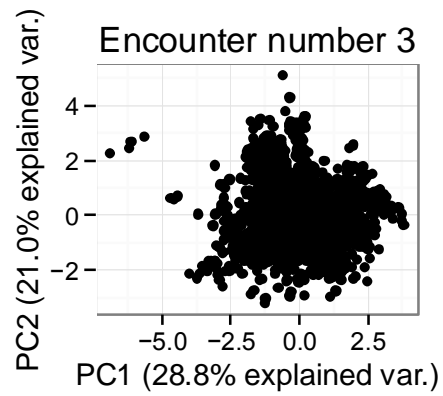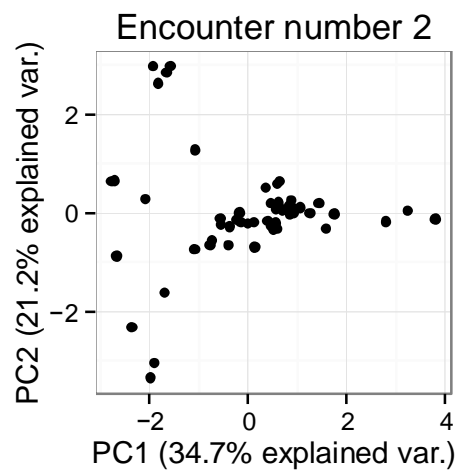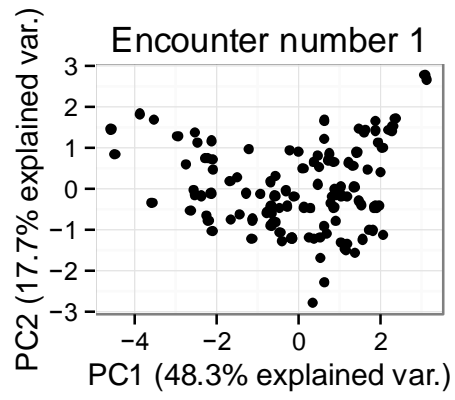
214

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

216

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).

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

| Group | PC | Proportion of Variance | -3dB | -10dB | 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 |

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 can't 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 three weeks 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*

235  *al.* 2011), which presumably helps make them more capable of diving with their mothers

236  immediately after birth. Our observations suggest that they dive in synchrony with their

237  mothers, even as neonates, and recent data on diving behavior from satellite transmitter

238  tags also indicates that the mother of a dependent calf dove with similar frequency and to

239  similar depths as females without calves (J. Durban, unpublished data). As neonates are

240  not vocalizing immediately after birth, they may be eavesdropping on their mothers'

241  clicks and therefore the vocal behavior of both mothers and calves may allow the calves

242  to follow their mothers during foraging dives shortly after birth to minimize the time that

243  the calf is alone at the surface and vulnerable to predation.

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