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# First year sperm whale calves echolocate and perform long, deep dives

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27**Abstract**

28Deep diving sperm whales have a complex social structure and the biggest brains on the planet, but very

29little is known about the ontogeny of their diving, foraging, echolocation, and communication skills. In large

30brained terrestrial species, social skills develop earlier than locomotor abilities; but this may not be feasible

31for sperm whales, which require locomotor skills from birth to breathe, swim, and suckle. Here we show

32the first evidence in any wild toothed whale for the relative development of social and locomotor

33capabilities. Sound and movement recording tags deployed on three first-year sperm whale calves for a

34total of 15 hours revealed that these calves rarely produced codas for communication with adult whales,

35but likely tracked the ample passive acoustic cues emitted by clicking adults. The calves' diving capabilities

36were well developed (maximum dive depth: 285, 337, and 662 m, maximum dive time: 11, 31, and 44 min)

37and they all produced clicks in a way that is consistent with echolocation. The calf performing the longest

38and deepest dives additionally emitted two echolocation buzzes, suggesting that it attempted to forage.

39Thus, sperm whales calves may supplement their milk diet with food caught independently at depth much

40earlier than previously believed. Contrary to terrestrial mammals, we propose that the maturation of

41locomotor, diving, and echolocation skills are favored over investment in developing social communication

42skills at an early age in sperm whales.

43

44**Significance statement**

45The life of deep diving toothed whales have up until recently been a mystery and the understanding of their

46behavior has been limited to surface observations and rare captive studies. Fortunately, the rapid

47development of animal-borne bio-logging devices has markedly improved our knowledge of the behavior of

48adult whales. The behavior and development of young calves are, however, still largely unknown. Sperm

49whale calves are challenged by being air breathing marine mammals, which must learn to hunt prey at

50great depths. Using Dtags, we here show that sperm whale calves have a much more pronounced diving

51capabilities than previously thought. The onset of independent foraging and foraging effort seem linked to

52the diving capability of the calf. These results show that young members of this otherwise slowly maturing

53species of apex predators do learn to dive and may hunt much earlier than previously believed.

54

55**Key words**

56**Behavior – Ontogeny – Dive capability – Echolocation – Coda – Sperm whale**

**INTRODUCTION**

58All newborn animals face the challenge of developing the physical and cognitive skills required to survive

59and cope in the novel environment they enter at birth. Fast physiological development often characterizes

60precocial species such as antelopes (Grillner 2011), chickens (Muir et al. 1996), and rabbits (Carrier 1995),

61which acquire adult walking, running, and jumping capabilities soon after birth. Conversely, altricial species

62such as humans have a prolonged ontogeny of locomotor skills (Carrier 1996; Grillner 2011). Intensive

63parental care enables neonates of altricial species to retard the development of locomotor skills in favor of

64increased investment in brain development leading to larger brains (Iwaniuk and Nelson 2003; Shultz and

65Dunbar 2010; West 2014). Social groups with pronounced inter-individual relationships and extended

66parental care, are often characteristic of altricial, big brained species (Dunbar and Shultz 2007; Emery et al.

672007; Shultz and Dunbar 2007; Dunbar 2009; West 2014). Hence, it has been hypothesized that social

68animals have evolved large brains to solve complex ecological tasks in a social context; as well as, to

69remember social interaction histories with their conspecifics in order to solve the dilemma of with whom to

70cooperate (Joffe 1997; Shultz and Dunbar 2007, 2010; Dunbar 2009). However, the advantages of being

71able to manage such social interactions comes at the cost of a prolonged developmental period of learning

72(Zeveloff and Boyce 1982; Joffe 1997; Shultz and Dunbar 2010). Additionally, the time and energy invested

73in acquiring complex social skills may affect the development of other faculties and, hence, likely explain

74the late maturation of advanced locomotor skills and thereby independent foraging of humans and other

75large apes.

76Despite living in a markedly different environment, many cetaceans possess many of the key features

77expected of altricial species: highly complex social lives (Connor et al. 1998; Rendell and Whitehead 2001),

78large brains allowing for complex cognition (Marino 2002; Marino et al. 2004, 2007), functionally diverse

79communication systems (Payne and McVay 1971; Rendell and Whitehead 2003; Filatova et al. 2012; King

80and Janik 2013), prolonged parental care (Whitehead and Rendell 2015), and extensive learning capacities

81(Janik and Slater 2000). However, due to their aquatic environment, neonate cetaceans require basic

82locomotor skills to get to the surface to breathe, to suckle, and to keep up with highly mobile mothers in

83their typically vast three-dimensional oceanic habitat. This raises the conundrum of how cetaceans handle

84the apparent conflict between timing of the ontogeny of their locomotor skills and social behavior. This

85dilemma is particularly relevant to sperm whales (*Physeter macrocephalus*) who possess the largest brain in

86the animal kingdom (Marino et al. 2004), employ a complex, long range biosonar system (Madsen et al.

872002b), live in a complex, multileveled social structure with long lasting, stable social units at its base

88(Whitehead et al. 1991; Christal et al. 1998; Whitehead 1999; Gero et al. 2015), and whose social

89interactions appear to be mediated through a diverse click-based communication system (Rendell and

90Whitehead 2003; Gero et al. 2016). Yet, this species lives in a pelagic habitat where they range widely and

91hunt for squid during deep (ca. 750 m) and long (ca. 45 min) foraging dives (Watwood et al. 2006;

92Whitehead et al. 2008).

93Observations of a sperm whale birth suggests that newborn sperm whales acquire basic locomotor skills

94within hours after birth (Weilgart and Whitehead 1986), and that young calves appear able to track the

95movements of their natal social unit from the surface (Gordon 1987; Whitehead 1996). The increased

96predation risk for calves staying near the surface appears to be mitigated through alloparental care in the

97form of babysitting (Whitehead 1996; Gero et al. 2009). As such, the current understanding of neonate calf

98behavior is that they spend most of their time at the surface and so do not urgently need to develop the

99locomotor, sensory, and diving skills to either avoid predation or to perform deep foraging dives (Best et al.

1001984), thereby allowing for an early energy allocation towards social development. However, current

101evidence of sperm whale calf diving abilities is ambivalent. As is the case for all mammals, sperm whale

102calves initially gain all their energy by suckling (Best et al. 1984). However, the stomach contents of one

103year old calves have been found to include some solid food items which may reflect independent foraging

104or food provisioning by adults, while milk in turn has been found in the stomach of a 13 year old juvenile

105male (Best et al. 1984); providing mixed evidence for when the onset of independent, deep, foraging dives

106might occur. Gordon (1987) demonstrated that two sperm whale calves dove to approximately 300 m

107suggesting significant diving capabilities although this is only half of the depth routinely reached by foraging

108adult females (Watwood et al. 2006).

109Studies of captive sperm whale calves undergoing rehabilitation have shown that neonate and young calves

110(up to 7 meters) are able to produce low frequency clicks which may be precursors for echolocation clicks

111(Watkins et al. 1988; Madsen et al. 2003). Recent studies have further shown that wild sperm whale calves

112at the age of three months can emit clicks in the form of codas (Gero et al. 2016). Amongst adults, these

113vocalizations serve a communicative function (Watkins and Schevill 1977). It may be speculated that such

114communication is important for facilitating reunion of calves with mothers or babysitters ascending from

115foraging dives. Sperm whale calves have been proposed to emit a click-based contact call similar to

116northern fur seal pups (*Callorhinus ursinus*) and chacma baboons (*Papio cynocephalus ursinus*) (Rendall et

117al. 2000; Insley 2001). This notion is based on the omni-directional, low frequency, and long duration clicks

118emitted by neonate sperm whales in captivity (Madsen et al. 2003). Alternatively, calves near the surface

119may track foraging adults (Gordon 1987) by eavesdropping on their echolocation. Thus, contrasting

120conclusions may be drawn from the current evidence leaving open the question of whether resources are

121invested more in developing diving or social capabilities in sperm whale calves.

122To shed light on this question, we deployed multi-sensor sound and movement tags on three first-year

123calves, to obtain the first data on locomotor and vocal capabilities for any wild toothed whale calf.

124Specifically, we sought to assess whether calves participate actively in social communication by emitting

125codas; and further if calves emit codas in the context of reuniting with their mothers. Secondly, we wanted

126to evaluate if sperm whale calves, like large-brained terrestrial species, postpone their locomotive

127development by examining the extent of their dive behavior. Given their presumably smaller oxygen stores,

128we hypothesized that calves are not able to dive as deep and for as long as adult sperm whales. Thirdly, we

129attempted to examine whether first year sperm whale calves gain energy exclusively from suckling or

130supplement it by foraging. We expected that when calves start foraging they would echolocate for shorter

131periods than adults as a consequence of potentially shorter dives and hence less time within the prey field.

132Lastly, if young calves forage, we anticipated that their inexperience in locating and catching prey would

133manifest in fewer and longer buzzes. We show that sperm whale calves less than one year old, have

134unexpectedly well-developed diving capacities and that they emit echolocation clicks and buzzes consistent

135with foraging. In comparison, social sounds are rarely produced, suggesting vocal communication may

136develop later or calves did not need to vocalize during these relative short periods of tagging – through

137which they seemed to be diving for much of the time. Hence, delayed locomotor ontogeny is not a strict

138prerequisite for developing complex social skills and may be circumvented in instances where the

139environment necessitates an early and rapid development of physiological capabilities.

140

141MATERIAL AND METHODS

142**Field site, animals and tagging**

143Field research was conducted as a part of a longitudinal study of well-known sperm whale social units off

144the coast of the island of Dominica (15.30⁰ N 61.40⁰ W) (Gero et al. 2014). Tagging was performed from an

14511 m rigid-hulled inflatable boat that also served as the primary observation platform during three

146consecutive field seasons in 2014, 2015, and 2016.

147Sperm whales were located acoustically using an HTI-96 hydrophone in a baffle to provide directionality.

148Clusters containing calves were approached from behind and priority was given to tagging calves before

149any adult whale. Dtag version 3 sound and movement tags (Johnson and Tyack 2003) were attached to the

150whale by four silicone suction cups and deployed using a 9 m hand-held, carbon fiber pole. All adults, the

151juvenile, and Calf R and A all showed none or minor reactions such as small flinches and/or a short shallow

152dive in response to tagging. We carefully evaluated response to each tagging of the calves to ensure that it

153was safe to proceed. Calf J performed several shallow dives for the first two minutes after tagging. No

154invasive sampling was conducted during or after the tagging and a minimum distance of 100 m, was kept

155after tagging to minimize the potential for disturbance. All whales, including tagged whales, were identified

156by photo-identification of distinct markings of the trailing edge on their flukes for adults, or the dorsal fins

157for calves (Arnbom 1987; Gero *et al.* 2009). Surface observations of cluster composition (sensu Gero et al.

1582014) was performed throughout the day to determine the calves' association with adult whales. Finally,

159far field recordings as well as sloughed skin and fecal samples were collected in the flukeprint after whales

160made deep fluke-up dives. Data was not collected blindly because our study involved focal animals in the

161field.

162The Dtags sampled audio on two channels (to get a bearing to the sound source) at 120 or 125 kHz with a

163resolution of 16 bits, providing a flat (±2 dB) frequency response between 0.4 and 50 kHz, and a clipping

164level of 184 dB re 1 μPa. Pressure and acceleration were sampled at a rate of 100 Hz and 500 Hz,

165respectively, both with 16 bit resolution, decimated to 25 Hz for analysis. All analyses were performed in

166Matlab (ver. 9.0 R2016a, Mathworks, Inc) using custom written scripts (http://www.soundtags.org).

167

168**Dive behavior**

169Calf dives were divided into two categories, deep dives (> 50 m) and potential suckling dives (< 50 m and

170longer than 30 s). The 50 m separation value is based on the division between the multiple shallow dives

171and the fewer deeper dives performed by the three calves using histograms of the data following Watwood

172et al. (2006). Adult dives deeper than 50 m were similarly termed deep dives and used for comparisons

173between adult and calves. Calf and adult deep dives were divided into three phases based on the body

174pitch angle; the descent phase, the bottom phase, and the ascent phase (sensu Watwood et al. 2006). To

175avoid transient pitch oscillations falsely shortening the descent and the ascent phases, the end of the

176 descents and the start of ascents were constrained to occur at a depth greater than 50 % of the maximum

177 depth of the dive.

178 For deep dives, the percentage of time gliding (periods of no fluking) was determined for the calves and the

179 adults by obtaining the root mean square (RMS) of the differentiated pitch in 10 s block. This block size was

180 chosen to cover 2 fluke strokes assuming a stroke rate of 0.2 strokes/s (Sato et al. 2007). Each 10 s block of

181 the dive with a RMS lower than 20% of the mean RMS of the dive was regarded as a period of gliding. The

182 20% threshold was set from visual examination of the acceleration signals for all dives (Fig. 2). The

183 dominant stroke frequency (sensu Sato et al. 2007) was calculated for periods with continuous fluking;

184 predominantly descent phases for adults and ascent phases for calves. Swim speed during descent and

185 ascent was estimated from vertical velocity and body pitch angle (in turn, calculated from the triaxial

186 acceleration low-pass filtered at one half of the dominant stroke frequency) using a two-state Kalman filter

187 and a Rauch smoother (Zimmer et al. 2005).

188 Randomization tests were conducted to compare the dive duration and maximum depth of the calves and

189 the adults. For each calf, the median of dive durations, maximum dive depths, stroke frequencies, and

190 percentages of time spent gliding were extracted across all deep dives. Similar medians were extracted

191 from six dives for each of the adults. This number of dives was chosen based on the lowest number of dives

192 recorded from the individual calves. Six random dives were chosen for each adult individual, potentially

193 from several tag deployments, however with a criterion that one of these six dives was the first dive on a

194 tag recording. This was done to ensure that the sampling method of adults matched that of calves, where

195 all dives, including the first dive with potential, but not apparent tagging effects, were included. This

196 resulted in a pool of 66 adult dives for bootstrap analysis. When comparing calves and adults, an adult

197 median value was extracted for each dive parameter from a randomly chosen subset of these dives. The

198 number of dives in the subset for comparison against a calf was equal to the number of dives made by the

199 given calf (i.e. 7, 15, and 6 for Calf J, R, and A). This was done to ensure similar sample size of calf and adult

200dives. Such an adult median was drawn 1000 times and the proportion of times that the median value

201for the calf was lower or higher than the median value for the adults was calculated.

202

203**Acoustic activity**

204All calf recordings were examined using a custom Matlab tool that allowed listening and visual examination

205of successive 15 s long windows of the tag recording using a spectrogram display (Hamming window, NFFT

206= 512 and 50 % overlap). Potential echolocation signals from the tagged calf (having a high and stable

207amplitude above 125 dB re 1 μPa peak) were marked for further assessments along with any associated

208buzzes and codas. Individual echolocation and coda clicks for both calves and adults were identified using

209an automated click detection algorithm. The detected clicks were subsequently visually evaluated by a

210single observer (PT) to make sure that no clicks were missed and that obvious false detections, such as

211noise or distant whales, were eliminated.

212

213**Echolocation**

214The inter-pulse interval (IPI), the angle of arrival (AOA) on the stereo hydrophones, and apparent output

215level (AOL) (Fais et al. 2015, 2016) were examined for all detected echolocation clicks recorded on the calf

216tags to determine whether they were produced by the tagged calf or a nearby adult. Detected clicks were

217low-pass filtered using a second order Butterworth filter with a cut-off frequency of 5 kHz. Clicks with a

218signal to noise ratio (SNR) below 20 dB or a received level at the tag of less than 154 dB re 1 μPa peak were

219removed to exclude weak signals that were either misdetections or clicks from distant animals. The SNR

220was calculated from the RMS of a 1 ms window centered on each detected click (signal) and a 3 ms window

221starting 15 ms before the click (noise). Clicks with a peak amplitude within 10 % of full-scale were excluded

222to avoid clipping. The IPIs of the accepted clicks were then obtained from inspections of the envelope of

223the click waveform, computed as the absolute value of the Hilbert transform. The two highest peaks of the

224envelope were identified, corresponding to the first and second pulse of the click, and the time difference

225between these was taken as the IPI (based on Bøttcher et al. 2018). We set an upper limit of 5 ms for the IPI

226corresponding to a maximum body length of roughly 12 m (Gordon 1991), as the average length of mature

227female sperm whales off Dominica is 9.2 m (Bøttcher et al. 2018).

228AOA was estimated using the time delay between the recordings of the same click from the two

229hydrophones of the Dtag. For clicks emitted by the tagged whale, the AOAs are expected to be stable as the

230position of the sound producing organ changes very little relative to the tag. Abrupt changes in AOA might

231however occur due to sliding of the tag on the whale. If another nearby whale, on the other hand, produces

232the clicks, the AOAs are likely to vary continuously due to changes in the relative position and orientation of

233the tagged whale and an echolocating conspecific. The AOA was calculated using the following expression:

$$234 \quad AOA = \sin^{-1}\left( \frac{\frac{\Delta time * c}{fs} * 1}{dist} \right)$$

235where $\Delta$time is the time difference between when a click was recorded by the two hydrophones, $fs$ is the

236sampling rate, $c$ is the speed of sound in water (1,500 m/s) and $dist$ is the distance between the two

237hydrophones (50 mm). This time difference was estimated from the cross-correlation of the click recorded

238on the two hydrophones. To help resolve the peak time in the cross correlation, the click signals were

239interpolated by a factor of eight.

240Lastly, the peak to peak apparent output level ($AOL_{pp}$) was used to aid the evaluation of whether the calf or

241a nearby adult was echolocating. Assuming that the calf emits clicks of a near constant amplitude, which

242seems to be the case for an adult sperm whale (Madsen et al. 2002a), there should be little variation in the

243recorded $AOL_{pp}$, whereas $AOL_{pp}$ of a nearby echolocating whale will fluctuate according to the distance to,

244and the heading of, the echolocating whale. All clicks with an IPI lower than 2 ms were assigned to the

245calves and clicks with an IPI higher than 2 ms were assigned to a nearby adult, this approach is supported

246by the stability of AOA and AOL (see Fig. 3). The SNR and clipping criterion excluded none or very few clicks

247across all whales. Clicks that did not get assigned an IPI due to a low amplitude, were ascribed to the animal

248producing the preceding and subsequent IPI confirmed clicks. To summarize, candidate clicks were

249presumed to come from the tagged calf if: i) The click SNR was > 20 dB and AOL > 154 dB re 1 µPa peak, ii)

250The AOAs were fairly constant except for occasional step changes due to tag sliding and iii) IPI < 2ms.

251All adult echolocation data used for comparison stems from six dives from each of 10 adult individuals,

252which performed six or more dives during recording. For adults, clicks with consistently high amplitudes

253were classified as produced by the tagged adult. Buzzes performed in the second and third dive of each of

254these 10 individuals were used to compare against the calf buzzes. Adult and calf buzzes were defined as a

255succession of clicks with an ICI lower than 0.2785 s based on the distribution of all adult echolocation clicks

256(Fig. 4, method sensu Teloni et al. 2008). Due to the high decay rate of the pulses within buzz clicks and

257their low signal to noise ratio, it was not possible to obtain IPIs of buzz clicks. However, buzzes recorded on

258the calf tags were assigned to the calf or an adult based on the IPI of clicks before and after the buzzes.

259Echograms (Johnson et al. 2004) were made to test if any echoes from ensonified objects such as prey

260could be detected during the calf buzzes. This was done by plotting low-pass filtered (fourth order

261Butterworth filter with a cut-off frequency of 5 kHz) envelopes of sound segments of subsequent, outgoing

262clicks. A Hanning-window was additionally applied to the sound segments to emphasize potential echoes

263and deemphasize the outgoing clicks. The distance to potential echoic objects was calculated from the

264arrival time of the echo assuming a sound speed of 1500 m/s.

265

266**Codas**

267The IPIs of clicks within all detectable codas in the calf recordings were examined to determine if the calves

268emitted any of the codas. All clicks with an IPI less than 2 ms were visually inspected to eliminate clicks with

269no apparent pulse structure. This cut-off value was chosen, as echolocation clicks judged to be from the

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270tagged calves had IPIs shorter than 2 ms for all three calves. An IPI of 2 ms corresponds to a body length of

2717.7 m (Gordon 1991), slightly greater than the average body length of 6 m reported for first year calves

272(Lockyer 1981) while the IPI of echolocation clicks from adults off Dominica range between 2.73 and 3.34

273ms (Bøttcher et al. 2018).

274IPIs of coda clicks were estimated following the same procedure as for echolocation clicks, except that the

275SNR criterion was omitted to avoid missing any calf codas. Since the calves only emitted codas sporadically,

276the stability of AOA and AOL could not be used to support the determination of whether the tagged calves

277or the adults emitted the codas. A coda was therefore assigned to a calf if the IPI of three or more clicks

278within the coda could be reliably determined and if these IPIs were all lower than 2 ms.

279

280**RESULTS**

281Dtags were deployed on three first-year calves (1 in 2015 and 2 in 2016) for a total of 15 hours. The three

282calves came from three different social units: Calf J from Unit J, which consisted of three adult females, Calf

283R from Unit R, which consisted of five adult females and two other calves, and Calf A from Unit A, which

284consisted of three adult females and a juvenile male. For future reference, Calf J, R, and A were named

285Jonah, Riot, and Aurora within The Dominica Sperm Whale Project. Unit J and A were engaged in foraging

286throughout the tag deployment, whereas Unit R socialized during 3 of 7 hours of the tag deployment based

287on hourly sampling of group-level behavioral state determined as per observed behavioral events

288(Whitehead and Weilgart 1991). As none of the calves were observed with their social unit during the

289previous year's field season, they were assumed to be less than a year old It appeared from field

290observations that calf A was slightly bigger than the two others. Calf J and A were genetically sexed using

291sloughed skin as females (Konrad 2017), whereas the sex of Calf R is unknown. Calf J, R, and A were tagged

292for 3.9, 6.4, and 4.7 hours and performed 7, 15, and 6 deep dives, respectively, during these recording

293periods (Fig. 1). Most of these dives were V-shaped, but Calf R and A each made four dives with a bottom

294phase (Fig. 1). The calves often initiated and surfaced from deep dives in the immediate company (within

29540 m and within <1 min) of one or more adults (diving: 3 of 3 and 0 of 1 observations, surfacing: 3 of 3 and

2962 of 2 observations for Calf J and A respectively, data not available for Calf R).

297Additionally, 19 tags (5 in 2014, 12 in 2015, 2 in 2016) were deployed on 11 different adult whales and one

298juvenile male across 6 social units (A, F, J, S, U, and one unknown unit) and used for comparison with the

299calves. The juvenile male was analyzed as described for the adults. Four of these whales were tagged twice

300and two were tagged three times, within one or two field seasons. A maximum of four adults were tagged

301during the same day and the calves were either the only one tagged that day (Calf R) or one adult was

302additionally tagged on the same day (Calf J and A).

303

304**Suckling**

305Calf J, R, and A made 43, 52, and 28 potential suckling dives with median durations of 2.1 min (IQR: 0.8-4.3

306min), 0.9 min (IQR: 0.6-2.2 min), and 1.2 min (IQR: 0.6-2.8 min). These potential suckling dives occurred at a

307median depth of 2.7 m (IQR: 2.3-5.3 m), 2.2 m (IQR: 1.7-3.6 m), and 3.3 m (IQR: 2.8-5.5 m) for Calf J, R, and

308A respectively. The amount of time spent potentially suckling differed between the calves. Calf J spent 47 %

309of the time potentially suckling whereas Calf R and A only spent 20 % and 22 % of their tag deployments

310potentially suckling. No acoustical cues or sounds of physical contact (rubbing) were audible during the

311potential suckling dives.

312

313**Deep dive behavior**

314All three calves performed several deep dives. In total they made 28 deep dives deeper than 50 m. The

315maximum depth of Calf J and R's dives were approximately 300 m, whereas Calf A made four dives to

316around 600 m (Fig. 1). The duration of the dives varied between individuals, with Calf J diving for a

317maximum of 11 min, Calf R staying submerged for up to 31 min and Calf A's longest dive lasting 44 min. The

318median dive depth and duration of the calf dives were significantly shallower (Randomization tests:

319numbers of iterations = 1000, $p \leq 0.001$) and shorter (Randomization tests: numbers of iterations = 1000, p

320< 0.001) for all three calves than the median adult dive depth and dive duration (median depth: 833 m, IQR:

321734-909 m, median duration: 48 min, IQR: 44-50 min, Fig. 5). During the recording periods Calf J, R, and A

322spent 25, 47, and 56 % of the time performing dives beyond 50 m, whereas adults spent a median of 76 %

323(IQR: 63-81 %) of their time diving (> 50 m, pooling data from different tag deployments for the same

324individual).

325All three calves glided significantly more during descents of deep dives (Calf J median 44% (IQR: 2-65%),

326Calf R median 18% (IQR: 0-28%), and Calf A median 31% (IQR: 0-67%), Randomization tests: numbers of

327iterations = 1000, $p < 0.001$ for all calves) than did adults (median 2% (IQR: 0-5%)). In contrast, the calves

328barely glided during ascents (median 0 % (IQR: 0-0%) for all calves), whereas adults spent a median of 20 %

329of ascents gliding (IQR: 8-41%, Randomization tests: numbers of iterations = 1000, $p < 0.001$ for differences

330between each calf and the adults). During the bottom phases, adults fluked constantly (median: 100 % (IQR:

331100-100%)) presumably to approach and catch prey. Calf R and A each made 4 dives with bottom phases

332during which they similarly fluked almost continuously (Calf R median 95% (IQR: 86-99%) and Calf A median

33395 % (IQR: 82-99%)). Calf J, R, and A ascended with a median dominant stroke frequency of 0.37, 0.41, and

3340.41 strokes per s (IQR: 0.33-0.39, 0.34-0.46, and 0.39-0.46 strokes per s), which for all calves was

335significantly higher (Randomization tests: numbers of iterations = 1000, $p < 0.001$ for all three calves) than

336the dominant stroke frequency of descending adults (median: 0.21 strokes per s, IQR: 0.20-0.22 strokes per

337s). Calf R and A both ascended significantly faster (median: both 1.6 m/s, IQR: 1.2-1.7 m/s and 1.4-1.7 m/s,

338Randomization tests: numbers of iterations = 1000, $p < 0.001$ for both calves) than the adults descended

339(median: 1.4 m/s, IQR: 1.3-1.5 m/s). Calf J on the other hand ascended significantly slower (median: 1.2

340m/s, IQR: 1.2-1.4 m/s, Randomization tests: numbers of iterations = 1000, p = 0.038) than the adults

341descended. We compare stroke frequencies during ascends for calves with descends for adults to use

342epochs where the buoyancy works against the relatively heavy calves (less body fat) and relatively light

343adults (more body fat) (Miller et al., 2004).

344

345**Echolocation**

346Given that all three calves performed dives to 300 m depth and Calf A further reached adult foraging depth,

347we examined the IPI, AOA, and AOL of clicks recorded by the tags on the calves to determine if the tagged

348calves were clicking. As an example, Fig. 3 shows these three parameters for calf clicks recorded by the

349Dtag on Calf A during dive I to IV (Fig. 1). The IPI estimates of clicks differ between and within dives,

350suggesting that the recorded clicks came from different individuals. In dive I and IV, the median IPI was 3.06

351ms (IQR: 2.92-3.18 ms) and 2.88 ms (IQR: 2.19-3.02 ms), which is similar to the IPI estimates of adult sperm

352whales in Dominica (Bøttcher et al. 2018). These IPIs indicate a body length of 9.3 and 9.0 m (Gordon 1991),

353which is the typical length of sexually mature female sperm whales (Lockyer 1981). During dive II and III the

354initial median IPIs of 1.45 ms (IQR: 1.38-1.51 ms) and 1.48 ms (IQR: 1.43-1.53 ms) shifted to a median of

3552.82 ms (IQR: 1.99-2.99 ms) and 3.00 ms (IQR: 2.60-3.08 ms) toward the end of the clicking. This change in

356the IPIs indicates a shift from a smaller whale to an adult whale clicking. The low IPI clicks had little variation

357in AOA (IQR: 4.2 and 4.8 degrees for dive II and III), whereas the AOA of the high IPI clicks varied more (IQR:

3584.8, 11.3, 14.7, and 10.7 degrees for dive I, II, II, and IV). Moreover, the AOL of the low IPI clicks varied less

359(IQR: 2.6 and 3.2 dB for dive II and III) than the AOL of the high IPI clicks (IQR: 12.8, 12.3, 9.6, and 10.5 dB

360for dive I, II, II, and IV). In combination, these observations of IPI, AOA, and AOL suggest that Calf A emitted

361the low IPI clicks and nearby adults emitted the high IPI clicks occurring right before the calf started its

362ascents (Fig. 1). Additionally, Calf A produced two of the eight buzzes recorded by its tag (Fig. 3).

363Following the same method it was found that Calf J and Calf R each produced one bout of regular clicks (Fig.

3641). However, no buzzes were recorded from these calves.

365During the full recordings, Calf J and R emitted clicks for 80.5 and 89.5 s, Calf A on the other hand

366echolocated for 18.4 and 28.5 s in two of its approximately 600 m dives (dive II and III in fig. 1). In

367comparison the median adult search phase duration (i.e., from first to last regular click in a dive as defined

368in Watwood et al. 2006) was 37.8 min (IQR: 35.5-41.1 min). Even accounting for the shorter duration of the

369calf dives compared to adult dives, the percentage of time spent in the search phase per dive was lower for

370the calves (13.9 and 16.2 % for Calf J and R, and 55.4 and 65.2 % for Calf A versus adults: median: 78.1 %,

371IQR: 76.3-80.5 %). Calf J and R both emitted their clicks at approximately 200 m depth, with Calf J clicking

372during the last part of its descent while Calf R emitted clicks during the initial part of its ascent (Fig. 1). Calf

373A started echolocating at 426 and 340 m during the last part of it descent, similar to adults (median depth:

374339 m, IQR: 235-371 m), but stopped clicking during the last part of the bottom phase (Fig. 1), which is

375earlier than adults (Watwood et al. 2006). The ICI of Calf R and A, median 0.46 and 0.41 s (IQR: 0.46-0.56 s

376and 0.40-0.46 s) respectively, was close to the median ICI of 0.49 s (IQR: 0.44-0.54 s) for adults. Calf J on the

377other hand had a higher median ICI of 0.81 s (IQR: 0.72-0.86 s).

378The two buzzes (one per dive) made by Calf A lasted 27.7 and 12.4 s, substantially longer than the median

379duration of 4.3 s (IQR: 4.2-4.8 s) for adult buzzes. Adults also produced a median of 17 (IQR: 14-19) buzzes

380per dive. Even when accounting for the different search phase durations, Calf A produced an order of

381magnitude fewer buzzes per minute than adults (median of 0.045 for Calf A compared to a median of 0.430

382buzzes per minute of the search phase for the adults). Calf A produced its buzzes at 556 and 470 m,

383considerably shallower than the median depth of 771 m (IQR: 722-789 m) for adult buzzes. The median ICI

384of Calf A's buzzes (0.025 and 0.019 ms) was similar to the median ICI of adult buzzes (0.019 ms, IQR: 0.017-

3850.020 ms) (Fig. 4). The echogram (Johnson et al. 2004) of the second buzz revealed the presence of an

386object 4.0 m in front of the calf 5.5 s into the buzz (Fig. 6). The distance to this object decreased to 2.7 m

387over a 2 s period, suggesting that the calf closed in on this object at a net speed of 0.7 m/s.

388

389**Codas**

390No codas with an IPI corresponding to a calf were recorded by the tags on Calf J and A, whereas 26 calf

391codas were recorded by the tag on Calf R. Codas and echolocation from other sperm whales were audible

392in 97.1, 95.5, and 94 % of the recording time of Calf J, R, and A respectively (Fig. 1e). Codas were audible in

3934, 29, and 5 % of the recording time of Calf J, R, and A respectively (Fig. 1e).

394

395**DISCUSSION**

396In this first detailed study of the fine-scale behavior of large toothed whale calves in the wild, we used

397multi-sensor Dtags to show that less than a year old calves can dive to depths at which adults forage, and

398can emit echolocation clicks and buzzes. However, contrary to adults the calves employed gliding during

399descents instead of ascents. Thus, despite a difference in locomotor requirements, the tagged calves

400appeared to be developing the capacity for independent foraging. In comparison, the calves rarely

401produced codas, perhaps suggesting that investment in locomotor, diving, and echolocation skills may be

402favored over the development of social communication skills.

403

404**Suckling**

405The calves made several potential suckling dives, a behavior that made up an estimate of 47, 20, and 22 %

406of the recording time for Calf J, R, and A. The variability between these three values may stem from

407different suckling efficiencies between the calves or may relate to the calves' stage of transition from

408exclusively suckling to increasingly supplementing their diet with prey. The three calves additionally

409performed shorter shallow dives similar to the peduncle dives observed by Gero and Whitehead (2007).

410Underwater observations have shown that the calves press their blowhole against the escorting adults'

411genital area during such dives (Gero and Whitehead 2007) probably to induce milk let down as observed in

412other cetaceans (Asper et al. 1988; Peddemors et al. 1992; Xian et al. 2012) and in terrestrial mammals

413(Lent 1974).

414Successful transfer of milk requires behavioral coordination between the adult female and the calf. A

415recent study show that humpback whale calves opt for mechanical cues rather than vocal cues to indicate

416their readiness to suckle (Videsen et al. 2017). Similarly, no vocal cues were associated with the potential

417suckling behavior of the sperm whale calves. However, contrary to the situation for humpback calves, no

418acoustic signs of physical contact were apparent from the recordings in this study, which may be due to

419posterior tag placement on the calves. Such lack of acoustic cues may be an adaptation to avoid the risk of

420eavesdropping predators such as killer whales at or near the surface as suggested for humpback calves

421(Videsen et al. 2017).

422

423**Communication**

424It has previously been documented that calves less than a year are able to produce codas (Schulz et al.

4252011), but that they produce codas far less frequently than adults (Marcoux et al. 2006). Despite the

426sparsity of codas, calves are reported to produce a higher diversity of coda types compared to adults

427(Schulz et al. 2011; Gero et al. 2016) and it appears to take several years before calves converge on their

428natal unit's dialect (Gero et al. 2016). In concert, these results suggest that social communication is a

429complex skill to acquire. We recorded codas on only one of three tags in this study. Unit R socialized during

4303 of 7 hours of the tag deployment while Units J and A were foraging the entire time and only produced few

431codas (see Fig. 1d, e). Given that coda production rate is correlated with group behavioral state (Whitehead

432and Weilgart 1991), we were presumably more likely to record codas on Calf R's tag. However, it would

433appear that young calves may not have a high need to participate acoustically in the social bonding during

434these periods of socializing at the surface. Nonetheless, based on the absence of codas produced by Calf A

435and J, our results indicate that the calves do not need to emit dedicated social cues to maintain and re-

436establish contact with deep diving adult whales; the ample presence of acoustic cues from adult sperm

437whales (Fig. 1e) seems sufficient for the calves to track as suggested by Gordon (1987).

438

439**Dive behavior**

440Contrary to our expectation based on surface observations (Gordon 1987; Whitehead 1996) and the

441assumed smaller oxygen stores of calves, we show that first year calves have well developed diving abilities.

442Calf J and R both dove to around 300 m, but Calf J's longest dive lasted only 11 minutes, whereas Calf R

443performed three dives lasting between 22 and 31 minutes (Fig. 1). Calf A on the other hand performed four

444even longer dives (ranging from 31-44 minutes) during which it reached 600 m (Fig. 1), which more closely

445resembles adult dive behavior in this geographical area. These differences may imply that the calves are at

446different stages of developing their diving ability. It further seems that all three calves stayed within close

447proximity of one or several adult whales during descent and ascent, as they most often initiated and

448surfaced from deep dives simultaneously with one or more adults, cues of physical contact were recorded

449during their descents and ascents, and high-level adult echolocation clicks were recorded right before Calf

450A ascended from its four deep dives (Fig. 1). Thus, sperm whale calves can tolerate the increased pressure

451at depth and have sufficient oxygen stores for deep diving within their first year of living.

452Noren et al. (2001) suggested that the age at which dolphins' and pinnipeds' oxygen stores are fully

453developed relates to the species life history traits and especially how early the calf or pup transitions to

454independent foraging. Based on their purported life history traits (Gero et al. 2009), sperm whales may be

455hypothesized to have a protracted development of oxygen stores. However, their relatively large size

456compared to delphinid calves and phocid pups, for example, gives sperm whale calves a built-in advantage

457as oxygen stores scale proportionally with body mass ($M$) whereas metabolic rate scales with $M^{0.7}$ (Kleiber

4581975). This advantage may allow sperm whale calves to supplement milk with independent foraging earlier

459than expected from their otherwise characteristically slow life history traits. Additionally, deep diving

460toothed whales such as sperm whales and presumably Blainville's beaked whales (*Mesoplodon densirostris*,

461Dunn et al. 2017) may have a more rapid development of muscle and blood oxygen stores compared to

462deep diving phocids, such as northern elephant seals (*Mirounga angustirostris*, Noren et al. 2001) that

463spend their first months on land (Reiter et al. 1978).

464The long duration of several of the calf dives and the energetic ascents may have resulted in these calves

465exceeding their aerobic dive limit (ADL). Assuming that their mass specific oxygen stores are fully

466developed, the ADL of the three calves may be estimated by scaling the diving metabolic rates from adults

467(sensu Watwood et al. 2006):

$$468 ADL_{calf} = ADL_{adult} * \left( \frac{M_{b,adult}}{M_{b,calf}} \right)^{-0.25}$$

469where $M_b$ is body mass. To perform that estimation a minimum and maximum $M_{b,calf}$ of 1 and 2 ton were

470chosen for neonate and first year sperm whale calves (Lockyer 1981). The average $M_{b,adult}$ was set to 7.2 ton

471(Lockyer 1981) corresponding to the median body length of 9.2 m for adult females in the area (based on 472Bøttcher et al. 2018). Hence, assuming the median adult dive duration of 48 min approximates their ADL 473(Watwood et al. 2006), the estimated ADL of the calves ranges from 28 to 34 min. This approach takes the 474difference in mass specific metabolic rate into account, but assumes equal oxygen stores per unit of body 475mass, which may cause an overestimation of the calf ADL. The duration of dives made by Calf J (maximum 47611 min) was well within this estimated ADL, whereas the longest dives of Calf R and A reached and 477exceeded the estimated ADL. Hence, these calves may have faster maturation of oxygen stores than seal 478pups on land and shallow water odontocetes (Dolar et al. 1999; Noren et al. 2001), but may still need long 479surface intervals to process the accumulated lactate from possible anaerobic metabolism (Kooyman et al. 4801980). Indeed, all calves spend less time deep diving than the adults. This may, however, also be the 481consequence of the calves engaging in specific behaviors confined to the surface or near-surface zone, such 482as nursing.

483Unlike adults, all three calves spend more time gliding during ascents and less time during descents 484compared to the adults. This suggests that the calves are negatively buoyant due to a lower percentage of 485blubber, spermaceti oil and/or junk (Miller et al., 2004). Getting a negatively buoyant body back to the 486surface requires well-developed locomotor skills and careful timing of dives to ensure sufficient oxygen 487resources for an energetic ascent. The three calves had stroke frequencies higher than adult whales, when 488comparing the phase of the dives in which each whale worked against its buoyancy, i.e. ascents for calves 489and descents for adults. This difference is likely due to scaling of body size (Sato et al. 2007). However, Calf 490R and A attained speeds that in some cases exceeded those of adults during powered swimming, 491highlighting that they can indeed follow and keep up with adults during some deep dives and/or that they 492had not yet learned to manage their oxygen stores to maximize dive duration. The third calf swam at lower 493speeds than the two other calves and the adults in general, possibly because the adults of its social unit 494were swimming at slow speeds. Alternatively, this difference may imply that the three calves were at 495different stages of locomotor development.

496

## **Echolocation**

498One explanation for the pronounced diving behavior of these three calves may be that they, despite their
499young age, are catching food to supplement their milk-based diet. Our study shows that these free-ranging
500calves produced click trains, which in accordance with earlier suggestions (Ridgway and Carder 2001;
501Madsen et al. 2003) indicates that young sperm whale calves may echolocate. It was previously assumed
502that echolocation was a very complex sensory process that took cetacean neonates a long time to master
503(Bowles et al. 1988; Lindhard 1988). However, our findings are in line with recent studies on smaller
504toothed whales; harbor porpoises (*Phocoena phocoena*) emit clicks within minutes after birth and adjust
505their echolocation to match that of adults within a few days (Delgado 2016). Similarly, wild bottlenose
506dolphins (*Tursiops aduncus*) emitted clicks a few days after birth and after 17-21 days these clicks were
507similar to adult echolocation clicks (Delgado 2016). This early development of echolocation fits the rapid life
508history traits of these species, but sperm whales, in contrast, are known for their slow maturation and
509hence perhaps would be expected to start echolocating much later. We show that this is not the case, and
510taken in combination with similar observations for Blainville's beaked whales (Dunn et al. 2017), this
511suggest that echolocation skills develop rapidly after birth in both small and large toothed whales.

512Calf J and R both emitted one short click train at a depth of approximately 200 m. The absence of buzzes
513and the fact that these two calves did not reach depths where the adults were foraging suggest that these
514calves were not engaged in biosonar based prey interception. However, the clicking may represent an early
515stage of their echolocation development, which could explain why the longer ICI of Calf J, which may be
516due to the calf needing longer processing time of the echoic scene of each click. In contrast, Calf A emitted
517two long bouts of clicks with ICIs similar to adult ICIs; and additionally, produced two buzzes at a depth
518where adults were also buzzing (Fig. 1). The presence of buzzes within echolocation bouts is a possible
519indication that Calf A was echolocating to catch prey. This interpretation is further supported by the

520presence of an echoic object that the calf approached during the second buzz (Fig. 6). Calf A made only two

521long buzzes, but these had ICIs similar to those of adults. This is consistent with the calf engaging in the

522approach and buzz phases of biosonar-based foraging, but perhaps not managing to catch the prey as

523quickly or at all, leading to a protracted capture attempt.

524The great variability in echolocation effort between the three calves of this study may reflect that these

525calves were at different stages in the transition from suckling to early independent foraging, or that we

526simply sampled them too little to capture the full range of vocal behaviors. Field observations suggest that

527the calf which performed the buzzes was the largest and therefore maybe the oldest of the three calves,

528implying that the difference in diving behavior and echolocation effort observed here may be an effect of

529age, within the inherent limitations of our small data set.

530

531

532**Conclusion**

533Here we have used miniaturized bio-logging devices to obtain a unique first snapshot of the early

534development of social and foraging behavior in the largest tooth-bearing predator on the planet, the sperm

535whale. Due to practical difficulties in tagging calves this study is based on a sample size of three calves and a

536total recording time of 15.7 hours. With this reservation in mind, the data has enabled us to shed some

537light on the gradual and complex ontogeny of sperm whale calves in unprecedented detail; as well as

538allowing for greater insight into what sperm whales are capable of in their first year of life and the pace at

539which they go on to become sound mediated, highly social apex predators in a deep oceanic environment.

540Contrary to large brained and highly social terrestrial mammals, our data potentially suggest that sperm

541whale calves do not postpone their locomotor development to favor the maturation of complex social

542skills. Instead, the first-year calves performed deep and long-lasting dives where they seem to employ

543echolocation as part of their sensory scene acquisition, and one calf may have engaged in biosonar

544mediated prey capture attempts. Furthermore, the calves seemed to primarily rely on passive acoustic cues

545from the adults rather than emit codas themselves to maintain and restore contact with adults. Hence, it is

546implied that sperm whales are an example of a large-brained, highly social mammal that perhaps prioritize

547locomotor and diving development potentially at the cost of slower development of social and

548communicative skill, which in turn may explain their prolonged dependency of their social unit compared to

549delphinids.

550

551**Compliance with ethical standards:**

552**Ethical approval**

553The study complied with the laws of Dominica and was approved by Aarhus University IACUC, Denmark.

554The whales were tagged under permits # P-122/4W-2, P-40/2W-7, and RP16-04/88FIS-9 issued by the

555Fisheries Department, Dominica.

556**Conflict of Interest**

557The authors declare that they have no conflict of interest.

558

559**Data availability**

560The data used in the current study are available from the corresponding author on reasonable request.

561

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733**Figure captions**

734**Fig. 1** Dive profiles over the entire tag deployments showing changes in depth over time for Calf J (a), Calf R

735(b), Calf A (c, with specific dives I-IV, see Fig. 3) and an adult from Unit J (d). Periods of calf clicking (red),

736loud adult echolocation (blue), coda bouts (magenta), calf buzzes (black circles in c), adult buzzes (black

737circles in d) and physical contact with another whale (yellow) are superimposed on the dive profile. Insert

738(e) shows the percentage of the recording time containing codas (black), echolocation clicks (dark grey) or

739no apparent sounds emitted by all audible sperm whales (light grey) and insert (f) shows the tag placement

740on Calf A

741

742**Fig. 2** Dive profile (black) and change in pitch (blue) for Calf A (a) and one of the adults (b), vertical lines

743indicates the end of the descent phase and the start of the ascent phase. RMS values for each 10 s block of

744the dive for Calf A (c) and the same adult (d), the red line indicates upper threshold for gliding periods set

745to 20 % of the mean RMS value of the dive

746

747**Fig. 3** Dive profiles for Calf A's four deepest dives (a-d), inter-pulse interval IPI (e-h), angle of arrival AOA (i-l)

748and apparent output level AOL (m-p) of high-level clicks recorded by the tag on Calf A during dive a, b, c,

749and d. Blue indicates nearby adult echolocation (a-d) and buzzes (l, k-m and o-p), red indicates Calf A's

750echolocation (b-c) and buzzes (j-k and n-o). Red vertical lines indicate the shifts from calf to adult click

751production

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753**Fig. 4** Histogram of inter-click intervals (ICI) of echolocation clicks of Calf J (green), Calf R (yellow), Calf A

754(light blue) and adults (dark blue). Bi-modal distribution demonstrates the change in ICI between normal

755echolocation and buzzes

756

**Fig. 5** Distribution of dive duration and maximum dive depth for Calf J (green), Calf R (yellow), Calf A (light blue) and adults (dark blue). The lines indicate the minimum (dashed) and maximum (solid) estimated aerobic dive limit for calves

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**Fig. 6** Echogram of Calf A's second buzz during dive c

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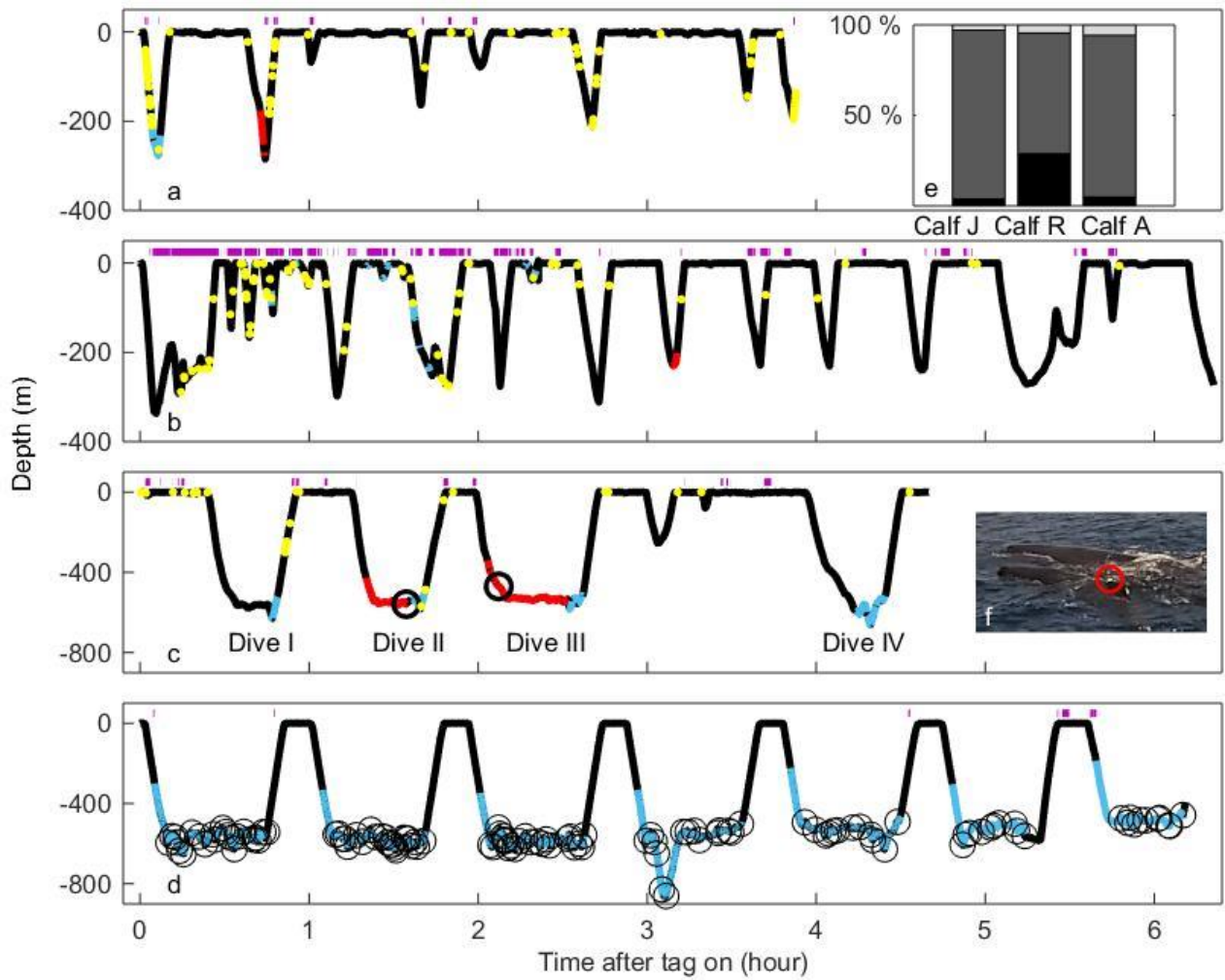**Figures for "First-year sperm whale calves echolocate and perform long, deep dives" Tønnesen et al. 2018**
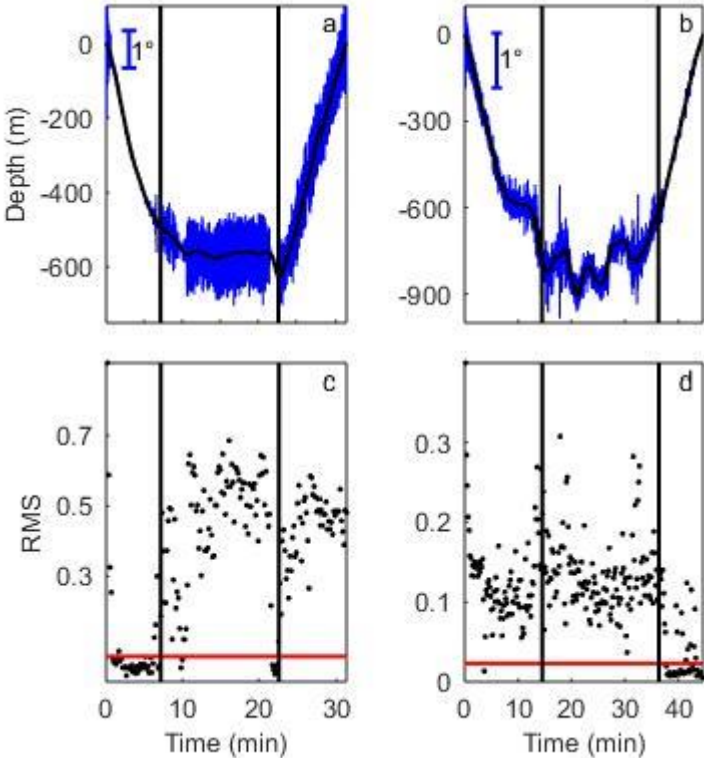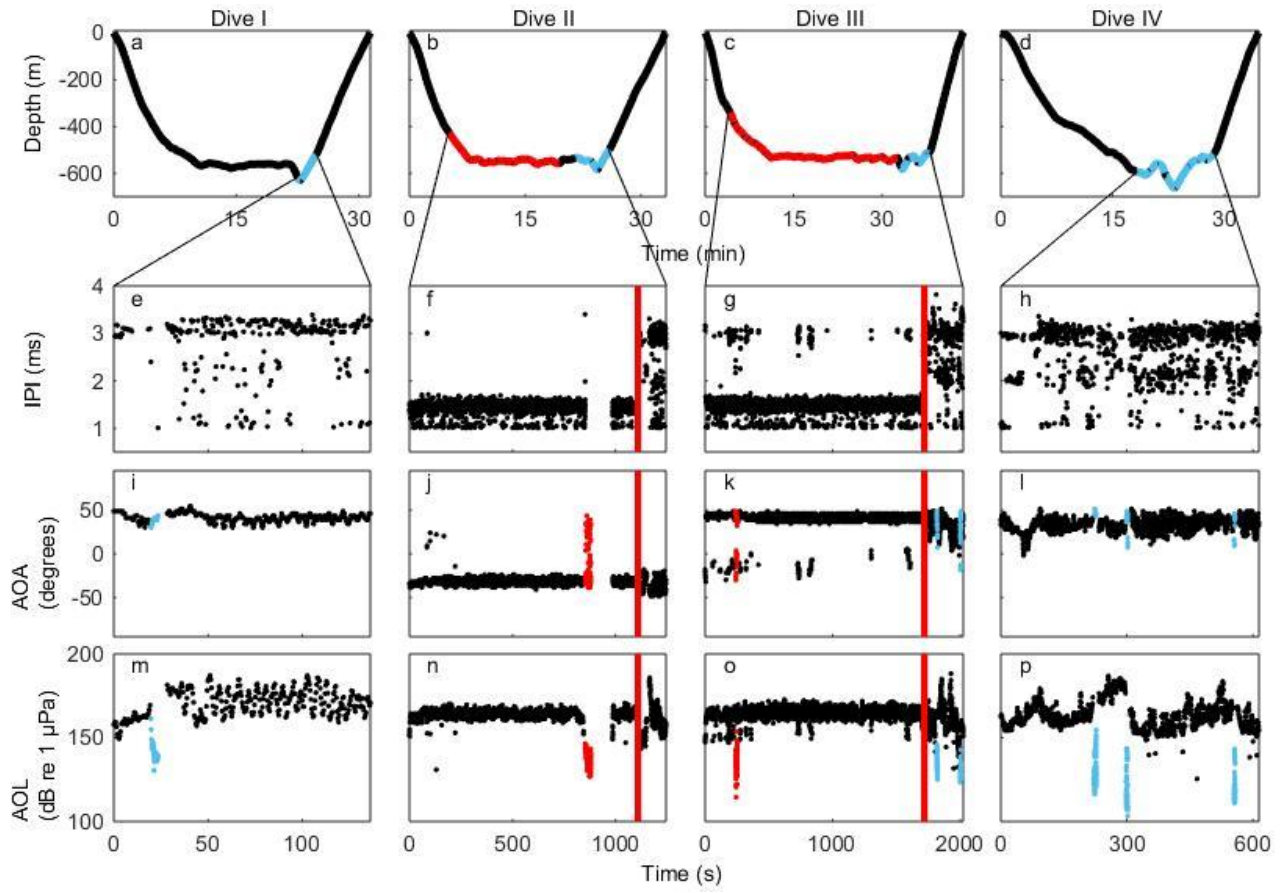
**Figure 1**

**Figure 2**

**Figure 3**

**Figure 4**

**Figure 5**

**Figure 6**