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## Ontogeny and synchrony of diving behavior in Humpback whale mothers and calves on their breeding ground

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4 **Ontogeny and synchrony of diving behavior in Humpback whale mothers and calves on**  
5 **their breeding ground**

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16 For humpback whales, the mother-calf pair is the only stable social unit with calves following  
17 their mother soon after birth and staying in close proximity. This following strategy ensures  
18 the maintenance of such close proximity between the mother and her calf, with calves  
19 benefiting from maternal protection and care. Using multi-sensor tags, we recorded the diving  
20 behavior of calves at 3 different age-classes (C1, C2, C3) to assess how calves developed in  
21 their natural environment at an early stage of their life. From 29 deployments on calves, we  
22 extracted the diving metrics from two C1 neonate calves, eight C2 calves and nineteen C3  
23 calves, and we found that some diving metrics (dive duration, time at bottom, maximal depth  
24 or maximal dive duration) differed among calves' age classes. On 23 tagged mothers, we  
25 analyzed if their diving profiles also varied depending on calf's age class. We showed that  
26 only two dive metrics of mothers varied with the age of their own calves (time spent at the  
27 bottom, and time interval between dives), but all others were not reliant on the calf's age.  
28 Simultaneous deployments on seven mother-calf pairs in 2016 and 2017 revealed highly  
29 synchronized dives, with mothers leading the diving pattern. This work represents an  
30 extensive study investigating the diving behavior in humpback whale mother-calf pairs on  
31 their breeding ground.

32 Key Words: breeding ground, diving behavior, humpback whale, mother-calf interaction,  
33 ontogeny.

34 Maternal strategies in mammals are diverse. Indeed, either mothers hide their young  
35 and leave them alone in a safe place while they forage (i.e., hiding strategy), or they travel  
36 with their young within close proximity (i.e., following strategy) (Lent 1974). The following  
37 strategy can be found in both terrestrial mammals (in ungulates, Lent 1974; in macropods,  
38 Fisher et al. 2002) and marine mammals (in humpback whale *Megaptera novaeangliae*, Szabo  
39 and Duffus 2008; in odontocetes, Mann 2019). Neonates will follow their mothers after birth  
40 and such spatial proximity persists until weaning when they separate permanently (Lent  
41 1974). Such close proximity between the neonate and its mother benefits both the young and  
42 the mother. The young benefits from continuous maternal care (nursing and protection against  
43 predators), while the female is able to continue travelling and feeding activities (Lent 1974;  
44 Szabo and Duffus 2008). In cetaceans, the following strategy is possible as cetacean neonates  
45 are precocial and thus have the abilities to swim, dive and nurse without physical support  
46 from their mother soon after birth (Szabo & Duffus 2008, Mann 2019). Swimming and  
47 nursing behaviors have been well documented in odontocetes (Mann & Smuts 1999, Noren  
48 2008, Sakai et al. 2013). Infant position is defined as the position where the calf usually  
49 swims in a close position to its mother (calf being less than 2m from its mother, Mann and  
50 Smuts 1999). In mysticete species, the swimming positions of calves and their close proximity  
51 to their mothers have been described for southern right whales, *Eubalaena australis* (Taber &  
52 Thomas 1982), grey whales, *Eschrichtius robustus* (Swartz 2018) and humpback whales  
53 (Szabo & Duffus 2008, Saloma et al. 2018).

54 Observational studies of humpback whales in both breeding and foraging grounds  
55 document calves staying within close proximity of their mothers (Szabo & Duffus 2008,  
56 Cartwright & Sullivan 2009, Zoidis 2014). Spatial proximity decreases with age when calves  
57 become more independent and have improved motor skills (Szabo and Duffus 2008). Previous  
58 studies on calves diving and surfacing behavior have been assessed using surface observations

59 from boats following animals or from snorkelers/divers swimming near focal animals (Zoidis  
60 et al. 2008, Cartwright & Sullivan 2009).

61 The development of miniature, multi-sensor tags deployed on whales have allowed  
62 researchers to investigate natural behaviors freely in their environment and without the  
63 presence of a boat and/or of humans (Cooke et al. 2004, Donaldson et al. 2014, Hussey et al.  
64 2015, Lennox et al. 2017). These animal-borne devices allow researchers to collect  
65 information on whale various behaviors (e.g. vocal communication, foraging, mating,  
66 navigation, predator avoidance...) and migration (Johnson et al. 2009). Tagging large adult  
67 whales induces some stress and reactions however these reactions have been mostly reported  
68 to be mild and short-term for tags with suction cups (Hooker & Baird 2001, Johnson et al.  
69 2009). Tagging young animals is less common for cetaceans however, if the tagging process  
70 is performed with a conservative approach and limited animals' disturbance as reported by  
71 Stimpert and colleagues (2012), the knowledge gained by tagging calves is highly valuable  
72 (Tyson et al. 2012, Videsen et al. 2017).

73 Understanding of mother-calf diving behavior during the early stage of calf's age is  
74 biologically important. This is a critical period during which the calf develops a strong bond  
75 with its mother and acquires essential respiratory and motor skills before the long migration to  
76 their foraging grounds. While diving ontogeny related to their feeding activities has already  
77 been investigated in foraging grounds (Szabo and Duffus 2008; Tyson et al 2012), less is  
78 known about diving behavior and diving ontogeny in breeding areas (Stimpert et al. 2012). In  
79 the present study, we investigated the diving behavior of humpback whale calves and mothers  
80 between 2013 and 2017 on the breeding ground off Sainte Marie Island, Madagascar. We  
81 deployed multi-sensor tags on calves of different ages and on adult mothers accompanied by  
82 calves of different ages. We also investigated mother-calf pair diving patterns during  
83 simultaneous tagging sessions to better understand the diving dynamics of the pairs. We

84 aimed to determine (a) if the diving behavior of calves and mothers vary with the calf's age,  
85 and (b) if mother-calf pairs synchronize their dives.

86

87

## MATERIALS AND METHODS

88 *Study site and animals.*—Acoustic and diving data were collected during five successive  
89 winters from 2013 to 2017 during the breeding season in the Sainte Marie channel, North-East  
90 of Madagascar (49°50' E-50°10 E, 16°60'S-17°55' S). The Sainte Marie channel is a  
91 relatively shallow channel showing a maximal depth at 60 meters and an average depth  
92 between 25 to 35 meters (Trudelle et al. 2018).

93 Age-classes of calves were estimated by both their skin characteristics and the  
94 inclination of the dorsal fin. Descriptions of newborn calf characteristics in the Sainte-Marie  
95 channel have documented newborn dorsal fins as completely unfurled and lying to one side at  
96 birth, with fluke tips curled (Faria et al. 2013). Calf dorsal fins straighten as they get older  
97 (Cartwright and Sullivan 2009). For this study, three relative age-classes were considered as  
98 follows; C1: neonates with some fetal folds, scars on different body parts, skin color light  
99 grey on the dorsal side and white ventrally, with the dorsal fin completely furled (Faria et al.  
100 2013) or semi furled with the fin at an angle less than 44° (Saloma, pers. com.). C2: calves  
101 with dorsal fins unfurled at an angle more than 45° but less than 62°, and C3: older calves  
102 with dorsal fins unfurled between 72° to fully erected fin (90°) (Cartwright and Sullivan  
103 2009). From our dataset, C1 calves showed an inclination angle ranging between 32° and 35°  
104 (n=2), C2 calves between 45° and 62° (n=10), and C3 calves between 72° and 87° (n= 36).

105 *Tagging procedure.*—Tagging mother-calf pairs, especially groups with neonate  
106 calves requires a strategic approach. Passive and active approach methods were used  
107 depending on mother-calf behavior (static or slow travelling), as well as the choice of the  
108 targeted individual to tag within the group (mother or calf). Passive approach, drifting with

109 the current, previously described by Stimpert *et al.* (2012) is most effective in limiting the  
110 disturbance of mother-calf pairs. This approach was used when groups were static or when  
111 calves were observed alone at the surface. If the pairs were travelling slowly, the boat was  
112 placed parallel to them at the same speed and within visual range of the mother. The animal  
113 closest to the boat was then tagged. For simultaneous tagging, mothers and calves were  
114 tagged either during the same approach (this involved two researchers) or if the double  
115 tagging was unsuccessful, a second approach was required. The maximum time spent with  
116 each pair (i.e. time spent attempting to tag the animals) never exceeded 30 minutes, following  
117 official Madagascar's agreement for mother and calf observations (inter-ministerial decree  
118 March 8<sup>th</sup>, 2000). As soon as the tag(s) were attached to the animal(s), the vessel slowly  
119 moved away in an opposite direction to avoid any further disturbance to the pair. All mother-  
120 calf pairs were photo-identified to avoid double-sampling within the breeding season.

121 The tags used in this study were two Acousonde 3B. The Acousonde (Acoustimetrics,  
122 Santa Barbara, California) is a miniature, self-contained, autonomous acoustic/ultrasonic  
123 recorder designed for underwater applications. Acousondes were deployed on mothers and/or  
124 calves using a non-invasive attachment system (suction cups). Since mother-calf pairs were  
125 not followed after tagging, each Acousonde was coupled with a VHF emitter (ATS F1835B,  
126 Advanced Telemetry System, Isanti, Minnesota) in order to retrieve the tag once detached  
127 from the animal using a VHF receiver (ATS R410, Advanced Telemetry System, Isanti,  
128 Minnesota) connected to an antenna. The duration of the attachment on the animal varied  
129 greatly among individuals from 30 minutes to up to 35 hours (Fig. 1).

130 All procedures involving live animals followed the American Society of  
131 Mammalogists guidelines (Sikes *et al.* 2016) and were approved by the Ministry of Fisheries  
132 Resources, Madagascar under national research permits n° 44/13, 44/14, 46/15, 28/16, 26/17  
133 MRHP/DGPRH.



134

135 *Data collection and analysis.* —Pressure sensor (resolution: 1.2 cm) was recorded at a  
136 10 Hz frequency sampling rate and down-sampled at 1Hz for automatic analyses. In 2016, we  
137 used a second Acousonde 3B that allowed us to tag both the mother and the calf of a given  
138 pair. Diving profiles were extracted from the pressure data using a custom routine in Matlab  
139 version r2016b. In order to compare with previous studies on diving behavior of humpback  
140 whale calves, a dive was considered as an excursion below 2m with the animal reaching a 10-  
141 m threshold during its excursion (10m corresponding to approximately 2 body lengths of a  
142 calf), as described in Stimpert et al. 2012. Such criterion was used for both mothers and calves  
143 to enable comparisons, and allowed us to exclude all sub-surface activities (0-5m, as shown  
144 on Figure 4.A1) from our analysis, and thus we analyzed only dives deeper than 10m.

145 To characterize the dives, we chose some of the dive metrics proposed by Hooker and  
146 Baird (2001) to describe cetacean dive behavior and those previously used for humpback  
147 whale calves (Stimpert et al. 2012). For automatic dive detection and slope computations,  
148 diving data were low-pass filtered (low pass filter frequency: 0.25Hz). We then extracted the  
149 following dive metrics: number of dives per hour (Dhour, in nb/h), maximum dive duration  
150 (maxDur, in s), maximum dive depth (maxDep, in m), surface time ratio (SurfaceR, in %),  
151 dive duration (diveDur, in s), dive depth (diveDep, in m), bottom time (BotDur, in s), post-  
152 dive surface interval (PostDSI, in sec), ascent slope (AscSlope, in  $m \cdot s^{-1}$ ), descent slope  
153 (DesSlope, in  $m \cdot s^{-1}$ ). The first four parameters (Dhour, maxDur, maxDep, surfaceR) were  
154 extracted from each deployment, and averaged values over individuals across age classes (C1,  
155 C2, C3 for calves, and M-C1, M-C2, M-C3 for mothers accompanied with C1, C2 and C3  
156 calves respectively) are given in the results section. For the last six parameters (diveDur,  
157 diveDep, BotDur, postDSI, AscSlope, DesSlope), values were extracted from each single  
158 dive. All dive metrics are summarized in Table 1.

159 Dive duration was defined as the time spent below the 2m/10m threshold. Dive depth  
160 represented the deepest point of each dive. The bottom time was defined as the time spent at  
161 >85% of the maximal dive depth for each dive. Post-dive surface interval was computed as  
162 the time between each dive (calculated from 2m). Descent slopes were computed from the  
163 point at which the whale starts a dive (below 2 meters) down to the first deepest point (if a  
164 plateau was observed during the dive). Ascent slopes were computed from the last deepest  
165 point to the end of the dive (above 2 meters).

166 Finally, during the 2016 and 2017 breeding seasons, we tagged both mother and calf  
167 of a given pair to investigate their diving pattern. This allowed us to assess if there were  
168 similarities in their diving profiles and the occurrence of diving synchrony. We also assessed  
169 if the mother or the calf initiated the dives.

170 We measured the averaged values of 11 dive metrics for each calf and mother: the  
171 number of dives performed during the overlap duration (Nb dives), the number of mother's  
172 dive during which the calf returned to surface (MDCsurface), the maximum dive duration  
173 (maxDur, in s), the maximum and modal dive depth (maxDep and modDep, in m), the  
174 duration at bottom (BotDur, in s), dive per hour (Dhour, in nb/h), post-dive surface interval  
175 (PostDSI, in s), vertical speed for both ascent and descent (AscSlope, DesSlope, in m/s) and  
176 the percentage of time spent at the surface (SurfaceR, in %). Depth difference between mother  
177 and calf was computed by subtracting mother and calf diving profiles at each point in time,  
178 and referred to as "vertical distance". Note that "vertical distance" is not equivalent to  
179 Euclidian distance as it only refers to the vertical axis. From all the extracted values,  
180 histograms were computed using either all the values (in order to assess the vertical distance  
181 distribution) or only at the maximal depth of each calf's dive (in order to assess the  
182 distribution of the relative depth of calves and mothers).

183

184            *Statistical analysis.* —From the six dive metrics measured on all dives (diveDur,  
185 diveDep, BotDur, postDSI, AscSlope, DesSlope) obtained during the five successive breeding  
186 seasons, we investigated if the dive characteristics for calves different among the three  
187 different age classes. For each dive metric we performed a linear mixed model (lmer function,  
188 lmerTest package) with the calf's age-class as a fixed factor and identity of the tagged  
189 individual as a random factor. For the four dive metrics (Dhour, maxDur, maxDep, surfaceR)  
190 we averaged the total duration of the deployment and performed Welch ANOVAs. Post-hoc  
191 tests were performed when a dive metric significantly differed among age-classes to assess  
192 pairwise comparisons (Tukey's tests, multcomp R package, and Games-Howell test,  
193 userfriendlyscience R package)(R Core Team 2020)

194            To analyze the diving pattern obtained from simultaneous deployments, we plotted  
195 together the diving profiles of the mother with her calf to visually assess similarities in diving  
196 profiles using MATLAB. We performed a cross-correlation test between profiles of mothers  
197 and calves on the common recording duration of the dives. A first correlation coefficient was  
198 measured with a sliding time-window to assess the maximal normalized correlation between  
199 the two diving profiles (the diving profiles are normalized so that their autocorrelations at  
200 zero-lag equal to 1). The time lag corresponding to this maximal correlation allowed us to  
201 assess the leader of the dive (either the mother or calf). A second coefficient was measured  
202 without time sliding to assess the correlation between the two diving profiles with their  
203 original time axes. Finally, we compared the 10 averaged dive metrics between the mothers  
204 and their calves using Wilcoxon rank sum tests in R. All plots were done in R using the  
205 package ggplot2 for violin plots.

206

207

## RESULTS

208 Over the five breeding seasons, we had successful deployments on 31 calves and 24 mothers  
209 (Fig. 1), but 3 deployments (i.e., 2 calves and 1 mother) were not included in our analysis  
210 because deployments were too short (less than 30 minutes). During the breeding seasons 2016  
211 and 2017, we performed 13 simultaneous mother-calf deployments, but only 7 showed  
212 sufficient overlapping time (at least 30 minutes) to measure dive metrics for both mother and  
213 calf of the targeted pair.

214

215 *Calves' diving behavior.* —Among the 10 dive metrics measured, 5 varied  
216 significantly among the 3 age classes (Table 2, Fig. 2). Calves increased the duration of their  
217 dives with age. The mean duration was significantly different between C1 and C3 calves  
218 (Figure 2), and the maximum dive duration for C1 calves were significantly shorter than C2  
219 and C3 calves (see Supplementary Data S1). They also increased the time spent at the bottom,  
220 with C3 calves spending significantly more time than C2 and C1 calves (Figure 2). The  
221 maximal dive depth increased also with age, with C2 and C3 showing significant maximal  
222 depth greater than C1 (see Supplementary Data S1). The ascending vertical speed did not vary  
223 with age.

224

225 *Mothers' diving behavior.* —Among the 23 mothers, we only had 2 mothers with C1  
226 calves, and one mother did not dive during the tag deployment (recording duration: 1.36  
227 hours). For the 6 dive metrics extracted on each single dive (diveDur, diveDep, BotDur,  
228 postDSI, AscSlope, DesSlope), we included only mothers with C2 and C3 calves (we could  
229 not run the analysis with only one mother with C1 calf). We included the two mothers with  
230 C1 calves for four dive metrics averaged on the total duration of the deployment (Dhour,  
231 maxDur, maxDep, surfaceR). When analyzing the diving behavior of mothers in regards to  
232 their calf's age class, only 2 dive metrics were found significantly different among mothers

233 with C2 and C3 calves (Table 2, Fig. 3). Mothers with C3 calves spent longer time at the  
234 bottom (BotDur) than mothers with C2 calves, and the duration between dives (postDSI) was  
235 shorter in mothers with C3 than mothers with C2 calves. However, we did not find any  
236 significant differences regarding the dive durations (mean or maximum), or maximal dive  
237 depth as found in calves.

238

239 *Simultaneous deployments.* —When plotting the dive profiles of the 7 mother-calf  
240 pairs, we found that mother and calf showed highly synchronized dives (Table 3, Fig. 4 A1-  
241 A3, see Supplementary Data S2). The dive metrics for mother-calf pairs, as well as correlation  
242 coefficients between mother-calf dive profiles are shown in Table 3. We found a very high  
243 synchrony between the dive profiles of mothers and calves, with the maximal correlations  
244 ranging from 0.81 to 0.98. As shown in Table 2, the number of dives was not similar between  
245 mother and calf as the calf sometimes returned to the surface while the mother stayed at  
246 bottom (see examples on Fig 4A1-A2). The number of mother's dives during which the calf  
247 returned to surface (MDCSurf) is given in Table 3. We observed 24 of these events, and  
248 during which the calf went back to the surface 2 to 4 times. When comparing the 10 dive  
249 metrics measured between mothers and calves of the pairs, six were found significantly  
250 different (Fig. 5). Calves showed shorter dive durations as in many instances the mother  
251 stayed at the bottom, so this also explained why the bottom duration was longer in mother and  
252 thus the time spent at the surface was longer in calves. The maximal dive depth was also  
253 found significantly different, with calves being slightly (i.e., within 5 meters) at a deeper  
254 position compared to their mother. Significant differences between mothers and calves were  
255 also found on the vertical speed during both ascending and descending phases, with calves  
256 showing higher vertical speeds when going back to the surface and when descending. On the  
257 7 mother-calf studied pairs, all showed that mothers were leading the dive (i.e. negative delta

258 values on Table 2), thus in all cases, calves followed the diving pattern of their mothers.  
259 Finally, mother-calf vertical distances ranged from -38 to 31m (Fig. 4B), showing that calves  
260 can be separated from their mother by at least 30m, with the calf being either below or above  
261 its mother. The histogram tail between -8m and -20m corresponds to events during which  
262 calves were going back to the surface while mothers stayed at the bottom. However, we can  
263 see that most of time they are together within 4m from each other. The time spent above or  
264 below the mother varies greatly among calves (Fig. 4B), but we found that, when the pair is  
265 diving, the calf was mostly below its mother (Fig. 4C) and rarely above her.

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## DISCUSSION

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*Ontogeny of diving behavior in calves.* — Here we investigated the diving pattern of calves at different ages. As two of the tagged calves were neonates (C1, but only one performed dives during the recordings), our results present the earliest diving behavior of baleen whales during their first days, when calves are extremely dependent of their mother. Such knowledge is quite important as we do not have many observations on their behavior at this early age, and we showed that even neonates can perform frequent dives with their mothers.

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Our findings are consistent with the previous studies done on humpback whales calves in their breeding grounds (Cartwright & Sullivan 2009, Tyson et al. 2012, Ejrnaes & Sprogis 2021). Of the 29 studied calves, we found that 4 out of the 10 analyzed dive metrics varied significantly with age. When getting older, calves increased the duration of their dives and thus the time spent at the bottom was also longer (Fig. 4, Table 2, see Supplementary Data S1). Calves also dove deeper (maxDep only) when they were older, but our post-hoc comparisons showed that the main difference was between neonate (C1) and older calves (C2, C3). Note that statistics were computed using the total number of dives as sample size, with

283 individuals included as nested factor in order to account for random effects due to inter-  
284 individual variations. However, since we could record dives only on two C1 calves, great care  
285 should be taken in generalizing the present results. Nevertheless, these findings suggest that  
286 older calves showed higher swimming and breathing abilities, as previously found in  
287 humpback whales (Cartwright & Sullivan 2009, Ejrnaes & Sprogis 2021) and observed in  
288 right whales (Cusano et al. 2019, Dombroski et al. 2021). As suggested in previous studies,  
289 neonate calves have limited lung capacity as they are still learning to manage their breathing  
290 cycle and buoyancy. In mammals, the alveolar saccules must expand and subdivide to  
291 increase the gas exchange, and then the volume of the lungs will grow (Weibel 2000). Also,  
292 larger animals have a proportionately greater oxygen storage capacity leading to a greater  
293 diving capacity (Schreer & Kovacs 1997). Indeed, diving capacity is among those skills  
294 developed gradually by calves (Stimpert et al. 2012). The number of dives per hour did not  
295 increase with age, and that both the time spent at the surface and the interval between dives  
296 did not decrease with age. This indicates that calves do not increase their dive rate when they  
297 age, and the time spent at the surface is not related to their age. So, even if their lung capacity  
298 increases with age, they do not seem to use it to dive more often. As suggested by Stimpert et  
299 al. (2012), calves might rather use such aerobic resources toward growth and development.  
300 Recent investigations on muscular myoglobin stores in mysticetes have revealed calves  
301 present very low levels of myoglobin stores in muscles compared to juveniles and adults  
302 (Cartwright et al. 2016). This would explain their limitations in respiratory and diving  
303 capacities.

304 Our results on calves are consistent with those reported by Stimpert et al. (2012) on  
305 breeding grounds in Hawaiian waters. The most striking difference between the two studies is  
306 the difference in dive depth that can be easily explained by the topography of our study site  
307 (averaged depth between 25-35 meters), and not a difference in diving abilities.

308 *Effect of calf's age on the mother's diving behavior.* —From the 23 tagged mothers, we  
309 were able to follow the diving behavior of 21 mothers accompanied with C2 and C3 calves.  
310 The two mothers with C1 calves were included in the descriptive analysis (four dive metrics:  
311 *Dhour, maxDur, maxDep, surfaceR*), but not in our general analysis as one female did not  
312 dive during the deployment duration (Table 2). Mothers modified their diving profile with  
313 regards to their calf's age. Mothers with C3 calves stayed longer at the bottom, and showed  
314 shorter time interval between dives than mothers with C2 calves. This indicates that mothers  
315 tended to increase their time away from their calves as they get older. There is also a  
316 possibility that the shorter time interval between dives for mothers with older calves (C3) may  
317 reflect the great respiratory capacities of the young. Our synchronous deployments on mother-  
318 calf pairs revealed such pattern with mothers staying at the bottom while calves come back to  
319 the surface for breathing in several instances (Fig. 4A1). Longer bottom time and shorter  
320 surface interval of mothers with older calves were also found in Southern right whales  
321 (Dombroski et al. 2021). In contrast, UAV monitoring of mother-calf pairs in Western  
322 Australia did not report any change of breathing rate in mothers with regards to calf length  
323 (i.e., age) (Ejrnæs & Sprogis 2021).

324  
325 *Mother-calf synchronized dives.* —Among the mother-calf pairs tagged  
326 simultaneously, mothers and calves show a high synchrony in their diving profiles. This is  
327 consistent with previous studies on humpback and right whales mother- calf pairs (Taber &  
328 Thomas 1982, Szabo & Duffus 2008, Tyson et al. 2012). Vertical distance measurements  
329 suggested high synchronicity and spatial proximity between the pairs (under the hypothesis  
330 that the horizontal separation was also small). Even though calves have to perform short dives  
331 to breathe, the vertical distance separating the pairs was mostly between 1 and 4 m (Fig. 4B)  
332 suggesting that mother-calf pairs on the breeding ground stay at the same depth and likely at



333 close range to each other in all their activities. Similar vertical proximity has been described  
334 by Tyson *et al.* (2012) on the feeding ground even though this distance tends to be greater ( $\pm$   
335 20m) compared to our results where mother-calf pairs were much closer ( $\pm$  4 m).

336 Mothers were the first to initiate dives to help facilitate the mobility of the calf. As it  
337 was shown on dolphins (Weihs 2004, Noren 2008), when calves swim in echelon (within  
338 30cm to its mother, on the mother's lateral flank, Weihs 2004) or in infant position (below its  
339 mother), they may benefit from the hydrodynamic flow of their mothers, and thus dive with  
340 reduced muscular effort (Noren & Edwards 2011). Such close proximity brings hydrodynamic  
341 benefits during diving, but most importantly allows the mothers to provide continuous  
342 maternal care and protection towards predators. As calves become older and more  
343 autonomous, distance between the mother and her calf increases (Szabo and Duffus 2008),  
344 and calves become more responsible for maintaining proximity to their mother (Taber and  
345 Thomas 1982, Tyson *et al.* 2012).

346 Our findings confirm that humpback whale calves exhibit a following strategy, and  
347 this was previously observed in feeding grounds (Szabo and Duffus 2008; Tyson *et al.* 2012).  
348 On several occasions, we also found that calves dove 1-3 m deeper than their mothers  
349 confirming that calves positioned themselves below their mothers (Glockner-Ferrari & Ferrari  
350 1985). This position allows calves to stay at the bottom as they cannot yet properly control  
351 their buoyancy (Tyson *et al.* 2012).

352 This study has given additional knowledge on the ontogeny of diving behavior of  
353 humpback whale calves in their breeding ground, especially on very young calves (C1  
354 calves). However, there still remains many more questions to be answered. Future direction of  
355 this work should investigate the ontogeny of the swimming behavior of calves by analyzing  
356 data from 3D-accelerometers. Such exhaustive analysis will allow us to assess the proportion  
357 of gliding and active swims while traveling and diving (*i.e.*, during both vertical and

358 horizontal movements), and how swimming performance and swimming styles (i.e., infant  
359 position, in echelon position) develop with calf age.

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368

**SUPPLEMENTARY DATA**

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**Supplementary Data S1.** —Dive metrics (Dhour, maxDur, maxDep, surfaceR)

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extracted from each deployment, and averaged over calves across age classes (C1 with n=2,

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C2 with n= 8, C3 with n=19) and over mothers accompanied with calves of different age

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classes (M-C1 with n=2, M-C2 with n=5, M-C3 with n=17).

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**Supplementary Data S2.** —Diving patterns of the four other mother-calf pairs

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obtained during simultaneous deployments.

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470

**FIGURE LEGENDS**

471 **Fig. 1.** —Summary of deployments performed on 23 adult mothers and 20 calves between  
472 2013 and 2017 (durations of deployments, and repartition of calves among the 3 age-classes).

473

474 **Fig. 2.** —Graphical representation (violin plots) of the 6 dive metrics calculated on each dive  
475 for the 3 age-classes of calves (C1 with n= 2, C2 with n= 8 and C3 with n=9).

476

477 **Fig. 3.** —Graphical representation (violin plots) of the 6 dive metrics calculated on each dive  
478 for mothers accompanied with calves of different age-classes (M-C1 with n = 1, M-C2 with n  
479 = 5, M-C3 with n = 17).

480

481 **Fig. 4.** —Mother-calf pair simultaneous deployments. A. Examples of diving profiles of 3  
482 mother-calf pairs with calves of different age class (C3, C2 n=and C1). B. Histogram of  
483 vertical distances measured between mothers and calves on the entire duration of the  
484 deployment. Data ranged from -38m to 31m, however the time spent below its mother at  
485 distances greater than 10m represented only 1.233 minutes, and thus was not visible on the  
486 plot, therefore not shown in the figure. C. Histogram of vertical distances measured only  
487 during calves' dives.

488

489 **Fig. 5.** —Boxplots of calves and mothers dive metrics found significantly different in mother-  
490 calf pairs during simultaneous deployments (n=7).



491 **Table 1. —Description of the different dive metrics extracted from the diving profiles. \*only**  
 492 for synchronous deployments.

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Dive metrics computed on each dive (one value per dive)

diveDur	diveDepth	BotDur	PostDSI	AscSlope	DesSlope
dive duration (seconds)	dive depth (meters)	time spent at bottom (seconds)	post-dive surface interval (seconds)	ascending slope (meters/second)	descending slope (meters/second)

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Dive metrics computed on each deployment (one value per deployment)

Dhour	maxDur	maxDepth	SurfaceR	MDC surface (*)
number of dives per hour	maximum dive duration (seconds)	maximum dive depth (meters)	surface time ratio (%)	number of mother's dives during which the calf returned to surface

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494 **Table 2.—Comparisons of dive metrics for calves of different age classes and for mothers with calves of different age classes.\***

495 for p values < 0.05, \*\* for p values < 0.005 # n= 21 for the 6 dive metrics extracted on each single dive (diveDur, diveDep, BotDur,

496 postDSI, AscSlope, DesSlope , the two M-C1 were excluded), n=23 for four dive metrics averaged on the total duration of the

497 deployment (Dhour, maxDur, maxDep, surfaceR, two M-C1 were included). See Table 1.

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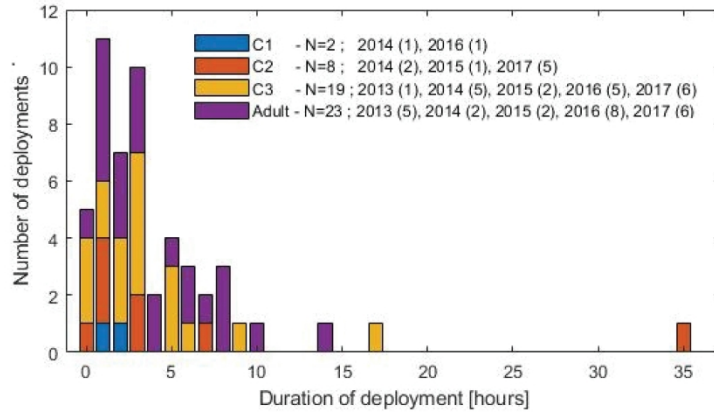
	diveDur	diveDep	BotDur	PostDSI	AscSlope	DesSlope	Dhour	maxDur	maxDep	SurfaceR
<b>CALVES</b>										
Difference among age classes n=29	*	NS (0.34)	*	NS (0.39)	NS(0.06)	NS (0.92)	NS (0.63)	**	*	NS (0.24)
	F = 3.86	F = 1.11	F = 5.04	F= 0.98	F= 3.3	F= 0.08	F= 0.54	F= 10.73	F=8.87	F= 2.04
Post-hoc Comparisons (2C1, 8C2, 19C3)	C1 ≠ C3		C3 ≠ C1 C3 ≠ C2					C1 ≠ C3 C1 ≠ C2	C1 ≠ C2 C1 ≠ C3	
<b>MOTHERS</b>										
Difference among age classes (# n=21 or 23)	NS (0.14)	NS (0.84)	*	*	NS (0.37)	NS (0.79)	NS (0.55)	NS (0.1)	NS (0.66)	NS (0.63)
Comparisons (5C2, 16C3)	F=2.33	F=0.04	F=4.41	F=4.97	F= 0.85	F= 0.07	F=0.76	F=4.82	F=0.48	F=0.56
			C3 ≠ C2	C3 ≠ C2						

499

500 **Table 3. —Diving behavior of simultaneous deployments on 7 mother-calf pairs in 2016 and 2017.** Dive metrics for mother-calf  
 501 pairs and correlation coefficients between mother and calf diving profiles. Delta indicates the time difference between mother-calf dive  
 502 profiles, a negative value means that the mother dove first, and thus led the dive. *Nb dives*: number of dives during synchronous  
 503 deployment ; *MDCsurface*: number of mother's dives during which the calf returned to surface, *maxDur*: maximum dive duration;  
 504 *maxDepth*: maximal dive depth ; *modDepth*: modal dive depth ; *BotDur*: average bottom duration ; *Dhour*: number of dives per hour ;  
 505 *PostDSI*: post-dive surface interval ; *AscSlope*, *DesSlope*: vertical speed for ascent and descent ; *SurfR*: percentage of time spent at the  
 506 surface (See Table 1).

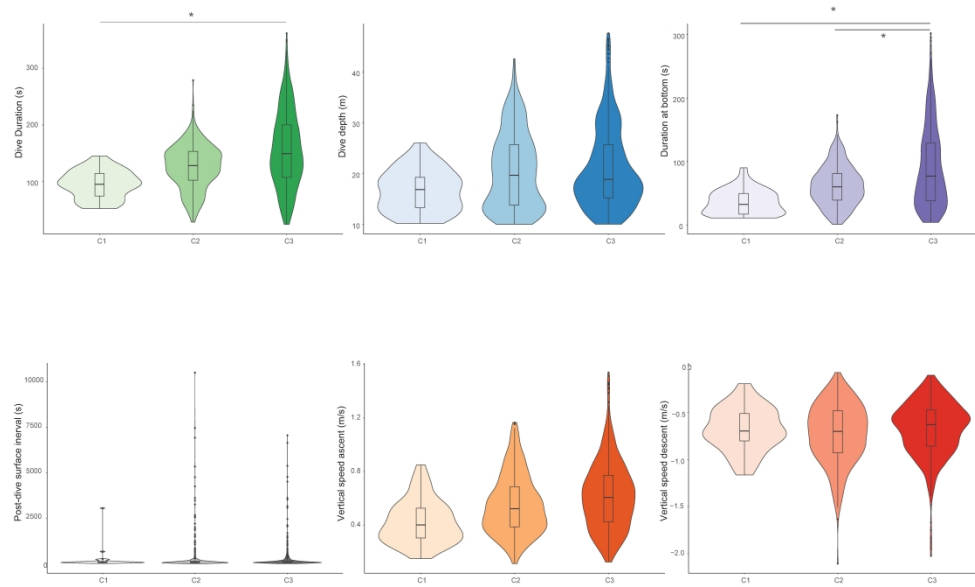
Dep #	Ind	Nb dives	MDC Surface	maxDur (sec)	maxDep (m)	modDep (m)	BotDur (sec)	Dhour (nb.h <sup>-1</sup> )	PostDSI (sec)	AscSlope (m.s <sup>-1</sup> )	DesSlope (m.s <sup>-1</sup> )	SurfaceR (in %)	Correl. max	Correl.	Delta (s)
2.16	C	16		185	37	7	57	13.1	134	-0.66	0.84	60	0.812	0.811	-2
2.16	M	8	5	668	36	11	165	6.6	183	-0.37	0.57	36			
4.16	C	9		146	18	13	45	16.4	32	-0.56	0.52	42	0.918	0.910	-5
4.16	M	7	1	404	17	11	45	12.8	11	-0.50	0.22	28			
7.16	C	32		260	24	13	95	12.6	90	-0.46	0.60	39	0.980	0.980	-1
7.16	M	32	0	319	21	11	99	12.6	73	-0.30	0.45	35			
8.16	C	10		123	22	14	41	18.8	90	-0.87	0.37	50	0.906	0.895	-8
8.16	M	10	0	214	22	14	65	18.8	40	-0.33	0.37	27			
9.16	C	55		294	39	9	135	7.1	289	-0.54	0.69	51	0.935	0.926	-12
9.16	M	27	14	1008	38	14	225	3.5	473	-0.23	0.52	32			
4.17	C	18		251	33	15	104	14.6	59	-0.79	0.63	26	0.932	0.904	-22
4.17	M	15	2	490	33	14	141	12.2	21	-0.53	0.41	11			
18.17	C	13		206	29	8	55	9.3	112	-0.41	0.43	62	0.941	0.939	-4
18.17	M	9	2	791	28	10	99	6.5	97	-0.37	0.36	37			

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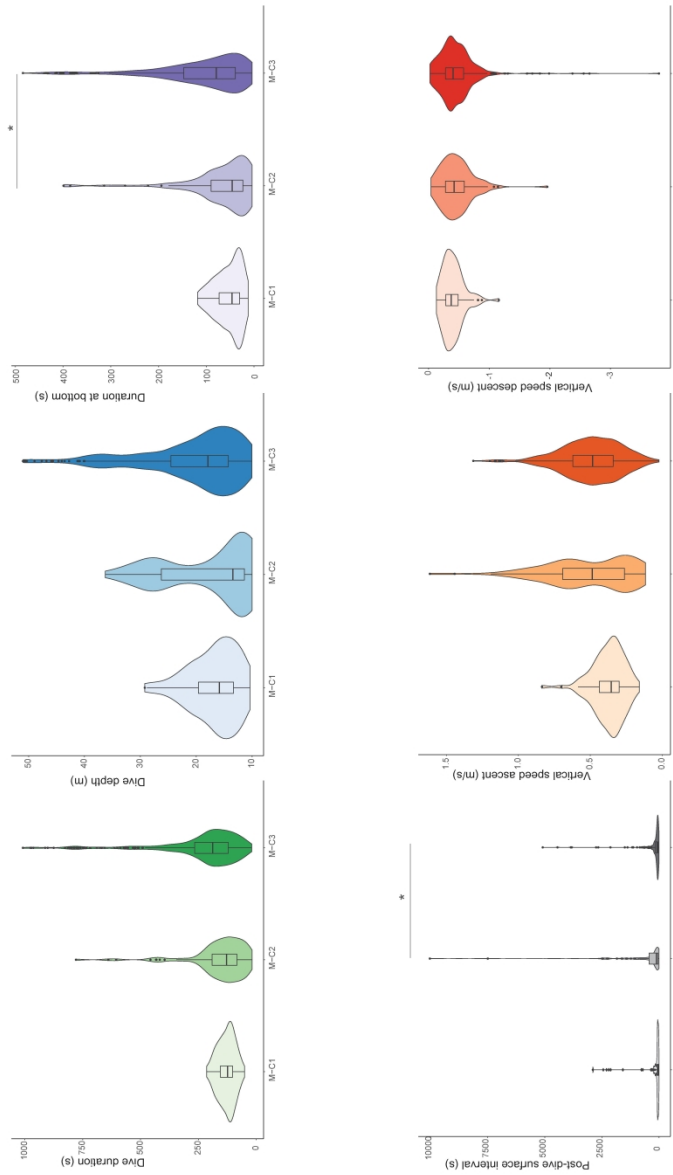
Summary of deployments performed on 23 adult females and 20 calves between 2013 and 2017 (durations of deployments, and repartition of calves among the 3 age-classes).

297x210mm (600 x 600 DPI)



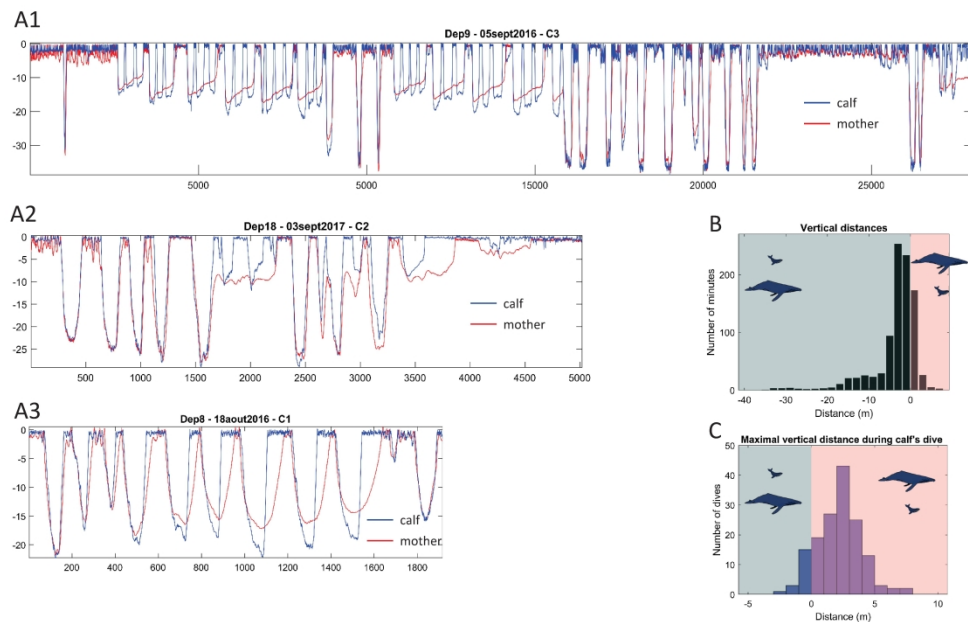
Graphical representation (violin plots) of the 6 dive metrics calculated on each dive for the 3 age-classes of calves (C1 with n= 2, C2 with n= 8 and C3 with n=9).

297x209mm (600 x 600 DPI)



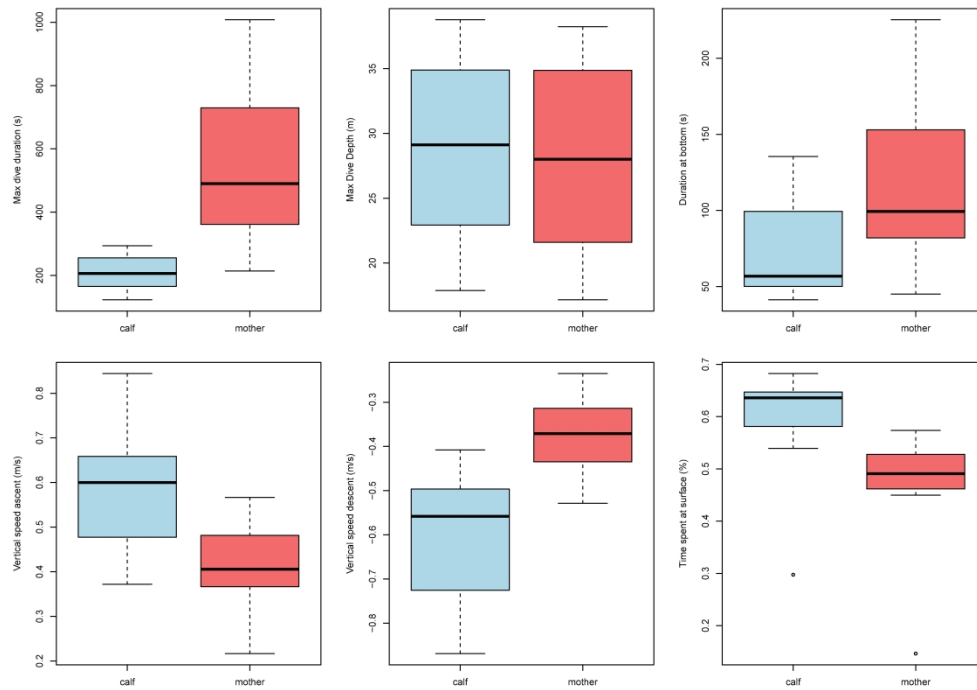
Graphical representation (violin plots) of the 6 dive metrics calculated on each dive for mothers accompanied with calves of different age-classes (M-C1 with n = 1, M-C2 with n = 5, M-C3 with n = 17).

209x297mm (600 x 600 DPI)



Mother-calf pair simultaneous deployments. A. Examples of diving profiles of 3 mother-calf pairs with calves of different age class (C3, C2 n=and C1). B. Histogram of vertical distances measured between mothers and calves on the entire duration of the deployment. Data ranged from -38m to 31m, however the time spent below its mother at distances greater than 10m represented only 1.233 minutes, and thus was not visible on the plot, therefore not shown in the figure. C. Histogram of vertical distances measured only during calves' dives.

254x190mm (600 x 600 DPI)



Boxplots of calves and mothers dive metrics found significantly different in mother-calf pairs during simultaneous deployments (n=7).

296x209mm (600 x 600 DPI)



For Review Only

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