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Chloé Huetz, Anjara Saloma, Olivier Adam, Aristide Andrianarimisa, Isabelle Charrier. Ontogeny and synchrony of diving behavior in Humpback whale mothers and calves on their breeding ground. *Journal of Mammalogy*, 2022, 103 (3), pp.576-585. 10.1093/jmammal/gyac010 . hal-03823711

HAL Id: hal-03823711

<https://hal.science/hal-03823711v1>

Submitted on 21 Oct 2022

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

Journal:	<i>Journal of Mammalogy</i>
Manuscript ID	JMAMM-2020-290.R6
Manuscript Type:	Feature Article
Date Submitted by the Author:	n/a
Complete List of Authors:	HUETZ, Chloé; Université Paris-Saclay, CNRS, UMR 9197, Institut des Neurosciences Paris-Saclay SALOMA, Anjara; Université Paris-Saclay, CNRS, UMR 9197, Institut des Neurosciences Paris-Saclay; University of Antananarivo, Zoology and Animal Biodiversity, Faculty of Sciences ADAM, Olivier; Université Paris-Saclay, CNRS, UMR 9197, Institut des Neurosciences Paris-Saclay; Sorbonne Université, CNRS, Institut Jean Le Rond d'Alembert, UMR 7190 ANDRIANARIMISA, Aristide; University of Antananarivo, Zoology and Animal Biodiversity, Faculty of Sciences CHARRIER, Isabelle; Université Paris-Saclay, CNRS, UMR 9197, Institut des Neurosciences Paris-Saclay
Keywords:	breeding ground, diving behavior, humpback whale, mother-calf interaction, ontogeny

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Manuscripts

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3 Running Header: Diving behavior in Humpback whales

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 8th, 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.

266

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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.

360

361

ACKNOWLEDGEMENTS

362 We would like to warmly thank the Cétamada team (François-Xavier Mayer, Henry Bellon,
363 and Didier Cabocel) and all the eco-volunteers who donated their time and energy to this
364 project. We are extremely grateful to Dr. Vanessa Pirotta for her invaluable corrections and
365 review of our manuscript and two anonymous referees for their helpful comments. This work
366 was supported by the Total Foundation, the WWF Education Fund for nature program and the
367 CeSigma Company.

368

SUPPLEMENTARY DATA

369

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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LITERATURE CITED

Cartwright R., Newton C., West K.M., Rice J., Niemeyer M., Burek K., Wilson A., Wall A.N., Remonida-Bennett J., Tejada A. et al. 2016. Tracking the development of muscular myoglobin stores in mysticete calves. *PLoS One* 11:1–18.

Cartwright R., Sullivan M. 2009. Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters. *Marine Mammal Science* 25:659–680.

Cooke S.J., Hinch S.G., Wikelski M., Andrews R.D., Kuchel L.J., Wolcott T.G., Butler P.J. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* 19:334–343.

Cusano D.A., Conger L.A., Van Parijs S.M., Parks S.E. 2019. Implementing conservation measures for the North Atlantic right whale: considering the behavioral ontogeny of mother-calf pairs. *Animal Conservation* 22:228–237.

Dombroski J.R.G., Parks S.E., Nowacek D.P. 2021. Dive behavior of North Atlantic right whales on the calving ground in the Southeast USA: Implications for conservation. *Endangered Species Research* 46:35–48.

Donaldson M.R., Hinch S.G., Suski C.D., Fisk A.T., Heupel M.R., Cooke S.J. 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers in Ecology and the Environment* 12:565–573.

Ejrnæs D.D., Sprogis K.R. 2021. Ontogenetic changes in energy expenditure and resting behaviour of humpback whale mother-calf pairs examined using unmanned aerial vehicles. *Wildlife Research* 20186.

Faria M-A., DeWeerd J., Pace F., Mayer F.X. 2013. Observation of a humpback whale (*Megaptera novaeangliae*) birth in the coastal waters of Sainte Marie Island, Madagascar. *Aquatic Mammals* 39:296–305.

- 401 Fisher D.O., Blomberg S.P., Owens I.P.F. 2002. Convergent maternal care strategies in
402 ungulates and macropods. *Evolution* 56:167–176.
- 403 Glockner-Ferrari D.A., Ferrari M.J. 1985. Individual identification, behavior, reproduction,
404 and distribution of humpback whales, *Megaptera novaeangliae*, in Hawaii. Annual
405 Report of the Marine Mammal Commission.
- 406 Hooker S.K., Baird R.W. 2001. Diving and ranging behaviour of odontocetes: a methodological
407 review and critique. *Mammal Review* 31:81–105.
- 408 Hussey N.E., Kessel S.T., Aarestrup K., Cooke S.J., Cowley P.D., Fisk A.T., Harcourt R.G.,
409 Holland K.N., Iverson S.J., Kocik J.F., et al. 2015. Aquatic animal telemetry: a
410 panoramic window into the underwater world. *Science* 348:1255642.
- 411 Johnson M., De Soto N.A., Madsen P.T. 2009. Studying the behaviour and sensory ecology of
412 marine mammals using acoustic recording tags: a review. *Marine Ecology Progress
413 Series* 395:55–73.
- 414 Lennox RJ, Aarestrup K, Cooke SJ, Cowley PD, Deng ZD, Fisk AT, Harcourt RG, Heupel M,
415 Hinch SG, Holland KN, et al. 2017. Envisioning the future of aquatic animal tracking:
416 technology, science, and application. *Bioscience* 67:884–896.
- 417 Lent P. 1974. Mother-infant relationships in ungulates. *The behaviour of ungulates and its
418 relation to management* 1:14–55.
- 419 Mann J. 2019. Maternal care and offspring development in odontocetes. In: Würsig B., editor.
420 *Ethology and behavioral ecology of odontocetes. Ethology and behavioral ecology of
421 marine mammals.* Springer, Cham; p 95-116.
- 422 Mann J., Smuts B.B. 1999. Behavioral development in wild bottlenose dolphin newborns (
423 *Tursiops* sp.). *Behaviour* 136:529–566.
- 424 Noren S.R. 2008. Infant carrying behaviour in dolphins: costly parental care in an aquatic
425 environment. *Functional Ecology* 22:284–288.

- 426 Noren S.R., Edwards E.F. 2011. Infant position in mother-calf dolphin pairs : formation
427 locomotion with hydrodynamic benefits. *Marine Ecology Progress Series* 424:229–236.
- 428 R Core Team. 2020. R: a language and environment for statistical computing. Vienna
429 (Austria): R Foundation for Statistical Computing. <https://www.R-project.org>
- 430 Sakai M., Morisaka T., Iwasaki M., Yoshida Y., Wakabayashi I., Seko A., Kasamatsu M.,
431 Kohshima S. 2013. Mother-calf interactions and social behavior development in
432 Commerson's dolphins (*Cephalorhynchus commersonii*). *Journal of Ethology* 31:305–
433 313.
- 434 Saloma A., Marchesseau S., Charrier I., Andrianarimisa A., Antogiorgi E., Adam O. 2018. Do
435 the new-born calves of humpback whales (*Megaptera novaeangliae*) have a preference
436 to position themselves at the side of their mother? *West Indian Ocean Journal of Marine*
437 *Science* :1–9.
- 438 Schreer J.F., Kovacs K.M. 1997. Allometry of diving capacity in air-breathing vertebrates.
439 *Canadian Journal of Zoology* 75:339–358.
- 440 Sikes R.S., and the animal care and use committee of the American Society of Mammalogists.
441 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild
442 mammals in research and education. *Journal of Mammalogy* 97:663–688.
- 443 Stimpert A., Mattila D., Nosal E., Au W. 2012. Tagging young humpback whale calves:
444 methodology and diving behavior. *Endangered Species Research* 19:11–17.
- 445 Swartz S. L. 2018. Gray Whale. In: Würsig B., Thewissen J.G.M., Kovacs K.M., editors.
446 *Encyclopedia of marine mammals*. Academic Press, London, p 422–428
- 447 Szabo A., Duffus D. 2008. Mother-offspring association in the humpback whale, *Megaptera*
448 *novaeangliae*: following behaviour in an aquatic mammal. *Animal Behaviour* 75:1085–
449 1092.
- 450 Taber S., Thomas P. 1982. Calf development and mother-calf spatial relationships in southern

- 451 right whales. *Animal Behaviour* 30:1072–1083.
- 452 Trudelle L., Charrassin J., Saloma A., Pous S., Adam O. 2018. Temporal and spatial patterns
453 of humpback whales (*Megaptera novaeangliae*) in the Sainte Marie channel, Madagascar
454 breeding ground. *African Journal of Marine Science* 40:1–12.
- 455 Tyson R., Friedlaender A., Ware C., Stimpert A., Nowacek D. 2012. Synchronous mother and
456 calf foraging behaviour in humpback whales *Megaptera novaeangliae*: insights from
457 multi-sensor suction cup tags. *Marine Ecology Progress Series* 457:209–220.
- 458 Videsen S.K.A., Bejder L., Johnson M., Madsen P.T. 2017. High suckling rates and acoustic
459 crypsis of humpback whale neonates maximise potential for mother–calf energy transfer.
460 *Functional Ecology* 31:1561–1573.
- 461 Weibel E.R. 2000. *Symmorphosis: on form and function in shaping life*. Harvard University
462 Press.
- 463 Weihs D. 2004. The hydrodynamics of dolphin drafting. *Journal of Biology* 3:1-16.
- 464 Zoidis A.M. 2014. Effects of sex, seasonal period, and sea state on calf behavior in hawaiian
465 humpback whales (*Megaptera novaeangliae*). *Aquatic Mammals* 40:44–58.
- 466 Zoidis A.M., Smultea M.A., Frankel A.S., Hopkins J.L., Day A., McFarland A.S., Whitt A.D.,
467 Fertl D. 2008. Vocalizations produced by humpback whale (*Megaptera novaeangliae*)
468 calves recorded in Hawaii. *Journal of the Acoustical Society of America* 123:1737–1746.

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.

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)

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

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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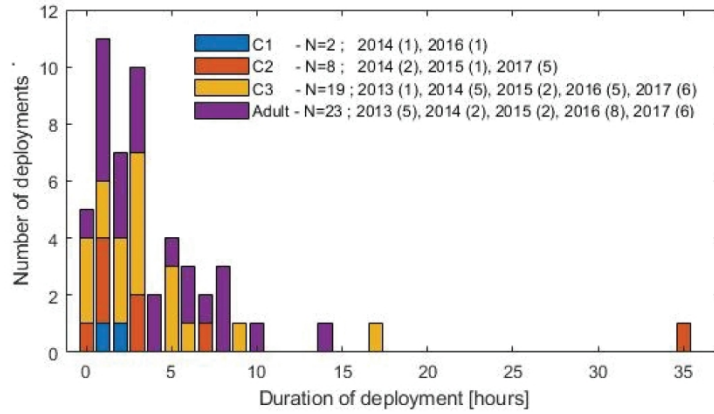
	diveDur	diveDep	BotDur	PostDSI	AscSlope	DesSlope	Dhour	maxDur	maxDep	SurfaceR
CALVES										
Difference among age classes n=29	*	NS (0.34)	*	NS (0.39)	NS(0.06)	NS (0.92)	NS (0.63)	**	*	NS (0.24)
	F = 3.86	F = 1.11	F = 5.04	F= 0.98	F= 3.3	F= 0.08	F= 0.54	F= 10.73	F=8.87	F= 2.04
Post-hoc Comparisons (2C1, 8C2, 19C3)	C1 ≠ C3		C3 ≠ C1 C3 ≠ C2					C1 ≠ C3 C1 ≠ C2	C1 ≠ C2 C1 ≠ C3	
MOTHERS										
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).

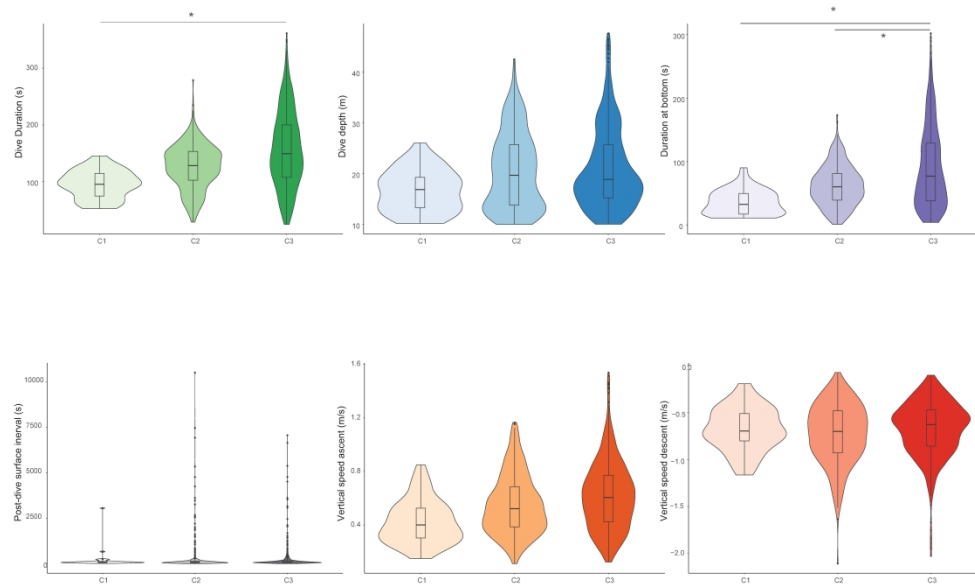
Dep #	Ind	Nb dives	MDC Surface	maxDur (sec)	maxDep (m)	modDep (m)	BotDur (sec)	Dhour (nb.h ⁻¹)	PostDSI (sec)	AscSlope (m.s ⁻¹)	DesSlope (m.s ⁻¹)	SurfaceR (in %)	Correl. max	Correl.	Delta (s)
2.16	C	16		185	37	7	57	13.1	134	-0.66	0.84	60	0.812	0.811	-2
2.16	M	8	5	668	36	11	165	6.6	183	-0.37	0.57	36			
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			

507



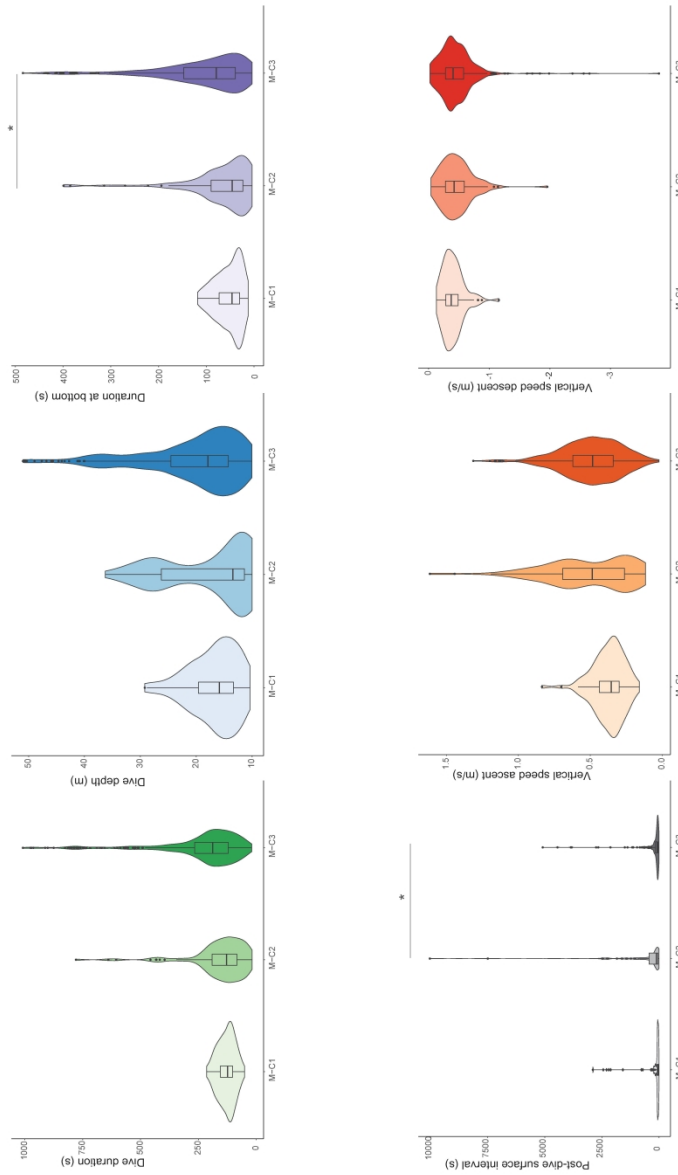
Summary of deployments performed on 23 adult females and 20 calves between 2013 and 2017 (durations of deployments, and repartition of calves among the 3 age-classes).

297x210mm (600 x 600 DPI)



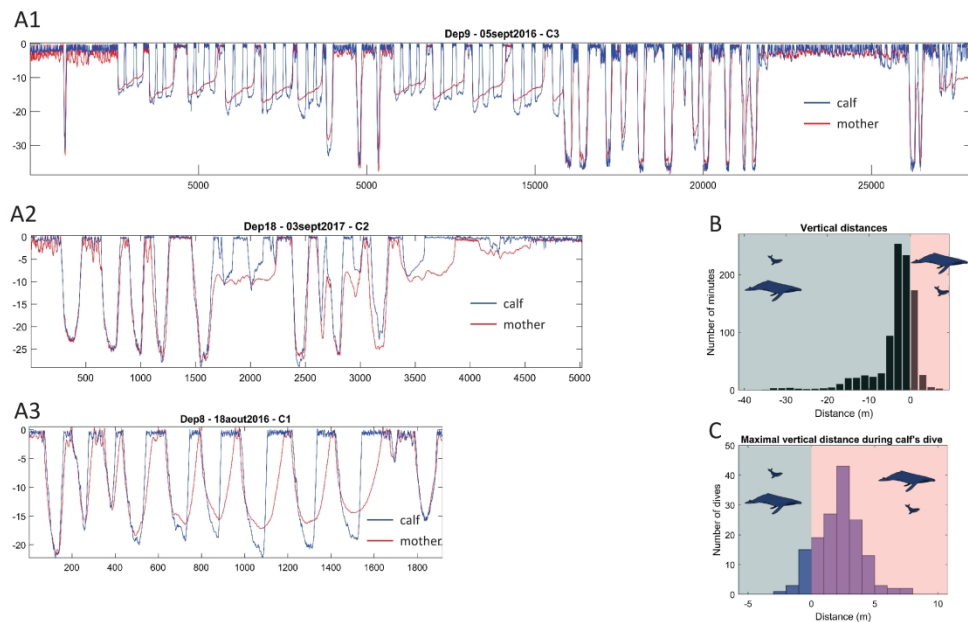
Graphical representation (violin plots) of the 6 dive metrics calculated on each dive for the 3 age-classes of calves (C1 with n= 2, C2 with n= 8 and C3 with n=9).

297x209mm (600 x 600 DPI)



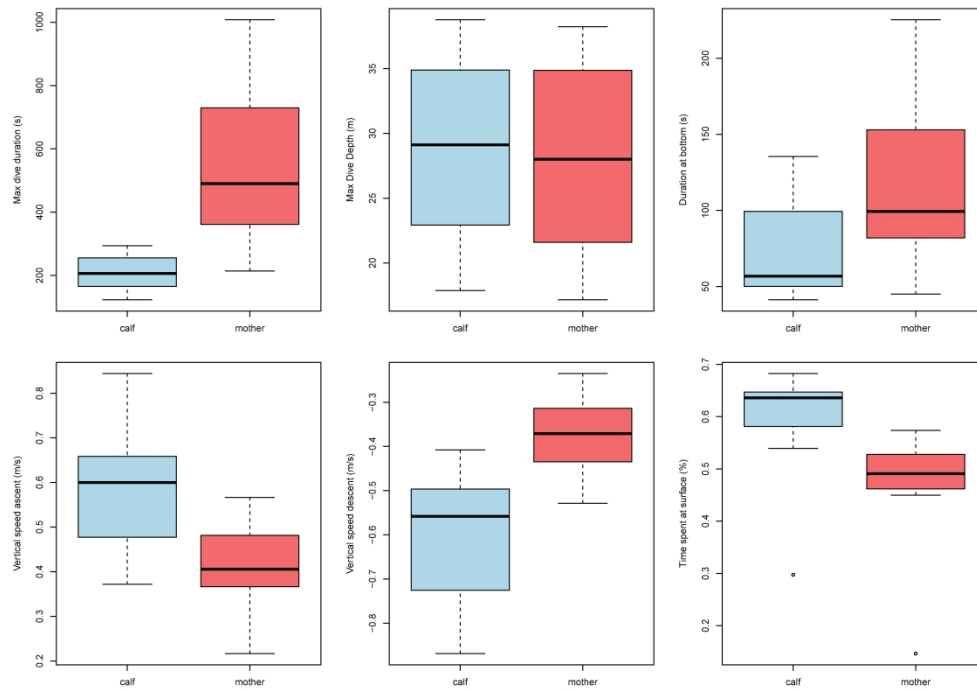
Graphical representation (violin plots) of the 6 dive metrics calculated on each dive for mothers accompanied with calves of different age-classes (M-C1 with n = 1, M-C2 with n = 5, M-C3 with n = 17).

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

For Review Only