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

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

Key words: breeding ground, diving behavior, humpback whale, mother–calf interaction, ontogeny

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

Observational studies of humpback whales in both breeding and foraging grounds document calves staying within close proximity of their mothers (Szabo and Duffus 2008; Cartwright and Sullivan 2009; Zoidis 2014). Spatial proximity decreases with age when calves become more independent and have improved motor skills (Szabo and Duffus 2008). Previous studies on calves diving and surfacing behavior have been assessed using surface observations from boats following animals or from snorkelers/divers swimming near focal animals (Zoidis et al. 2008; Cartwright and Sullivan 2009).

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

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

Materials and Methods

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

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

Tagging procedure.—Tagging mother–calf pairs, especially groups with neonate calves requires a strategic approach. Passive and active approach methods were used depending on mother–calf behavior (static or slow traveling), as well as the choice of the targeted individual to tag within the group (mother or calf). Passive approach, drifting with the current, previously described by Stimpert et al. (2012) is most effective in limiting the disturbance of mother–calf pairs. This approach was used when groups were static or when calves were observed alone at the surface. If the pairs were traveling slowly, the boat was placed parallel to them at the same speed and within visual range of the mother. The animal closest to the boat was then tagged. For simultaneous tagging, mothers and calves were tagged either during the same approach (this involved two researchers) or if the double-tagging was unsuccessful, a second approach was required. The maximum time spent with each pair (i.e., time spent attempting to tag the animals) never exceeded 30 min, following official Madagascar's agreement for mother and calf observations (interministerial decree 8 March 2000). As soon as the tag(s) were attached to the animal(s), the vessel slowly moved away in an opposite direction to avoid any further disturbance to the pair. All mother–calf pairs were photo-identified to avoid double-sampling within the breeding season.

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

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

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

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

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

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

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

Statistical analysis.—From the six dive metrics measured on all dives (diveDur, diveDep, BotDur, postDSI, AscSlope, DesSlope) obtained during the five successive breeding

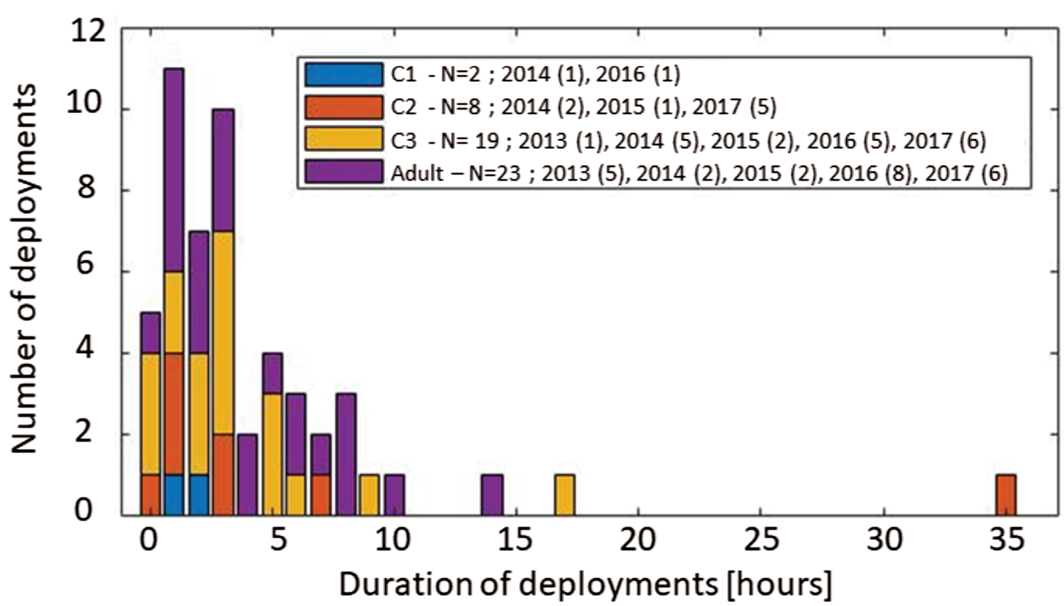

Fig. 1.—Summary of deployments performed on 23 adult mothers and 20 calves between 2013 and 2017 (durations of deployments, and repartition of calves among the three age-classes).

Table 1.—Description of the different dive metrics extracted from the diving profiles. *Only for synchronous deployments.

Dive metrics computed on each dive (one value per dive)					
diveDur	diveDepth	BotDur	PostDSI	AscSlope	DesSlope
dive duration (s)	dive depth (m)	time spent at bottom (s)	postdive surface interval (s)	ascending slope (m/s)	descending slope (m/s)
Dive metrics computed on each deployment (one value per deployment)					
Dhour	maxDur	maxDepth	SurfaceR	MDC surface (*)	
number of dives per hour	maximum dive duration (s)	maximum dive depth (m)	surface time ratio (%)	number of mother's dives during which the calf returned to surface	

seasons, we investigated if the dive characteristics for calves different among the three different age-classes. For each dive metric we performed a linear mixed model (lmer function, lmerTest package) with the calf's age-class as a fixed factor and identity of the tagged individual as a random factor. For the four dive metrics (Dhour, maxDur, maxDep, surfaceR) we averaged the total duration of the deployment and performed Welch ANOVAs. Post hoc tests were performed when a dive metric significantly differed among age-classes to assess pairwise comparisons (Tukey's tests, multcomp R package, and Games–Howell test, userfriendlyscience R package) (R Core Team 2020).

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

Results

Over the five breeding seasons, we had successful deployments on 31 calves and 24 mothers (Fig. 1), but three deployments (i.e., two calves and one mother) were not included in our analysis because deployments were too short (less than 30 min). During the breeding seasons 2016 and 2017, we performed 13 simultaneous mother–calf deployments, but only seven showed sufficient overlapping time (at least 30 min) to measure dive metrics for both mother and calf of the targeted pair.

Calves' diving behavior.—Among the 10 dive metrics measured, five varied significantly among the three age-classes (Table 2; Fig. 2). Calves increased the duration of their dives with age. The mean duration was significantly different between C1 and C3 calves (Fig. 2), and the maximum dive duration for C1 calves was significantly shorter than C2 and C3 calves (see Supplementary Data SD1). They also increased the time spent at the bottom, with C3 calves spending significantly more time than C2 and C1 calves (Fig. 2). The maximal dive depth increased also with age, with C2 and C3 showing significant maximal depth greater than C1 (see Supplementary Data SD1). The ascending vertical speed did not vary with age.

Mothers' diving behavior.—Among the 23 mothers, we only had two mothers with C1 calves, and one mother did not dive during the tag deployment (recording duration: 1.36 h). For the six dive metrics extracted on each single dive (diveDur,

Table 2.—Comparisons of dive metrics for calves of different age-classes and for mothers with calves of different age-classes. *P-values < 0.05, **P-values < 0.005. [#]n = 21 for the six dive metrics extracted on each single dive (diveDur, diveDep, BotDur, postDSI, AscSlope, DesSlope), the two M-C1 were excluded), n = 23 for four dive metrics averaged on the total duration of the deployment (Dhour, maxDur, maxDep, surfaceR, two M-C1 were included). See Table 1.

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

diveDep, BotDur, postDSI, AscSlope, DesSlope), we included only mothers with C2 and C3 calves (we could not run the analysis with only one mother with C1 calf). We included the two mothers with C1 calves for four dive metrics averaged on the total duration of the deployment (Dhour, maxDur, maxDep, surfaceR). When analyzing the diving behavior of mothers in regards to their calf's age-class, only two dive metrics were found significantly different among mothers with C2 and C3 calves (Table 2; Fig. 3). Mothers with C3 calves spent longer time at the bottom (BotDur) than mothers with C2 calves, and the duration between dives (postDSI) was shorter in mothers with C3 than mothers with C2 calves. However, we did not find any significant differences regarding the dive durations (mean or maximum), or maximal dive depth as found in calves.

Simultaneous deployments.—When plotting the dive profiles of the seven mother–calf pairs, we found that mother and calf showed highly synchronized dives (Table 3; Fig. 4 A1–A3; see Supplementary Data SD2). The dive metrics for mother–calf pairs, as well as correlation coefficients between mother–calf dive profiles are shown in Table 3. We found a very high synchrony between the dive profiles of mothers and calves, with the maximal correlations ranging from 0.81 to 0.98. As shown in Table 2, the number of dives was not similar between mother and calf as the

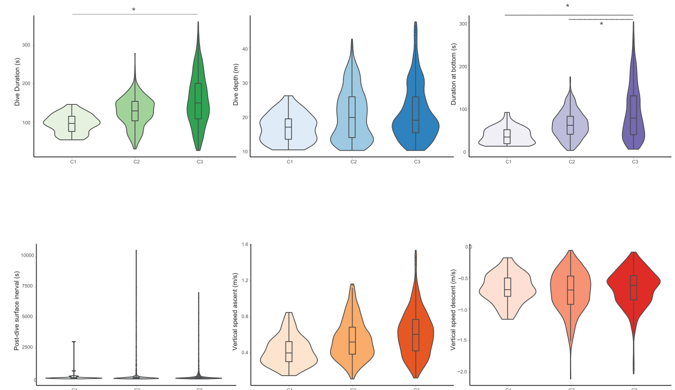

Fig. 2.—Graphical representation (violin plots) of the six dive metrics calculated on each dive for the three age-classes of calves (C1 with n = 2, C2 with n = 8, and C3 with n = 9).

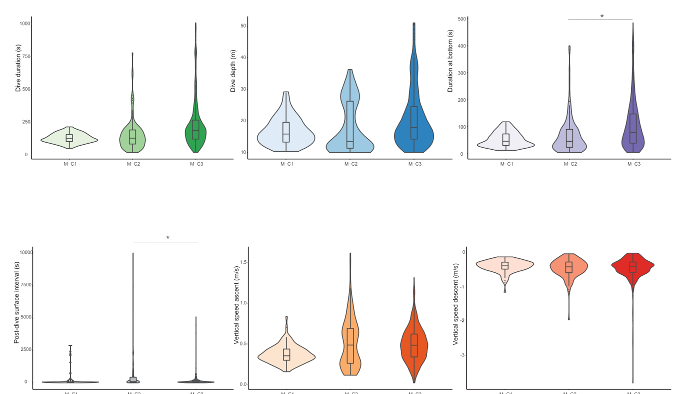

Fig. 3.—Graphical representation (violin plots) of the six dive metrics calculated on each dive for mothers accompanied with calves of different age-classes (M-C1 with n = 1, M-C2 with n = 5, M-C3 with n = 17).

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

Dep #	Ind	Nb dives	MDC Surface	maxDur (s)	maxDep (m)	modDep (m)	BotDur (s)	Dhour (nb/h)	PostDSI (s)	AscSlope (m/s)	DesSlope (m/s)	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	1,008	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			

calf sometimes returned to the surface while the mother stayed at bottom (see examples on Fig. 4A1 and A2). The number of mother's dives during which the calf returned to surface (MDCSurf) is given in Table 3. We observed 24 of these events, and during which the calf went back to the surface 2–4 times. When comparing the 10 dive metrics measured between mothers and calves of the pairs, six were found significantly different (Fig. 5). Calves showed shorter dive durations as in many instances the mother stayed at the bottom, so this also explained why the bottom duration was longer in mother and thus the time spent at the surface was longer in calves. The maximal dive depth was also found significantly different, with calves being slightly (i.e., within 5 m) at a deeper position compared to their mother. Significant differences between mothers and calves were also found on the vertical speed during both ascending and descending phases, with calves showing higher vertical speeds when going back to the surface and when descending. On the seven mother–calf studied pairs, all showed that mothers were leading the dive (i.e., negative delta values on Table 2); thus, in all cases, calves followed the diving pattern of their mothers. Finally, mother–calf vertical distances ranged from −38 to 31 m (Fig. 4B), showing that calves can be separated from their mother by at least 30 m, with the calf being either below or above its mother. The histogram tail between −8 and −20 m corresponds to events during which calves were going back to the surface while mothers stayed at the bottom. However, we can see that most of time they are together within 4 m from each other. The time spent above or below the mother varies greatly among calves (Fig. 4B), but we found that, when the pair is diving, the calf was mostly below its mother (Fig. 4C) and rarely above her.

Discussion

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.

Our findings are consistent with the previous studies done on humpback whales calves in their breeding grounds (Cartwright and Sullivan 2009; Tyson et al. 2012; Ejrnæs and Sprogis 2021). Of the 29 studied calves, we found that four 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 SD1). 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 individuals included as nested factor in order to account for random effects due to interindividual variations. However, since we could record dives only on two C1 calves, great care should be taken in generalizing the present results. Nevertheless, these

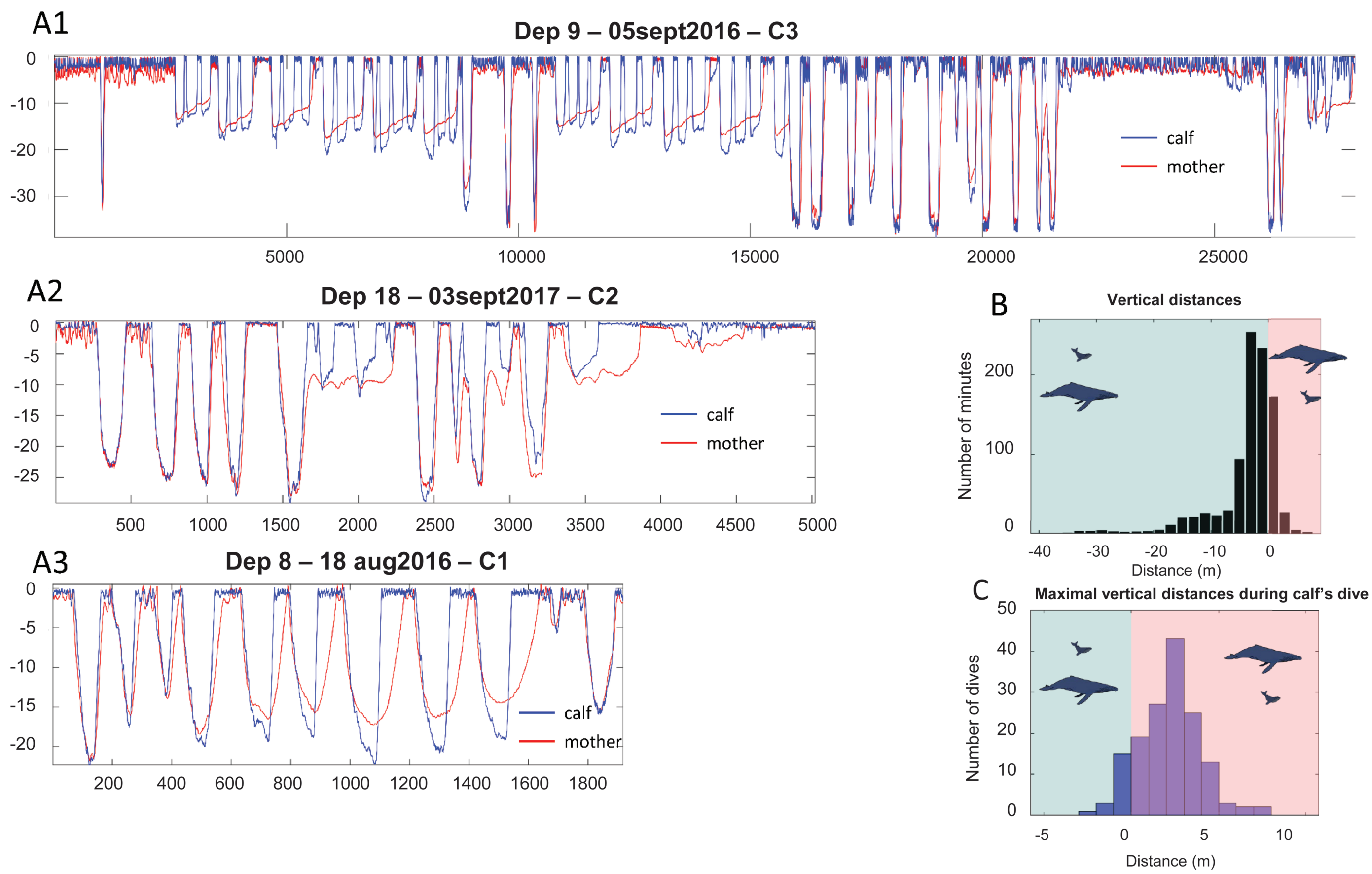

Fig. 4.—Mother–calf pair simultaneous deployments. (A) Examples of diving profiles of three mother–calf pairs with calves of different age-class (C3, C2, and C1). (B) Histogram of vertical distances measured between mothers and calves on the entire duration of the deployment. Data ranged from −38 to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

findings suggest that older calves showed higher swimming and breathing abilities, as previously found in humpback whales (Cartwright and Sullivan 2009; Ejrnæs and Sprogis 2021) and observed in right whales (Cusano et al. 2019; Dombroski et al. 2021). As suggested in previous studies, neonate calves have limited lung capacity as they are still learning to manage their breathing cycle and buoyancy. In mammals, the alveolar saccules must expand and subdivide to increase the gas exchange, and then the volume of the lungs will grow (Weibel 2000). Also, larger animals have a proportionately greater oxygen storage capacity leading to a greater diving capacity (Schreer and Kovacs 1997). Indeed, diving capacity is among those skills developed gradually by calves (Stimpert et al. 2012). The number of dives per hour did not increase with age, and that both the time spent at the surface and the interval between dives did not decrease with age. This indicates that calves do not increase their dive rate when they age, and the time spent at the surface is not related to their age. So, even if their lung capacity increases with age, they do not seem to use it to dive more often. As suggested by Stimpert et al. (2012), calves might rather use such aerobic resources toward growth and development. Recent investigations on muscular myoglobin stores in mysticetes have revealed calves present very low levels of myoglobin stores in muscles compared to juveniles and adults (Cartwright et al. 2016). This would explain their limitations in respiratory and diving capacities.

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

Effect of calf's age on the mother's diving behavior.—From the 23 tagged mothers, we were able to follow the diving behavior of 21 mothers accompanied with C2 and C3 calves. The two mothers with C1 calves were included in the descriptive analysis (four dive metrics: *Dhour*, *maxDur*, *maxDep*, *surfaceR*), but not in our general analysis as one female did not dive during the deployment duration (Table 2). Mothers modified their diving profile with regards to their calf's age. Mothers with C3 calves stayed longer at the bottom, and showed shorter time interval between dives than mothers with C2 calves. This indicates that mothers tended to increase their time away from their calves as they get older. There is also a possibility that the shorter time interval between dives for mothers with older calves (C3) may reflect the great respiratory capacities of the young. Our synchronous deployments on mother–calf pairs revealed such pattern with mothers staying at the bottom while

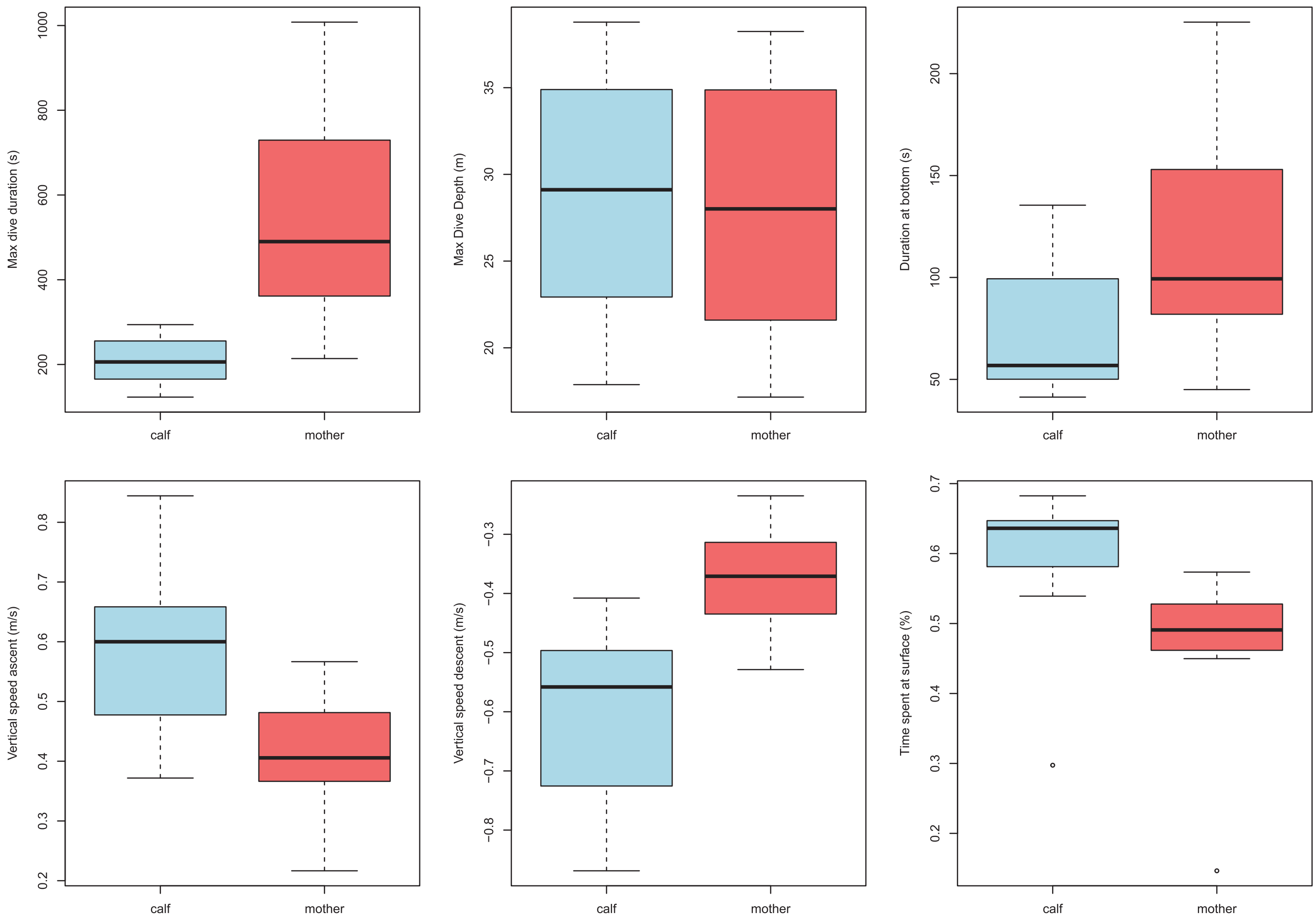

Fig. 5.—Boxplots of calves and mothers dive metrics found significantly different in mother–calf pairs during simultaneous deployments (n = 7).

calves come back to the surface for breathing in several instances (Fig. 4A1). Longer bottom time and shorter surface interval of mothers with older calves were also found in Southern right whales (Dombroski et al. 2021). In contrast, UAV monitoring of mother–calf pairs in Western Australia did not report any change of breathing rate in mothers with regards to calf length (i.e., age) (Ejrnæs and Sprogis 2021).

Mother–calf synchronized dives.—Among the mother–calf pairs tagged simultaneously, mothers and calves show a high synchrony in their diving profiles. This is consistent with previous studies on humpback and right whales mother–calf pairs (Taber and Thomas 1982; Szabo and Duffus 2008; Tyson et al. 2012). Vertical distance measurements suggested high synchronicity and spatial proximity between the pairs (under the hypothesis that the horizontal separation was also small). Even though calves have to perform short dives to breathe, the vertical distance separating the pairs was mostly between 1 and 4 m (Fig. 4B) suggesting that mother–calf pairs on the breeding ground stay at the same depth and likely at close range to each other in all their activities. Similar vertical proximity has been described by Tyson et al. (2012) on the feeding ground even though this distance tends to be greater (±20 m) compared to our results where mother–calf pairs were much closer (±4 m).

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

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

This study has given additional knowledge on the ontogeny of diving behavior of humpback whale calves in their breeding ground, especially on very young calves (C1 calves). However, there still remains many more questions to be answered. Future direction of this work should investigate the ontogeny of the swimming behavior of calves by analyzing data from 3D accelerometers. Such exhaustive analysis will allow us to assess the proportion of gliding and active swims while traveling and diving (i.e., during both vertical and horizontal movements), and how swimming performance and swimming styles (i.e., infant position, in echelon position) develop with calf age.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Dive metrics (Dhour, maxDur, maxDep, surfaceR) extracted from each deployment, and averaged over calves across age-classes (C1 with $n = 2$, C2 with $n = 8$, C3 with $n = 19$) and over mothers accompanied with calves of different age-classes (M-C1 with $n = 2$, M-C2 with $n = 5$, M-C3 with $n = 17$).

Supplementary Data SD2.—Diving patterns of the four other mother–calf pairs obtained during simultaneous deployments.

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