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Nursing Behavior in Sperm Whales (*Physeter macrocephalus*)

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Abstract – In mammals, lactation is the universal behavior of feeding offspring and has a fundamental nutritional and social value with offspring staying near their mothers. In order to obtain milk, terrestrial mammal offspring squeeze the breast of lactating females and suckle the nipples with their tongues. In the specific case of cetacean species, it was reported that lactating females intentionally eject milk from their mammary slit into the calves' mouths. Nursing behavior in sperm whales has already been broadly described, but the results of our current study, based on 127 underwater videos, recording over 7 years and displaying explicit nursing behavior, bring a higher level of understanding. We first showed that sperm whale calves are proactive in getting milk. We were then able to illustrate and describe with a high level of precision their suckling behavior: firstly, the calf bumps its head onto the female's genital area to signal the mother its willingness to suckle; secondly, the calf introduces its lower jawbone into the genital slit, this action makes the nipple pop up from its slit; thirdly, the calf squeezes the nipple with its tongue against the hard palate and suckles; fourthly, the calf removes its jawbone from the female and swims off. Moreover, our underwater visual observations provided the first direct evidence for allosuckling in sperm whales, a situation during which a calf obtains milk from an adult female who is not its mother.

Keywords – Sperm whale, Nursing, Allonursing, Suckling, Underwater observations

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For the almost 6,000 mammal species, newborns start their life on a diet of milk, obtained from their mother or from an adult female nurse (Feldhamer et al., 2007; Klopfer, 1981). All mammalian species, terrestrial, aerial and marine, provide milk to their offspring through the mammary glands. Lactation is the universal process to feed offspring (Pond, 1977) and strengthens social bonds between mother and offspring (Wilson, 1975). Lactation has a fundamental nutritional benefit; depending on the type of placenta, the antibodies (specific to the mother's environment and therefore to the calf) will be transmitted mainly via the colostrum. This is the case for cetaceans: antibodies are not fully transmitted during gestation but during the ingestion of colostrum in the first days of life of the neonates. Lactation is also the most energetically expensive reproductive state for females (Clutton-Brock et al., 1989, Hinde et al., 2009).

Nursing refers to the behavior of adult females providing milk, while suckling refers to the calf behavior to obtain milk from the female adult (Cowie et al., 1951). Nursing or suckling behaviors have been less well documented in cetaceans than in terrestrial mammals because it is difficult to observe them closely, especially in the wild marine environment. Nevertheless, it was reported that the milk seems to be actively ejected by the females directly into the calves' mouth (Slijper, 1962). In bottlenose dolphins (*Tursiops truncatus*), calves stimulate their mother by bumping their head onto the genital regions (Kastelein et al., 1990). Humpback whale (*Megaptera novaeangliae*) calves position themselves under the genital slit, then stimulate the mother by bumping the mammary slit with the head. Then they roll over on their side to be able to use their tongue to guide milk into their mouth (Ratsimbazafindranahaka et al., 2022).

Alloparental care, defined as caregiving by a nonparent (Woodroffe & Vincent, 1994; Whitehead, 1996), is not rare in mammals. A review of 63 species that live in family groups revealed that the majority (55) engage in alloparental care (Emlen, 1995). Allonursing has also been described in mammals (Briga et al., 2012), with allonursing defined as the nursing of a non-filial young, and allosuckling as young that suckle an adult female who is not its mother (Gero et al., 2009). It often occurs when females live in groups (Packer et al., 1992). Croft et al. (2017) suggested that the benefits of alloparental care increase the chance of survival of young born into a group with other young animals. Allocare was also observed to correlate with increased fertility in females (Cerrito & Spear, 2022). In orcas (*Orcinus orca*), calves born into a group with another lactating mother may benefit from allosuckling during the first year of life (Croft et al., 2017). Hetereospecific alloparental care has also been observed in dolphins in the wild (Conry et al., 2022).

Sperm whales (*Physeter macrocephalus*) are the largest Odontoceti species. Females and their offspring live together in stable matrilineal groups (Christal & Whitehead, 1999; Sarano et al., 2021). Most females spend their entire lives in their natal unit while juvenile males disperse before puberty, at an estimated age of 6 years (Christal & Whitehead, 2001; Whitehead, 2003). Males can then be found at high latitudes in aggregations called bachelor schools, with other males of about the same size and age (Letteval et al., 2002). After reaching social maturity in their late twenties, large males return to tropical breeding waters to reproduce (Girardet et al., 2022). After a gestation period, lasting about 14 to 16 months, female sperm whales give birth to a single calf. Calves are dependent on adult females for survival including nursing, protection and energy conservation (Christal et al., 1998; Whitehead et al, 2012; Whitehead & Weilgart, 1991).

Sperm whale nursing behavior was previously observed and partially described (Gero & Whitehead, 2007). The authors hypothesized that suckling could be performed during repeated and short dives alongside an adult escort, known as peduncle dives (Gordon et al., 1998). Gero and Whitehead (2007) observed a calf positioning itself under a lactating adult female and repeatedly pressing its blowhole onto her genital area. Thus, it was assumed that sperm whale calves could ingest milk through the nasal passage. However, Johnson et al. (2010) observed two captive newborn sperm whales ingesting milk through their mouth with active suckling by wrapping their tongue around the nursing bottle. They also did complementary experiments and noticed that the calf was powerfully sucking the author's finger positioned inside its mouth (Johnson et al., 2010). Moreover, two underwater films were recorded in the wild showing calves with open mouths approaching female sperm whales suggesting that they might get milk through their mouth even though it is not explicitly shown in these videos (Johnson et al., 2010). Mouth-feeding in sperm whales has, therefore, yet to be accurately observed, photographed, and described, and this was the aim of our work.

Since 2011, we have used underwater observations and skin sampling to study a particular social group of sperm whales off Mauritius Island (Indian Ocean). This social group consisted of adult females and juveniles. These long-term underwater observations allowed us to identify all individuals (Sarano et al., 2022) and to decipher familial relationships between group members (Sarano et al., 2021). These underwater observations provided evidence that some adult males who joined the unit to socialize were also reproductive and may exhibit social fidelity (Girardet et al., 2022).

The aim of the current study was to describe the nursing and suckling behaviors in sperm whales. We took advantage of the dataset collected during this long-term study, allowing us to visually observe in detail adults and calves in many instances and to precisely study each step of their nursing behavior. We firstly described how sperm whale calves access milk thanks to their specific morphology. We also assessed whether nursing/suckling were allosuckling events.

Methods

Ethics Statement

To respect cetaceans and their habitats, the observers strictly followed the ethical rules of the official Charter for responsible approach and observation of marine mammals and the Maritimes zones regulations (Conduct of Marine Scientific Research/ Notice n°57 of 2017) promulgated by the Mauritius Government. This study was placed under the policies of the Mauritius Department for continental shelf, maritime zone administration and exploration, with the appropriate permit to conduct underwater observations, underwater videos and marine scientific research on sperm whales.

Study Area

Field work was carried out off Mauritius Island, which is part of the Mascarenes Islands in the Indian Ocean. The studied area extended from latitude 19°55' S to 20°20' S, and up to 15 km off the Leeward Western coast. Opportunistic underwater observations took place between 2011 and 2019, as part of a global comprehensive study directed by the French NGO Longitude 181, part of the project called "Maubydick", led by the Marine Megafauna Conservation Organisation (Mauritius Island). The dataset was collected every year between February and May from 2013 to 2017 and 2019, and from February to August in 2018, representing a total of 263 fieldwork days (Sarano et al., 2022). Few occasional observations were also made from September until January during these years. Fieldwork was conducted daily when the weather conditions were good enough to proceed with marine observations (sea state code < 3) (WMO, 2022). Starting from the harbor of Trou aux Biches (20°01'S - 57°33'E), searches for sperm whales began around 8 am and ended around noon, according to administrative Mauritian policies.

Sperm Whale Social Unit

For this study, we used observations from 30 sperm whales belonging to two social units (28 sperm whales belonged to Irene's unit and two to Reshna's unit). All individuals were already identified thanks to external morphological marks on their body (Sarano et al., 2022). Genetic analysis of sloughed skin samples of all individuals had also been performed to assess their kin relationships (Sarano et al., 2021). These genetic relationships are listed in Table 1, as well as the given name of both mothers and calves, and the sex and the year of birth of the calves.

Passive Underwater Observations and Video Recordings

When the social unit was located, the boat stopped 100 m away from the sperm whales, dropped off the observers, then moved away but remained about 200 m away from the whales. Passive underwater observations and audio-video recordings were performed by a professional tank diver cameraman and three experienced marine biologist snorkelers. Observers waited for cetaceans to swim by to identify them with certainty from our catalog of individuals (Sarano et al., 2022) and to start the video recordings. If sperm whales did not move, observers slowly and carefully swam to them in order to position themselves close enough to provide best visual observations of nursing activities. Distances between observers and cetaceans depended on the sperm whale behaviors and on the water visibility. Usually, around 10 m of distance between the sperm whales and the observers allowed careful observations and precise filming. All the observations were done between the sea surface and a 30 m depth.

Fieldtrips have been conducted every year since 2013, allowing to collect more than 200 hours of underwater video recordings using a GoPro camera, a Sony F55 4K camera and a Sony EXIR HD camera. Then, we manually selected the video sequences when nursing activities were observed and when we were able to doubtless identify the involved sperm whale individuals. It was possible because these individuals were all identified from their own external markings, including the shape of the tail fluke, the dorsal fin marks, the body scars, and the skin pigmentation. For a previous study, numerous photographs were collected in a catalog and individual cards were already made for each sperm whale (Sarano et al., 2022).

Table 1

Kin Relationships of Mothers-Calves, with Sex and Year of Birth of the Calves

Mother	Calf	Sex	Year of birth
Adélie	Eliot	M	2011
Caroline	Zoé	F	2013
Caroline	Alexander	M	2019
Delphine	Chesna	F	2018
Dos Calleux	Baptiste	M	2017
Irène	Arthur	M	2013
Irène	Lana	F	2019
Issa	Miss Tautou	F	2016
Lucy	Roméo	M	2013
Lucy	Daren	M	2018
Mina	Ali	M	2018
Reshna	Cindy	F	2018

Description of the Nursing Behavioral Repertoire

To describe the nursing behavior, we used the software BORIS (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016). We defined four events (*E*) to describe all the successive steps of the nursing behavior in sperm whales:

E#1 - The preliminary phase. The calf approaches an adult female under her rear ventral part, makes physical contact with her, then rubs its head and bumps onto the female's genital area (for a detailed description, see Figure S1).

E#2 - The roll-over phase. The calf rolls onto its back, opens its mouth to introduce its lower jaw into the female's genital slit making one of the two nipples to come out of its mammary slit.

E#3 - The suckling phase. Once the nipple is outside of its slit, the calf grasps it, squeezes it in its mouth, wraps around it with its tongue and makes active strong repetitive suckling movements. Note that suckling is one of the different phases of the nursing event.

E#4 - The final phase. After removing its lower jaw from the genital slit, the calf swims off, either to the sea surface to breathe or swims to another individual of the social unit or stays by the suckled female. We also defined the beginning and the end of the suckling activity with two behavioral states, in contrast to events that last longer:

O#1 - The jaw introduction. The calf introduces its lower jaw into the adult female's genital slit.

O#2 - The jaw extraction. The calf removes its lower jaw from the female genital slit. Note that it is possible to observe a milk cloud at this moment. In multiple suckling events, the sequence goes back to *O#1*.

We also defined the following six parameters:

Presence of milk. We distinguished a nursing event with evidence of milk, where a milk cloud is clearly seen on the video footage, from nursing events without evidence of milk where no milk was released from either the calf's mouth or from the female mammary slit.

Nursing without suckling activity. We defined as a nursing event without suckling an event when the calf was observed to repeatedly bump onto the female's genital area and prepare to suckle but did not introduce its lower jaw inside her genital slit (i.e., switching directly from *E#1* to *E#4*).

Maternal nursing vs allonursing. We labelled maternal nursing or allonursing the instances where the calf respectively suckled its mother or another female. This work was only possible because 1) video recordings were done close enough to have clear pictures of the involved sperm whale individuals, 2) all individuals of the social unit were previously identified (Sarano et al., 2022) and 3) all their kin relationships were assessed (Sarano et al., 2021).

Number of involved calves. We provided the number of calves involved in each nursing event.

Position of the adult female during the nursing. We also divided the behavior of the adult female into 4 categories: 1) the female is in a static vertical position (*vertical static*), 2) the female is in a static position but not vertically (*static*), 3) the female moves slowly with no visible fluke movements (*slow swim*), and 4) the female actively swims at a speed exceeding the speed that can be reached by the underwater observers (*swim*).

The estimated depth. We categorized the depths at which nursing occurred into 3 classes: *zone 1* when a part of the body of the adult female was seen out of the water, *zone 2* when the female was close to the surface but with her entire body under the sea surface (< 10 m deep), and *zone 3* for any depths greater than 10 m.

Data Analysis

We calculated the time duration of both maternal nursing and allonursing events. Data normality and homoscedasticity were checked respectively by doing a Shapiro-Wilk test and a Levene test with the Brown-Forsythe modification. Hence and considering the low number of observations (<30) in most of the conditions, we conducted a non-parametric test Kruskal-Wallis followed by Wilcoxon-Mann-Whitney test using R. When the p value was < .05, the test provided a significant result. Finally, a binomial test was used to assess the effect of the different depths on nursing events.

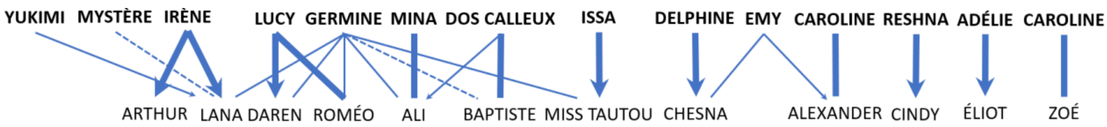
Results

Adult-Offspring Interactions During Nursing Events in this Social Unit

Our catalog of all the sperm whale individuals was used to identify the adults and the calves involved in nursing events. We were able to classify them into maternal and allonursing events. From our underwater visual dataset, the first result was that all the calves were observed during maternal events but not all during allonursing sequences. Indeed, calves DAREN, ELIOT, ROMÉO, ZOÉ, CINDY and ARTHUR only suckled their mothers (Figure 1).

Figure 1

Nursing and Allonursing in this Social Unit



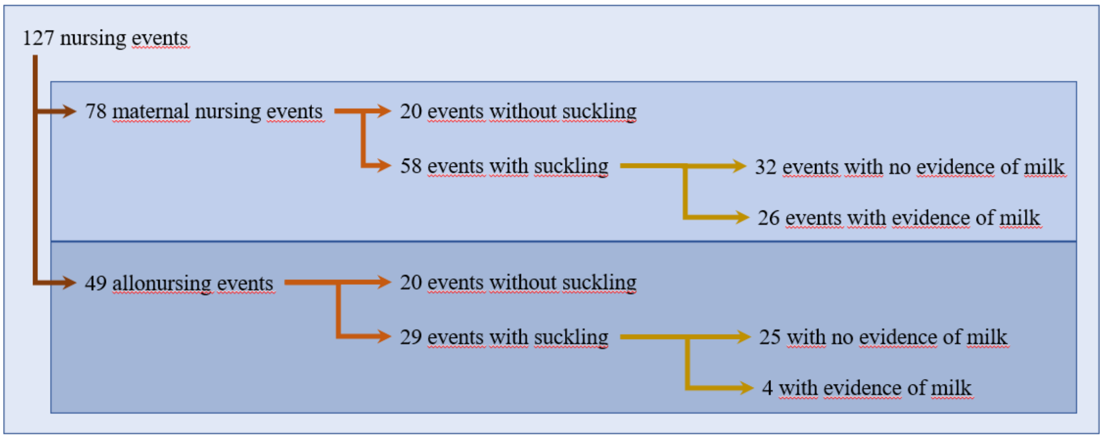
Note. Normal/bold: name of the calf/adult female; thick/normal line: mother/nurse; solid/dashed line: nursing event with/without suckling event; line ending without/with arrow: no evidence/evidence of milk.

We found that even if calves had nurses (i.e., non-maternal females who provided allonursing), there was no significant differences between the average time spent with their mothers and the time spent with the nurses. Only three calves went more often to their nurse for allonursing events than to their mother. Our data showed 127 nursing events, including 78 maternal and 49 allonursing events (Figure 2). For each, we distinguished events when the calves suckled (or not) their mother and the nurse, respectively 58 (20) and 29 (20) events. Finally, for suckling events, we noticed if we were able to observe milk clouds (or not), respectively 26 (32) for maternal nursing and 4 (25) for allonursing (Figure 2).

Calf ALEXANDER (male, estimated age: 2 to 4 months old) rarely suckled his mother CAROLINE, and for the majority of time (90%) he suckled nurse EMY. On the contrary, BAPTISTE (male, estimated age: 4 o 17 days old) suckled nurse GERMINE, 20% of the time, and the rest of the time his mother DOS CALLEUX. ALI (male, estimated age: 1 week to 1 year old) suckled his mother 36% of the time and also two nurses, GERMINE and DOS CALLEUX, 64% of the time, but the average time spent with each adult was not significantly different (p = .978), even if the two nurses are grouped together (p = .850). CHESNA (female, estimated age: 2 months to 1 year old) had only one nurse, EMY, that she suckled 20% of the time, however, the average time spent with her mother or her nurse was not significantly different (p = .433). LANA (female, estimated age: 2 days to 2 months old) had three nurses in addition to her mother, while MISS TAUTOU (female, estimated age: 1 month to 2 years old) had one nurse. They suckled 53% and 40% respectively of the time with their nurses but the averages were not significant (p = .446 and .189, respectively).

Figure 2

Analysis of the 127 Collected Nursing Events in Two Classes: Maternal Nursing and Allonursing.



Note. For each subclass, we recorded whether the calves suckled, or not, from the adult females, and if milk clouds were observed.

In the following subsections, we describe the time order of the nursing steps in sperm whales. Then we showed some specific features of the behaviors and interactions between adult females and juveniles, including time durations, depths, and relative positions (Table 2). We also separately considered nursing events with and without suckling. Finally, we focus on maternal nursing and allonursing, especially to show the different role of the nurses compared to the mother.

Table 2

Maternal and Allonursing Events

	Maternal nursing				Allonursing			
Position of the adult female	Zone depth (1-2-3)	Duration of nursing (sec)	Duration of suckling (sec)	Evidence of milk (yes/no)	Zone depth (1-2-3)	Duration of nursing (sec)	Duration of suckling (sec)	Evidence of milk (yes/no)
vertical static	2	30	14	y	3	100	18	y
	2	96	1	y	2	20	5	n
	2	141	55	y	2	34	14	n
	2	360	3	y	2	96	21	n
	3	50	9	y	2	147	2	n
	3	60	14	y	2	150	16	n
	3	83	32	y	2	160	2	n
	3	94	26	y	2	174	12	n
	3	108	17	y	2	427	75	n
	3	108	29	y	3	35	1	n
	3	225	8	y	3	42	6	n
	3	285	69	y	3	108	4	n
	1	115	2	n	3	176	15	n
	1	278	36	n	2	28	0	-
	2	10	12	n	2	30	0	-
	2	125	2	n	2	63	0	-
	2	160	21	n	2	140	0	-
	3	45	12	n	3	26	0	-
	3	47	15	n	3	56	0	-
	3	68	9	n	3	85	0	-
	3	100	12	n	3	100	0	-
	3	149	1	n	3	125	0	-
	3	165	32	n	3	135	0	-
	3	358	36	n				
	2	40	0	-				
	2	62	0	-				
	2	155	0	-				
	2	280	0	-				
	3	20	0	-				
	3	23	0	-				
	3	39	0	-				
	3	50	0	-				
	3	54	0	-				
	3	120	0	-				
	3	147	0	-				
	3	249	0	-				
static	1	52	8	y	1	111	6	y
	1	72	16	y	1	228	7	n
	1	80	8	y	1	228	21	n
	1	121	19	y	1	322	1	n
	1	170	59	y	2	22	6	n
	2	230	5	y	2	90	3	n
	1	26	21	n	2	155	2	n
	1	40	11	n	2	320	3	n
	1	80	4	n	3	71	1	n

	1	34	0	-	3	77	12	n
	1	67	0	-	1	22	0	-
	2	29	0	-	1	80	0	-
					1	87	0	-
					1	103	0	-
					1	124	0	-
					1	155	0	-
					2	55	0	-
	1	60	9	y	2	50	22	y
	1	60	11	y	3	132	2	y
	2	45	21	y	1	84	13	n
	2	72	8	y	2	118	15	n
	2	200	69	y	2	185	2	n
	3	44	4	y	1	66	0	-
	1	30	6	n	2	43	0	-
slow swim	1	74	74	n	2	110	0	-
	1	97	5	n				
	2	101	11	n				
	3	90	7	n				
	3	97	76	n				
	1	180	0	-				
	2	19	0	-				
	2	21	0	-				
	3	66	0	-				
	2	30	9	y	2	46	1	n
	3	30	26	y				
	1	42	1	n				
	1	84	34	n				
	2	25	22	n				
	2	28	15	n				
	2	29	11	n				
swim	2	33	32	n				
	2	39	1	n				
	2	60	35	n				
	2	68	1	n				
	3	17	11	n				
	3	59	29	n				
	2	39	0	-				

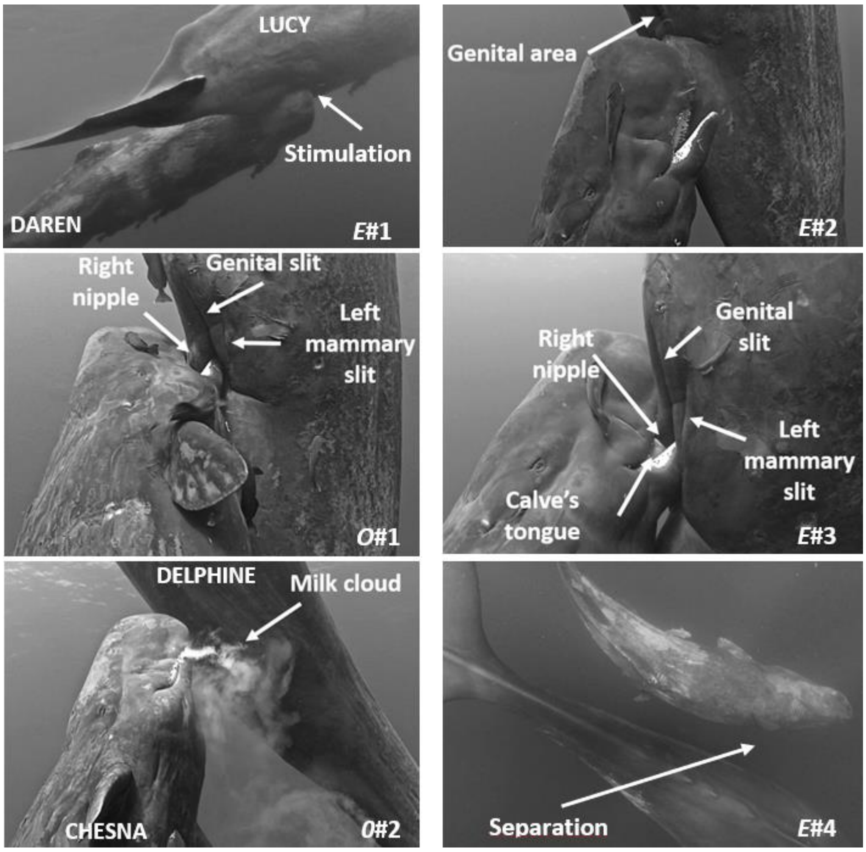
Note. Highlighted in gray are the two nursing events shown in supplemental videos S1 and S2.

Successive Steps of Nursing

Underwater videos allowed for the full description of nursing activities (Figure 3). Calves initiated by approaching one adult female (as shown in videos S1 and S2). Nursing events started either with *E*#1 or *E*#2. During the preliminary step *E#1*, calves usually made several attempts and swam along with the adult females to finally position themselves in infant position, so close enough to the genital slit, even if they did not start a suckling event. Then, the suckling phase E#3 followed, but not systematically. Indeed, the calf can switch directly to *E#4*. Sometimes, E#3 was performed several times during one given nursing event. Finally, the calves ended these nursing activities with phase *E*#4.

Figure 3

Illustration of the Different Nursing Events (E) and the Occurrences (O)



Note. Sperm whale calf swims towards the adult female and bumps the genital slit to stimulate her (*E*#1). Then, the calf rolls onto its back to position its mouth on the female ventral side and opens its mouth (*E*#2). Next, the calf introduces its lower jaw inside the genital slit that put the nipple out of its slit (*O*#1). The calf actively and strongly uses its tongue around the nipple, as shown on the photo (*E*#3). When the suckling activity is over, the calf drops the nipple and removes its jaw from the genital slit (*O*#2). Evidence of milk can sometimes be observed at this specific moment. Finally, the calf is no more in contact with the female's body (*E*#4). Photo credit: Photos of DAREN (M, 1 month old) with his mother LUCY, except for O#2 with CHESNA (F, 1 month old) and her mother DELPHINE (© René Heuzey/ Label Bleu/ MMCO / Longitude 181).

From our visual observations over seven successive years, 11 calves were observed during nursing events. Eight of the 11 displayed allonursing behaviors. Five of the 18 adult females of the group were involved in allonursing events. However, 53% of the allonursing events were performed by a single female, *GERMINE*. This female could sometimes allonurse two or three calves in the same time period, so she could be considered as the primary "babysitter" (Gero et al., 2008).

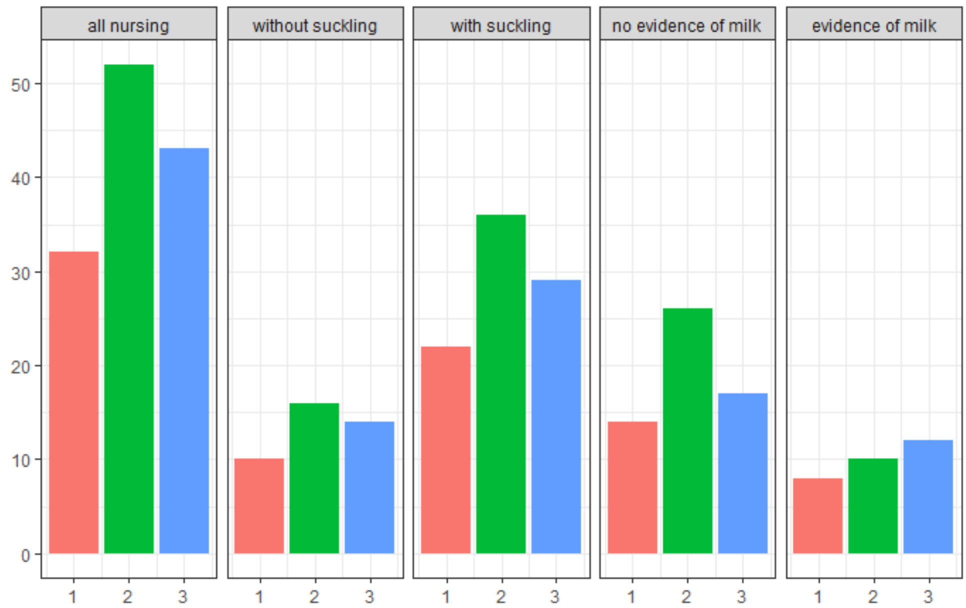
From the 127 observed nursing events, 87 events (69%) included a suckling event (Figure 2). Fifty-eight (67%) were done during maternal nursing and 29 (33%) during allonursing events. From our observation, we found a statistical trend for the duration of the nursing durations between the 78 maternal and the 49 allonursing events (p = .071). The mean (standard deviation) of the durations of maternal nursing and allonursing events were respectively 94.1 sec (79.0) and 113.1 sec (83.1).

Relative Positions between Adult and Juvenile Sperm Whales

From the collected nursing events, we extracted specific features, including the estimated depths of the female adults and the offspring, their relative positions, and their swimming. The 127 nursing events were video recorded at different depths close to the sea surface (Figure 4): 25% of these observations occurred when the adult females were at the sea surface (zone 1), 41% at a depth lower than 10 m (zone 2) and 34% below a depth of 10 m (zone 3). Depth zone 2 was similarly chosen during both maternal nursing and allonursing events (respectively 28 and 24 events), while zones 1 and 3 were favored during maternal nursing events (67% and 33% respectively for maternal nursing and allonursing events). Considering only suckling events with evidence of milk, 27% of the observations were done while adult females were at the sea surface, and 73% were done while they were below 5 m.

Figure 4

Depths of the Adult Females across the Different Nursing Behaviors Recorded

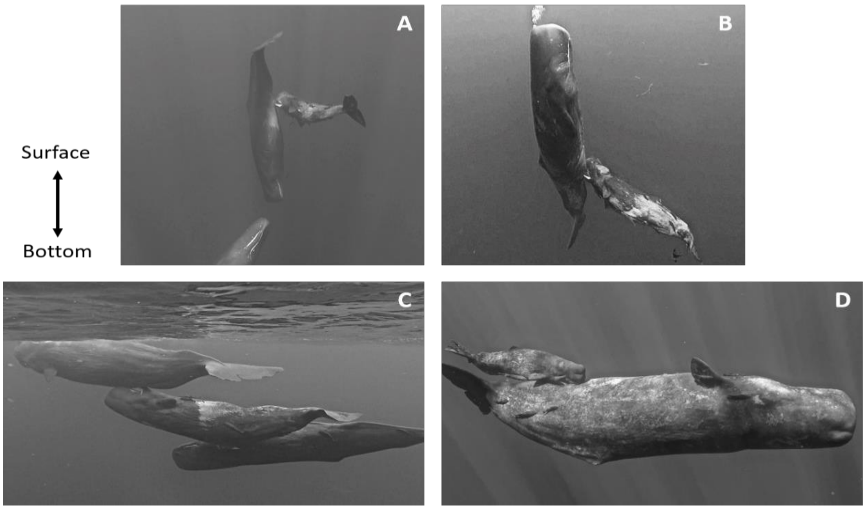


Note. Data are grouped by depth zone, where zone 1: sea surface (red), zone 2: 5-10m deep (green), and zone 3: >10m deep (blue)

We then investigated the relative positions between the adult females and the juveniles. We noticed in our video recordings that nursing behavior could take place in the following four positions (Figure 5): 1) For both maternal nursing and allonursing events, in 46% cases, the adult females were in vertical static position. Of these 88 instances, they stayed in *static* 29 times versus in a *vertical static* 59 times. In vertical positions, the adult females were either head down (Figure 4A) or up toward the surface (Figure 4B). 2) In 31% of our observations, the adult females were *swimming*, mainly in a *slow swimming* (24 times vs 15 times for higher swim). Adult females were either with their back (Figure 4C) or their belly towards the sea surface (Figure 4D). During both *swimming* and *slow swimming* situations, suckling events were observed for 82% and with evidence of milk for 26% (Figure 5).

Figure 5

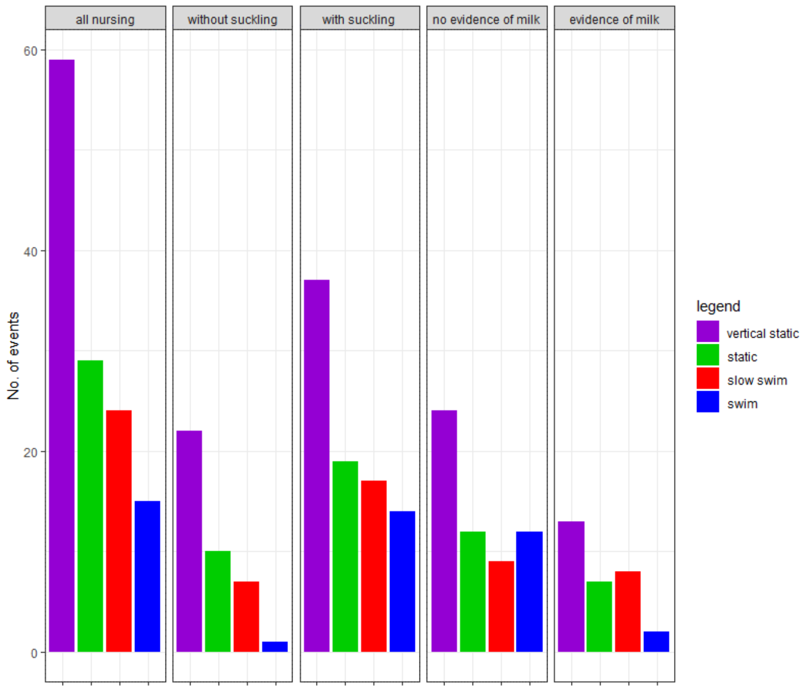
Different Nursing Positions Performed by Females and Calves



Note. Vertical static positions of the adult females with head down (A) or up toward the surface (B) and horizontal swimming positions of adult females with their back (C) or their belly towards the sea surface (D). Photo credit : © Axel Preud'homme, Francois Sarano, Fabrice Guerin / MMCO / Longitude 181 / Label Bleu.

Figure 6

Locomotion Behavior of Adult Females



Nursing with Suckling

Our observations showed that the suckling phase, E#3, lasted between 1 to 76 seconds, with a mean duration around 16.7 sec (standard deviation = 18.2). During the 58 maternal suckling events, the mean duration was 19.8 sec (standard deviation = 19.2), whereas for the 29 allonursing suckling events, the mean duration was 10.6 sec (standard deviation = 14.2). The suckling lasted almost two times higher for maternal nursing (mean = 19.8 sec, standard deviation = 19.1) than for allonursing events (mean = 10.6 sec, standard deviation = 14.2). This difference is statistically significant ($p = .010$). On the other hand, the mean duration for nursing events without suckling in maternal nursing was 84.7 sec (standard deviation = 78.1) versus 81.7 sec (standard deviation = 41.4) in allonursing ($p = .394$). During allonursing, the calves did not pursue the nursing events by suckling (40.8%).

Evidence of Milk

Among the 127 nursing events, 87 (68.5%) were observed with sequences of one to five successive active suckling events. The shortest time duration of a complete nursing event was 10 sec and the longest amounted to 7 min and 7 sec.

Evidence of milk was observed during 30 suckling events: 26 times (45%) for maternal suckling, and four times (14%) for allonursing. Involved calves were aged from few hours old to five-years old. These underwater observations explicitly showed that calves older than two years could continue to suckle. This result is consistent with the presence of milk found in the stomach of a 13-year-old sperm whale (Best et al., 1984). Note that two of these four allonursing suckling events with evidence of milk occurred between the calf ALI and its grandmother DOS CALLEUX, who lost her own calf one year before the birth of ALI.

We also noticed that, during maternal nursing, mothers did not always accept suckling from their own calf. Indeed, in 25.5% of our observations, adult females rolled onto their side away from the calves' mouths.

Influence of Age

Although observations were completely opportunistic and our team members did not intentionally choose to preferentially film any particular sperm whale individual, it appears that the studied dataset is heterogeneous with respect to offspring age, with a large majority of video recordings (76%) when the individuals were less than one year old (0 years old: 102 observations, 1 years old: 19, 2 years old: 9, 3 years old: 2, 5 years old: 2) (Table 3).

Each offspring was individually seen more often with its nurse than with its mother, regardless of age. In addition, the age distribution did not reveal significant depth preferences for nursing events (zone 1 = 28%, zone 2 = 40%, zone 3 = 32%). However, the number of suckling events was higher during maternal nursing than during allonursing.

For juveniles less than one year old, maternal nursing represented 73% of the observations, half of them with evidence of milk. For one-year-olds, this proportion is found again. However, for older juveniles, the number of observations was unfortunately not sufficient to confirm this trend and future work must be considered.

Table 3

Nursing Events Event of Each Juvenile According to its Age

			Positions				Depth Zone			Without suckling	With suckling	
Type	Age	Name	Slow swim	Swim	Vertical static	Static	1	2	3		No milk	Evidence of milk
Allonursing	0	Alexander	2	0	4	3	3	6	0	3	5	1
Allonursing	0	Ali	0	0	2	9	5	2	4	5	5	1
Allonursing	0	Baptiste	0	0	2	0	0	2	0	2	0	0
Allonursing	0	Chesna	1	0	2	0	0	2	1	1	2	0
Allonursing	0	Daren	0	0	0	4	4	0	0	2	2	0
Allonursing	0	Lana	5	1	9	2	1	12	4	4	11	2
Allonursing	0	Miss Tautou	0	0	0	1	0	1	0	0	1	0
Allonursing	1	Miss Tautou	0	0	3	1	1	1	2	3	1	0
Allonursing	1	Ali	0	0	1	0	0	0	1	1	0	0
Allonursing	2	Miss Tautou	0	0	1	2	2	0	1	3	0	0
Allonursing	5	Roméo	0	0	0	1	1	0	0	0	1	0
Maternal	0	Alexander	0	1	0	0	1	0	0	0	1	0
Maternal	0	Ali	1	0	3	0	0	2	2	1	3	0
Maternal	0	Arthur	2	0	1	0	0	0	3	1	1	1
Maternal	0	Baptiste	1	2	0	1	2	2	0	0	4	0
Maternal	0	Chesna	2	3	9	1	2	5	8	5	4	6
Maternal	0	Cyndi	1	0	0	0	0	1	0	0	0	1
Maternal	0	Daren	1	0	5	2	2	0	6	2	3	3
Maternal	0	Lana	3	6	3	3	1	13	1	5	5	5
Maternal	0	Miss Tautou	0	0	0	2	2	0	0	0	0	2
Maternal	0	Roméo	0	0	1	0	0	1	0	1	0	0
Maternal	0	Zoé	1	0	0	0	0	0	1	0	1	0
Maternal	1	Chesna	0	0	1	0	0	0	1	0	1	0
Maternal	1	Daren	0	0	5	1	3	3	0	1	3	2
Maternal	1	Miss Tautou	2	0	3	1	3	0	3	3	2	1
Maternal	1	Roméo	0	0	1	0	0	0	1	0	1	0
Maternal	2	Eliot	0	1	0	0	1	0	0	0	1	0
Maternal	2	Miss Tautou	2	0	2	0	2	0	2	0	0	4
Maternal	2	Roméo	0	0	1	0	0	0	1	0	1	0
Maternal	3	Eliot	0	1	0	0	0	1	0	0	0	1
Maternal	3	Roméo	0	0	0	1	1	0	0	0	1	0
Maternal	5	Eliot	0	0	1	0	0	0	1	1	0	0

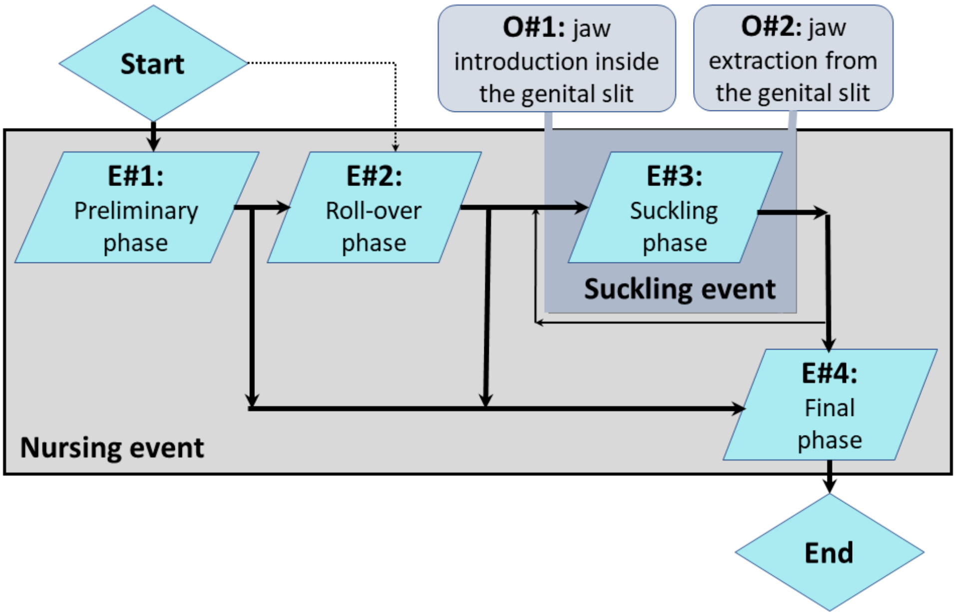
Discussion

Nursing Behavior Repertoire in Sperm Whales

Our underwater observations resulted in the schematic diagram illustrating the successive phases of the nursing behavior in sperm whales (Figure 7). Nursing usually started with stimulation from the calves bumping their head on the adult female body in the mammal slit area. Such behavior is common in mammal offspring to stimulate the female (Clutton-Brock, 1991) and was previously observed in cetacean calves (e.g., Barbara, 1999; Oftedal, 1997). Then calves turned over to have their jaw close to the ventral side of the adult female.

Figure 7

Diagram Describing the Sequential Events for Nursing and Suckling Behaviors in Sperm Whales



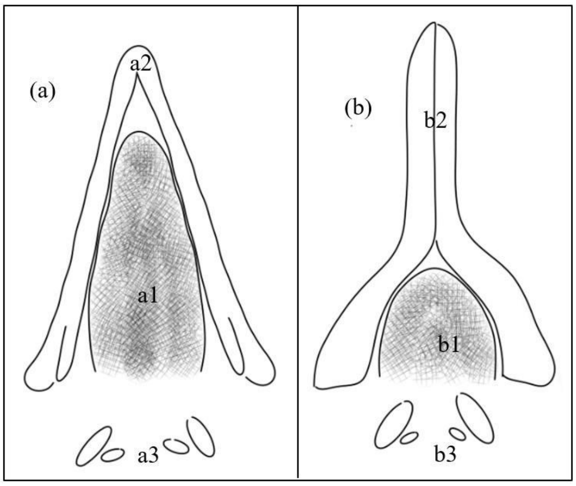
Note. More than one suckling activity could be observed during the same nursing event.

Our underwater observations did not support the hypothesis that calves can ingest milk through their nasal passage, as suggested by Gero and Whitehead (2007). Rather, the calves ingested milk through their mouth, a result which is consistent with Johnson et al. (2010), upheld by anatomical data showing that, for odontocetes, the respiratory system is disconnected from the digestive tract by the rostral laryngeal cartilages and the soft palate (MacLeod et al., 2015; Werth, 2007). Moreover, this study showed that sperm whale calves have a unique biomechanical process to obtain milk: our closest videos revealed how calves suckle the adult female's nipples with active movements of their tongue, consistent with observations from Johnson et al.'s (2010).

This suckling method is perfectly adapted to this cetacean species because of their specific anatomy. On one hand, the nipples are internal, so not easily accessible by the calves, but sperm whale females have their mammary glands located close to their genital slit, allowing the calf to reach the nipples through this genital slit. On the other hand, the location of the sperm whale tongue is atypical, and short, compared to the length of the jaw. A longer tongue over the whole mouth could form a straw shape to carry the milk ejected by the mother, as done in dolphins (Figure 8). In sperm whales, the tongue reaches only the last caudal teeth (Werth, 2004). So, the introduction of the jaw in the genital slit is needed to allow the calf the use of its tongue on the nipple. Also, despite of their hypertrophied head, the position, the stiffness, the length, and the width of their long jawbones allow them to introduce it into the adult female genital slits. Risk of injury of the female adults is reduced as calves' mandibles are toothless. However, the introduction of the lower jaw inside the mother's urogenital slit is not specific to sperm whales, as it was already described for beluga whales (Drinnan & Sadleir, 1981).

Figure 8

Frontal Section Comparison between Common Dolphin and Sperm Whale



Note. (a) Drawing of a frontal section (ventral view) of a common dolphin head: a1. Long tongue that can form a straw to carry the milk ejected by the mother; a2. Mandibula with short symphysis; and a3. Hyoid. (b) Drawing of a frontal section (ventral view) of a sperm whale head: b1. Short tongue that can't form a straw but that have muscles adapted to suckle; b2. Mandibula with long symphysis. Jawbones adapted to introduce it into female genital slits; and b3. Hyoid, bone essential for sucking. The scale is not respected between the two species.

We showed that nursing events took place in various static or swimming positions. When calves are hungry, they begin a nursing event, even when female adults are sleeping, or their position does not seem to be the most suitable and requires the calves to swim around the female to position themselves in front of the genital slits. Sometimes, when females have their bellies towards the sea surface, calves can lay down on the adult female and therefore reduce their energetic cost during nursing events. These different situations clearly show that the nursing events can be achieved whether the females are static or swimming.

Maternal Nursing and Allonursing

In mammals, parental care is mostly provided by mothers rather than fathers (Kleiman & Malcolm, 1981). This is true in sperm whales. Allocare, including babysitting, contributes to strengthening the social bonds of the unit (Whitehead, 1996). From our visual observations of this specific social unit, allonursing is done by adult females that are genetically related to the mother (grandmother, aunt, or distant cousins). Moreover, the allocaring events were also provided by juveniles who took care of the youngest animals. These caregivers were 3 and 4 years older than the calves, often juvenile males, closely related to the mother's calf, as shown by Gero et al. (2008).

Strong kin relationships were already described for this social unit, and our dataset tended to show a negative association between relatedness and group size, that it is consistent with Briga et al. (2012). Our observations suggested that allosuckling was predominantly provided by three nurses (YUKIMI, DOS CALLEUX, and EMY) and a babysitter (GERMINE), all of them without a filial calf, suggesting that the interindividual variability or individual temperaments could be drivers for such behaviors. Even if calves have more than one nurse, they obtained milk only from a single nurse: calf LANA from the nurse YUKIMI but not from the nurse GERMINE, calf ALI from the nurse DOS CALLEUX but not from the nurse GERMINE. Accordingly, GERMINE took care of different calves but did not give milk to all of them (i.e., no evidence of milk during suckling activities). However, each nurse seemed to give milk to only one calf: for example, the nurse EMY provided milk to calf ALEXANDER but not to calf CHESNA. Such behavior does not seem to be directed by kin relationship, as we noted that only the nurse DOS CALLEUX is the grandmother of ALI. EMY and YUKIMI have no direct kinship with ALEXANDER and LANA respectively (Sarano et al., 2021). Moreover, our visual observations showed that the nurses displayed rotation movements or swim away to avoid providing milk to a second calf. Hypotheses to explain such specific behaviors could be that: 1) an adult female can only physiologically produce enough milk for a single calf, 2) a nurse might choose to provide milk to one calf only, 3) the association nurse-calf may result from the choice of the mother, the nurse and/or the calf. It could also be a combination of these 3 hypotheses. In this sperm whale unit, social relationships, including allocare, could be reinforced by the relatively small size of the social group, and because of the cultural transmission of the clan made up of individuals of up to three generations (Sarano et al., 2021).

Direct Evidence for Allosuckling

In sperm whales, nurses took care of their own calves of their own social unit, by helping them to swim, to breathe, and to let them interact socially (Christal and Whitehead 2001; Whitehead, 2003). Our observations showed that calves suckled the nurse, even if all the studied calves were observed, at least once, suckling their mother with evidence of milk. From our dataset, eight out of the 10 allonursing events with sequence of suckling involved the same two adult females of the social unit, GERMINE and EMY. Interestingly, none of these females were seen with their own calf since 2011, as for YUKIMI; however, evidence of milk was observed from EMY and YUKIMI, indicating that these two adult sperm whales were lactating females. The allonursing events mainly involved calves with no close parenting relationship with these nursing females, except for a female, DOS CALLEUX, who was the grandmother of the allonursed calf ALI. For this female DOS CALLEUX, the allonursing was observed with evidence of milk showing that her milk production is still active after the loss of her own calf BAPTISTE, one year earlier, or that milk production can be re-induced by repetitive attempts to suckle by this "grand-calf". Such hypothesis is consistent with hunting data indicating that, in groups of harvested females, there were consistently more lactating females than calves (Best et al., 1984), and thus potentially more opportunities for allocaring and allosuckling. It also seems from our dataset that the allosucklings were done by nurses to only one calf: DOS CALLEUX to ALI, EMY to ALEXANDER, YUKIMI to LANA.

Otongenesis of Nursing

The age distribution of juveniles in our database was heterogeneous and limited, which does not allow a true study of age-related behavioral changes. However, opportunistic observations showed that each individual did more allonursing events than maternal nursing events. The number of suckling events were slightly higher with their mother. Future work should be considered to further investigate these results. Also, the fact that there are more observations in static (static and vertical static) is probably due to the data collection method. To confirm this result, it would be preferable to use video cameras to be fixed directly on the back of the juveniles.

Difference between Peduncle Dive and Suckling

Suckling positions in sperm whales do not match with peduncle dives defined by Gordon et al. (1998). We considered that these peduncle dives were unlikely an indication that suckling is occurring as suggested by Gero and Whitehead (2007) and in a more restrained way by Konrad et al. (2018) who mentioned that nursing was difficult to observe from the boat and that they never saw milk clouds.

From our dataset, no suckling events were observed during these peduncle dives. It thus means that peduncle dive should rather be considered as swimming infant position only (Figure S3). Note that infant position is an affiliative behavior displayed with mothers and non-mother females of the social unit. Indeed, we observed this behavior in eight out of the 18 adults of the social unit. Interestingly, those eight non-mother females were never involved in allonursing events. This affiliative position may thus play an important role in the maintenance of social bonds among members of social unit. For dolphin calves who also swim in similar peduncle dive (Simard & Gowans, 2004), it was also suggested to have both social and vital advantages, such as being a camouflage strategy from predators (Nore & Edwards, 2011) or a way to benefit from the hydrodynamic of their mothers (Nore & Edwards, 2011).

Our underwater observations have allowed us to show that peduncle dives are not involved in nursing behavior as previously suggested by Gero and Whitehead (2007) and Konrad et al. (2019), but only participate to social bonds between members of the social unit.

About the Data Collection

Our dataset was made from opportunistic visual passive observations. The underwater videos allowed us to cumulate information about the group structure, some of its activities and different types of interactions. Firstly, we were able to describe the whole nursing behavior from 127 nursing events, which is a large enough number to be statistically significant and to avoid potential bias. Secondly, aerial visual observations are inappropriate to describe the specific sperm whale nursing activity for at least two reasons: 1) our dataset showed that such activities can occur at different depths, even greater than 10 m, and 2) close underwater videos are needed to assess when calves suckle by introducing their jawbone inside the genital slit of the female adult. Thirdly, using an underwater robot was not an alternative as it would have been too slow and too difficult to safely maneuver between individuals (i.e., high risk of entanglements), and thus the use of human experts is more appropriate.

Animal disturbance cannot be excluded when human swimmers are around sperm whales. However, sperm whale adults and calves did not exhibit any avoidance or escaping behavior during both our approach and underwater observations. No individuals displayed any annoyance or any agonistic behavior (e.g., abrupt changes of behavior and/or swimming directions, tail slap). Calves stayed heavily focused on their nursing activities and never stopped suckling because of swimmer presence. Furthermore, our team has observed these calves since their birth and probably got them used to our presence. As it was done in primates' studies in the wild, habituation to humans, which can take from a few days to several years, plays a key role in the increasing quality of the observations (Narat et al., 2015). The increasing number and quality of our nursing observations (77% in 2019/2018 compared to 23% from 2013 to 2017) could be an indication of the increased habituation to humans (and thus decreased disturbance).

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Author Contributions: F. S. designed the study. F. S., V. S., A. P.-H., and R. H. worked on sperm whale observations and have collected the underwater video recordings. O. A. worked on the scientific contents. F. S., V. S, O. A., J. G., J.-L. J, I. C. and F. D. worked on the references. F. S., V. S., O. A., A. Y., and M.-L. T extracted the behavioral sequences. A. Y., M.-L. T. and O. A. performed the statistical analyses. F. S., V. S., O. A., J.-L. J, M. A., and I. C. developed the discussion. O. A. and I. C. organized and compiled the manuscript. M. A. added specific comments on the anatomy. All authors worked on the previous versions of the manuscript and reviewed this current version.

Conflicts of Interest: René Heuzey was employed by the company Label Bleu Production. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Barbara, J. M. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops sp*.). *Behaviour*, *136*(5), 529-566. https://doi.org/10.1163/156853999501469

Best, P. B., Canham, P. A. S., & MacLeod, N. (1984). Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission*, Special Issue, *6*, 51–79. https://doi.org/10.1007/978-1-4684-2985-5_7

Briga, M., Pen, I., & Wright, J. (2012). Care for kin: within-group relatedness and allomaternal care are positively correlated and conserved throughout the mammalian phylogeny. *Biology Letters*, *8*, 533–536. https://doi.org/10.1098/rsbl.2012.0159

Cerrito, P., & Spear, J. K. (2022). A milk-sharing economy allows placental mammals to overcome their metabolic limits. *Proceedings of the National Academy of Sciences*, *119*(10), e2114674119 https://doi.org/10.1073/pnas.2114674119

Christal J., & Whitehead, H. (2001). Social affiliations within sperm whale (*Physeter Macrocephalus*) groups. *Ethology*, 107(4), 323-340. https://doi.org/10.1046/j.1439-0310.2001.00666.x

Christal, J,, & Whitehead, H. (1999) Sperm whale social units: variation and change. *Canadian Journal of Zoology*, *76*, 1431-1440. https://doi.org/10.1139/z98-087

Christal J., Whitehead H., & Lettevall, E. (1998). Sperm whale social units: variation and change. *Canadian Journal of Zoology*, *76,* 1431–1440. https://doi.org/10.1139/z98-087

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press. https://doi.org/10.1515/9780691206981

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, *337*(6204), 260–262. https://doi.org/10.1038/337260a0

Conry, D. S., Nico de Bruyn, P. J., Pistorius, P., Cockcroft, V. G., & Penry, G. S. (2022). Alloparental care of a bottlenose and common dolphin calf by a female Indian Ocean humpback dolphin along the Garden Route, South Africa. *Aquatic Mammals*, *48*(3), 197–202. https://doi.org/10.1578/am.48.3.2022.197

Cowie A. T., Folley, S. J., Cross, B. A., Harris, G. W., Jacobsohn, D., & Richardson, K. C. (1951). Terminology for use in lactational physiology. *Nature*, *168*, 421. https://doi.org/10.1038/168421a0

Croft, D. P., Johnstone, R. A., Ellis, S., Nattrass, S., Franks, D. W., Brent, L. J. N., Mazzi, S., Balcomb, K. C., Ford, J. K. B., & Cant, M. A. (2017). Reproductive Conflict and the Evolution of Menopause in Killer Whales. *Current Biology*, *27*(2), 298–304. https://doi.org/10.1016/j.cub.2016.12.015

Drinnan, R. L., & Sadleir, R. M. F. S. (1981). The suckling behavior of a captive beluga (*Delphinapterus leucas*) calf. *Applied Animal Ethology*, *7*(2), 179-185. https://doi.org/10.1016/0304-3762(81)90097-3

Emlen, S. T. (1995). An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, *92*, 8092–8099. https://doi.org/10.1073/pnas.92.18.8092

Feldhamer, G. A., Drickamer, L. C., Vessey, S. H., Merritt, J. F., & Krajewski, C. (2007). *Mammalogy: Adaptation, Diversity, Ecology*. 3rd Ed, Johns Hopkins University Press, 592 p., ISBN: 9780801886959.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gero, S., & Whitehead, H. (2007). Suckling behavior in sperm whale calves: observations and hypotheses. *Marine Mammal Science*, *23*(2), 398–413. https://doi.org/10.1111/j.1748-7692.2007.00113.x

Gero, S., Engelhaupt, D., & Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, Physeter macrocephalus, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology*, *63*,143–151. https://doi.org/10.1007/s00265-008-0645-x

Gero S., Engelhaupt D., Rendell L., & Whitehead H. (2009). Who cares? Between-group variation in alloparental care giving in sperm whales. *Behavioral Ecology*, *20*, 838–843. https://doi.org/10.1093/beheco/arp068

Gero, S., Gordon, J., & Whitehead, H. (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131113, http://dx.doi.org/10.1098/rspb.2013.1113

Girardet, J., Sarano, F., Richard, G., Tixier, P., Guinet, C., Alexander, A., Sarano, V., Vitry, H., Preudhomme, A., Heuzey, R., Garcia, A., Adam, O., Madon, B., & Jung, J.-L. (2022). Long distance runners in the marine realm: New insights into genetic diversity, kin relationships and social fidelity of Indian Ocean male sperm whales. *Frontiers in Marine Science*, *9*, 815684. https://doi.org/10.1101/2021.04.23.440733

Gordon J., Moscrop A., Carlson C., Ingram S., Leaper R., Matthews, J., & Thompson, K. (1998). Distribution, movements and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: Implications for the development and regulation of the local whale watching industry. *Report of the International Whaling Commission*, *48*, 551–57.

Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology*, *138*(2), 148–157. https://doi.org/10.1002/ajpa.20911

Johnson, G., Frantzis, A., Johnson, C., Alexiadou, V., Ridgway, S., & Madsen, P. T. (2010). Evidence that sperm whale (*Physeter macrocephalus*) calves suckle through their mouth. *Marine Mammal Science*, *26*(4), 990–96. https://doi.org/10.1111/j.1748-7692.2010.00385.x

Kastelein, R. A., Dokter, T., & Zwart, P. (1990). The suckling of a Bottlenose dolphin calf (*Tursiops truncatus*) by a foster mother, and information on transverse birth bands. *Aquatic Mammals*, *16*, 134–138. https://doi.org/10.1578/am.32.1.2006.10

Kleiman, D. G., & Malcolm, J. R. (1981). The evolution of male paternal investment in mammals. In: Gubernick DJ, Klopfer PH, editors. *Parental care in Mammals*. New York: Plenum Press. pp. 347–387. https://doi.org/10.1007/978-1-4613-3150-6_9

Klopfer, P. H. (1981). Origins of parental care. In D.J. Gubernick and P.H. Klopfer, Eds. *Parental Care in Mammals*, pp. 1–13. New York: Plenum Press. https://doi.org/10.1126/science.214.4523.899

Konrad, C. M., Frasier, T. R., Whitehead, H., & Gero, S. (2018). Kin selection and allocare in sperm whales. *Behavioral Ecology, 30*(1), 194–201, https://doi.org/10.1093/beheco/ary143

Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., & McCall Howard, P. (2002). Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology, 80*, 1189–1196. https://doi.org/10.1139/z02-102

MacLeod, K. J., McGhee, K. E., & Clutton-Brock, T. H. (2015). No apparent benefits of allonursing for recipient offspring and mothers in the cooperatively breeding meerkat. *Journal of Animal Ecology*, *84*, 1050–1058. https://doi.org/10.1111/1365-2656.12343

Narat, V., Pennec, F., Simmen, B., Bokika Ngawolo, J. C., & Krief, S. (2015). Bonobo habituation in a forest–savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context. *Primates*, *56*(4), 339–349. https://doi.org/10.1007/s10329-015-0476-0

Nore, S. R., & Edwards, E. (2011). Infant position in mother-calf dolphin pairs: formation locomotion with hydrodynamic benefits. *Marine Ecology Progress Series*, *424*, 229–236. https://doi.org/10.3354/meps08986

Oftedal, O. T. (1997). Lactation in whales and dolphins: Evidence of divergence between baleen- and toothed-species. *Jounal of Mammary Gland Biology and Neoplasia*, *2*, 205–230. https://doi.org/10.1023/a:1026328203526

Packer, C., Lewis, S., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour*, *43*, 265–281. https://doi.org/10.1016/s0003-3472(05)80222-2

Pond, C. M. (1977). The Significance of Lactation in the Evolution of Mammals. *Evolution*, *31*(1), 177. https://doi.org/10.2307/2407556

Werth, A. J. (2004). Functional morphology of the sperm whale (*Physeter macrocephalus*) tongue, with reference to suction feeding, *Aquatic Mammals*, *30*(3), 405–418. https://doi.org/10.1578/am.30.3.2004.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Cambridge. Massachusetts: Harvard University Press.

Ratsimbazafindranahaka M. N., Huetz, C., Andrianarimisa, A., Reidenberg, J. S., Saloma, A., Adam, O., & Charrier I. (2022). Characterizing the suckling behavior by video and 3D-accelerometry in humpback whale calves on a breeding ground. *PeerJ*, *10*, e12945. http://doi.org/10.7717/peerj.12945

Sarano, F., Girardet, J., Sarano, V., Vitry, H., Preud'homme, A., Heuzey, R., Garcia-Cegarra A. M., Madon, B., Delfour, F., Hervé, G., Adam, O., & Jung, J.-L. (2021). Kin relationships in cultural species of the marine realm: case study of a matrilineal social group of sperm whales off Mauritius island, Indian Ocean. *Royal Society Open Science*, 8201794201794. http://doi.org/10.1098/rsos.201794

Sarano, V., Sarano, F., Girardet, J., Preud'homme, A., Vitry, H., Heuzey, R., Sarano, M., Delfour, F., Glotin, H., Adam, O., Madon, B., and Jung, J-L. (2022). Underwater photo-identification of sperm whales (*Physeter macrocephalus*) off Mauritius. *Marine Biology Research, 18*(1-2), 131-146.

Simard, P., & Gowans, S. (2004). Two calves in echelon: An alloparental association in Atlantic white-sided dolphins (*Lagenorhynchus acutus*). *Aquatic Mammals*, *30*(2), 330-334. https://doi.org/10.1578/am.30.2.2004.330

Slijper, E. J. (1962). *Whales*. 1st English ed. Hutchinson and Co., London. 475pp.[Translation of the Dutch book Walvissen published in 1958].

Werth, A. J. (2007). Adaptations of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, *290*(6), 546–568. https://doi.org/10.1002/ar.20538

Whitehead, H. (1996). Babysitting, dive synchrony and indication of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology,* 38: 237–244. https://doi.org/10.1007/s002650050238

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean*, University of Chicago Press.

Whitehead, H., & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour*, *118*, 275–296. https://doi.org/10.1163/156853991x00328

Whitehead, H., Antunes, R., Gero, S., Wong, SNP., Engelhaupt, D., & Rendell, L. (2012). Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *International Journal of Primatology*, *33*, 1142–1164. https://doi.org/10.1007/s10764-012-9598-z

Woodroffe, R., & Vincent, A. (1994). Mother's little helpers: patterns of male care in mammals. *Trends in Ecology & Evolution*, *9*, 294–297. https://doi.org/10.1016/0169-5347(94)90033-7

World Meteorological Organization, https://en.wikipedia.org/wiki/Sea_state [Date of access: 04/30/2022]

Appendix

Video S1

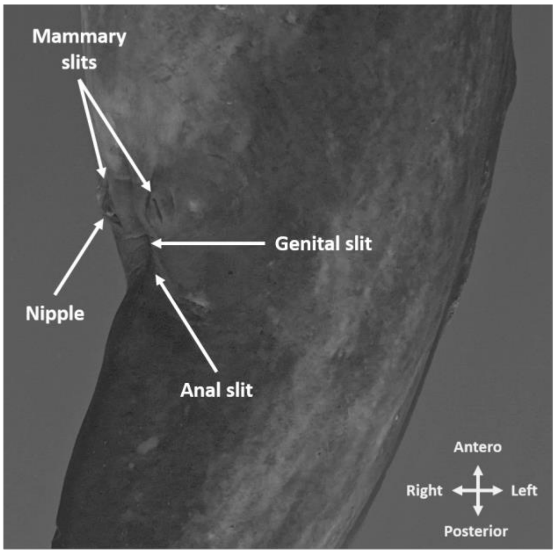
Underwater observation of a maternal nursing (May 5, 2018):
https://drive.google.com/file/d/12sRtGec3tl58k6D0U-AEhMEtYiSmeZ-M/view?usp=sharing

Video S2

Underwater observation of an allonursing (May 5, 2018):
https://drive.google.com/file/d/1EdlJF9yTIzRoNefY29WostVgO03KlbWw/view?usp=sharing

Figure S1

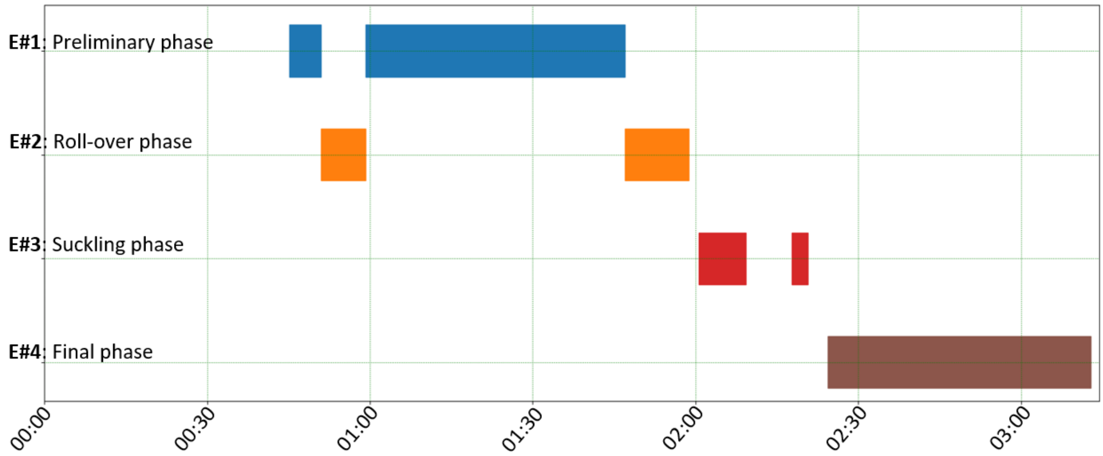
Description and Identification of the Different Slits of an Adult Female Sperm Whale



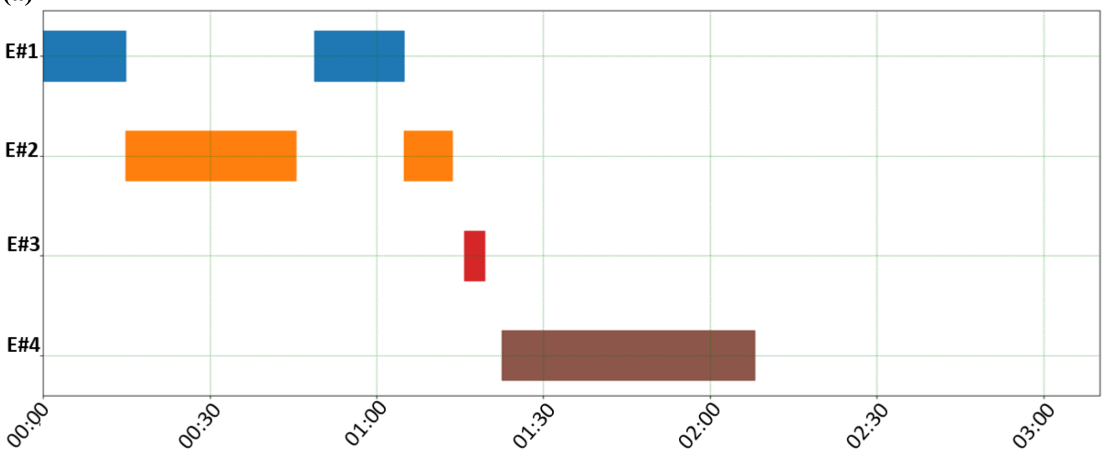
Note. On the female's belly, in the anteroposterior order are: the navel, the genital slit framed by two mammary slits, and the anal slit. Each mammary slit houses a nipple. As with other cetacean species, the nipples stay inside the mammary slit optimizing the hydrodynamic of the female body. Nevertheless, our underwater videos clearly document the nipple exhibited out of the mammary slit; here the right nipple can be clearly seen outside of its slit (© René Heuzey/Label Bleu/MMCO/Longitude 181).

Figure S2

Illustration of Behavioral Repertoire for 2 Nursing Events including Suckling Activities (a) maternal nursing (Miss Tautou and her mother Issa) and (b) allonursing (Miss Tautou and the nurse Germine)



(a)



Note. (a) maternal nursing (Miss Tautou and her mother Issa) and (b) allonursing (Miss Tautou and the nurse Germine)

Figure S3

Infant position swimming of ELIOT (M, 6 year old) with ADÉLIE (mother)

Note. Photo credit:© Axel Preud'homme / MMCO / Longitude 181/ Label Bleu.

Table S1

Visual observations of 127 nursing events documented from underwater videos. Durations of nursing and suckling events are given in sec (we uses “>” when the video starts after or ends before the whole sequence). Evidence of milk is specified for suckling activities. In italic, the 2 nursing events are given shown in supplementary video files.

Year	Date (mm dd)	Calf	Adult Female	Position of the Female	Type of Nursing	Zone Depth	Start Time (hh:mm)	Duration Nursing (sec)	Duration Suckling (sec)	Evidence of Milk (yes/no)
2019	05 05	ALEXANDER	EMY	vertical static	allonursing	2	10:04am	28		
2019	05 05	ALEXANDER	EMY	vertical static	allonursing	2	09:48am	174	12	n
2019	05 03	DAREN	LUCY	vertical static	maternal	2	10:09am	40		
2019	05 01	ALEXANDER	EMY	slow swim	allonursing	2	11:54am	185	2	n
2019	05 01	ALEXANDER	EMY	vertical static	allonursing	2	11:36am	34	14	n
2019	05 01	CHESNA	DELPHINE	vertical static	maternal	3	10:34am	149	1	n
2019	05 01	ALEXANDER	EMY	static	allonursing	1	11:23am	111	6	y
2019	04 29	LANA	GERMINE	vertical static	allonursing	2	09:37am	96	21	n
2019	04 27	ALEXANDER	EMY	slow swim	allonursing	1	09:52am	84	13	n
2019	04 19	LANA	GERMINE	vertical static	allonursing	2	11:01am	63		
2019	04 19	LANA	GERMINE	slow swim	allonursing	2	10:13am	118	15	n
2019	04 19	LANA	GERMINE	vertical static	allonursing	2	10:53am	147	2	n
2019	04 12	ALEXANDER	EMY	vertical static	allonursing	2	08:41am	30		
2019	04 12	LANA	GERMINE	static	allonursing	2	10:10am	155	2	n
2019	04 12	LANA	IRÈNE	vertical static	maternal	2	09:30am	62		
2019	04 05	LANA	GERMINE	static	allonursing	2	10:10am	320	3	n
2019	04 05	LANA	YUKIMI	vertical static	allonursing	2	09:18am	160	2	n
2019	04 05	LANA	GERMINE	vertical static	allonursing	2	09h58am	427	75	n
2019	04 05	LANA	YUKIMI	vertical static	allonursing	3	09:07am	176	15	n
2019	04 05	LANA	MYSTÈRE	vertical static	allonursing	3	08:54am	125		
2019	03 31	ALEXANDER	CAROLINE	swim	maternal	1	09:07am	42	1	n
2019	03 29	DAREN	LUCY	vertical static	maternal	1	10h51am	278	36	n
2019	03 29	LANA	YUKIMI	vertical static	allonursing	3	10:36am	35	1	n
2019	03 25	DAREN	LUCY	static	maternal	1	10:56am	170	59	y
2019	03 25	LANA	IRÈNE	static	maternal	1	10:54am	121	19	y
2019	03 25	DAREN	LUCY	vertical static	maternal	2	10:49am	141	55	y
2019	03 25	DAREN	LUCY	vertical static	maternal	2	10:18am	125	2	n
2019	03 25	LANA	YUKIMI	slow swim	allonursing	3	10:07am	132	2	y
2019	03 25	ALI	DOS CALLEUX	vertical static	allonursing	3	10:01am	26		
2019	03 21	LANA	IRÈNE	vertical static	maternal	2	10:54am	360	3	y
2019	03 20	ALEXANDER	EMY	static	allonursing	1	09:46am	124		
2019	03 19	LANA	GERMINE	vertical static	allonursing	2	09:13am	20	5	n
2019	03 19	LANA	YUKIMI	slow swim	allonursing	2	08:38am	50	22	y

2019	03 19	LANA	IRÈNE	vertical static	maternal	2	08:36am	96	1	y
2019	03 14	LANA	IRÈNE	static	maternal	2	10:43am	230	5	y
2019	03 14	LANA	IRÈNE	slow swim	maternal	2	10:04am	19		
2019	03 14	LANA	IRÈNE	slow swim	maternal	2	09:53am	200	69	y
2019	03 12	LANA	IRÈNE	swim	maternal	2	10:40am	39	1	n
2019	03 12	LANA	GERMINE	swim	allonursing	2	10:23am	46	1	n
2019	03 12	LANA	IRÈNE	swim	maternal	2	09:34am	39		
2019	03 12	LANA	IRÈNE	swim	maternal	2	10:41am	28	15	n
2019	03 11	DAREN	LUCY	vertical static	maternal	1	10:06am	115	2	n
2019	03 01	ALEXANDER	EMY	static	allonursing	2		90	3	n
2019	03 01	LANA	YUKIMI	slow swim	allonursing	1		66		
2019	02 27	LANA	IRÈNE	static	maternal	2	10:16am	29		
2019	02 27	LANA	IRÈNE	swim	maternal	2	10:05am	25	22	n
2019	02 22	LANA	YUKIMI	slow swim	allonursing	2	09:22am	43		
2019	02 22	LANA	IRÈNE	slown swim	maternal	2	09:21am	21		
2019	02 22	LANA	IRÈNE	swim	maternal	2	08:49am	68	1	n
2019	02 22	LANA	IRÈNE	swim	maternal	3	07:18am	59	29	n
2018	08 03	DAREN	LUCY	vertical static	maternal	3	11:44am	165	32	n
2018	07 02	ALI	MINA	vertical static	maternal	3	12:19pm	47	15	n
2018	05 15	ALI	GERMINE	vertical static	allonursing	3	11:01am	135		
2018	05 15	DAREN	LUCY	static	maternal	1	09:51am	80	4	n
2018	05 05	ALI	DOS CALLEUX	vertical static	allonursing	3	12:03pm	100	18	y
2018	05 05	ALI, DAREN and ROMÉO	GERMINE	static	allonursing	1	11:59am	228	7	n
2018	05 05	DAREN	LUCY	static	maternal	1	01:18pm	52	8	y
2018	05 05	DAREN	LUCY	vertical static	maternal	3	01:20pm	120		
2018	05 05	DAREN	LUCY	vertical static	maternal	3	01:23pm	94	26	y
2018	05 05	ALI	GERMINE	static	allonursing	2	11:38am	22	6	n
2018	05 05	ALI and DAREN	GERMINE	static	allonursing	1	11:48am	87		
2018	05 05	ALI and DAREN	GERMINE	static	allonursing	1	11:49am	22		
2018	05 05	ALI	GERMINE	static	allonursing	3	12:00pm	71	1	n
2018	05 04	ALI and DAREN	GERMINE	static	allonursing	1	10:30am	228	21	n
2018	05 03	DAREN	LUCY	slow swim	maternal	3	12:56pm	90	7	n
2018	05 02	DAREN	LUCY	vertical static	maternal	3	01:05pm	20		
2018	05 02	MISS TAUTOU	ISSA	vertical static	maternal	3	10:26am	83	32	y
2018	05 02	MISS TAUTOU and ALI	GERMINE	static	allonursing	1	10:34am	103		
2018	05 01	ALI	MINA	vertical static	maternal	3	12:01pm	147		
2018	05 01	ALI	GERMINE	static	allonursing	2	10:41am	55		
2018	04 28	ALI	DOS CALLEUX	static	allonursing	3	01:16pm	77	12	n
2018	04 28	DAREN	LUCY	vertical static	maternal	3	12:47pm	285	69	y
2018	04 23	CHESNA	DELPHINE	vertical static	maternal	2	11:51am	155		
2018	04 20	CHESNA	DELPHINE	vertical static	maternal	3	12:17pm	23		
2018	04 20	CHESNA	DELPHINE	vertical static	maternal	2	12:15pm	160	21	n
2018	04 20	CHESNA	DELPHINE	vertical static	maternal	2	12:14pm	30	14	y
2018	04 20	CHESNA	DELPHINE	vertical static	maternal	3	12:35pm	60	14	y

2018	04 20	CHESNA	DELPHINE	vertical static	maternal	3	12:32pm	108	17	y
2018	04 11	CHESNA	EMY	vertical static	allonursing	2	02:11pm	150	16	n
2018	04 11	CHESNA	EMY	vertical static	allonursing	3	11:48am	42	6	n
2018	04 03	CHESNA	DELPHINE	slow swim	maternal	2	09:17am	72	8	y
2018	04 01	CHESNA	DELPHINE	vertical static	maternal	3	10:28am	249		
2018	04 01	CHESNA	DELPHINE	vertical static	maternal	3	09:39am	225	8	y
2018	04 01	CHESNA	DELPHINE	vertical static	maternal	3	09:21am	39		
2018	04 01	CHESNA	DELPHINE	static	maternal	1	08:50am	34		
2018	03 09	MISS TAUTOU	ISSA	slow swim	maternal	1	11:25am	60	11	y
2018	03 09	MISS TAUTOU	ISSA	slow swim	maternal	1	12:31pm	60	9	y
2018	03 09	CHESNA	DELPHINE	swim	maternal	3	10:48am	17	11	n
2018	03 09	CHESNA	DELPHINE	slow swim	maternal	1	09:36am	30	6	n
2018	03 09	CHESNA	DELPHINE	swim	maternal	2	09:42am	29	11	n
2018	03 03	MISS TAUTOU	ISSA	vertical static	maternal	3	10:57am	50	9	y
2018	03 02	CHESNA	DELPHINE	swim	maternal	3	10:02am	30	26	y
2018	03 02	CHESNA	EMY	slow swim	allonursing	2	10:00am	110		
2018	03 01	CINDY	RESHNA	slow swim	maternal	2	10:56am	45	21	y
2018	02 07	ALI	MINA	vertical static	maternal	2	09:35am	10	12	n
2018	02 07	MISS TAUTOU	GERMINE	static	allonursing	1	09:06am	155		
2018	02 07	MISS TAUTOU	GERMINE	vertical static	allonursing	3	09:09am	85		
2018	02 06	ALI	MINA	slow swim	maternal	2	10:04am	101	11	n
2017	05 05	MISS TAUTOU	ISSA	vertical static	maternal	3	11:07am	50		
2017	05 05	MISS TAUTOU	ISSA	static	maternal	1	11:03am	67		
2017	05 05	MISS TAUTOU	ISSA	vertical static	maternal	3	11:00am	108	29	y
2017	05 05	MISS TAUTOU	ISSA	vertical static	maternal	3	10:56am	100	12	n
2017	05 04	MISS TAUTOU	GERMINE	vertical static	allonursing	3	11:38am	56		
2017	05 04	MISS TAUTOU	GERMINE	vertical static	allonursing	3	11:34am	108	4	n
2017	04 28	MISSTAUTOU	ISSA	slow swim	maternal	1	10:19am	97	5	n
2017	04 05	MISS TAUTOU	ISSA	slow swim	maternal	1	10:44am	180		
2017	03 24	BAPTISTE	DOS CALLEUX	slow swim	maternal	1	10:56am	74	74	n
2017	03 24	BAPTISTE	DOS CALLEUX	static	maternal	1	10:55am	40	11	n
2017	03 24	MISS TAUTOU and BAPTISTE	GERMINE	vertical static	allonursing	2	09:16am	100		
2017	03 24	BAPTISTE	GERMINE	vertical static	allonursing	2	8:16am	140		
2017	03 24	MISS TAUTOU	GERMINE	static	allonursing	1	8:16am	80		
2017	03 16	BAPTISTE	DOS CALLEUX	swim	maternal	2	09:33am	33	32	n
2017	03 11	BAPTISTE	DOS CALLEUX	swim	maternal	2	11:47am	60	35	n
2016	05 05	ROMÉO	LUCY	static	maternal	1	morning	26	21	n
2016	04 27	ELIOT	ADÉLIE	vertical static	maternal	3	12:20am	54		
2016	04 13	MISS TAUTOU	ISSA	static	maternal	1	10:58am	80	8	y
2016	03 19	MISS TAUTOU	GERMINE	static	allonursing	1	08:04am	322	1	n
2016	03 15	MISS TAUTOU	ISSA	static	maternal	1	10:51am	72	16	y
2015	04 12	ROMÉO	LUCY	vertical static	maternal	3	12:40am	45	12	n
2014	11 26	ELIOT	ADÉLIE	swim	maternal	2	morning	30	9	y
2014	03 20	ROMÉO	LUCY	vertical static	maternal	3	10:42am	68	9	n

2013	12 16	ZOÉ	CAROLINE	slow swim	maternal	3	10:07am	97	76	n
2013	12 16	ROMÉO	LUCY	vertical static	maternal	2	12:03pm	280		
2013	12 16	ARTHUR	IRÈNE	vertical static	maternal	3	11:51am	358	36	n
2013	10 11	ELIOT	ADÉLIE	swim	maternal	1	09:31am	84	34	n
2013	04 05	ARTHUR	IRÈNE	slow swim	maternal	3	08:27am	66		
2013	04 05	ARTHUR	IRÈNE	slow swim	maternal	3	08:03am	44	4	y