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Humpback whales (*Megaptera novaeangliae*) mother-calf interactions

Anjara Saloma

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Humpback whale (*Megaptera novaeangliae*) mother-calf interactions

Thèse de doctorat de l'Université Paris-Saclay
Préparée à l'Université Paris-Sud et à l'Université d'Antananarivo

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PREFACE

The word "whale" refers to a very large animal, whose history is closely related to that of humans. Wanted for their flesh, their baleen plates and their blubber, several species were decimated by the intensive hunting of the XIXth and XXth centuries, bringing them to near extinction. International treaties now strictly limit hunting, contributing to the recovery of some species. However, the current numbers are still very far from the initial population estimations and their status still depends entirely on conservation measures.

The history of whaling in Madagascar, is not well documented, and has focused on humpback whale populations' migrations along Malagasy coastal waters during their breeding and calving season (from July to October). Females, and consequently their foetuses, mainly resided along the east coast, showing that pregnant females appear in the season and concentrate in the waters along the coast from Fort Dauphin (extreme southeast) to Sainte-Marie Island (northeast). This population also experienced a period of intensive hunting, particularly in the XXth century. Neither males, nor females, nor their offspring were spared from hunting, even though the minimum size limit for hunted individuals was set at 10.66 m. Humpback whales are vulnerable to hunting due to a slow average swimming speed (5.55 km/h); their cruising speed hovers around 10 km/h. They can reach maximum speeds of 25 km/h when are frightened by harpoons blasts, but this speed gradually decreases, and they are easily overtaken after an hour of uninterrupted pursuit.

According to oral tradition, traditional hunting on Sainte-Marie Island has existed since the XVth century. The wise men of the villages all know the story of "*Rabesamondra*" the strong man who could tame whales. Hunting being an activity reserved for men, the women, for their part, remained at home and chanted while waiting for the men to return from the sea. The first report of traditional whale hunting dates from 1786 and describes the ease of approach and the

abundance of individuals caught by pirogue at the rate of 25 harpooned individuals per season. The Saints-Marians of the time were familiar with and very skilled at this hunt, which they learned from the pirates. The Whalers' Tower, that still stands to this day, is a reminder of these legendary residents.

In 1914, a provincial order was issued, authorizing a private individual to set up a whaling and processing plant on Sainte-Marie Island (oil extraction facility, preparation of guano and other by-products). The area concerned measured 1ha 54a 80ca and occupancy was granted for 30 years - renewable, against payment of a symbolic annual fee. The abundant stock of whales passing through Sainte-Marie Channel ensured supply for the factory. In 1949 and 1950, whaling expeditions were carried out by the *Société des Pêcheries Coloniale à la Baleine* (SOPECOBA) which simultaneously sent two fleets, one to Gabon, in support of the floating factory "*Jarma*", the other to Madagascar, in support of the factory ship "*Anglo-Norse*", which was accompanied by whaling ships. The most frequent anchorages were along the south coast, between Cap Sainte-Marie and Fort Dauphin, with other stops along the east coast, the largest of which was at Sainte-Marie Island. A total of 1335 individuals were captured in 1949 and oil extraction produced 60,400 barrels, or 10,227.7 tones. All individuals were humpback whales. In 1950, 737 whales were caught, 719 of which were processed, and supplied 38,485 barrels, or 5,670 tones (33,011 barrels of Megaptera oil and 474 barrels of Sperm whales oil). Whales were mainly hunted for their oil. On average, an 11.58 m individual, possesses blubber 15 to 16 cm thick, or approximately 1.3% of the total girth. In terms of sex ratio, more males were generally the products of hunting than females. Megaptera frequently travel in pairs. If they are hunted, both individuals stay together. If a female is harpooned, the male remains in the vicinity of his companion until she gives no sign of life. On the contrary, if the male is taken, the female inevitably flees.

The scientific report on whaling expeditions around Madagascar during the 1949 and 1950 seasons, written by M. Angot, documented the general status of population decline. The author recommended the immediate cessation of hunting for the protection of cetaceans. A few days prior to the printing of this report, SOPECOBA spontaneously decided to suspend hunting. These events mark the first and only documented case of industrial whaling around Madagascar. Since 1979, in response to the Seychelles Islands' proposal, the Indian Ocean area has become one of dozens of whaling sanctuaries. The International Whaling Commission (IWC) has therefore banned all commercial whaling. This status is reviewed every ten years. Nowadays, the Sainte-Marie channel is considered a hot spot for whale watching in the southwest Indian Ocean. Whale watching activities are regulated by an interministerial decree, dated March 2000, which defines distances and duration of observation. Hundreds of females accompanied by their newborns are there each year.

This thesis was born from the unique qualities of Sainte-Marie Island, along with the author's desire to discover and understand more about the biology of this iconic species that is the Megaptera. Mother-calf pairs were chosen because they represent the only stable formation of these sea nomads. The first three months of calves' lives are a critical phase of life and their survival ensures the survival of the species. Understanding mother-calf interactions could help in establishing species-wide conservation strategies, in line with their biology. The results of these studies would contribute in strengthening laws already in force: approach charters, and especially maintenance of sanctuaries to ensure their long term protection.

"Great whales are so-called umbrella species. By protecting them and conserving their habitats, we are protecting many other species and thus the oceans at large".



De Bry, *Icones quartæ partis Indix orientalis*, 1601, pl. IV.

Pêche à la baleine à l'île Sainte-Marie de Madagascar.

Sources:

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For Magalie Chaigneau and Romain Bollon

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EXTENDED SUMMARY

Humpback whales (*Megaptera novaeangliae*) perform annual migrations between high-latitude feeding ground and low-latitude breeding and calving grounds. This species displays obvious social behaviours during breeding period, which vary according to the productive status of individuals (solitary individuals, pair associations: male/female, male/male or female/female, females accompanied by their calves, and competitive surface groups characterized by aggressive males in competition). Numerous studies have highlighted the strong competition among males for access to females. Males in this context are known to produce complex but organized sound emissions, commonly called "song" which was first described by Payne and McVay in 1971. In addition to male songs, adult and calf vocalizations defined as "social calls" have been described (Dunlop *et al.* 2007; Silber 1986; Zoidis *et al.* 2008). These social calls present a less complex organisation than that observed in male songs. Although recent studies have focused on these social sounds, details are lacking about their function and the biological contexts in which they are produced.

Females are mainly observed close to shore, especially when accompanied by their newborn. Calves are born and spend the first months of their lives in a noisy environment not far from the competing males. Social interactions between females and their calves are poorly documented. Humpback whales are generally solitary; they form social groups for specific reasons: reproduction and feeding, however, these formations remain ephemeral. The only stable association is that of a female and her calf. Visual observation has shown that mother-calf pairs have a very close relationship and seem to use different sensory modalities to assure communication. In this work, I study mother-calf acoustic communication, diving behaviour and spatial behaviour, in order to establish a global view of their communication system.

To study their acoustic communication, we analysed acoustic recordings from an Acousonde tag deployed on mother-calf pairs during the years 2013-2014. The temporal and frequency characteristics of the social calls have been described and categorized in **Chapter 1a**. Half of the social sounds described are low-frequency harmonic sounds and 30% are similar to the sound units of male songs in the same population. Some of the social calls described in this study are similar to those described in other populations in other breeding areas. Hypotheses on the sounds produced by mothers and calves were made by considering the temporal and frequency characteristics of certain calls, as well as their production contexts, in the 16-studied mother-calf groups. It has been suggested that females mainly produce low-frequency sounds, especially in the context of vocal exchanges with their young. The presence of sound units of male songs suggests that females could have a large vocal repertoire and could use them in different contexts. Calves were suggested to produce low and medium frequency sounds and can produce composite sounds as well. Mother-calf pairs produce low amplitude sounds, at least 40 dB lower than male songs. The vocal repertoire of calves is detailed in **Chapter 1b**. This study was carried out by analysing the data collected in 2016-2017, in addition to the data in Chapter 1a. Analyses were based on calf and mother-calf group vocalizations described in Chapter 1 and in other breeding areas. Calves' vocalizations are short and relatively simple in structure. They mainly produce medium frequency sounds, low-frequency sounds and amplitude modulated sounds. The results showed that calves emitted combined sounds, composite sounds and sequenced sounds. These results suggest a degree of complexity in calves' sound production.

In **Chapter 2**, I focused investigations on six types of social calls attributed to mothers and calves (the most frequent sounds in Chapters 1a and 1b). This chapter deals with two different analyses. The first analysis aims at determining the source of low-frequency sounds attributed to mothers, using Acousonde accelerometer data (sampled at 400 Hz) and following the detection method for these low-frequency sounds in the tagged individual, described by Goldbogen *et al.* 2014. The second analysis investigates the individual vocal signature in the six selected social calls. In total two different types of low-frequency sounds could be detected on the accelerometer, suggesting that they were produced by the individual on which the tag was attached (the mother). All six social sounds have a fairly high individuality rate, suggesting that these 6 types of analysed sounds may well belong to each group studied.

The behavioural contexts of these six selected social sounds, as well as the dive profiles of the mother-calf pairs are presented in **Chapter 3**. The results showed that social calls attributed to calves are mostly produced during surface activities. The same production pattern was found for two of the social calls attributed to mothers. Two of the mothers' other calls are, on the other hand, produced during dives and one call was produced both during surface and diving activities. Analysis of dive profiles showed that there was a difference in the duration of dives and average time spent at depth between newborn and older calves. Finally, dive profiles between five mothers and their calves (simultaneous deployments) showed a perfect synchronization of dives with the mothers leading such behaviour.

Humpback whales with their calves spend much of their time on the surface of the water. Mothers are often static at the surface while calves move around them. In **Chapter 4a**, using opportunistic underwater videos, we analysed the positioning of the calves in relation to their mothers. By considering only calf's movements, we have shown that calves prefer to position themselves next to the mother's rostrum on the left and/or right. During the calves resting



phases, they are preferably below the mother's rostrum or below their pectoral fin. In **Chapter 4b**, I went further into the analysis of the calf's behaviour around the mother by using aerial videos captured by drone. Based on calves' only, they remain mostly in their mothers' fields of vision and move in the same way to the left or right of their mothers. However, in the presence of other congeners, calves positioned themselves more significantly to the right side of their mother and followed the right-side lateralization rule previously observed in Odontocetes. Using the photogrammetry method, we measured the body lengths of both mothers and calves to determine minimum and maximum lengths. Finally, the maximum distance between mother and calf was also measured and the dynamics of this mother-young distance in relation to calf size was studied.

RESUME ETENDU

Les baleines à bosse (*Megaptera novaeangliae*) effectuent chaque année une longue migration entre les zones d'alimentation de haute altitude et les zones de reproduction et de mise bas de *bass* altitude. Chez cette espèce, les comportements sociaux sont très prononcés durant la période de reproduction et varient selon le statut producteur des individus (individus solitaires, les associations par couples : mâle/femelle, mâle/mâle ou femelle/femelle, les femelles accompagnées de leurs baleineaux, et les groupes compétitifs de surface caractérisés par une compétition agressive des mâles). De nombreuses études ont mis en évidence les fortes compétitions entre les mâles pour l'accès aux femelles. Les mâles dans ce contexte, sont connus pour produire des émissions sonores complexes mais organisées, communément appelés « chant » qui fut décrites pour la première fois par Payne et McVay en 1971. En dehors des chants des mâles, il a été démontré la production par les adultes et les baleineaux de vocalisations définies comme des « sons sociaux » (Dunlop *et al.* 2007; Silber 1986; Zoidis *et al.* 2008). Ces sons sociaux présentent une organisation syntaxique bien moins complexe que celle observée dans les chants des mâles. Bien que de plus en plus d'études soient concentrées sur ces sons sociaux, leur fonction et le contexte biologique dans lesquels ils sont produits sont encore peu connus.

Les femelles évoluent principalement à proximité des côtes, notamment lorsqu'elles sont accompagnées de leur nouveau-né. Les baleineaux naissent et passent les premiers mois de leur vie dans un environnement bruyant et non bien loin des mâles en compétition. Les interactions sociales entre les femelles et leurs petits sont très peu documentées. Les baleines à bosse sont généralement solitaires, ils ne forment un groupe social que pour des raisons bien précises : la reproduction et l'alimentation, toutefois, ces formations restent éphémères. La seule association

stable est celle d'une femelle et son baleineau. Au vue des observations, ce couple mère-baleineau a un lien très étroit et semble utiliser différentes modalités sensorielles pour assurer leur communication. Dans ce travail, j'étudie leur communication acoustique, leur comportement de plongée et leur comportement spatial afin d'avoir une vision globale de leur système d'interactions.

Pour étudier leur communication acoustique, les enregistrements acoustiques collectées à partir de la balise Acousonde déployés sur les groupes mère-baleineau durant les années 2013-2014 ont été analysés. Les caractéristiques temporelles et fréquentielles des sons sociaux ont été décrites selon leur catégorie, **Chapitre 1a**. La moitié des sons sociaux décrits sont des sons harmoniques de *bass* fréquences et 30% sont similaires aux unités sonores des chants des mâles de la même population. Certains des sons sociaux décrits dans cette étude sont similaires aux sons sociaux décrits chez d'autres populations appartenant à d'autres zones de reproduction. Des hypothèses sur les sons appartenant aux mères et aux baleineaux ont été émises en considérant les caractéristiques temporelles et fréquentielles de certains sons ainsi que leurs contextes de production chez les 16 groupes mère-baleineau étudiés. Il a été suggéré que les femelles produisent majoritairement des sons de *bass* fréquences, notamment dans les contextes d'échanges vocales avec leurs petits. La présence des unités sonores des chants des mâles suggère que les femelles pourraient avoir un large répertoire vocal et pourrait les utiliser dans certains contextes. Les baleineaux quant à eux produisent des sons de *bass* et de moyenne fréquence et peuvent produire des sons 'composites'. Les mère-baleineaux produisent des sons de faibles amplitudes, 40 dB de moins que les chants des mâles. Le répertoire vocal des baleineaux est détaillé dans le **Chapitre 1b**. Cette étude été réalisée en analysant les données collectées en 2016-2017 en complément des données du Chapitre 1a. Les analyses se sont basées sur les vocalisations des baleineaux et des groupes mère-baleineau décrites dans d'autres

zones de reproduction. Les vocalises des baleineaux sont courtes et relativement simples en structure. Ils produisent majoritairement des sons de moyennes fréquences, des sons de *bass* fréquences et des sons à amplitude modulés. Les résultats ont montré l'émission par les baleineaux des sons combinés, des sons composites et des sons en séquence. Ces résultats suggèrent un degré de complexité de la production sonore des baleineaux.

Dans le **Chapitre 2**, l'étude se base sur 6 types de sons sociaux attribués aux mères et aux baleineaux (les sons les plus fréquents dans les études du Chapitre 1a et 1b). Ce chapitre traite deux analyses différentes. La première a pour objectif de déterminer la source des sons de basse fréquence attribués aux mères en utilisant les données de l'accéléromètre de l'Acousonde (échantillonnés à 400 Hz) et en suivant la méthode de détection de ces sons de basse fréquence chez l'individu tagué, décrite par Goldbogen *et al.* 2014. La deuxième analyse les signatures vocales de 6 sons sociaux sélectionnés. Au total deux types de sons de basse fréquence ont pu être détectés sur l'accéléromètre, suggérant qu'ils ont été produits par l'individu qui porte le tag (la mère). Les 6 sons sociaux présentent un taux d'individualité assez élevé, suggérant que les 6 types de sons analysés pourraient bien appartenir à chaque groupe étudié.

Les contextes comportementaux de ces 6 sons sociaux sélectionnés ainsi que les profils de plongées des couples mère-baleineaux sont présentés dans le **Chapitre 3**. Les résultats ont permis de voir que les sons sociaux attribués aux baleineaux sont produits majoritairement lors des activités de surface. Il en est de même pour deux des sons sociaux attribués aux mères. Les 2 autres sons des mères sont par contre produits lors des plongées et le dernier son produit en même temps lors des activités en surface et de plongées. L'analyse des profils de plongée a montré qu'entre les baleineaux nouveau-nés et les baleineaux plus âgés, il y a une différence sur la durée de leur plongée et le temps moyen qu'ils passent en profondeur. Les résultats des profils de plongée de 5 mères et de leurs baleineaux (déploiements simultanés) ont montré une

synchronisation presque parfaite de leur profil de plongée avec les mères qui dirigent les comportements.

Les femelles baleines à bosse accompagnées de leurs petits passent une grande partie de leur temps à la surface de l'eau. Les mères sont souvent statiques à la surface tandis que les baleineaux évoluent autour d'elles. Dans le **Chapitre 4a**, en utilisant des vidéos sous-marines opportunistiques, nous avons analysé les positionnements des petits par rapport à leurs mères. En ne considérant que les initiatives de déplacement des baleineaux, nous avons montré que les petits choisissent préférentiellement de se positionner à côté du rostre de la mère à gauche et/ou à droite. Pour leurs phases de repos, ils sont préférentiellement en dessous du rostre de la mère ou encore en dessous de leur nageoire pectorale. Pour aller plus loin dans les analyses des comportements des baleineaux autour de leur mère, nous avons analysés des vidéos aériennes capturés par drone. Toujours en ne tenant compte que les initiatives des baleineaux, les résultats de leurs positionnements dans le **Chapitre 4b** montrent que les baleineaux restent majoritairement dans les champs de visions de leurs mères et ils évoluent de la même manière à gauche et à droite de leurs mères. Cependant, en présence d'autres congénères, les baleineaux se positionnent significativement du côté droit de sa mère et suivent la règle de la latéralisation côté droit observé chez les Odontocètes. En utilisant la méthode de la photogrammétrie, nous avons mesuré les longueurs des groupes mère-baleineaux étudiés ayant permis de déterminer les tailles minimales et maximales des individus étudiés. Enfin, la distance maximale séparant les deux ont également été mesurés et l'évolution de cette distance par rapport à la taille des baleineaux a été calculée.



INTRODUCTION



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Maternal care in cetaceans

Effective reproduction in mammals implies not only success in fertilization, gestation and birth, but also in behaviours associated with parental care to ensure juvenile survival. In many vertebrates, male and female can both contribute (disregarding gestation and lactation) to offspring care. Nonetheless, other than in cooperative breeding mammals, all mammals including cetaceans, care and survival of offspring rely entirely on females. There are no known cases of paternal care and investments reported in any cetaceans, with the possible exception of Baird's beaked whale (*Barardius bairdii*) (Kasuya *et al.* 1997). Neonatal survival also relies on an ecologically appropriate environment throughout the early development stage, and on offspring's optimum interactions with the mother (Gubernick 1981).

Mother-offspring interactions require behaviours such as gazing, clinging, approach and vocal communication to achieve reunion and maintain proximity (Gubernick 1981). In an aquatic environment, sound is far less attenuated than light and smell, therefore acoustic signalling remains the most effective way to ensure communication. Consequently, cetaceans use vocalizations in many social interactions, including offspring care (Tyack 1997). For cetaceans living in social groups, such as bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*), signature whistles are different among individuals (Sayigh *et al.* 1990) and are associated with close-range communication between individuals, but can also be emitted during long-range exchanges when they are dispersed (Thomsen *et al.* 2002). Signature whistles exchanged between mother-calf dolphins play a major role on individual recognition and allow the pair to maintain contact (Sayigh *et al.* 1990). Visual cues also play an important role in mother-calf association. Belugas and dolphins maintain continuous visual contact between mothers and calves. Karenina *et al.* (2010) shows the importance of visual contact between the

pair, observed during dolphins' monocular sleep, during which the calf's eye in the mother's direction is open more often than the other eye. Moreover, studies focusing on belugas, orcas, and dolphins highlighted the presence of calves right-biased positioning towards their mothers (Karenina *et al.* 2010; Karenina *et al.* 2013). Calves observe their mothers with the left eye to analyse the information on a socially significant object in the right brain hemisphere. However, sperm whale (*Physeter microcephalus*) calves do not follow this rule with a bias to mothers' left side, a distinction that could be explained by sperm whales' unique blowholes, displaced to the left and probable calves' nasal suckling (Karenina *et al.* 2010). Lateralized behaviour's in mysticetes have been poorly studied and thus no conclusion can really be drawn. Adults humpback whales were reported to exhibit behavioural asymmetry during bottom-feeding behaviour using a right-biased turning position (Clapham *et al.* 1995). The same right-bias was reported in humpback whale calves suckling behaviour (Zoidis & Lomac-macnair 2017) and southern right whale calves (*Eubalaena australis*) were described to be right-bias positioned in relation to their mothers (right whale data were only obtained from photographs) (Karenina *et al.* 2017). When observing cetacean mother-calf pairs, physical contact also appears to be an important component of their behavioural interactions. Flipper-to-body contacts have been reported in many Odontocete species, between individuals belonging to the same social group as well as in mother-calf interactions (Sakai *et al.* 2006; Karenina *et al.* 2010). For Mysticetes, body contact have also been well observed, especially in mother-calf interactions. Female humpback whales have been observed to use their long flippers to maintain physical contact with their calves and calves usually stay below these pectoral fins while resting. Using their rostrum, female humpback whales have been observed carrying their newborn, especially during the calves' first days (Faria *et al.* 2013; Ferreira *et al.* 2011).

Lactation in cetaceans differs from land and semi-aquatic mammals (i.e., pinnipeds, sea otters, polar bears for marine mammals). Indeed, mammary gland mechanisms and postnatal development have evolved in a different way in terrestrial and aquatic mammals. Cetaceans have developed a fusiform body terminated by a powerful tail fluke to maximize swimming efficiency, and their mammary glands followed the same evolutionary pattern. Contrary to terrestrial and semi-aquatic mammals, the mammary glands of cetaceans are internal and located on either side of the genital slot (Slijper 1962). Calves need to stimulate the mammary glands to eject milk so that it may be drunk. Whaling stations provided opportunities to study cetacean reproduction and lactation. Mysticetes' mammary tissues appear to be deep in the body. Among mysticetes, the depth of lactating mammary glands averages about 20-25 cm in fin whales, right whales, 10-13 cm for sei whales and minke whales (Laws 1961; Gambell 1968; Best & Rüther 1992). Blue and fin whales (*Balaenoptera musculus* and *Balaenoptera physallus*) have relatively flat mammary glands 1.5-2 m long, 65 cm wide and 20-30 cm thick (Mackintosh 1929). Humpback whales' mammary glands have similar length (1.7 m long) but appear to be narrower, only 45 cm at their widest point (Lillie 1915). Information on odontocetes is also scarce. Long-finned pilot whales' (*Globicephala melas*) lactating glands are 45 cm long, 15 cm wide and 7.5 cm deep (Sergeant 1962), spotted and spinner dolphins are an average of 27 cm long and 2.8 cm deep (Pilson & Waller 1970). Mysticetes' lactation patterns follow their annual migration patterns and start in the breeding area, where they give birth until calves' weaning. There are three families of baleen whales, and calves' weaning periods varied widely: estimated at 6 to 7 months before arrival in the feeding ground for the Balenopteridae (Rorquals) (Best 1982), about 4 to 8 months for the Eschrichtiidae (Grey whale) (Rice & Wolman 1971) and an average of 12 months for the Balaeinidae (Right whales) (Hamilton *et al.* 1995). Limited data from breeding grounds and migration routes (from low to high latitude) suggest that mothers feed in these areas despite continuous milk production. When arriving on

feeding grounds, females begin an intensive foraging activity to regain better body condition for the next migration. Large marine mammals acquired the ability to deposit excess nutrients in blubber, as well as in other tissues during their foraging period, an advantage that supports lactation during fasting periods. During mid to late lactation period, the great baleen whales produce high-fat milk containing 300-400 g/kg fat, 110-150 g/kg protein, and probably 10-20 g/kg sugar (Oftedal 1997). Based on calf growth rates and mammary gland mass, the predicted amount of milk produced for blue whales (*Balaenoptera musculus*) is 220 kg milk/day. Throughout the entire lactation period (6 months), they produce a total of about 40 000 kg of milk, containing 16 000 kg fat, 4 500 kg protein and 710 000 MJ energy transferred to the calf (Oftedal 2000), from which calves increase body mass by 17 000 kg (Lockyer 1981). Determination of lactation stage is more difficult in odontocetes as they have prolonged calving seasons, long lactation periods and less established migratory patterns (Oftedal 1997). Atlantic spotted dolphins (*Stenella frontalis*) were observed lactating and nursing calves until the birth of the next offspring. Thus, lactation period averages about 3 years, with some females continuing to nurse for up to five years (Herzing 1997). There is also strong variation in milk composition among odontocetes species. Compared to mysticetes, odontocetes milk contain 30% less fat. For instance, the fat content (30%) of common dolphin milk is about three times that of humpback dolphins (10%) while dwarf and pigmy sperm whales' milk has moderate fat content (15-19%) and great sperm whales 26% (Oftedal 1997).

“Following” is a species' strategy in which neonates accompany their mother as early as post-parturition, and are rarely distant from the mother until permanent separation or weaning (Lent 1974). Therefore, females' foraging activity is not constrained by the need to hide their offspring for protection. By maintaining close proximity, the follower offspring benefit from maternal vigilance, defence and protection against predators (Espmark 1971). Follower strategy

has been documented in several mammalian species including primates (Struhsaker 1971; Nash 1978) and hoofed mammals living in mobile and large groups (Hayssen, V. & Orr 2017). Studies of maternal care in baleen whales have suggested the use of the follower strategy (Lent 1974; Taber & Thomas 1982; Szabo & Duffus 2008; Tyson *et al.* 2012) in which calves benefit from hydrodynamic advantages during travels by staying close to their mother (Smultea *et al.* 2017). Mother-offspring spatial associations in Mysticetes are similar to those observed in terrestrial followers (Szabo & Duffus 2008). Nevertheless, baleen whale followers are faced with possible separation during foraging activities (Szabo & Duffus 2008), as they perform prolonged and deep dives during foraging bouts (Croll *et al.* 2001) that calves cannot perform. However, recent studies of humpback whales mother-calf feeding behaviour have shown synchronized diving, allowing the pair to maintain proximity while feeding (Tyson *et al.* 2012) thus reducing exposition to potential predators.

Vocal production and communication in Mysticetes

Baleen whales (Mysticetes) and toothed whales (Odontocetes) differ in morphology and feeding habits. Vocal communication is an important part of social life for both. Anatomically, Odontocetes and Mysticetes share the same particularity of vocal folds that lie in parallel to the long axis of larynx and trachea, in contrast to terrestrial mammals where vocal folds are perpendicular (Reidenberg & Laitman 2007a). However, the evolution of their vocal folds have both taken different rotations in opposite directions, and this difference supports the evolutionary divergence between the two suborders (Reidenberg & Laitman 2007b). If mechanisms of vocal production are well described for Odontocetes species, sound production in Mysticetes is less well understood. Sounds are described as being produced inside their respiratory system by airflow between the lungs and the laryngeal sac passing through the U-

fold system (Reidenberg & Laitman 2007b). This mechanism is described as the source of low-frequency sounds, and control of the airflow which allows adjustment of internal air pressure especially inside the laryngeal sac, may affect frequency or amplitude of produced sounds (Gandilhon *et al.* 2015).

Most baleen whales undertake annual migrations from high latitude regions where food is available to lower latitude regions where waters are warmer and suitable for breeding and birthing. For animals that travel so widely across oceans, the ability to communicate over short and long distances plays an important role in social interactions. Mysticetes produce different varieties of sounds that vary widely in frequency components and temporal characteristics: pulse, groan, moan, growl, upsweep, downsweep, whistle, click, ect (Parks *et al.* 2011; Dunlop *et al.* 2013; Rekdahl *et al.* 2015; Dunlop *et al.* 2007; Fournet *et al.* 2015; Wisdom *et al.* 2001; Clark 1983; Clark & Clark 1980; Goldbogen *et al.* 2013; Stimpert *et al.* 2015). Each species' vocal repertoire is still under investigation, but their structure and motivation appear to have similar rules in social motivation (Edds-Walton 1997). In birds and terrestrial mammals, frequency sweeps and variations in temporal patterns may contain important information to communicate their motivational state and/or behavioural context (Edds-Walton 1997). Long distance communication can be facilitated by call repetitions (Wiley & Richards 1978). Some baleen whales are known to produce repetitive calls. East Australian humpback whales frequently combine their social calls in bouts, which are produced in a specific social group composition and in a given behavioural context (Rekdahl *et al.* 2015). Similarly, sequences of calls in fin whales (*Balaenoptera physalus*) were described as call interactions that may function as contact calls to maintain social group cohesion (Širović *et al.* 2013). Broadband calls and frequency sweeps, which make vocalizations stand out from background noise, provide more information for binaural sound localization, compared to narrowband calls with

constant frequency (Wiley & Richards 1978). Songs performed by humpback whale males are used for territorial displays and mate attraction (Herman 2016). Considered as very complex, humpback whale songs show frequency sweeps, broadband and narrowband components, produced at different amplitudes, up to 190 dB (Thompson *et al.* 1986; Au *et al.* 2006). Blue whales (*Balaenoptera musculus*) produce low-frequency vocalizations (< 20 Hz) containing short frequency sweeps and lasting between 10 to 20 sec (Mellinger & Clark 2003). Gray whales produce brief series of pulses that stand out from the background noise due to their wide frequency bandwidth and sharp frequency onset (Fish *et al.* 1974) . Acoustic recordings have been made for all baleen whales. Even though acoustic signals have been well described, little information is available about the behavioural context of their sound production.

Social calls in humpback whales

Non-song vocalizations occur in all humpback whale social group compositions, both in breeding and feeding grounds. Initially described by Silber (1986) and Thompson *et al.* (1986), humpback whales' social calls were first reported to occur in large social groups composed of multiple males and few females' on breeding grounds. The investigation of social calls has recently received increasing attention and started with Dunlop *et al.* (2007, 2008), who published a detailed catalogue of humpback whale social sounds in migrating Australian whales departing from their breeding grounds. These social calls were classified into different main classes: harmonic sounds, separated into three categories (low, mid and high frequency), amplitude modulated sounds, repetitive sounds and the final class which includes all broadband, noisy and complex sounds (Dunlop *et al.* 2007). Rekdahl *et al.* (2013) showed the occurrence of 12 stable call types produced by the east Australian population of humpback whales.

First descriptions of humpback whale social sounds in their feeding grounds were done by D'Vincent, Nilson, and Hanna (1985) followed by Cerchio and Dahlheim (2001), describing feeding cries in South-eastern Alaska. This work was followed by Stimpert *et al.* (2007) who described a new type of sound recorded during night-time foraging activities in the Northwest Atlantic. Humpback whale vocal repertoire in feeding grounds were then described in details by Fournet *et al.* (2015) who classified these social calls into four main categories: low-frequency harmonic sounds, pulsed calls, tonal calls and the final class which pools noisy and complex calls (Fournet *et al.* 2015). If description of the different call types is getting more exhaustive among populations, further research is still needed on the behavioural context during which these vocalizations are produced, as well as their use in relation to gender, age and social context (mother-calf pair, adult groups, pairs, etc).

What do we know about humpback whale mother-calf association?

Humpback whales do not live in stable social groups (Baker *et al.* 1985; Clapham 1996) and they are scattered in wide breeding areas during winters (Winn *et al.* 1975; Baker *et al.* 1985; Whitehead & Moore 1982). Their mating system is considered either polygynous or promiscuous, with an aggregation of males gathered to engage competitive displays for the access to mature females (Cerchio *et al.* 2005; Clapham 1996; Herman and Travolga 1980). In some breeding areas they can cover expansive breeding habitats where males aggregate to sing and females visit these aggregations to assess potential mates. This suggests a large and mobile lek-mating strategy (Clapham 1996, Cerchio *et al.* 2016; Dulau *et al.* 2017). Males and females reach sexual maturity at a similar age (Chittleborough 1965), approximatively 5-year old (Barlow & Clapham 1997; Clapham 1992). Although females can mate and give birth at this age, the ability of males to successfully engage intra-sexual competition may not be possible

until physical/social maturity is reached at eight to 12 years (Chittleborough 1965). Studies of female humpback whale ovaries in the Western Australian population show that females ovulate once during winter, although a small minority, 16-28% and 8%, can ovulate twice and three times respectively (Chittleborough 1958; Chittleborough 1965). The gestation period is about 11-12 months (Chittleborough 1958) and birth intervals are reported to be between two to three years (Clapham 1992; Clapham & Mayo 1990) although females can give birth in two successive years (Glockner-Ferrari & Ferrari 1990).

Observations of cetacean births are rare, as are reports of mother-calf behaviours after birth. Scientists have only observed the births of a few Odontocete species in the wild (Weilgart & Whitehead 1986; Béland *et al.* 1990; Sciara & Gordon 1997). For mysticetes, only two documented descriptions of humpback whales' births are available: 27th August 2007 in North-eastern of Brazil (Ferreira *et al.* 2011) and 30th August 2010 in North-eastern Madagascar (Faria *et al.* 2013). These two observations differ in the number of individuals observed during these events. The female observed giving birth in Brazil was alone prior to and after birth, while the one observed in Madagascar was accompanied by 14 adults circling around her prior to and after parturition. In both cases, the water was blood coloured and the neonates' rostrum appeared in the middle of the pool of blood. Calves' first breaths were taken about two minutes after their first observation. Both calves were breathing with difficulty, and mothers used their rostrum to keep the calves at the surface just moments after birth. Calves body lengths were estimated to be one third of that the females. This length is consistent with the mean length at birth (about 4.5 m) reported by Chittleborough (1958). Caudal fins and ventral parts were entirely white, and the dorsal fin laid to one side, a characteristic of cetacean neonates (Scheidat *et al.* 2000). Calves were pale grey, and Faria *et al.* (2013) showed the presence of foetal folds over the whole body.

Humpback whales' nursing behaviour has been described during both surface and underwater observations and in both breeding and feeding areas. Nursing can be performed in different ways: with the mother stationary or swimming very slowly at a depth of 10-15 m (Glockner-Ferrari & Ferrari 1985) and occasionally at the surface with the mother's tail fluke extended into the air (position named "stable tail" that can also be observed in non-mother individuals) (Morete *et al.* 2003). Calves are usually positioned at an angle of approximately 30° to the midline of mother's body with rostrum up and tail down (Glockner & Venus 1983; Zoidis & Lomac-macnair 2017). The observation of nursing bouts is rare and infrequent even though humpback whale mother-calf pairs are widely observed (Zoidis & Lomac-macnair 2017). As in other mysticetes, humpback whale calves get energy transfer from fatty milk allowing an accelerated development phase during their first months (Glockner & Venus 1983).

Mother-calf pairs are the only stable social group in humpback whales, and last 12 to 18 months. Most calves leave their mothers shortly before or during their second winter, however, some association can remain for up to two years (Baraff & Weinrich 1993; Clapham & Mayo 1990). Humpback whales' site fidelity to a breeding and feeding ground are assumed to be maternally transferred (Barendse *et al.* 2013). Calves are born in low-latitude breeding regions and their habitat use can be influenced by the presence of escorts (one or multi-adult humpback whales accompanying lone female or females accompanied by calves). Mother-calf pairs were often reported to be accompanied by a single singing whale (Tyack & Whitehead 1983; Baker & Herman 1984). Association with one male could be a strategy to reduce harassment by males in competitive groups (Cartwright *et al.* 2012). Indeed, the pairs deal with the presence of competitive males displaying aggressive behaviours, and the association with such individuals increases their energy expenditure (Cartwright & Sullivan 2009a). Given the high energetic demands of lactation and the importance of optimizing calf growth rate, Mysticetes mothers

have a preference for warm waters (Rasmussen *et al.* 2007) and calm surface conditions (Elwen & Best 2004), and tend to avoid energetically costly association (Cartwright & Sullivan 2009a; Pack *et al.* 2017). Mother-calf habitat preference is also conditioned by calves' age ; their move towards deeper waters is correlated with calves' sizes (Pack *et al.* 2017). The residency of humpback females with calves in the breeding grounds are longer than females without calves. This extension is presumably beneficial to the survival of their calves despite the high costs of maternal energy transfer to calves while fasting (Herman 2016).

Maintaining interactions between pairs implies well-developed acoustic communication and an ability to maintain physical and visual contact, especially when evolving in a competitive group. Even though data on calves' sound production has been documented in opportunistic recordings, acoustic vocalizations seem to be common among wintering humpback calf pods (Zoidis *et al.* 2008). Despite acoustic studies of humpback whales' social calls in groups, including mother-calf pairs (Dunlop *et al.* 2007; Dunlop *et al.* 2008), call types used in mother-calf communication are still under scientific investigation. Moreover, there is no detailed information either on behavioural context of their sound production nor on their vocal interactions. Calves diving behaviour in the breeding ground have been described by Stimpert *et al.* (2012) but not correlated to mothers' diving patterns. Mother-calf foraging behaviour described by Tyson *et al.* (2012) shows synchronized behaviour between the pair within a vertical distance of ~ 20 m.

Research objectives

Humpback whales are the most observed baleen whales worldwide, as they are frequently (especially females accompanied with their newborns) encountered in coastal areas. Visual observations show a very close relationship between mother and calf using different sensory modalities such as hearing, touch and vision. Humpback whales' group compositions were reported to use social sounds other than male songs, which are mainly used as mating displays. Calves have been reported to vocalize (Zoidis *et al.* 2008) as well as females (Simao & Moreira 2005), even though little information is available concerning their sound production and even less on their vocal exchanges. Moreover, mother-calf pairs appear to keep in close proximity. Indeed, females have been frequently seen using their rostrum to regularly carry their calves during their first days of life, in order to assist them in breathing as they do not yet control their buoyancy very well. Calves have been observed staying to their mother's side while traveling or resting, which allows them to keep visual contact. The aim of my PhD is to describe mother-calf interactions in humpback whale, to better understand their close social interaction. In this study, I will use different methods to describe the vocal activities and behaviours exhibited by mother-calf pairs.

This dissertation explores my four main objectives, presented in 4 chapters.

What are the social calls present in recordings focused on mother-calf pairs and what type of social calls are used by mothers and their calves? What are calves' vocal repertoire?

Mother-calf vocal communication has rarely been studied, thus there is a lack of information on their vocal production. Using multi-sensor tags embedded on mother-calf pairs, I collected and analysed the vocal activity of mother-calf pairs. **Chapter 1a** describes the social sounds recorded in mother-calf pairs. In it, I discuss sounds assigned to females and those produced by

calves. **Chapter 1b** is dedicated to calves' vocal repertoire, giving detailed description of the temporal and frequency characteristics of their social calls. These works take into account the previous knowledge of humpback whale social sounds described in other populations (Dunlop *et al.* 2007; Fournet *et al.* 2015; Rekdahl *et al.* 2015; Zoidis *et al.* 2008).

How to detect the sound emitter? Is there an individual vocal signature?

When studying acoustic behaviour of marine mammals, especially cetaceans, recording their vocal behaviour at source is difficult, and determining the source of a given acoustic signal as well as assigning the emitted sound to a specific individual is challenging. In **Chapter 2**, we used methods described by Goldbogen *et al.* (2014) to identify the source of low-frequency signals from mother-calf pairs by using Acousonde accelerometer high-sample rate. We also investigated the presence of individual vocal signatures by analysing calls selected from mother-calf vocal repertoire and assessing call individuality.

What are the behavioural contexts of their sound production and what are the characteristics of mother-calf diving patterns?

Chapter 3 is dedicated to the description of the diving context of their vocal production. By linking the diving activity with the production of the principle social calls by females and calves, selected from Chapter 1 and Chapter 2, we investigated whether some of these are produced in specific diving contexts, thus hypothesizing the potential function of these vocalizations. By analysing diving data of all tagged calves and simultaneous tagging of given pairs, I described diving dynamics between all calves and between mother-calf pairs.

How can we describe the spatial organization of the calf around its mother?

Visual observations show continuous physical and visual contact between females and their offspring. **Chapter 4a** and **Chapter 4b** aim to describe mother-calf surfacing behaviours. Using both underwater and aerial observations, I will investigate the position of the calf in relation to its mother, and will assess if spatial laterality occurs in humpback whales as found in other Odontocetes species (taking into account the social association of the pairs with other conspecifics). We used a photogrammetric method to perform length measurement of pairs. Finally, I assess whether the distance of the calf, in relation to its mother changes with calf size.

MATERIALS AND METHODS



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Study area

This study was carried out in the Sainte-Marie Island, part of the Analanjirofo region, situated on the northeast coast of Madagascar. The island's total length is 60 km, and width seven km, with S-SW to N-NE orientation. The island itself covers an area some 160 km² and is separated from a smaller island named "Ile aux nattes" (3.75 km²) by a narrow 400 m channel. Both islands are surrounded by a barrier reef that protects a narrow, shallow water lagoon (<10 m). Sainte-Marie Channel (49°50' E-50°10' E, 16°60'S-17°55' S) is 60 km long and 30 km wide, characterized by a narrow passageway about seven km wide at the middle of the channel (Trudelle *et al.* 2018). This geographic location presents a great opportunity to observe migrating humpback whales a short distance from shore, in a shallow-water channel. Only a small portion of the coastal water reaches the maximum depth of 60 m, and the mean depth around Sainte-Marie is about 25-35 m (Figure 1).

Madagascar's east coast is the wettest area of the entire country. Due to its location, Sainte-Marie's weather is characterized by two seasons: the summer period that extends from November to May is warm and dry, and also includes cyclone season. Austral winter, from June to October, is rainy season, corresponding to humpback whales' breeding season in the southern hemisphere. Sea surface temperatures during the humpback whale breeding season from 2013 to 2017 ranged from 24.8 to 25.6 (obtained from NASA's Aqua-MODIS satellite: <http://disc.sci.gsfc.nasa.gov/giovanni>).

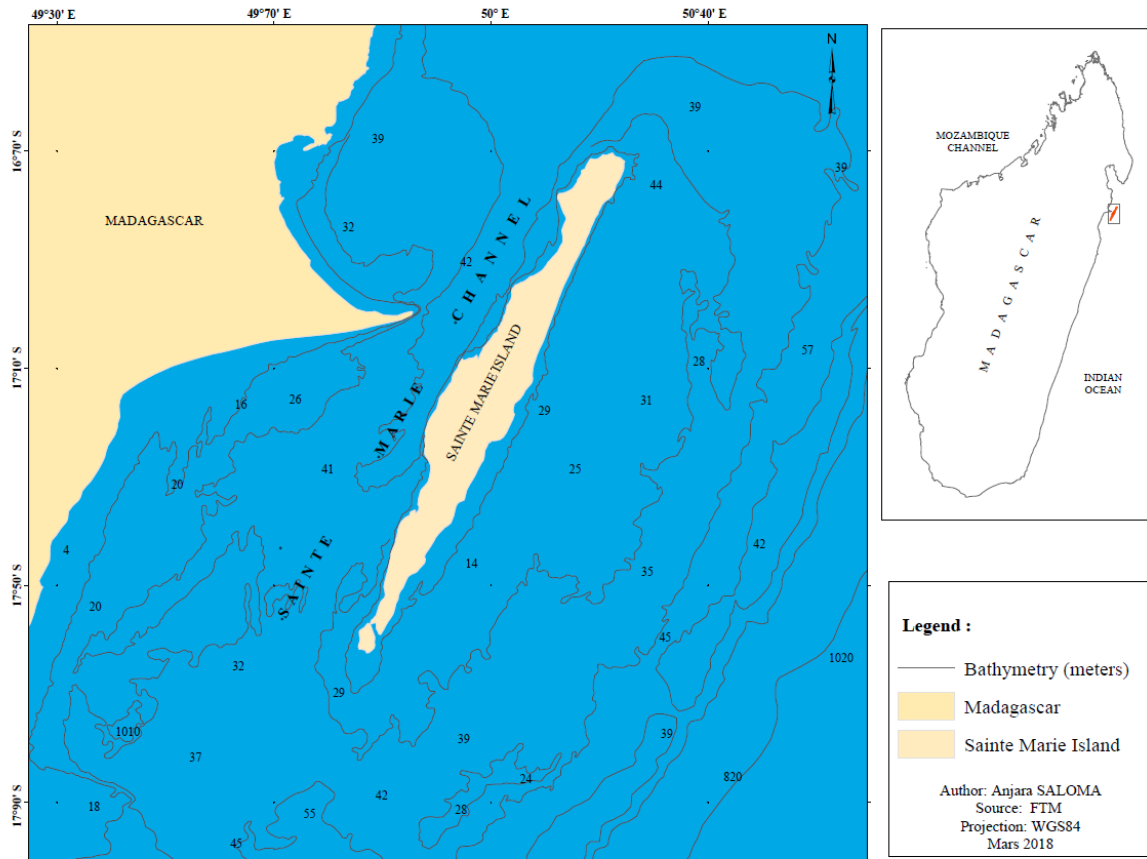


Figure 1: Map of the Sainte-Marie Island, North-East coast of Madagascar showing detailed bathymetry around the island.

All methods used in this thesis were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by the Fisheries Resources Ministry, Madagascar. National research permits were obtained during all five consecutive years of data collection: n° 44/13, 44/14, 46/15, 28/16, 26/17 MPRH/DGPRH.

Animal identification

Large cetacean identification is first based on observation of the characteristics and shape of their blows, which differ from one species to another. On an individual scale, various features, including notch patterns and trailing edges of dorsal and caudal fins, pigmentation patterns and scars present on their bodies, or callus patterns and scars were used for individual identification. Photo-identification methods provide quantitative estimates of population parameters such as abundance and survival, as well as fidelity to breeding or feeding sites (Hammond 1986). In 1988, the International Whaling Commission held a workshop to review and standardize photographic techniques, sampling protocols, and analytical methods (Hammond *et al.* 1990). The use of digital cameras (with lenses zooming up to 600 mm, waterproof casing) drastically changed photo-identification methods in the field, and data storage/sharing.

Among large baleen whales, humpbacks are known for the almost infinite variety of black and white patterns of their flukes and the variations in shapes of dorsal fins (Lillie 1915; Pike 1953; Katona *et al.* 1979). The patterns of the underside of flukes vary from nearly all black to all white, and may contain a wide variety of black or white patches, lines or streaks. They are the most effective means for individual identification. In addition to the colour pattern of caudal fins, five main categories have been described for the shape of dorsal fins (Figure 2) (Mizroch *et al.* 1990). These categories are commonly used by the international community during field identification and classification.

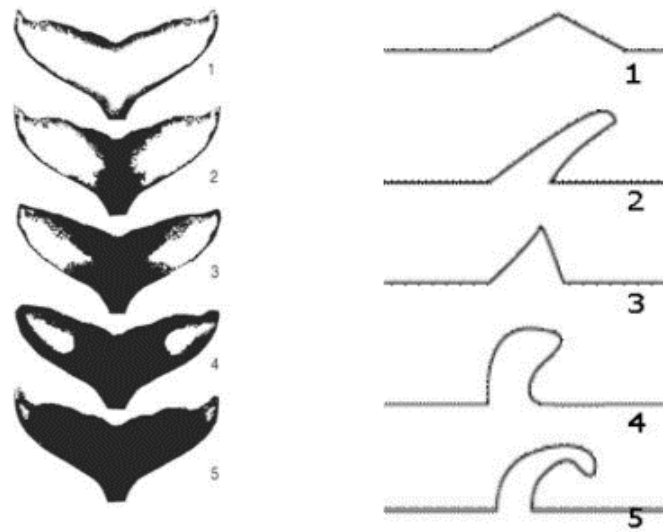


Figure 2: Classification of the humpback whales caudal and dorsal fins in five different classes (Mizroch et al. 1990).

For this study, mother-calf pairs were photo-identified before being tagged to avoid duplicate tagging during each season. Compared to other adults, female humpback whales accompanied with their calves often exhibit calmer behaviours (resting at the surface) and slow swimming. They may however, also exhibit active behaviours such as breach, or tail and pectoral slapping, during which both mother and calf often behave the same way. Mothers' tail flukes have rarely been photographed, as they seldom show "diving" behaviour that would allow observation of the internal face of the tail. The capture-recapture method performed during fieldwork to identify individuals is thus only based on mothers' dorsal fin pictures (left and right sides) (Figure 3). This protocol allowed us to avoid double sampling within season but also to identify recaptures between seasons.



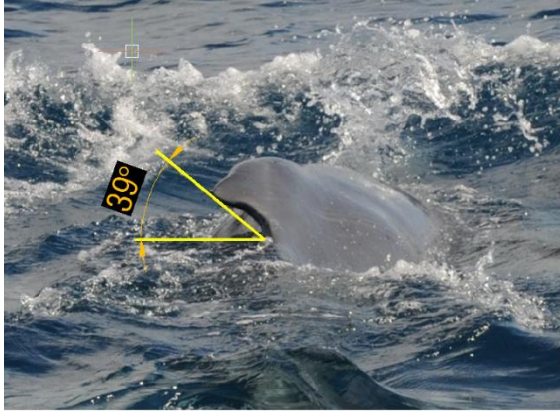
Figure 3: Female humpback whale dorsal fin photo identified (right and left sides) (©Cetamada).

Humpback whale calves were also photographed. Calves' photographs were taken at a six o'clock position (i.e., from behind) for each animal, to estimate their relative age. As changes in morphology of the dorsal fins are used as an indicator of calves' relative age, we measured the angle of unfurling of the dorsal fins, using the method described in Cartwright & Sullivan (2009b). Descriptions of new-born calf characteristics in the Sainte-Marie channel have shown that new-borns' dorsal fins are completely furled and lying to one side at birth (Figure 4) (Faria *et al.* 2013). For five calves with neonate traits documented in Hawaiian water, the mean dorsal fin angle was 45° and older calves (without neonate traits) had a mean dorsal fin angle of 79° . Dorsal fins were thus considered as furled when they had an angle $< 62^\circ$ and unfurled at an angle $> 72^\circ$. Two cases in this study have shown that a calf's dorsal fin can unfurl up to 8° in 7 days and 13° in 15 days (Cartwright & Sullivan 2009c).

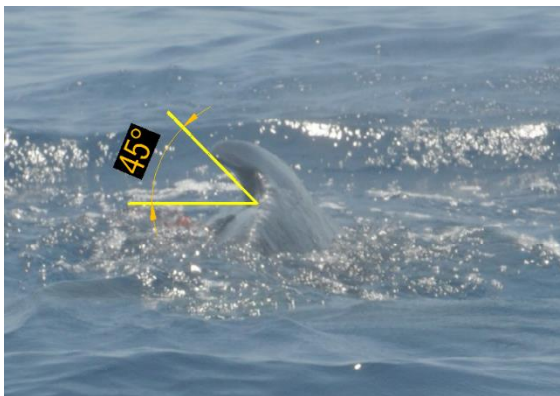


Figure 4: Humpback whale newborn with dorsal fin lying on left side (baby Maria, Sainte-Marie Island August 30th 2010) (©Cetamada – Fx. Mayer 2010).

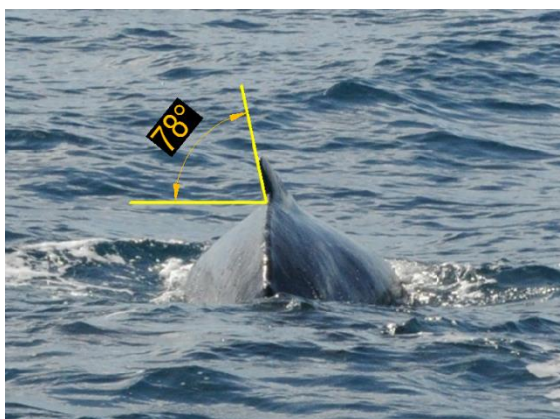
In our study, we based calves' relative ages using the criteria cited above and divided calves into three different age classes (Figure 5):



C1: calves showing the same characteristics as described by Faria and colleagues with dorsal fin $< 45^\circ$.



C2: calves having dorsal fins with an angle $\geq 45^\circ$ but less than 72°



C3: calves having dorsal fins that are unfurled at an angle going from 72° to fully erected (90°).

Figure 5: Measure of calf C1, C2 and C3 classes' dorsal fin angle. The angle of the fin relative to the horizontal axis measured in Adobe Photoshop 19.0.1 (© Cetamada).

Acoustic recordings

Acousonde suction cup tag

The Acousonde™ 3B is a self-contained underwater acoustic recorder which includes one hydrophone, sensors for speed, orientation, depth and temperature, a digital recorder, and a battery (Figure 7). When attached to an animal subject using four suction cups, the Acousonde records the vocalizations of the tagged animal as well as environment sounds surrounding the subject (i.e., other vocalising congeners, flow noise, boats, etc). These acoustic recordings can thus be linked to associated behaviours such as diving behaviour, travelling speed, etc.

The tag is programmed using a Palm Pilot M100 model connected to the Acousonde by an infrared port. We set up the acoustic sampling rate at 24 453 Hz, auxiliary sensors (temperature, 3D compass, pressure) at 10 Hz, and the 3D accelerometer at either 10 Hz or 400 Hz. The hydrodynamic floating part contains a receptacle for an HF transmitter. The HF transmitter is used to retrieve the Acousonde once detached from the tagged whale. The signal of the HF transmitter frequency can be detected within a 35-km range using a HF receiver ATS R410 model coupled with an antenna.

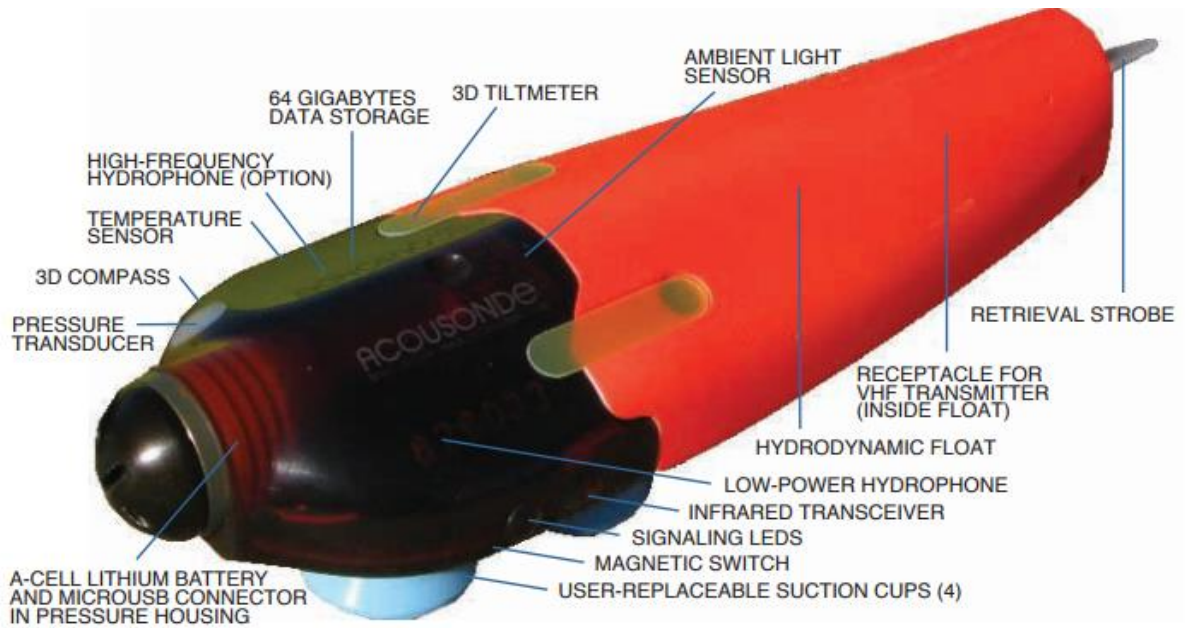


Figure 6: Acousonde™ 3B design (source: www.acousonde.com)

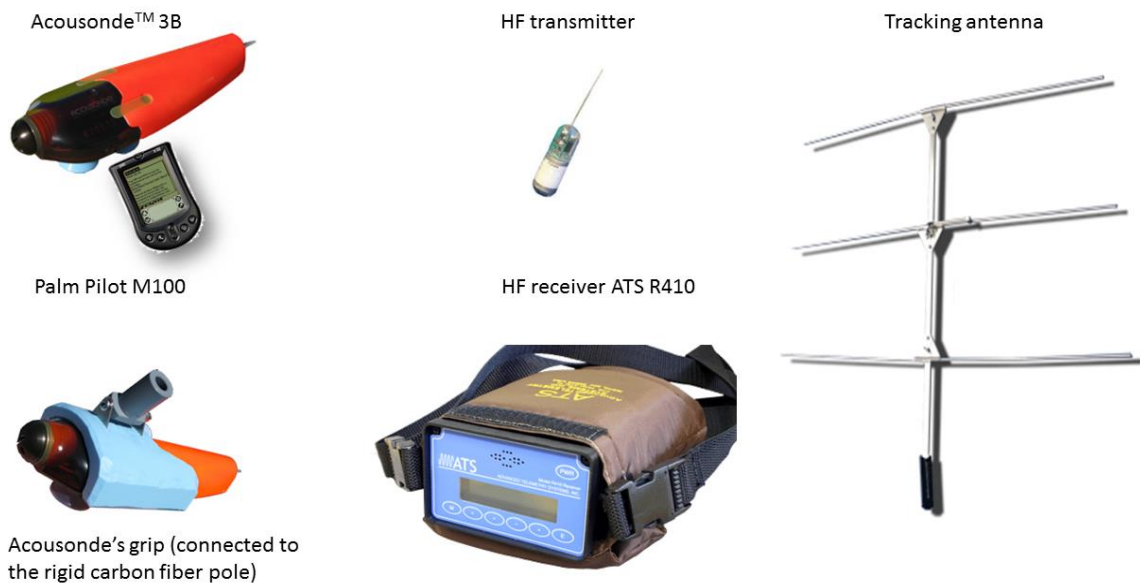


Figure 7: Acousonde™ accessories (palm, grip, HF transmitter, HF receiver) (sources: www.acousonde.com and www.astrak.com).

Deployment

The team consisted of 4 persons on board: one operator, one photographer, one note taker and one person identified to tag. Safety procedures were conducted prior to each deployment, to ensure the safety of people on board and the safety of whales. The major roles (tagging and operator) were only performed by highly experienced people possessing more than 6 years of experience on whale behaviour. This configuration allowed us to optimise all the approaches we performed and increase the chance of tagging success, while reducing the time spent with the targeted group.

To approach mother-calf pairs, a rigid boat TM 21 model (2.35 m width and 6.5 m long) equipped with a 115 CV engine was used. Daily trips were organised when weather permitted tag deployment (Beaufort scale ≤ 3 corresponding to a gentle breeze, wind speed of 12 km/h, wave height varying from 0.2-0.5 m). When a static or slow travelling mother-calf group (accompanied or not by single or more than 2 individuals) was spotted, the boat started to reduce engine speed at an 800 m distance from the group and a slow approach was then performed until the boat reached a 300 m distance from whales. The observation zone was within 200 m of the whales. Prior to tag deployment, groups were observed for 10 to 15 min and their group composition and behaviours were noted: MC for lone mother-calf, MCE for mother-calf accompanied by one escort and MCEs for mother-calf accompanied by 2 or more escorts. Different approaches were performed for each group: a drifting approach when MC pairs were static at the surface, or a parallel approach following the MC when the group was travelling slowly (following whales' speed, to a maximum of 4 km/h). Mother-calf pairs followed by escorts tend to change direction frequently therefore, the approach of such group types varied somewhat, depending on the context. However, in all instances, Acousondes were deployed on animals only when mother-calf groups were cooperative (i.e, did not exhibit aggressive or

escape behaviours in regards to the boat). The Acousonde was deployed from the boat using a 5-m rigid, handheld carbon fiber pole. The grip we used during the tagging procedure was modified to attach the Acousonde tag to the side of the whale and not on its back (Figure 8). The tag was placed on the lateral side of the whale as low as possible. This configuration allows optimized sound recordings while mother-calf pairs were resting for long periods at the surface (i.e., tag always in the water even during surface events).



Figure 8: Acousonde tag deployed on calf with a rigid handheld carbon fiber pole and acousonde tag attached to lateral side of humpback whale calf (© Cetamada).

Total time spent with tagged mother-calf groups started at the moment we aimed to deploy the tag and ended when the tag was attached to the target animal, and this time never exceeded 30 minutes to limit animal disturbance. For all our deployments, mother-calf pairs were not followed, the Acousonde tag was retrieved when the HF transmitter produced a constant beep indicating that the Acousonde was no longer attached to the animal.

Data analysis

Acoustic data from Acousonde were converted from .MT file format to .WAV using Goldwave (v5.70) and were analysed using Avisoft SASLab Pro (R. Spetch, version 5.207, Avisoft

Bioacoustics, Berlin, Germany). Spectrograms were produced using a FFT 1024-point window size, 75% overlap and Hamming window.

Video recordings

Underwater video footages

Underwater video recordings were opportunistically collected from various sources: from snorkelers (using GOPRO Hero 3 camera or professional camera, NIKON D300), from immersed GOPRO Hero 4 camera using one-meter rigid pole from a boat or from a kayak (see Figure 9). Video recordings were collected only when groups were cooperative. These videos were sampled on different geographic areas in the Indian Ocean (Reunion Island, France and Sainte-Marie Island, Madagascar) and in the Pacific Ocean (Polynesia). As videos were collected opportunistically, we mostly obtained short underwater recordings.

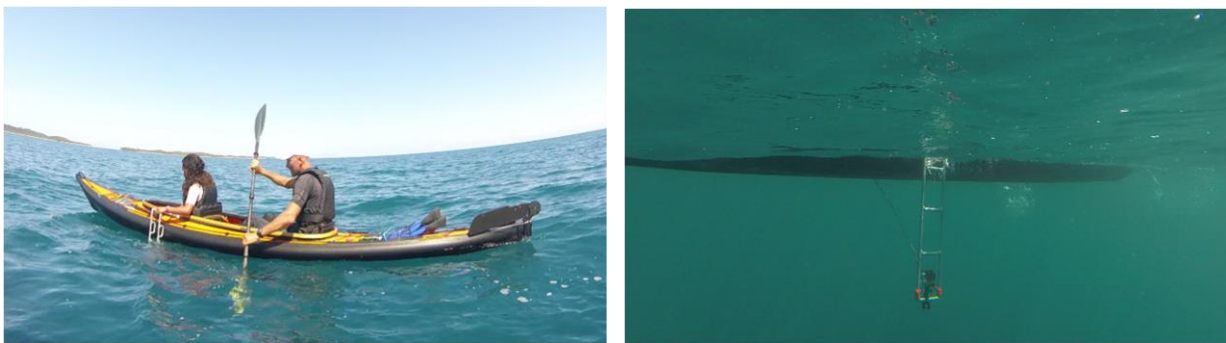


Figure 9: Underwater video recordings device from kayak (© Cetamada).

Aerial video

Aerial video recordings were collected using 3 models of drones: the phantom 3 and 4 models, as well as the Mavic PRO (all DJI models). To approach mother-calf pairs, the same rigid boat TM 21 model (2.35 m width and 6.5 m long) equipped with a 115 HP engine as during

Acousonde deployment was used. Daily trips were organised when the weather permitted drone flying (Beaufort scale ≤ 3 corresponding to gentle breeze, wind speed of 12 km/h, wave height varying from 0.2-0.5 m). At least 2 drone pilots were present on the boat. When a static or slow traveling mother-calf group (accompanied or not by a single or more than 2 escorts) was spotted, the boat started to reduce engine speed at an 800 m distance from the group, and a slow approach was performed until the boat reached the 300 m distance from the whales. All videos were obtained at 200 – 300 m distance from mother-calf groups with the engine off, with the altitude of the drone (ranging from 6 to 30 m) chosen depending on both behavioural context and environmental parameters. Prior to drone deployment, each group was observed for 10 to 15 min and its composition was noted: MC for lone mother-calf, MCE for mother-calf accompanied by one escort and MCES for mother-calf accompanied by 2 escorts or more. Drones were deployed when groups did not change their behaviour towards the boat. The use of drones reduces the impact of the boat on whales' behaviour, and thus allowed us to collect long observation sessions of mother-calf social interaction.



Figure 10: Drone deployment (DJI Phantom 3) from boat and mother-calf pair aerial photography (© Cetamada).

Data analysis

Video recordings were analysed by using Gom Player version 2.3.26.5283. This software allowed us to perform a precise temporal analysis of each video file (i.e., 1-sec step video analysis). Photography obtained by video files were analysed by using measurement tools in Inkscape version 0.92.2 and Autodesk Autocad 2014 SP1.

Sampling effort

Populations migrating in the Southwestern Indian Ocean region are described as “C-stock” by the International Whaling Commission (IWC 2008). The C-stock population is widely distributed along Africa’s west coast, Madagascar coastal areas and around Islands such as Mayotte, Mauritius, La Réunion and Seychelles (Rosenbaum *et al.* 1997; Best *et al.* 1998). Exchanges and distribution of this population among these different areas are not yet fully understood (Rosenbaum *et al.* 2009; Dulau *et al.* 2017; Salvatore Cerchio *et al.* 2016). Data were collected during austral winter corresponding to humpback whales’ annual migration from high to low latitude (July to September).

Acoustic and diving data

Acoustic data analysed in this work were collected from 2013 to 2017. In total 53 trips (337 hours and 29 minutes of sampling effort) were organised during these 5 breeding seasons. A total of 68 deployments were performed on 51 mother-calf groups including 33 MC, 15 MCE and 3 MCES groups (Table 1). Among these groups, were calves from the 3 different age classes: 3 calves from C1 class, 13 from C2 class and 35 from C3 class. Simultaneous tagging (two acoustic tags deployed at the same time on the same mother-calf pair) were performed on 10 pairs. For 67% of cases, Acousondes were deployed on the first group approached during

the tagging process. For the remaining 33% of cases where we had to change our target group, as the first group could not be approached, tagging was generally attempted on the second group approached.

Table 1: Summary of acoustic and diving data collected and analysed from 2013 to 2017 in the Sainte-Marie channel, Madagascar

Year	Tagged mothers	Tagged calves	Simultaneous tagging
2013	7	3	0
2014	3	8	0
2015	3	4	0
2016	8	7	6
2017	9	16	4
Total	30	38	10

Among the 68 deployments, 48 from 2013 to 2017 were analysed to study mother-calf vocal activity. To link the vocal activity to the diving behaviours of mother-calf pairs, and to analyse mother-calf diving patterns, we analysed 43 deployments from 2013 to 2016 for which we had both audio recordings and diving profiles.

Videos footage

We obtained 186 underwater videos from snorkelers for the period 2010- 2014, 2 drone videos in 2015 and 26 videos from immersed Go Pro from a boat or from a kayak between 2014 and 2016. These video files contained 91 mother-calf groups with a total observation time of 4 hours and 56 minutes.

Aerial footage was collected by drones during the 2017 field season. A total of 20 trips were performed and we obtained 225 video files from 65 groups for a total duration of 28 h 34 min.

CHAPTER 1a: Humpback whales mother-calf social calls



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Humpback whale (*Megaptera novaeangliae*) mother-calf social calls in the Sainte-Marie channel breeding ground, Madagascar.

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ABSTRACT

Humpback whales are born and spend their first months in an environment filled with songs and social calls. Social calls are defined as non-song vocalizations, presumably emitted from the same sound generator as songs and heard in all group compositions. Here, we present the repertoire of social calls recorded on mother-calf pairs, over two field seasons in Madagascar, using an Acousonde tag deployed either on the mother or on the calf. Sixteen deployments (on 9 calves and 7 mothers) were performed and a total of 26 social call types were extracted and classified into five categories: low, medium and high frequency sounds, amplitude modulated sounds and pulsed sounds. Among call types, 8 are part of unit songs heard during the 2 field seasons. Harmonic sounds constitute 90% of all social calls and low-frequency harmonic sounds are the most represented (50%). Calls attributed to calves vary from low to mid-frequency harmonic sounds while calls attributed to mothers were classified as low-frequency, pulsed and amplitude modulated sounds. Social calls were common in mother-calf pairs including newborns, suggesting that calves vocalize soon after birth, but their repertoire seems limited. The frequent production of low-frequency sounds suggests that females use such sounds to communicate with their calf.

INTRODUCTION

The maintenance of social bonds between parents and offspring in mammals requires various behaviours such as gazing, clinging and approaching as means of communication, which serve to reunite them in case of separation or to maintain proximity (Gubernick 1981). Various sensorial modalities are used between them. In an aquatic environment, sound is far less attenuated than light and smell; therefore acoustic signalling remains the most effective way to ensure communication. As a result, marine mammal species use vocalization in many social contexts such as mating, predator alert, offspring care, and foraging cooperation. Humpback whales (*Megaptera novaeangliae*) are a species that undertake annual migrations from high-latitude feeding grounds to low-latitude wintering, breeding and calving grounds. The breeding ground is generally considered as the place where male humpback whales produce their complex songs (Payne and McVay 1971), defined as highly structured and continuous repetitive units organized to constitute sequenced phrases and themes. Song units are produced from low (30 Hz) to high frequencies up to 24 kHz (Au *et al.* 2006). Humpback whales also produce non-song sounds, known as social sounds. These social sounds can be categorized into two different classes: the surface-generated percussive sounds performed during aggressive or learning behaviours such as breach, tail fluke or pectoral slapping, and the vocal sounds or social calls (Dunlop *et al.* 2007; Fournet, Szabo, and Mellinger 2015; Rekdahl *et al.* 2013, 2015; Silber 1986). Social calls as songs are presumably produced by the same sound generator as that used for song, located inside the respiratory system (Adam *et al.* 2013). Individuals in all group compositions produce social sounds: lone adults, singletons, multiple animals, pairs, and mother-calf pairs, whether accompanied or not by one or more than two escorts in the breeding area (Dunlop *et al.* 2008). Unlike songs, social calls have been described as variable through time, interrupted by silent periods, defined as unpredictable and as not showing the rhythmic,

consistent and continuous temporal pattern of songs and specific sequences, like sub phrases in songs (Silber 1986; Tyack 1981). A recent study has shown that depending on social context and social groups, humpback whales' social calls can be combined into bouts, and the composition of calls within bouts is variable. Social calls produced in bouts are assumed to be produced by multiple animals interacting with each other in close proximity or by a single individual (Rekdahl *et al.* 2015).

Social calls in adult humpback whales were first described as ranging from 50 Hz to over 10 kHz with fundamental frequencies below 3 kHz (Silber 1986). These social calls have been reported to be produced when whales are predominantly in groups of three or more adults, in an active surface group including both females and males (Silber 1986). However, even though their biological functions remain unclear, visual observations from surface activity suggest that social sounds could serve either as a sign of aggression among males competing for the “principal escort” status (Baker and Herman 1984; Silber 1986; Tyack 1983) or, depending on sex and group composition, among adults as a deterrent to dissuade approach from of other whales of same or opposite sex (Tyack 1983). Mother-calf pairs constitute the only stable observable social association on breeding grounds. Calves are born into a rich acoustic environment filled with songs and social calls. Despite existing acoustic studies on group social calls of humpback whales, including mother-calf pairs (Dunlop *et al.* 2007; Fournet *et al.* 2015), social calls assigned to females and their calves are still under scientific investigation. According to underwater acoustic data collection, calves have been reported to vocalize (Zoidis *et al.* 2008). It has been suggested that calves' vocal repertoire is limited and vocalizations are simple in structure, short in duration, predominantly composed of low frequencies and relatively narrow frequency bandwidth (Zoidis *et al.* 2008). Mothers' vocalizations have rarely been reported. A stable vocal unit repeated 47 times featuring only ascending frequencies with

harmonics, attributed to a female accompanied by a calf, was recorded in Arrayal Do Cabo, Brazil (Simao and Moreira 2005). The social call from this female was described to present similarity to feeding sounds produced by humpback whales on their feeding grounds.

This study aims to exhaustively describe the various social call types present on humpback whales mother-calf acoustic recordings at Sainte-Marie channel, Madagascar, during 2 successive breeding seasons. We recorded vocal activity using suction-cup acoustic tag (Acousonde 3B) deployed on females or calves, and herein describe and characterize the different main categories and sub-categories of social calls. By comparing the social call type recordings of different mother-calf pairs and their acoustic characteristics, we suggest and discuss the social call types likely produced by mothers or by calves.

METHODS

Study area

Acoustic data were collected during winters 2013 and 2014 in the Sainte-Marie Channel, North-East of Madagascar (49°50' E-50°10 E, 16°60'S-17°55' S). The maximum depth of the Sainte-Marie channel is 60 meters with an average depth between 25 to 35 meters (Trudelle *et al.* 2018). The Sainte-Marie channel is known as one of the most important breeding areas in the southwestern Indian Ocean region (Trudelle *et al.* 2018). Humpback whale birth was observed and described in 2010 (Faria *et al.* 2013).

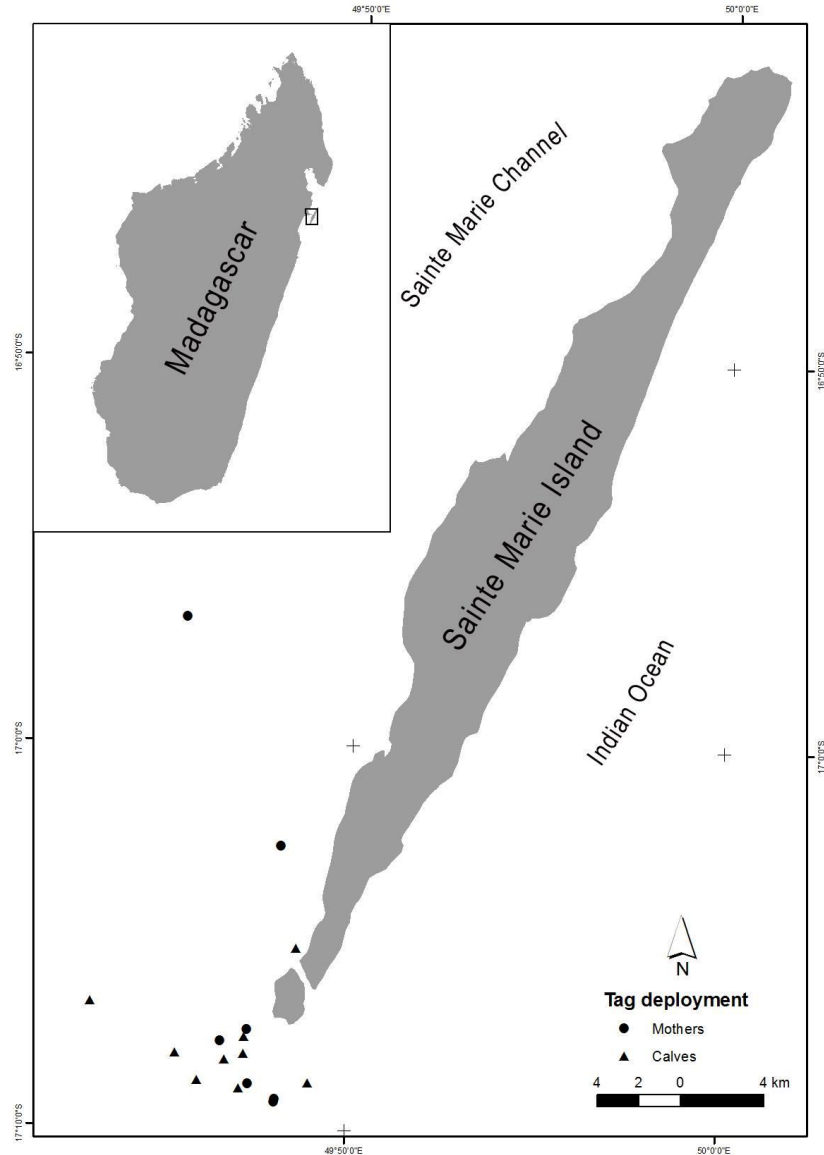


Figure 1: Map showing the survey area in the North-East coast of Madagascar (Sainte-Marie channel) including tag deployment locations on mothers and on calves [Shapefile source: FTM (Foiben'ny Taosaritanin'I Madagasikara, 2016), map generated by using ArcMap, version 10.4.1 march 2016)].

Data collection and tagging procedures

To record social calls, we used an Acousonde 3B tag (www.acousonde.com) attached to females or calves by 4 suction cups. Acoustic recordings were sampled at 24.453 Hz sample

rate, coded on 16 bits, with a +20-dB gain. The auxiliary sensors, including pressure, 3D accelerometers, 3D magnetometers and temperature, were sampled at a 10 Hz sampling rate.

All methods were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by the Fisheries Resources Ministry, Madagascar (national research permit n° 44/13 and 44/14 MPRH/DGPRH). To deploy the tag, we used a rigid boat TM 21 model, 6.5 m long and 2.3 m width. Acousonde deployment trips were organized when the Beaufort scale was ≤ 3 corresponding to gentle breeze, wind maximum speed of 12 km/h, wave height varying from 0.2-0.5 m. Even if newborn calves are observed by the end of June in the Sainte-Marie channel, we only deployed Acousonde tag from August to September during which weather corresponded to our criteria. The team consisted of 4 persons on board: one operator, one photographer, one note taker and one person identified to tag. Safety procedures were conducted prior to each deployment to ensure the safety people on board and the safety of whales. The major roles (tagging and operator) were only performed by highly experienced people possessing years of experience on whale behaviours. This configuration allowed us to optimise all the approaches we performed and increase the chance of tagging success while reducing the time spent with the targeted group.

The Acousonde tag was attached to a grip at the end of a 5-m rigid handheld carbon fiber pole. The grip we used during our tagging procedure was modified to attach the Acousonde tag to the side of the whale and not on its back. The tag was then placed on the lateral side of the whale, as low as possible, to ensure it permanently stayed underwater, even if tagged individual performed long surfacing activity with the upper back out of the water. As we did not follow the groups after tagging, we did not require VHF signal for tracking purpose, preferring continuous acoustic recordings, especially as the targeted groups often remain at the surface for long periods of time. When mother-calf accompanied or not by escort were spotted (blows were

usually seen at 1-2 km distance from boat), we performed similar approaches as touristic boats, in order to follow Madagascar's Code of Conduct for whale watching activities (inter-ministerial decree March 8th, 2000): the speed of the boat was reduced gradually at 800 m distance from spotted group. The observation area for mother-calf groups is set at a 200 m radius around them; this distance was used to observe the groups' behaviours and we noted group composition at the same time: mother-calf alone (MC) or accompanied by one escort (MCE) or more than two escorts (MCEs). Behavioural observations and photo-identification were obtained concurrently for each group and the calf's relative age was estimated by using the inclination of the dorsal fin, as the dorsal fin in humpback whale calves straightens with age (Cartwright and Sullivan 2009b). Three age classes were considered by measuring the angle of inclination of their dorsal fins: C1: newborns present some folds and scars and their skin colour tends to be light grey dorsally and white ventrally with the angle of dorsal fin less than 45° (Faria *et al.* 2013), C2: calves having furled dorsal fins more than 45° but less than 72°, and C3: older calves that have unfurled dorsal fins (> 72°). Tagging mother-calf pairs, especially groups with newborn calves requires a strategic approach. Passive and active approach methods were used depending on mother-calf behaviours (static or slow travelling; groups that travelled fast were not considered), 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) to be the best approach for mother-calf pairs was used when the groups were static or when calves were alone at the surface. This drifting approach usually starts from 100-200 m from the pair and was mostly possible for C1 and C2 calves. We tag tagged a total of 5 C1 and C2 calves and for 3/5 cases (Calf#3, Calf#7 and Calf #8, see Table 1), the group did not move away from the boat after tagging, in such cases we waited until the boat was drifted by the current to about 300 m from the group before restarting the engine to leave the group. Even if groups were stationary with newborn calves, drifting approaches were more difficult when both

the mother and her calf were at the surface. For instance, females are more aware of the presence of the motor boat and thus tend to place themselves between the boat and their calves. In such cases, if the group did not move away from the boat while we were drifting, we prioritized the tagging of females (cases of Mother#3 and Mother#7, Table 1) to minimize the disturbance of the mother-calf pair, especially when calves were placed to the far side of their mother. Similar difficulties in tagging stationary groups or when the mother-calf pairs were at the surface have been also reported by Stimpert *and colleagues* (A. Stimpert *et al.* 2012) due to the difficulty in predicting mothers' location when calves were at the sea surface, potentially requiring an active approach. The easiest achieved approaches were those performed on the 3 newborn calves. Indeed, newborns spend more time at the surface than older calves, and they also tend to approach the boat, giving us an ideal opportunity to tag them in a passive manner. Since the targeted groups were travelling slowly, the boat was placed parallel to them at the same speed and within visual range of the mother. The presence of escorts determined mother-calf pairs' behaviours during the tagging process. Almost half of tagged individuals were accompanied by escorts: 4 groups with one escort and 3 groups accompanied by more than 2 escorts (see Table 1). Escorts are males surrounding mother-calf pairs and competing for proximity to the female (Baker and Herman 1984). The presence of a single escort with the mother-calf pair was reported to not influence their behaviour (Cartwright and Sullivan 2009a). Indeed, in our study, mother-calves accompanied by single escort usually adopted static behaviour similar to lone mother-calf pairs. However, the presence of a single escort during the tagging process compelled us to adopt a different approach, especially when the single escort tended to display defensive behaviour towards the boat (going up in front of the boat or placing itself between the boat and the mother-calf pairs). In such case, we left the targeted group and aborted tagging procedure. Depending on the context, the boat was placed parallel to the calf or the mother and if the mothers placed their calves between themselves and the escort, we prioritize the tagging

of the mothers. In contrast, the presence of several escorts involved a greater energy expenditure for the mother-calf pair as they increase their traveling activity (Cartwright and Sullivan 2009a) and thus the group tends to act as an active surface group with frequent changes in direction. We tagged a total of 4 mother-calves accompanied by single escorts (Mother#3, Mother#5, Calf#3, Calf#5), 2 with two escorts (Mother#2, Calf#8) and one with 3 escorts (Mother#7) (see Table 1). Since the group was slow travelling, tagging the mother was prioritized except in the rare case (Calf#8) during which the female placed the calf on the same side as the boat to avoid the proximity of competing escorts.

Once tags were deployed, we left the groups and the Acousonde was retrieved when it was detached from the tagged subject. We then did not follow the groups, and the time spent with them did not exceed the tagging period, which was the time we were within 200 m distance (considered as starting contact) until the Acousonde was attached to the mother or calf (considered as ending contact with the group). Our tagging processes have had an average duration of 21 minutes, and never exceeding 30 minutes (i.e., our maximum duration to tag a whale).

In total, 21 mother-calf groups were tagged during 2013 and 2014 field seasons. Of these, 16 were analysed to describe mother-calf vocal repertoire, including 7 deployments on mothers and 9 on calves (Table 1). Five deployments (3 from 2013 and 2 from 2014) were not analysed due to the high level of background noise or for their short durations of attachment (less than 30 minutes). Background noise was mostly present either during the acceleration phase of the tagged individual (mostly the mother) or when the tag was placed in a higher position close to the dorsal fin and thus often out of the water, especially on calves for which surfacing activities occurred very often. For instance, two of the recordings presented short duration (< 15 min) and the tag was placed too high which not allowed us to extract any sounds. Two were sampled

at low gain amplitude level (0 dB and +10 dB), therefore no social calls were detected. The last one presented acceleration phases of the tagged individual 20 min after tagging and the recording was saturated by background noises.

We collected a total duration of 17h09min of audio recordings in 2013, and of 29h27min in 2014, thus a total of 46h36min were subsequently analysed. The average attachment duration of the tag on the target animal was 4h10min for mothers and 3h28min for calves. All recordings occurred during daylight, and only 1 case showed an overnight activity as the deployment lasted 14h30min (Group 10, Mother#7).

Table 1: Details of the tagging sampling effort: date, group ID, group composition while tagged, an estimation of the calf age, and duration of tag deployment on the animal.

Date	Group #	Tagged individual	Group type	Calves relative ages	Time of tagging	Recording duration
					(hh : mn)	(hh : mn)
05/08/2013	1	Mother#1	MC	C3	12 : 18	05:15
07/08/2013	2	Mother#2	MCEs	C3	12 : 10	04:05
16/08/2013	3	Mother#3	MCE	C1	08 : 21	01:22
08/09/2013	4	Mother#4	MC	C3	08 : 37	01:26
09/08/2013	5	Mother#5	MCE	C3	10 : 03	00:39
12/09/2013	6	Calf#1	MC	C3	09 : 44	03:14
15/09/2013	7	Calf#2	MC	C3	10 : 54	01:06
20/08/2014	8	Calf#3	MCE	C2	11 : 10	00:50
24/08/2014	9	Mother#6	MC	C3	11 : 31	02:00
26/08/2014	10	Mother#7	MCEs	C2	08 : 11	14:23
29/08/2014	11	Calf#4	MC	C3	07 : 59	00:27
08/09/2014	12	Calf#5	MCE	C3	09 : 31	03:27
09/09/2014	13	Calf#6	MC	C3	14 : 42	05:00
10/09/2014	14	Calf#7	MC	C1	13 : 52	02:15
11/09/2014	15	Calf#8	MCEs	C2	12 : 24	00:35
17/09/2014	16	Calf#9	MC	C3	12 : 30	00:28

Vocal repertoire and acoustic analysis

Audio files were converted from .MT file format to .WAV using Goldwave Software and were analyzed using Avisoft SASLab Pro (R. Spetch, version 5.207, Avisoft Bioacoustics, Berlin, Germany). Spectrograms of social calls were produced using 1024-point Fast Fourier Transform, 75% overlap and Hamming window. All social calls were labelled and only clearly audible calls, with no visible overlap, and presenting a signal-to-noise ratio greater than 10 dB were thus selected for further acoustic analysis.

A first qualitative classification was performed based on aural-visual classification of calls depending on spectrographic characteristics (Dunlop *et al.* 2007; Fournet *et al.* 2015; Rekdahl *et al.* 2015). Each social call was labelled, and for selected calls, temporal and spectral characteristics were measured. Depending on their frequency characteristics, social calls were classified into the 6 main categories previously described in Dunlop *et al.* (2007): low-frequency sounds, mid-frequency harmonic sounds, high-frequency harmonic sounds, amplitude modulated sounds, broadband noisy and complex sounds and repetitive sounds. Another main call category, the pulsed sound, used by Fournet *et al.* (2015), was used as well. Then, within each main category, we determined if calls could be classified into one of these categories or if a new call category should be created. As some social calls are also song units (Dunlop *et al.* 2007), we used 16 recordings of male songs during both seasons to detect which social units were also found in male songs.

After such qualitative classification of the social calls, acoustic parameters were measured. We measured both start and end times (s) of each social call on the oscillogram (cursor precision: 1ms) to determine the total duration of the call (Dur, s). From the averaged spectrum, we manually measured the fundamental frequency (F0, Hz), as well as the first, second and third peak frequencies (F_{max1}, F_{max2} and F_{max3}, Hz). Automatic measurements were also performed

on the average spectrum, such as peak frequency (Fmax, Hz), energy quartiles (Q, Hz) as the frequency below which 25% (Q25), 50% (Q50) and 75% (Q75) of the total energy occurs, and the frequency bandwidth within which the energy falls within 12 dB of the first peak (Bdw, Hz). When possible, we measured the frequency excursion (Fexc, Hz) as the difference between the end and start frequencies on the spectrogram. For harmonic-structure calls, Fexc (Hz) was measured on the first visible frequency band. Finally, for pulsed calls, we measured the pulse rate (PR, in Hz) using the pulse train analysis function of Avisoft SASLab Pro. These acoustic features were used to describe each main category and sub-categories of social calls, but also to confirm our aural-visual classification method. A total of 5 749 calls were labelled and 1 498 calls were measured (Figure 1). Following previous descriptions of social calls (Dunlop *et al.* 2007 et Fournet *et al.* 2015), social calls were categorized as followed: calls with frequencies below 160 Hz were categorized as low-frequency sounds (LF), the mid-frequency harmonic sounds (MF) included social calls with a peak frequency ranging from 170 to 550 Hz while high-frequency sounds included calls with a peak frequency above 700 Hz. Sounds consisting of a combination of long harmonic and amplitude modulated components with peak frequency ranging from 20 to 300 Hz were categorized as amplitude modulated sounds (AM). Finally, pulsed sounds (PS) are low-frequency sounds produced in series and at a constant rate. This main category classification was thus tested using a Discriminant Function Analysis (DFA), a classification method primarily used to predict group membership from a set of continuous variables. We also performed a cross-validation DFA, using the cross-validation leave-one-out method to assess the reliability of the DFA results. Six acoustic variables were included in this analysis: Dur, Fmax, Q25, Q50, Q75 and PR, and we used our selected 781 calls to perform such analysis. DFA has been used to classify Mysticetes social calls, especially for southern right whales (*Eubaleana australis*) (Clark 1982) and for humpback whales (Dunlop *et al.* 2007; Fournet *et al.* 2015).

Received level

We measured the received level (in dB) of a limited number of selected identified sounds in our recordings. This was done by using the root mean square (RMS, in V) function in AvisoftSASLab Pro on sounds presenting a signal to noise ratio above 10 dB and no overlap. Measurements were only performed on the most common call types and we chose the best exemplars to calculate the RL with the highest accuracy: three low-frequency sounds (*100 Hz*, *bass* and *boom*) and one amplitude modulate sound (*trill*) when tagged individual were mothers; and one mid-frequency sound (*heek*) when tagged individuals were calves. For these 5 call types, we then calculated the received level (in dB re 1 μ Pa RMS) for 10 calls.

RESULTS

Social call classification

Aural-visual analysis allowed extraction of 26 call types that were categorized into 5 main categories according to their frequency and temporal characteristics, reported in Supplementary Table 1 (Appendices Chapter 1a).

Low-frequency sounds constituted 51% of all social calls, mid-frequency 22% and high-frequency 18%, while amplitude modulated sounds constituted 6%, and pulsed sounds 3% of all vocalizations. Among all identified social call types, 8 presented similarities to unit songs recorded in 2013 and 2014 in the Sainte-Marie channel, which is consistent with results from Dunlop *et al.* 2007.

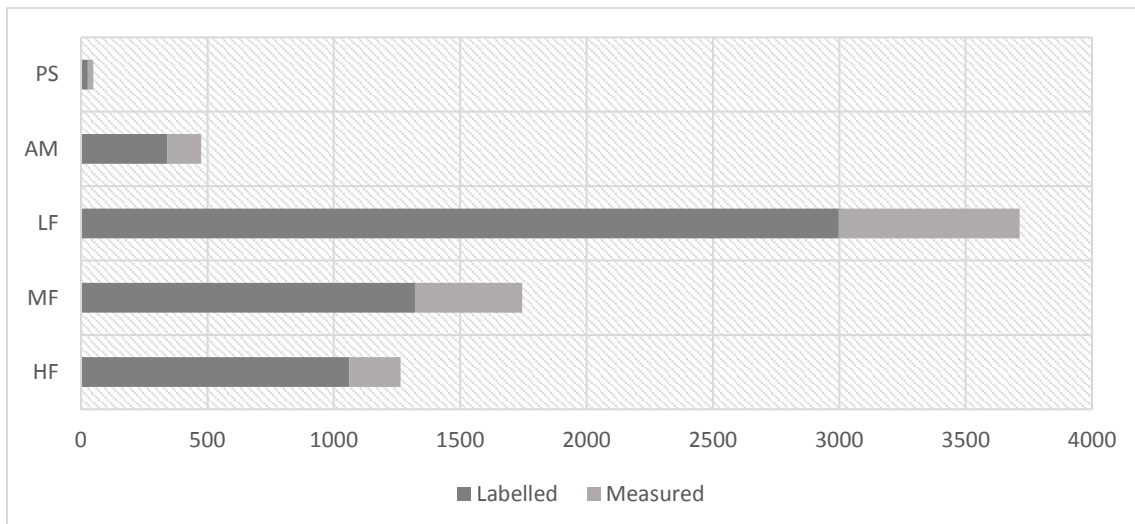


Figure 2: Distribution of labelled and measured social calls among the 5 main categories. ($n=5749$ labelled sounds and $n=1498$ measured sounds in 2013 and 2014; PS: pulsed sounds, AM: amplitude-modulated sounds, LF: low-frequency sounds, MD: mid-frequency sounds, HF: high-frequency sounds).

Low-frequency sounds (LF):

Nine call types were classified as low-frequency sounds. The *100 Hz* sound (Figure 3A) is a long, relatively flat call, frequently heard during both seasons and in 8 out of the 16 groups. *Bass* (Figure 3B), is a harmonic sound with a fundamental frequency below 40 Hz and was heard in 8/16 groups. *Boom* and *boom2* (Figure 3C and 3D) are similar harmonic sounds produced either in sequence or alone and detected in 5/16 groups. *Snort* (Figure 3E) are produced either singly or in a repetitive way and was heard in 3/16 groups (one deployment on mother and two on calves). *Gru*, *burp* and *guttural sound* (Figure 3F, 3G and 3H) are considered as rare sounds. Indeed, *gru* and *guttural sound* were heard in only 1/16 groups (2014). *Burp* was heard in 3/16 groups. *Thowp* and *wop* (Figure 3I and 3J) are brief harmonic upsweep sounds, similar in frequency characteristics but different in duration. Both are produced alone and were heard in 8/16 groups.

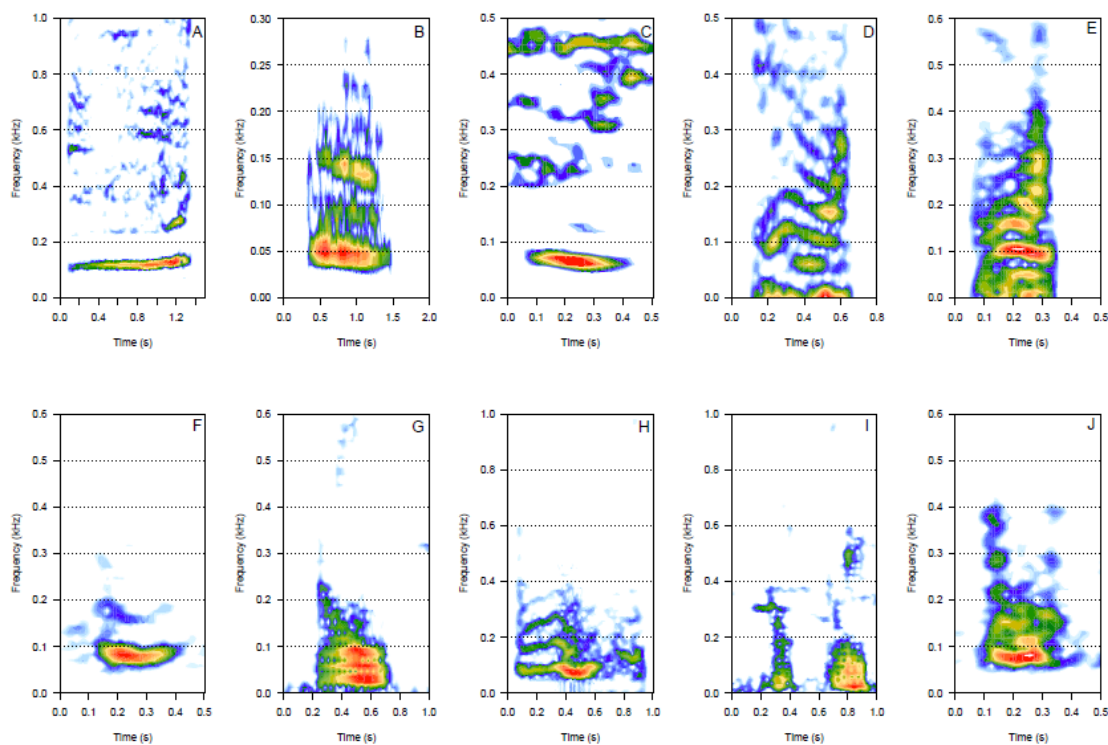


Figure 3: Spectrograms of low-frequency sounds (LF). A: 100 Hz, B: bass, C: Boom, D: Boom2, E: snort, F: gru, G: burp, H: guttural sound, I: thowp, J: wop. Most of LF sounds are harmonic-structure sounds, and produced alone, except Boom, Boom2 and snort that can be produced in sequences. Gru and guttural sound can be associated with heek (MF sound). [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap –performed using Seewave (Sueur, Aubin, and Simonis 2008)]

Mid-frequency harmonic sounds (MF):

Six call types were classified as mid frequency harmonic sounds: *groan* (Figure 4A), *downsweep* (Figure 4B), *woohoo* (Figure 4C), *trumpet call* (Figure 4D), *heek* (Figure 4E) and *whoop* (Figure 4F). *Groan* (Figure 4A) is a long harmonic call only heard in 2/16 groups. *Downsweep*, *woohoo* and *trumpet call* (Figure 4A, 4B and 4C respectively) were similar to song units heard in 2013 and 2014. *Woohoo* was heard in 8/16 groups and *whoop* in 9/16 groups, which makes it the most common mid-frequency call type found during the two seasons. *Heek* (Figure 4F) is a very short mid-frequency call produced either alone or associated with the LF sound *gru*, and it was heard in 4/16 groups (tags on 3 calves and 1 female).

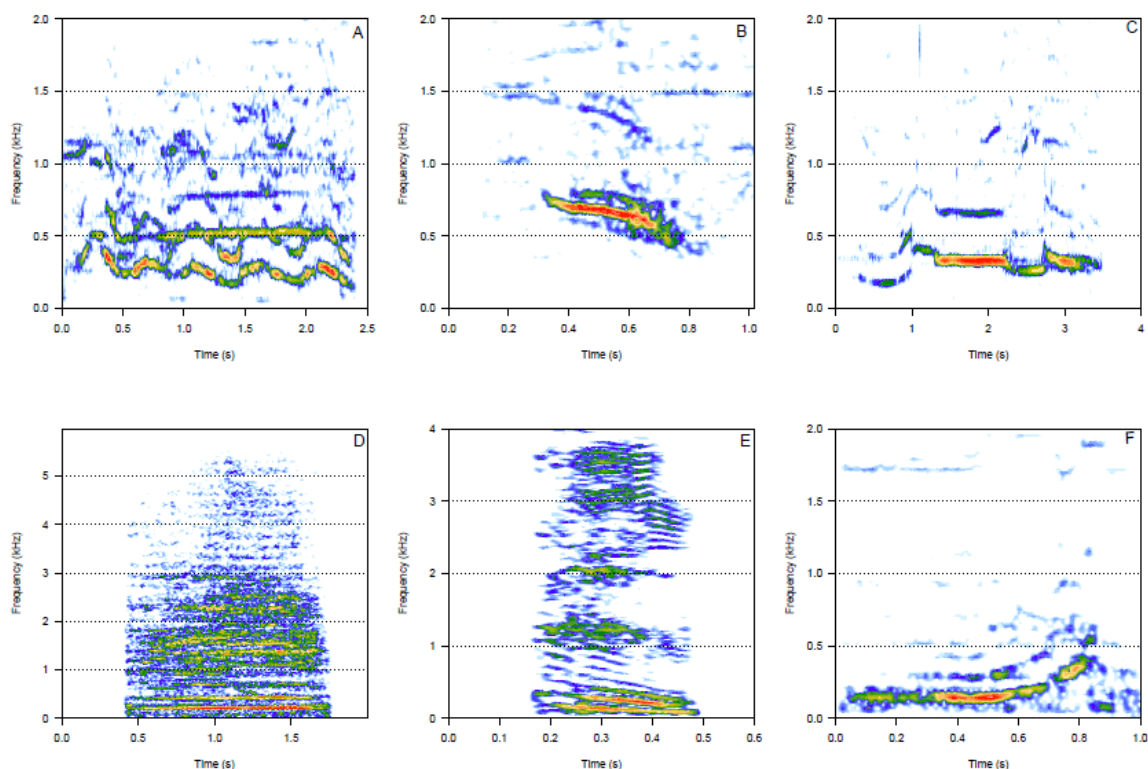


Figure 4: Spectrograms of mid-frequency sounds (MF). A: groan, B: downswEEP, C: woohoo, D: trumpet call, E: heek, F: whoop. DownswEEP, woohoo and trumpet call are similar to song units produced during the study period. Heek is produced alone or in association with the LF sound, Gru. Woohoo are the most common mid-frequency call types. [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

High-frequency harmonic sounds (HF):

Two social calls were classified in this category. The *squeak* (Figure 5A) is a very short call with frequencies above 1 kHz, and the *ascending shriek* (Figure 5B) is one of the longest social calls with the highest frequency amongst all social calls. *Ascending shriek* is also a song unit and was heard in 6/16 groups, while *squeak* is a more common call type heard in 9/16 groups.

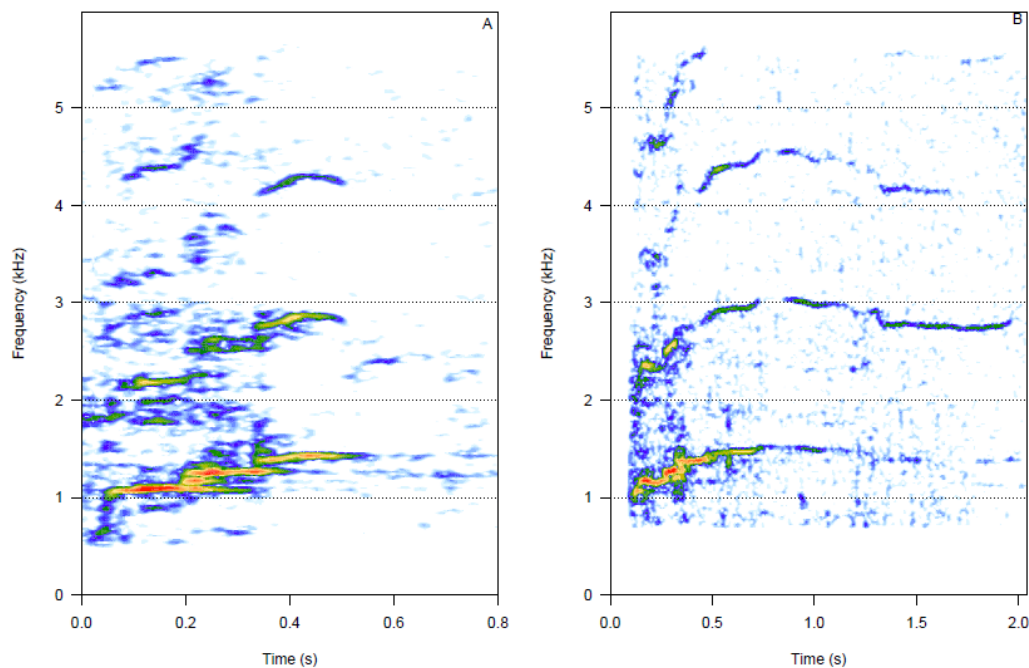


Figure 5: Spectrograms of high-frequency sounds (HF). A: squeak, B: ascending shriek. Squeak is a very short call with frequencies above 1 kHz; ascending shriek is one of the longest social call types with the highest frequencies values among all call types. [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

Amplitude modulated sounds (AM):

Four social calls were classified in this category, 3 of which were also unit songs from both seasons. *Door*, *whine*, *trill* and *bug sound* (Figure 6A, 6B, 6C and 6D respectively) are long in duration ranging from 1 to 5 seconds with a peak frequency ranging from 100 to 400 Hz, and produced in bouts of random durations. *Trill* was detected in 5/16 groups, whereas *door*, *whine* and *bug sound* were only heard in 1/16 groups.

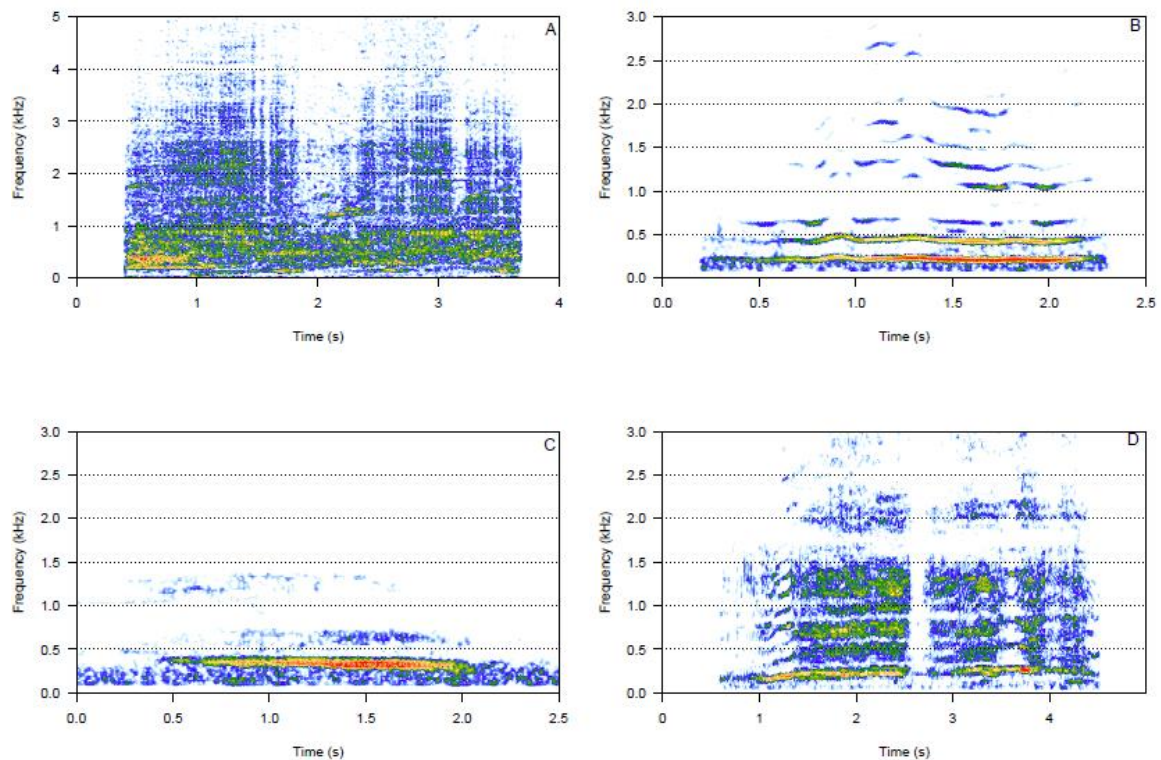


Figure 6: Spectrograms of amplitude-modulated sound (AM). A: door, B: whine, C: trill, D: bug sound. AM sounds are long calls ranging from 1 to 5 seconds with a peak frequency between 100 and 400 Hz, produced in bouts of random durations, and 3 out 4 call types are found as song units. [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

Pulsed sounds (PS):

Four social calls were classified in this category. These calls consist of a repetition of very short, low-frequency sounds: *fry* (Figure 7A), *bubble sound* (Figure 7B), *moped* (Figure 7C) and *gloop* (Figure 7D). *Fry* was found in only 2/16 groups and *gloop* in 6/16 groups. *Bubble sound* and *moped* are very rare calls, each of them being identified in only 1/16 groups. Each call type is characterized by its total duration and pulse rate, see Supplementary Table 1 (Appendices, Chapter 1a).

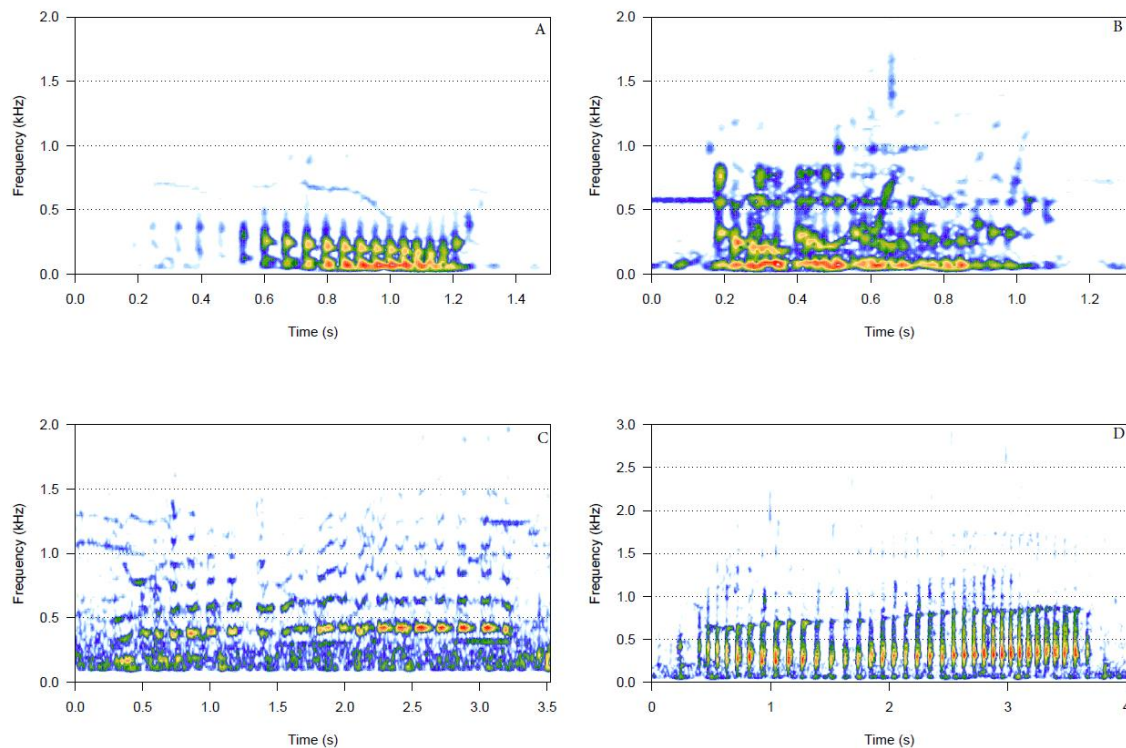


Figure 7: Spectrograms of pulsed sound (PS). A: fry, B: bubble sound, C: moped, D: gloop. PS are repetitive short and low-frequency sounds, and each call type differs by both its total duration and pulse rate. [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

Statistical analysis

Six acoustic variables were used (Dur, Fmax, Q25, Q50, Q75 and PR) to perform a DFA on 781 calls of the 5 main call categories. The DFA extracted four roots that account for 59.7%, 35%, 4.8% and 0.6% of the total variance respectively. The four spectral features (Fmax, Q25, Q50, Q75) were positively correlated to LD1, whereas Dur and PR were negatively correlated to LD2. Vocalizations were classified to the correct call type with an average rate of 88.2% and 87.7% with cross-validation, all rates being greater than random. As expected, LF, MF and HF frequency sounds can be differentiated by their spectral features (LD1). Some call categories show similar spectral features but differ in their temporal features (Dur and PR). For instance, PS and LF are both low-frequency sounds, but they differed in their duration and pulse rate

(LD2 axis). Similarly, MF and AM sounds were composed of mid-frequencies, but they differed in duration (LD2 axis).

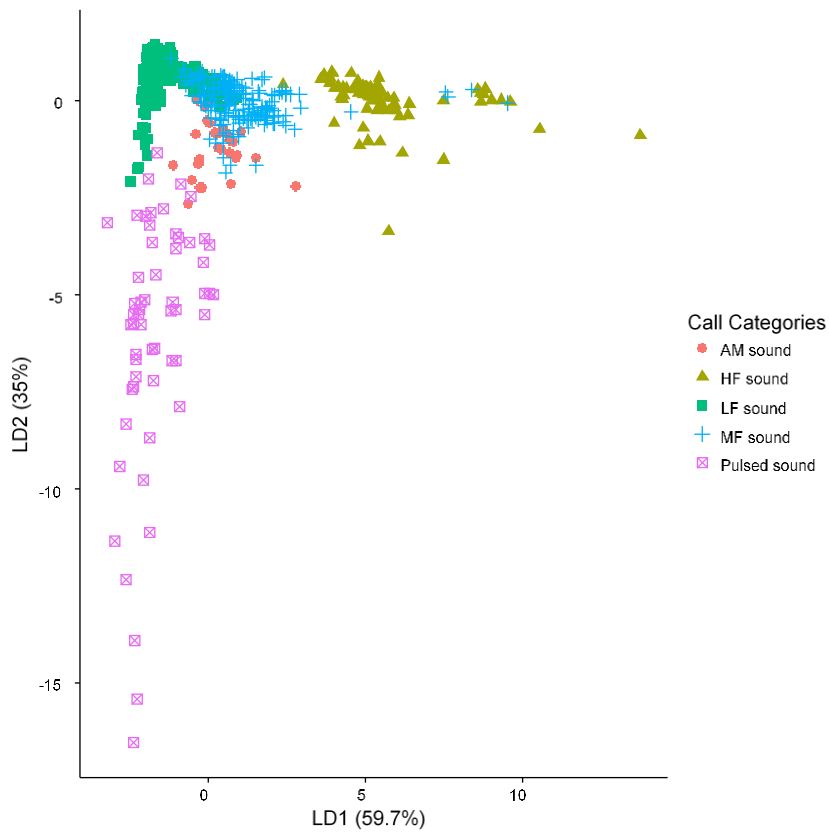


Figure 8: Scatterplot of LD1 and LD2 from the discriminant function analysis performed on the 5 main call categories (n=781 calls) using 6 acoustic variables (Dur, F_{max} , Q25, Q50, Q75 and PR). Spectral features explained most of the LD1 variations, whereas temporal features such as duration and PR explained most of the LD2 variations.

Table 1: Classification matrix of calls within the 5 main call categories.

	AM sounds	HF sounds	MF sounds	LF sounds	Pulsed sounds
AM sounds	15	0	8	7	7
HF sounds	0	93	5	0	0
MF sounds	15	1	141	23	4
LF sounds	1	0	23	392	2
Pulsed sounds	0	0	0	0	44
Total	31	94	177	422	57
% correct classification	48.39	98.94	79.66	92.89	77.19
% chance	3.96	12.04	22.7	54.03	7.30

Received level

Amplitude level of selected social calls (*100 Hz, bass, boom, trill* and *heek*, $n=10$ for each call type) ranged from 132 to 154 dB re $1\mu\text{Pa}$ RMS with an average of 141 dB re $1\mu\text{Pa}$ RMS. *Bass* present the highest amplitude level and *trill* the lowest.

Table 2: Amplitude of received level sounds for 3 low-frequency calls (*100 Hz, bass, boom*), 1 amplitude-modulated call (*trill*) and 1 mid-frequency call (*heek*).

Calls	Amplitude Received level	N (call)	Tagged individual
	(in dB re $1\mu\text{Pa}$ RMS)		
100Hz	141 ± 4	10	Mother
bass	154 ± 6	10	Mother
boom	135 ± 3	10	Mother
trill	132 ± 2	10	Mother
heek	145 ± 6	11	Calf

DISCUSSION

We successfully attached our acoustic tags to 16 mother-calf groups, 2 calves and 5 mothers in 2013 and 2 mothers and 7 calves in 2014. For all group composition (9 MC, 4 MCE and 3 MCEs of which 2 were accompanied by two escorts and 1 accompanied by 3), tagging effort varied widely and lasted from 5 min to 30 min. The presence of one or several escorts did not influence the duration spent with the target group (Comparison of tag durations between MC groups and MCE/MCES groups, Mann-Whitney test, $U=9$, $p=0.405$).

Humpback whales' vocal activity is well known for its diversity and complexity at individual group and population levels. Social calls occur in all group compositions, in both breeding and foraging ground as well as on migratory routes (Dunlop *et al.* 2007, 2008; Fournet *et al.* 2015; Rekdahl *et al.* 2013; Stimpert 2010; Zoidis *et al.* 2008). The combined results of aural-visual analysis and discriminant function analysis based on acoustic characteristics of each call allowed us to classify 26 social calls distributed into five main call categories. This is quite a large vocal repertoire, and based on their frequency characteristics, social calls recorded in mother-calf pairs in the Sainte-Marie channel present similarities to those described in east Australian humpback whale, ranging from less than 30 Hz to 2.5 kHz (Dunlop *et al.* 2007). Compared to the East-Australian catalogue, for which recordings were performed on all group compositions, the catalogue presented here contains fewer types of social calls. From the 26 social calls identified, 22 were heard in more than one group, of which the 2/2 high frequency harmonic sounds (*squeak* and *ascending shriek*), 4/6 mid-frequency harmonic sounds (*whoop*, *downsweep*, *woohoo* and *trumpet call*) and 3/4 amplitude modulated sounds (*whine*, *bug sound* and *trill*) were part of unit songs recorded in the Sainte-Marie channel during both seasons. These song units, used as social calls, were present in all group composition studied here: mother-calf pair (MC); mother-calf accompanied by one escort (MCE) and mother-calf

accompanied by two escorts (MCEs). Moreover, there are fewer song units in social call recordings of groups that included mother-calf pairs: 8 out of 26 social calls were also song units in our catalogue whereas 22 out of 34 social calls were similar to song units in Australia (Dunlop *et al.* 2007).

Six main categories were defined by Dunlop *and colleagues* (Dunlop *et al.* 2007) to classify the 34 social calls. In our study, we defined 5 main categories including 4 categories (LF, MF, HF, AM) previously described (Dunlop *et al.* 2007). The categories containing the broadband, noisy and complex sounds and repetitive sounds were not found in our recordings. The repetitive sounds, described as short, low-frequency discrete sounds were nevertheless present (*snort*, *boom*, *boom2*, and *100 Hz*), however they were grouped in the low-frequency main category. Indeed, these repetitive sounds could be produced alone or in bouts for short or long periods of time, therefore we did not classify them exclusively as repetitive sounds. Moreover, one of the main categories described by Fournet *and colleagues* (Fournet *et al.* 2015), the Pulsed Sound, was used to classify 4/26 social calls, since they presented characteristics similar (short repeated units with low fundamental frequency) to pulsed sounds described for Southeast Alaskan humpback whales. Anatomical study of the humpback whale sound generator showed that it can produce both harmonic vocalization and pulsed sounds, that have totally different acoustic features than clicks emitted by Odontocetes species (Cazau *et al.* 2013).

Madagascar social calls show similar frequency characteristics as other studied regions. Low-frequency calls are the main call category most represented. A similar ratio was found for social calls recorded in Southeast Alaskan humpback whales on their foraging grounds: 16 call types were identified and low-frequency sounds were the most represented (Fournet *et al.* 2015). Compared to the Australian catalogue (Dunlop *et al.* 2007) in which 5 low-frequency calls have been described, 10 were described in our study and 3 of them (*snort*, *thowp* and *wop*) presented

similarities with both these studied populations (Australia and Southeast Alaska). The most detected low-frequency sounds were *100 Hz*, *boom*, *bass*, *thowp* and *wop*. *Thowp* and *wop* seem to be shared between breeding and feeding grounds, and have been described to be commonly used in all group compositions (Dunlop *et al.* 2007; Stimpert 2010). *Wop* has a more cosmopolitan distribution since it was described in Australia (Dunlop *et al.* 2007), in the North Atlantic (Stimpert 2010) and in Southeast Alaska (Fournet *et al.* 2015) and seems to occur frequently in all group compositions. In our recordings, two of the most produced sounds were present both in mother-calf groups and in groups accompanied by at least one escort. However, most of them could not have been measured due to the high level of background noise (flow noise or songs) and/or overlap with other low-frequency pulsed or/and harmonic sounds. LF sounds such as *100 Hz*, *boom* and *bass* are commonly produced calls in our study area, but they have not been described on other breeding areas or feeding areas. *Bass* is a common call heard in any type of social group (MC, MCE, MCEs) and can be confused with background noises, while *100 Hz* and *boom* were produced most frequently in series, following a well-defined order (*100 Hz – boom – boom – 100 Hz*). As these short harmonic sounds arranged in sequence show lower frequencies compared to song units (ranging from 300 to 8.000 Hz), we could differentiate them when produced in sequence, even though recordings were saturated by singers. Three call types, *gru* (n=19), *guttural sound* (n=7), *burp* (n=19) were present in only one group (MC). *Gru* is a low-frequency sound that could also be produced with the *heek* sound to constitute a kind of “composite call” since the silence separating the two vocalizations is very short. *Guttural sounds* are likely to be a combination of *gru* sounds and *heek* sounds without the silence between the two call types and can explain why they present different duration and frequency characteristics.

Eleven mid-frequency sounds were described in the Australian repertoire and six in our study. *Groan* is the only social call of this category presenting similarities to the Australian catalogue and described as both a social call and a song unit. In contrast, *groan* is a rare social call in the Northeast Madagascar catalogue. *Whoop* is one of the most produced mid-harmonic sounds, and seems to be a common vocalization found in different reproduction areas (Cholewiak, Sousa-Lima, and Cerchio 2013; Rekdahl *et al.* 2013, 2015). *Whoop* and *downsweep* were part of song units, which could explain why they were heard on half of the tagged groups as we were not able to identify the vocalizing animals in our recording.

The two high frequency harmonic *ascending shriek* and *squeak* were visually similar to song units reported in the Australian catalogue (Dunlop *et al.* 2007). *Ascending shriek* was also produced on feeding grounds (Fournet *et al.* 2015). In this study, *squeak* was mostly detected in 2013 while *ascending shriek* was detected both years. In our results, 4 amplitude modulated sounds were described whereas only 3 were found in the East Australian catalogue. *Trill* was the most produced and presented similarities to the “*trill*” sound described by Dunlop *et al.* (2007). The *door* sound seems to share similarities to the “*purr*” sound described by Dunlop *et al.* (2007) and is a rare vocalization along with *whine* and *bug sounds*. Our pulsed call category is represented by four call types considered as highly rare social calls heard only in one or two groups, except for *bubble sounds* detected in 6 groups. Few pulsed calls have been measured due to overlap with other vocalizations or high level of background noise (flow or surfacing noise, as well as singing activity). *Fry* was heard in only one group but repeated many times during surface activity context.

Social call categories determined by Dunlop *and colleagues* (Dunlop *et al.* 2007) were used as a basis for our description of social call recordings only in mother-calf groups. Seven low-frequency sounds, 4 mid-frequency sounds and the 4 pulsed sounds are specific to our study

site. However, several social calls are similar between different breeding and feeding grounds suggesting that these types of social sounds are used in specific social and/or behavioural contexts. A comparative study among these different areas will allow us to better understand the production context of these vocalizations. Most of the social calls described in this study such as *100 Hz*, *boom*, *snort*, *bass*, *whoop*, *downsweep*, *woohoo*, *squeak*, *ascending shriek* and *trill* were often combined into bouts and frequently produced. The use of call bouts in humpback whales has been shown to be common and the temporal pattern of calls within bouts is generally highly variable (Rekdahl *et al.* 2015). Further investigations are still needed to better understand the temporal organization of social calls produced in bouts as they seem to exhibit some particular order in the sequence.

Vocalizations are common among wintering humpback whale groups containing mother-calf pairs (Dunlop *et al.* 2008; Zoidis *et al.* 2008). The methodology used in this study cannot confirm whether identified sounds were produced either by the mother or the calf or any nearby conspecifics. Indeed, we could not use accelerometer data (Goldbogen *et al.* 2014) to assign caller identity as a 10 Hz sampling rate was used. Received levels could not be used either to assign caller identity as most calls show low amplitude levels (> 150 dB). However, based on the 16 deployments analysed, we found that some call types are found in a majority of MC groups (more than 8/16 groups), and the similarities in their temporal pattern (in sequence or in association with other call types) and/or in their context of production (some vocalizations produced mainly during surfacing activities or some produced during quiet recording, (i.e. without any other conspecifics heard nearby) gave us cues on the potential identity of the emitter. Calves have been reported to vocalize and they can produce series of *grunts*, predominantly low-frequency sounds with relatively narrow bandwidth (Zoidis *et al.* 2008). In our recordings, we suggest that LF harmonic sounds such as *gru* and *guttural sound*, as well as

the MF sounds such as *heek* sounds could be produced by calves. These 3 call types could be produced in sequence and occurred 90% of time during surfacing activity, knowing that surfacing activities are easily detectable on recordings. As described by Zoidis and colleagues (Zoidis *et al.* 2008), calves have a limited vocal repertoire and their calls are relatively short in duration. Calves vocalizations reported here are mostly harmonic sounds, and the ability to produce composite sounds (*heek* associated with *gru*) suggests a certain degree of complexity in sound production with calls varying from low to mid-frequency calls. Further investigations are needed to confirm the development of more complex calls in calves. Social calls were audible in mother-calf pairs with newborns (C1 class), suggesting that calves can produce calls soon after birth, which in turn suggests a way to reinforce the social bond with the mother, but also to imprint the calf's voice on the mother.

Song units used as social calls were present in mother-calf groups' recordings (mostly amplitude modulated sound and mid-frequency harmonic sounds). They could have been produced either by the mother or by nearby conspecifics. Based on this, females might be able to produce song units even though they have never been shown to produce songs as males do. Low-frequency sounds such as *100 Hz*, *bass*, *boom*, *snort*, *burp*, *thowp* and *wop* can also be assigned to females since two of them, *100 Hz* and *boom*, were produced in bouts and most of the time over a long period especially when recordings were saturated by males' songs. We can suggest that in such a noisy context, this kind of "frequency partitioning" allowed the mothers to maintain a vocal contact with their newborn despite the very loud environment of singing males. Both *burp* and *snort* were heard during surface active behaviours, which could indicate they might be involved in a learning process to initiate and maintain contact with the calf, and thus reinforce the social bond. *Bass* was produced in both surface and diving context. Pulsed sounds such as *fry* and *gloop*, as well as low-frequency sounds such as *bass* and *snort* could

also be assigned to females, as they were often produced in a context of vocal interactions with *gru* sound and *heek* sound that can be assigned to calves (see supplementary Figure 1, 2, Appendices Chapter 1a). Such temporal concordance can be used as a strong argument for the use of low-frequency sounds by the female in the context of vocal interaction with her newborn. Finally, the presence of song units in this catalogue suggests that female humpback whales may have a larger vocal repertoire, whose calls usage varies according to both behavioural and social contexts. Mother-calf vocal interactions tend to differ widely among the different tagged groups (MC, MCE, MCEs) but also among the behavioural contexts (e.g. learning behaviours, surface activity...), however there is no obvious pattern exhibited by mother-calf pairs, as some pairs can be more or less quiet than others. Further investigation is still needed to confirm our hypotheses on the source of the emitter of such social calls, using both accelerometer data with high sampling rates, but also data from synchronous deployments on mother-calf pairs. Indeed, synchronous recordings might allow us to detect a single call on both tags, and difference in amplitude should give us the source identity. Similarly, when calves and mothers are spatially separated, we should be able to detect calls on a given tag and not the other, also helping to pinpoint the potential sound source.

Regarding our analysis on received levels, we found that both females and calves' vocalizations are produced at a low amplitude level as found previously (Zoidis *et al.* 2008), with received levels ranging from 132 to 145 dB re 1 μ Pa RMS compared to the estimated source level of singers of 149-169 dB re 1 μ Pa (Au *et al.* 2006) and likely to be even louder (185 dB re 1 μ Pa, from pers. obs. in Sainte-Marie channel). These received levels are consistent with a recent study performed on mother-calf pairs in Australia (136 to 141 dB re 1 μ Pa RMS, (Videsen *et al.* 2017a)). Such low-amplitude vocal production between mother-offspring is quite common in mammals, such as pinnipeds (walrus (Charrier, Aubin, and Mathevon 2010; Miller 1985)),

sheep (low-pitch bleats (Sèbe *et al.* 2010)), and cats (purring sounds (Peter, Forschungsinstitut, and Koenig 2002)). Such low amplitude level is not surprising as the communication between the mother and her calf is short to medium range, with the purpose of maintaining social contact but also to reinforce the social bond and maternal attachment with the calf.

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CHAPTER 1b: Humpback whale calves vocal repertoire



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Humpback whale calves' vocal repertoire in the Sainte-Marie channel breeding ground.

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ABSTRACT

Humpback whales use vocalizations during diverse social interactions or to organise activity such as foraging or mating. Unlike songs, which are confined to males, social calls are involved in social interactions, and have been reported to be produced by all types of individuals, adult males and females, juveniles and calves alike. Recent studies have described these social calls in different geographic areas; however, the context and biological functions of these social calls remains unknown. This study, aims to investigate the vocal repertoire of humpback whale calves during interaction with their mothers. We recorded mother-calf vocal activity during the breeding season in Madagascar by using Acousondes tags attached to mother-calf pairs (either mother or calf or both). Based on a previous description of the vocal repertoire of social sounds in the study area, we were able to identify 9 types of calls by calves, varying from low to mid-frequency, including one call presenting amplitude modulation. Two of the calves' vocalizations reported in this study were similar to calves' vocalizations described in the literature of other geographic area, and four call types appeared to be group-specific. Though humpback whale calves' vocalizations are in general relatively simple in structure, we found that calves are also able to produce combined calls, composite calls and sequenced calls. Such diversity in call production may be part of the vocal ontogeny of humpback whales, and could lead to a more stable and complex vocal repertoire at adulthood.

INTRODUCTION

In humpback whales, the term “social sounds” is used as a general expression for all sounds produced, excluding male songs (Payne 1978). Thus, social sounds include sounds generated by active surface behaviours (breach, tail or pectoral fins slapping) and social vocalizations called “social calls”. Humpback whales’ non-song vocalizations have been the subject of several studies, both in feeding or breeding grounds, as well as on migration routes (Cerchio and Dahlheim 2001; D’Vincent, Nilson, and Hanna 1985; Dunlop *et al.* 2007; Fournet *et al.* 2015; Jurasz and Jurasz 1979; Rekdahl *et al.* 2013, 2015; Silber 1986; Stimpert *et al.* 2011; Zoidis *et al.* 2008). These social calls vary from low to high-frequency calls, and also differ in general structure (*cries, grumbles, snorts, pulses, grunts*, etc.). The main difference between songs and social calls is that songs are long, continuous complex signals including different units repeated in themes, whereas social calls are short, with no temporal pattern, randomly produced, and not confined to males. In the breeding grounds and on migration routes, social calls have been recorded in all group compositions (containing males and females), including groups with calves (Dunlop *et al.* 2008; Silber 1986; Zoidis *et al.* 2008; Simao & Moreira 2005; Pack *et al.* 2005). Calves’ vocalizations from Hawaiian breeding grounds have been reported to be constituted of frequency modulated sounds, pulsed sounds and amplitude modulated sounds (Zoidis *et al.* , 2008). It has been suggested that some of these sounds are used by calves as ‘alarm’ calls to alert or call the mother. However, clear documentation on the biological significance and function of calf vocalizations is lacking.

The present study, analysed acoustic recordings collected using Acousondes tag attached to mother-calf pairs, with the main aim of describing calves’ vocalizations. Both temporal and frequency characteristics of these vocalizations were assessed and then compared to previous studies on humpback whale social calls and calves vocalizations previously described.

METHODS

Data collection

Acoustic recordings were collected in 2013, 2014, 2016 and 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). Sainte-Marie channel is a shallow channel which has a maximum depth of 60 meters and an average depth between 25 and 35 meters (Trudelle *et al.* 2018).

For sound recordings, we used Acousonde 3B (www.acousonde.com) that we attached to females and/or calves using 4 suction cups, a non-invasive attachment system. We used one Acousonde tag during the 2013 and 2014 seasons, and two Acousonde tags in 2016 and 2017 which allowed us to perform simultaneous recordings of the mother and her calf.

Tagging procedures

Acousonde tags were attached to a grip at the end of a 5-m rigid, handheld, carbon fiber pole and deployed from a rigid boat TM 21 model (6.5 m long and 2.3 m wide). Acousonde deployment trips were organized when the Beaufort scale was ≤ 3 corresponding to gentle breeze, wind a maximum speed of 12 km/h, and wave height varying from 0.2-0.5 m. Even if newborn calves are observed as early as the end of June in the Sainte-Marie channel, we only deployed Acousonde tags from August to September, as weather during these months corresponded to our criteria. The team consisted of 4 persons on board: one operator, one photographer, one note taker and one expert to tag. Safety procedures were conducted prior to each deployment to ensure the safety of people on board and the safety of whales. The major roles (tagging and operator) were only performed by highly experienced people, possessing more than 6 years of experience on whale behaviours. This configuration allowed us to optimise

all the approaches we performed and increase the chance of tagging success, while reducing the time spent with the targeted group.

When mother-calf pairs, accompanied or not by escort(s), were spotted (blows were usually seen at 1-2 km distance from boat), we performed approaches similar to tourist boats, in order to follow Madagascar's Code of Conduct for whale watching activities (inter-ministerial decree March 8th, 2000). At an 800 m distance from spotted group, the speed of the boat was gradually reduced. The observation area for mother-calf groups, is set at a 200 m radius around them. Observation of groups' behaviours took place within this distance, and we noted group composition at the same time: mother-calf alone (MC) or accompanied by one escort (MCE) or two to three escorts (MCEs). For each group, behavioural observations and photo-identification were concurrently obtained and the calf's relative age was estimated by observing the inclination of the dorsal fin, as the dorsal fin in humpback whale calves straightens with age (Cartwright and Sullivan 2009b). Three age classes were considered by measuring the angle of inclination of their dorsal fins: C1: newborns still presenting some folds and scars, and whose skin colour tends to be light grey dorsally and white ventrally, with the angle of dorsal fin less than 45° (Faria *et al.* 2013), C2: calves having dorsal fins unfurled more than 45° but less than 72°, and C3: older calves that have unfurled dorsal fins (> 72°). When groups were cooperative, tags were then placed on the lateral side of the whales, as low as possible, to ensure they remained permanently underwater, even when tagged individuals performed long surfacing activity with the upper back out of the water. As we did not follow the groups after tagging, we did not require VHF signal for tracking purpose, preferring continuous acoustic recordings, especially as mother-calf groups often surface for long periods of time.

Tagging mother-calf pairs, especially in groups with newborn calves, requires a strategic approach. Passive and active approach methods were used depending on mother-calf

behaviours (static or slow travelling; groups that travelled fast were not considered), as well as the choice of the targeted individual to tag within the group (mother or calf or both). Passive approach, drifting with the current, previously described by Stimpert *et al.* (2012) to be the best approach for mother-calf pairs, was used when the groups were static or when calves were alone at the surface. This drifting approach usually starts from 100-200 m from the pair and was mostly possible for C1 and C2 calves. Even if groups with newborn calves were stationary, drifting approaches were more difficult when both the mother and her calf were at the surface. Females are generally more aware of the presence of the motor boat and thus tend to position themselves between the boat and their calves. In such cases, if the group did not move away from the boat while we were drifting, we prioritized tagging of females, to minimize the disturbance of the mother-calf pair, especially when calves were placed to the far side of their mother. Since targeted groups were travelling slowly, the boat was placed parallel to them, at the same speed and within visual range of the mother. The presence of escorts determined mother-calf pairs' behaviour during the tagging process. The presence of a single escort with the mother-calf pair did not greatly influence their behaviour; mother-calves accompanied by single escort usually adopted static behaviour similar to lone mother-calf pairs. Depending on context, the boat was placed parallel to the calf or the mother, and if mothers placed their calves between themselves and the escort, we prioritized tagging of the mothers. In contrast, the presence of several escorts involved a greater energy expenditure for the mother-calf pair as they increase their traveling activity (Cartwright and Sullivan 2009a) and the group therefore tended to act as an active surface group with frequent changes in direction. In such cases, we prioritize tagging the mother as well.

All methods and approaches were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by the Fisheries Resources Ministry, Madagascar (National Research Permit n° 44/13, 44/14, 46/15, 26/17 MRHP/DGPRH).

Acoustic analysis

Acoustic recordings were recorded at a 24453 Hz frequency sampling rate and auxiliary sensors (pressure, 3D accelerometers, 3D magnetometer and temperature) were sampled at a 10 Hz frequency sampling rate for the first Acousonde (2013-2014 seasons) and at 400 Hz for the second Acousonde (2016-2017 seasons).

Audio files were converted from .MT file format to .WAV using Goldwave Software and were analyzed using Avisoft SASLab Pro (R. Spetch, version 5.207, Avisoft Bioacoustics, Berlin, Germany). Spectrograms of social calls were produced using 1024-point Fast Fourier Transform, 75% overlap and Hamming window. All social calls were labelled and only clearly audible calls, with no visible overlap, and presenting a signal-to-noise ratio (SNR) greater than 10 dB were selected for further acoustic analysis.

A first aural-visual qualitative classification based on spectrographic characteristics was performed (Dunlop *et al.* 2007; Fournet *et al.* 2015; Rekdahl *et al.* 2013), and temporal and spectral characteristics were measured for each selected call. The following acoustic parameters were considered: start and end time(s) of each social call on the oscillogram (cursor precision: 1ms) to determine total duration of the call (Dur, s). Automatic measurements were performed on average spectrum, peak frequency (F_{\max} , Hz), energy quartiles (Q, Hz), where frequencies below 25% (Q25), 50% (Q50) and 75% (Q75) of total energy occur, and where frequency bandwidth within which the energy occurs is situated within 12 dB from the first peak (Bdw, Hz).

When performing our analysis, we considered social calls present on mother-calf recordings from deployment in 2013-2014. We then selected and used the following sounds, suggested to be produced by calves, as a basis: *heek*, *guttural sound* and *gru*. We also considered the *amplitude modulated grunt*, the *pulsed sounds* and *frequency modulated sounds* produced by calf described in Hawaiian breeding ground (Zoidis *et al.* 2008). All these known sounds were labelled and measured. We also identified any possible new call types that could be produced by calves. Social calls were then categorized into three different categories depending on their temporal and frequential characteristics (Dunlop *et al.* 2007; Saloma *et al.* in rev). Among the 62 deployments on 35 calves and 27 mothers performed during the 4 years of data sampling (2013-2017), we obtained good-quality calves' calls from 9 deployments on 7 different mother-calf groups: 4 deployments on calves, 1 on mother and 2 simultaneous mother-calf deployments (Table 1). As social calls have been shown to be produced at very low amplitude (Chen, Adam A. Pack, *et al.* 2016; Videsen *et al.* 2017a) and that social calls can thus only be recorded by the tag if the animal is a short distance from it, or if the tag is attached onto it, the present analysis, considered that as long as social calls could be detected in the recordings, these sounds belonged to the mother-calf pair.

RESULTS

Calves vocal repertoire

A total of 51h27min of recordings were analysed and 685 calls were labelled; of these, only 382 answered our criteria (no overlap and an SNR > 10 dB) and were considered for measurements (Table 2). The number of calls identified for each studied group varied widely. The longest recording duration belonged to the deployment of group #4 (C3-class calf), a

simultaneous mother-calf tagging. When analysing both deployments from the same group, we obtained a total recording duration of 11h23mn, and 55 calls were labelled. In contrast, we obtained a total recording duration of 5h27min from group #6 (C3-class calf), in which only the calf was tagged, but it contained the greatest number of labelled vocalizations, 372 calls (Table 1).

Table 1: Details of analysed tagging: date, group number, tagged individual ID, an estimation of calf's relative age, duration of tag deployment on the animal, number of calls labelled, and number of measured calls.

Date (m-d-y)	Group #	Tagged Ind. ID	Calf age class	Duration rec. (hr-min-sec)	Labeled calls	Measured calls
09/10/2014	1	Calf 11	C2	02:15:47	72	48
08/11/2016	2	Calf 15	C2	05:38:19	122	55
08-17-2016	3	Mother 17	C3	07:19:02	19	14
08-18-2016	4	Calf 18	C1	01:07:02	55	37
Sim. tagging		Mother 18		10:14:04		
09/05/2016	5	Calf 19	C3	09:04:02	12	7
Sim. tagging		Mother 19		07:46:08		
08-28-2017	6	Calf 28	C3	05:32:11	372	209
09/01/2017	7	Calf 29	C3	02:30:47	33	12
Total				51:27:22	685	382

Aural-visual analysis allowed us to extract 9 different call types: *gru*, *slight snort*, *guttural sound*, *slight bark*, *drum*, *heek*, *wiper*, *creak* and the *amplitude modulated grunt*. These calls were classified in 3 main categories according to their temporal and spectral characteristics: low-frequency sounds (LF) for calls with $F_{\max} < 160$ Hz and mid-frequency (MF) for calls with $170 > F_{\max} < 550$ Hz and amplitude modulated sound (AM) (Table 2).

Table 2: Mean and standard deviation of acoustic variables measured for 9 calls. N is the number of measured calls and N_{groups} the number of tagged groups containing the call. LF = low-frequency sound, MF = mid-frequency sound, AM = amplitude modulate sound, ms = milliseconds and Hz = hertz

	N_{calls}	N_{groups}	Dur (ms)	Fmax (Hz)	Q25 (Hz)	Q50 (Hz)	Q75 (Hz)	Bdw (Hz)
LF								
Gru	30	5	188 ± 89	60 ± 38	68 ± 42	209 ± 356	811 ± 788	33 ± 30
Slight snort	33	6	202 ± 138	65 ± 52	78 ± 49	175 ± 184	460 ± 501	43 ± 64
Guttural sound	4	1	976 ± 610	54 ± 55	77 ± 16	486 ± 675	1137 ± 1125	17 ± 4
Slight bark	2	1	329 ± 25	148 ± 1	143 ± 13	251 ± 62	719 ± 392	23 ± 0.7
Drum	74	2	115 ± 49	156 ± 70	144 ± 54	284 ± 152	878 ± 518	77 ± 62
MF								
Heek	181	7	386 ± 214	410 ± 447	469 ± 367	1019 ± 617	1868 ± 873	37 ± 28
Wiper	34	1	232 ± 54	390 ± 270	349 ± 173	702 ± 301	1371 ± 438	54 ± 36
Creak	4	1	205 ± 123	309 ± 189	668 ± 756	1207 ± 1239	2136 ± 1277	133 ± 92
AM								
AM grunt	20	3	437 ± 378	168 ± 320	164 ± 186	535 ± 559	1203 ± 1055	30 ± 41
	382							

Low-frequency sounds (LF):

The social calls classified in this category include all vocalization with a peak frequency below 160 Hz (*gru*, *slight snort*, *guttural sound*, *slight bark* and *drum*) and short in duration except for the *guttural sound*. The most common calls were *gru* and *slight snort* (Figure 1a, 1b) present in 5/7 and 6/7 groups, respectively. These vocalizations are relatively similar, very short (Dur: 188 ± 89 ms and 202 ± 138 ms) and can be produced alone or in combination with either *heek* (MF category) or the *modulated grunt* (AM category) (see Figure 2a, 2b). The *guttural sound* (Figure 1c) was only heard in 1/7 group and appeared to be a composite call combining two calls (i.e. no silence between the calls), the *gru* and the *heek* sounds (MF calls). This call type is much longer than other LF calls (976 ± 610 ms) but shows similar peak frequency as the other LF sounds (54 ± 55 Hz). The *slight bark* (Figure 1d) is a brief harmonic upsweep call that was only heard twice in 1/7 group. The spectrogram of this call type is similar to the bark sound described by Dunlop *et al.* (2007). However, they differ in both their temporal and frequencial

characteristics. For instance, the *slight bark* is much longer than the *bark* sound (329 ± 25 ms vs 205 ± 119 ms from Dunlop *et al.* 2007), and the peak frequency is lower in the *slight bark* (148 ± 1 Hz vs 225 ± 106 from Dunlop *et al.* 2007). This call type was detected during a simultaneous mother-calf tagging and was recorded by both Acousonde tags. As in *heek* and *amplitude modulated sound*, this call type was preceded by *slight snort* to form a combined call (i.e., short silence between the calls in contrast to composite calls that do not show silence between calls). This characteristic led us to select it among calves' vocalizations. Moreover, when comparing the amplitude level of this vocalization recorded on both tags, we found that the *slight bark* had a higher amplitude on the tag placed on the calf. Since this call type was only heard twice and in 1/7 group, we considered it as a rare call type.

Finally, the *drum* (Figure 1e) was heard in 2/7 groups and showed the shortest duration (115 ± 49 ms) but the highest peak frequency (156 ± 70 ms) among the LF category. This sound is a repetitive sound, never produced alone but always in series. For each of the 2 groups in which this call type was detected, the ~ 529 ms sequence was produced twice and composed of 18 to 19 *drums*. For one group, the sequence was directly followed by a *heek* (MF category). This temporal pattern is similar to a calf call type described by Zoidis *et al.* (2008) constituted of pulsed calls followed by a slight frequency modulated sound.

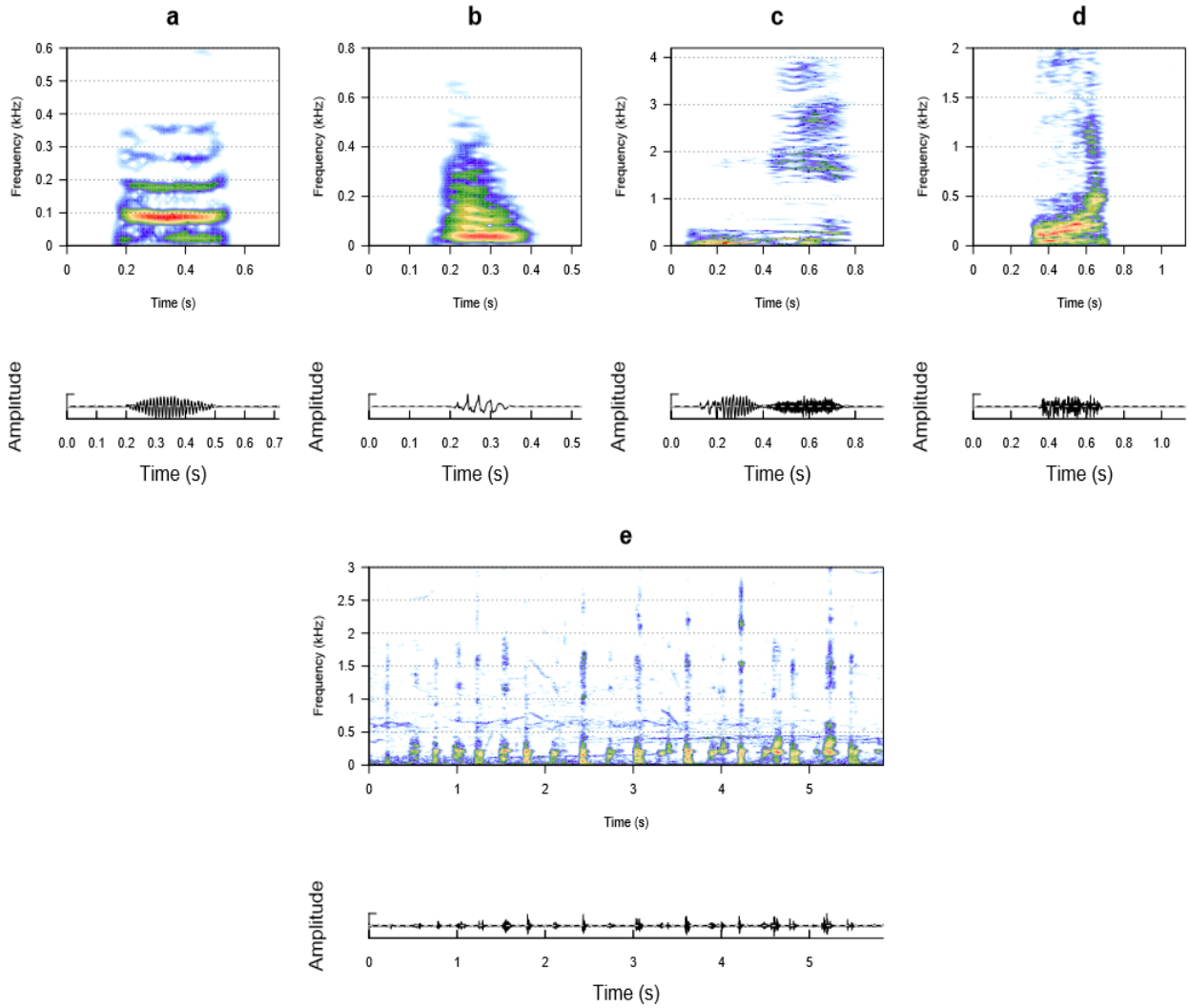


Figure 1: Spectrograms of low-frequency sounds (LF). a: gru, b: slight snort, c: guttural sound, d: slight bark, e: drum [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

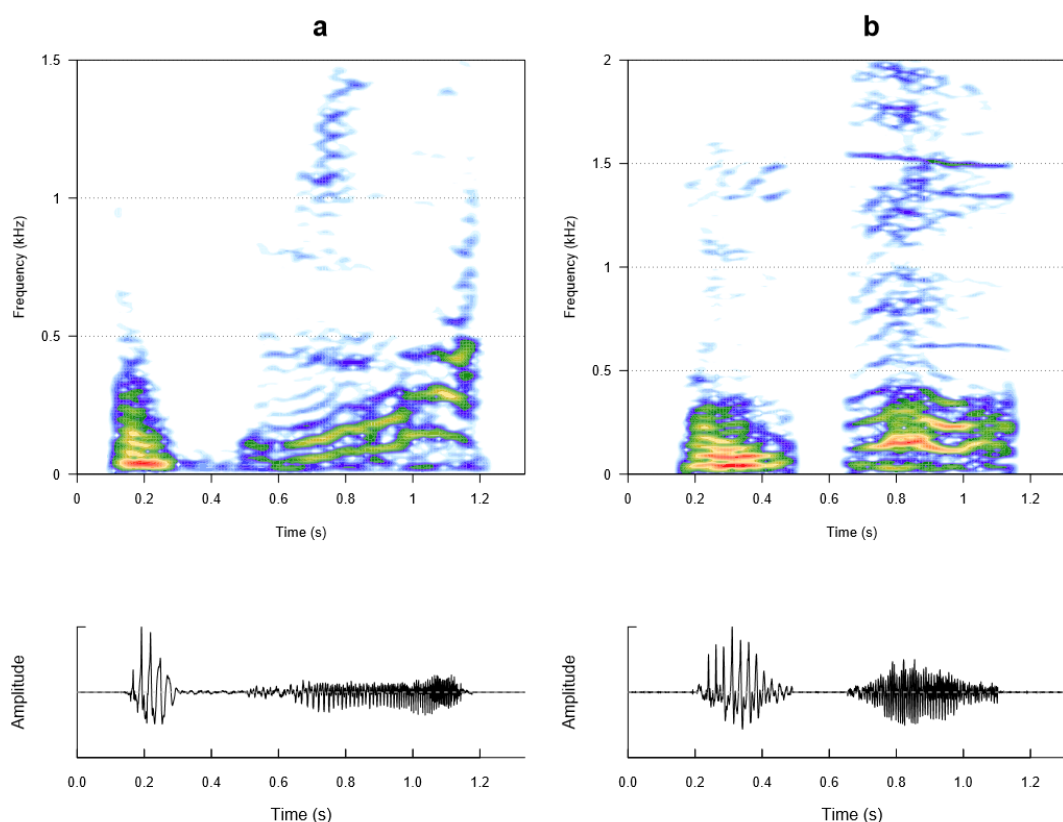


Figure 2: Spectrograms of combined social sounds. *a*: gru and heek, *b*: slight snort and heek. [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap – performed using Seewave (Sueur et al. 2008)]

Mid-frequency sounds (MF):

This category is represented by three call types: *heek*, *wiper* and *creak*. The *heek* (Figure 3a) was the most produced and measured call over all studied groups and was present in 7/7 groups. The sound is a brief harmonic sound (Dur: 386 ± 214 ms) relatively simple in structure and could be produced either alone or in combination with two LF calls (*gru* and *slight snort*) (Figure 2). This call type is also particular in that it is randomly produced in different frequency-modulation patterns: *downsweep*, *upsweep* and *modulated* (see Figure 4a, 4b and 4c).

The call type *wiper* (Figure 3b) is a short curved mid-frequency harmonic sound (Dur: 232 ± 54 ms, F_{\max} : 390 ± 270 Hz) produced in asynchronous sequence (i.e., about 4 to 5 repetitions of the same call, but in a random temporal pattern). In the mother-calf group in which this call

type was observed, the sequence was repeated 5 times throughout the entire recording. The *creak* (Figure 3c) is a composite call. The *creak* has the largest frequency bandwidth among all measured call types (133 ± 92 Hz) with the energy distributed over low to high-frequencies. Both *wiper* and *creak* were heard in 1/7 group and can thus be considered rare call types.

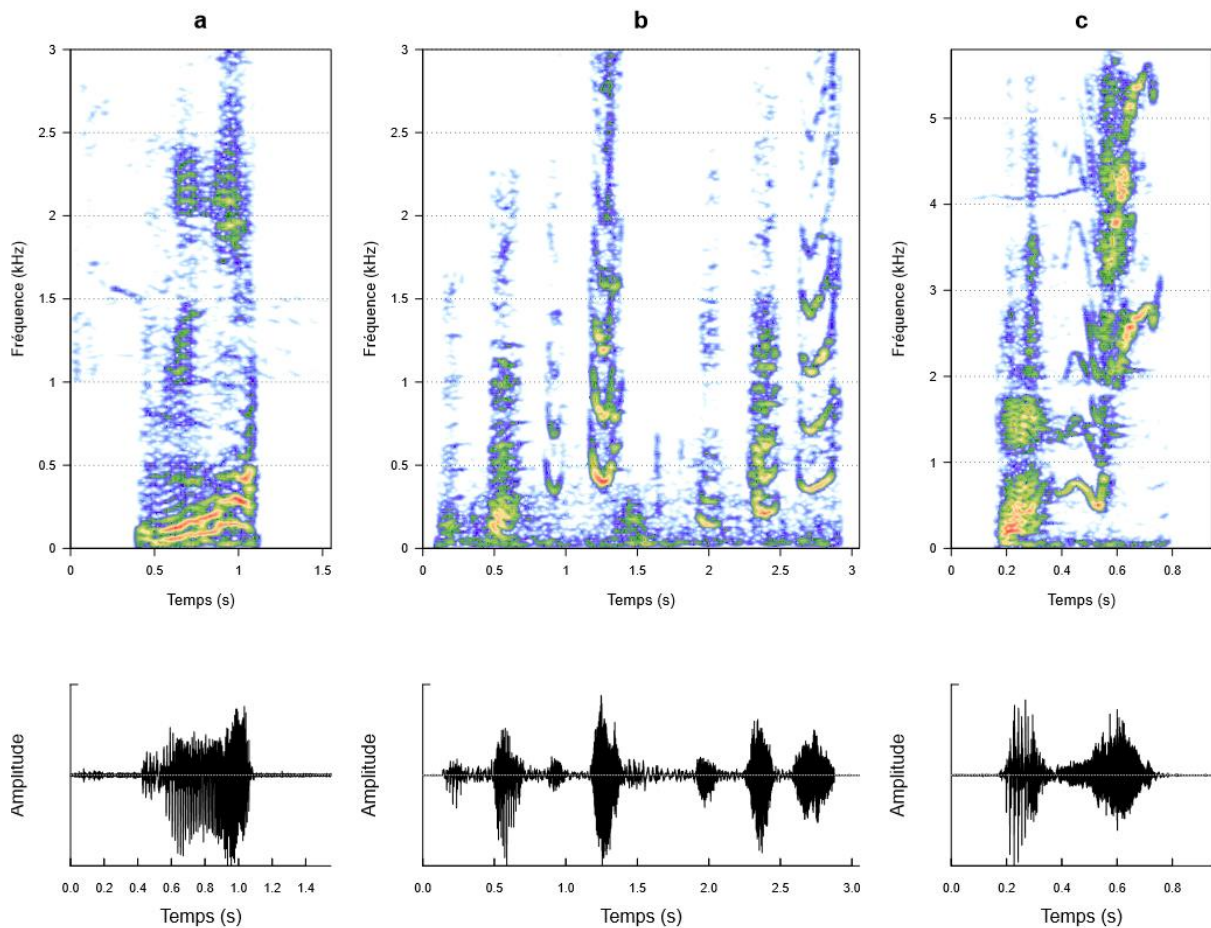


Figure 3: Spectrograms of mid-frequency sounds (MF). a: heek, b: wiper, c: creak. [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap – performed using Seewave (Sueur et al. 2008)]

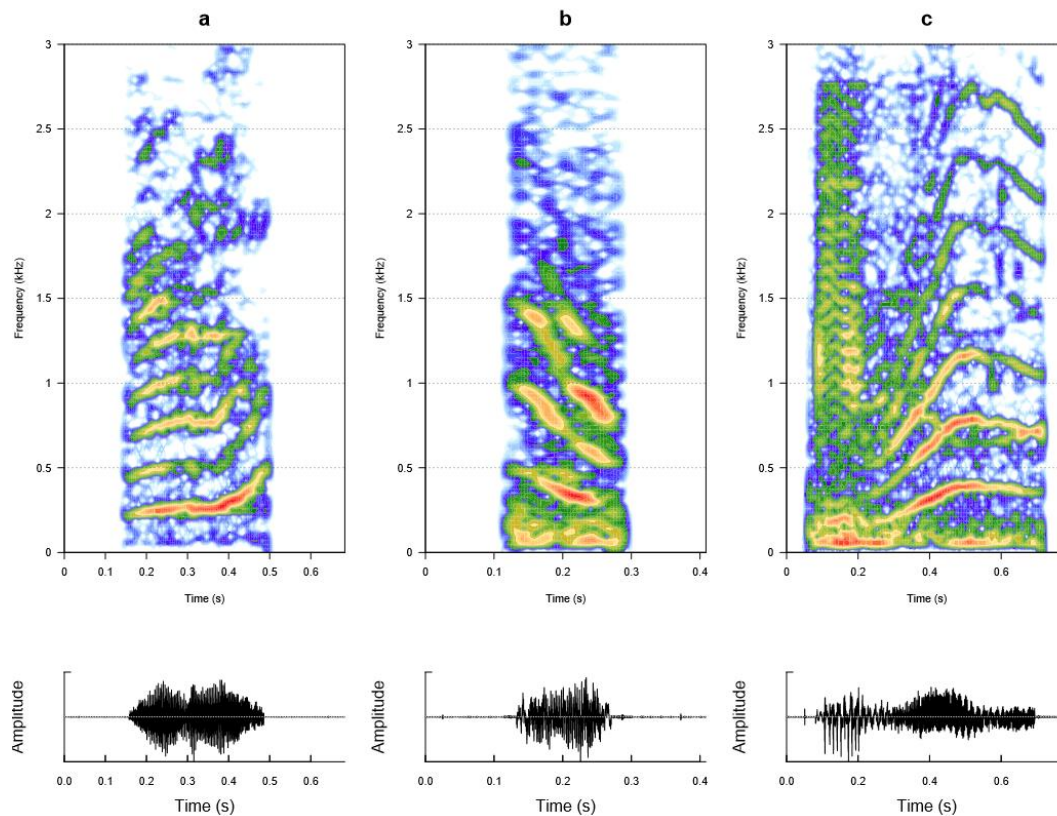


Figure 4: Spectrogram of mid-frequency sounds (AM). a: upsweep heek, b: downseep heek, c: modulated heek [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap –performed using Seewave (Sueur et al. 2008)]

Amplitude modulated sound (AM):

This category is represented by one call type only: the *amplitude modulated grunt* (Figure 5). This call type was heard in 3/7 groups and presents similarities with the amplitude modulated *grunt* described by Zoidis *et al.* (2008) of the Hawaiian population (which was one of calves' call types). These calls present similar duration (437 ± 378 ms in our study vs 469 ± 276 ms in Zoidis *et al.* 2008) and similar frequency features. Indeed, the lowest and highest frequencies for AM *grunt* from Zoidis *et al.* 2008 were 140 ± 39 and 279 ± 506 Hz respectively, and our AM *grunt* showed a peak frequency of 168 ± 320 Hz. In our recordings, this call type was usually produced alone, but in some instances it was associated with *gru* or *slight snort* (LF sounds).

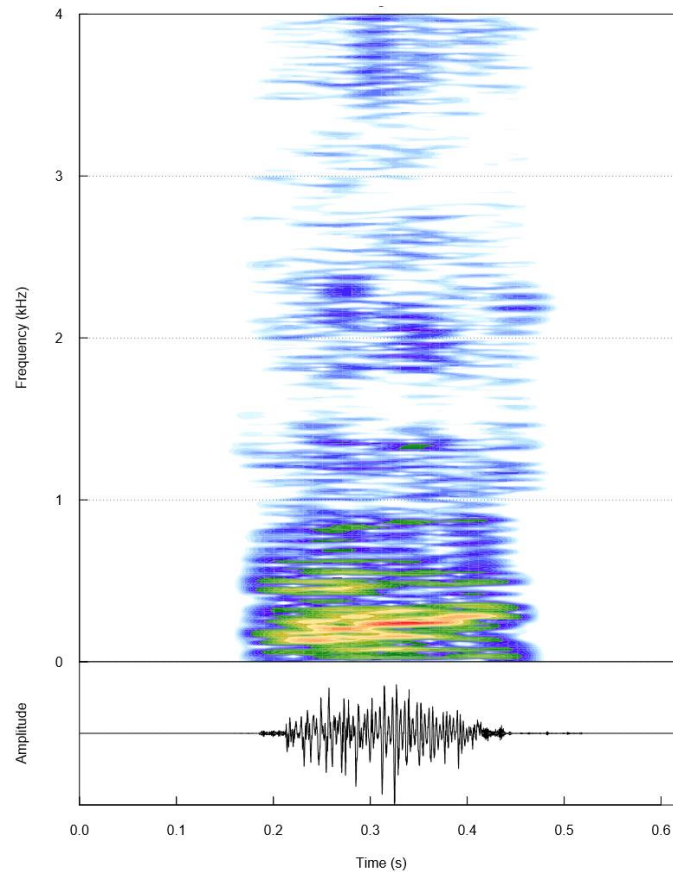


Figure 5: Spectrogram of amplitude modulated sound (AM): amplitude modulated grunt [Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap – performed using Seewave (Sueur et al. 2008)]

The 9 calls types described here appear to be randomly produced among the 7 studied mother-calf groups (Table 3). Except for group #6 which produced 6 out of the 9 call types, all other groups produced 3 to 4 different call types with the most common call types being *heek* followed by *gru* and *slight snort* associated with *heek*. Calf age does not seem to influence either the number of calls produced or the number of call types produced (Table 3).

Table 3: Number of each call types measured for each studied group. LF= low-frequency sound, MF = mid-frequency sound, AM = Amplitude modulated sound.

Group #	1	2	3	4	5	6	7	Total
Calf age class	C2	C2	C3	C1	C3	C3	C3	
LF								
Gru	13	3	1			12	1	30
Slight snort	11		3	1	3	12	3	33
Guttural sound	4							4
Slight bark					2			2
Drum						73	1	74
MF								
Heek	20	51	10	2	1	90	7	181
Wiper				34				34
Creak						4		4
AM								
AM grunt		1			1	18		20
Total	48	55	14	37	7	209	12	382
Nb of call types	4	3	3	3	4	6	4	

DISCUSSION

Humpback whales produce a large variety of social calls that range from very low to high-frequency sounds, from simple to complex structure, and from single to multiple repetition or calls in combination (Dunlop *et al.* 2007; Fournet *et al.* 2015; Rekdahl *et al.* 2013, 2015; Silber 1986; Stimpert *et al.* 2011; Zoidis *et al.* 2008). We based our analysis on calves' vocalizations described from previous studies, and we have been able to identify 2 call types in our recordings which show similarities to these vocalizations. We also described additional vocalizations and provided an exhaustive description of each call type according to their temporal and frequency characteristics. Even though we performed our analysis on a very large database, good-quality calves' vocalizations were only obtained and measured in 7 mother-calf groups. Mother-calf pairs evolve in a noisy environment full of conspecifics vocalizations and spent most of their time resting at the water surface. The possibility to extract high quality vocalizations for acoustic measurements (especially calls with no overlap, and low background noise) was

therefore very low. For instance, of the 685 labelled calls, only half could be measured, even though we optimized our chances to obtain quality recordings by attaching the tag as low as possible on the whale in order to ensure continuous recordings (i.e., tag always under water even during surface events).

Our findings are consistent with a previous study showing that humpback whale calves have a limited vocal repertoire (Zoidis *et al.* 2008). Indeed, among the 9 extracted call types, 3 (*slight bark*, *wiper* and *creek*) appeared to be specific to an individual, only 1 call type (*heek*) was present in all mother-calf groups, and 2 call types were found in 5 or 6 groups. *Heeks* represent half of the measured calves' vocalizations in our dataset, and as this call type was present in all studied groups, it suggests that humpback whale calves might have a common call type produced by calves at all ages studied. Furthermore, the vocal repertoire found in each mother-calf group is different among studied groups. Indeed, among the 7 studied groups, none produced the exact same call types, suggesting that each mother-calf pair could have developed its own vocal repertoire. The call types, *guttural sound*, *slight bark*, *wiper* and *creek* were each detected in one single group, and thus seem to be group-specific.

Calves' vocalizations from the Hawaiian breeding ground were predominantly low-frequency calls and short in duration except for the pulsed sounds. In our study, most call types were also short in duration, however, they varied from low to mid-frequency calls with a predominance of mid-frequency sounds. Zoidis *et al.* (2008) described the production of sequenced sounds by humpback whale calves. Our findings are consistent with this previous study. Indeed, the *drum* sound is a "repeated" sound only produced in sequence. The *drum* is composed of a single sound repeated at a constant rate. Unlike *drum*, the call *wiper* was also repeated to form a sequence but in a random temporal pattern. Two of our call types (*amplitude modulated grunt* and *drum*) presented structure similarities with calves' social calls described in the Hawaiian

breeding ground. However, the *drum* described in the present study was not categorized as a pulsed sound since there were clear silent intervals (ranging from 125 to 262 ms) between sound units, and such inter-call interval showed a consistent and stable pattern between the two groups in which it was observed. Thus, this suggests that *drums* are produced following a well-defined temporal pattern.

Calves vocalizations have been defined as simple in structure (Zoidis *et al.* 2008) and according to Pack *et al.* (2005), calf-attributed vocalizations were statistically similar to adults' social sounds but significantly different from male song units. Our results corroborate these findings. However, we showed here that calves could produce combined calls (composed of a LF and MF sounds separated by a silence) and composite calls (composed of a LF sound followed by MF sound without silence), which suggests a degree of complexity in their sound production. Calves vocal production is stereotyped, as we have been able to define 9 call types, however, each call type presents an important variation (see SD values on Table 1) suggesting a lack of well-controlled vocal production. The development of an adult call repertoire in most mammals seems to be primarily under genetic control and may be affected by maturation of vocal tract, coupled with motor and neuronal control (Ehret 1980; Nottebohm 1972, 1975). However, Cetaceans are able to mimic calls and to learn new vocal pattern. Captive dolphins and killer whales are well-known to mimic vocalizations (Caldwell and Caldwell 1972, Tyack 1986) and learning seems to play a major role in the development of their vocal behaviour (Caldwell & Caldwell 1979). An interesting case of social vocal learning is the ever-changing male humpback whale songs (Mercado, Herman, and Pack 2005; Noad *et al.* 2000; Payne and Payne 1985) which appear to have cultural transmission traits between populations from different areas (Garland *et al.* 2011; Garland *et al.* 2017). Humpback whale calves may need experience and practice to be able to correctly produce a call type with the simple structure of adults' non-song vocalizations. The study of the vocal ontogeny of a captive killer whale calf showed that

it learned and reproduces only the call of its mother (Bowles *et al.* 1988). Thus, the hypothesis of humpback whale calves vocal learning should not be rejected. Our sample size for each call type and for each group did not allow us to assess if vocal production varies with the age of the calf.

The number of call types analysed here show that their sound production is randomly distributed among studied groups. According to previous findings, their sound production may change depending on their social structure. It was reported by Green and Zoidis (2001) and Zoidis *et al.* (2008) that vocalizations were more common among lone mother-calf pairs than they were in those escorted by other individuals. In contrast, Silber (1986) and Dunlop *et al.* (2008) reported that vocalizations were more frequently produced on escorted pairs than on lone mother-calf pairs. As we did not follow the studied group after deployment of the acoustic tag, we could not determine if the vocal production changed with social group composition. Moreover, call rate could not be assessed, as some portions of our recordings were saturated by male songs or background noise (either due to flow noise or surfacing activities).

The function and biological significance of these vocalizations could not be investigated, however, we found that three call types (*gru*, *guttural sounds* and *heek*) were mostly produced during surfacing activities. Zoidis *et al.* 2008 has suggested the use of specific sounds, particularly repetitive *grunts* and frequency modulated signals, as “alarm” calls that the calf uses to alert and/ or to call its mother. In our recordings, calves’ vocalizations (mostly *heek*) were sometimes preceded, followed or overlapped with low-frequency sounds (*bass*, *heek*, *boom*, *100 Hz* and *wop* calls from mother-calf social calls) to constitute a sequence that could be considered a vocal exchange between the mother and her calf during surfacing activity. Among the 34 call types described by Dunlop *et al.* (2007), the short low-frequency call type “*wop*” was the most commonly heard in mother-calf groups, and authors suggested the use of

this call as a parent-offspring contact call (Dunlop *et al.* 2008). Further investigation is needed as mothers' vocalizations have been too rarely reported in the literature to enable comparison. Even though we have now acquired additional information about the characteristics of these calls, identification of the sound emitter remains a challenge. The uncertainty of the sound source complicates study of the behavioural context of a vocalization. Although the methodology used in this study cannot exactly rule out that sounds did not come from another whale that was nearby, it was however possible to extract call types showing similarities in structure, spectral characteristics and in their pattern of production among the 7-studied mother-calf groups. The simultaneous recordings performed on the same mother-calf pair allowed us to identify vocalizations present in both recordings. Unfortunately, it was difficult to find a clear vocal production on both tags as most often, when a call was detected on one recording, it could not be detected on the second, due to high background noise, overlaps with other vocalizations or just low amplitude sounds and their recordings are presumably conditioned by the place of the Acousondes tags on the whale. We were only able to detect and measure two clearly audible and present vocalizations in both tags (a *slight snort* followed by a *slight bark*). The tone difference of these calls recorded on both tags allowed us to conclude that the call was first recorded on the calf's tag and then recorded on the mother's tag. In this case, we were able to certify that the calf was the sound source. This was also confirmed by the difference in amplitude level, as the same sound showed a higher amplitude on the calf's tag compared to the mother's tag. A recent method using accelerometer data was developed, to assess if the tagged animal was the sound source of low-frequency calls (Goldbogen *et al.* 2014). In most of our recordings here analysed, the sampling frequency (400 Hz) of the 3D accelerometer was high enough to detect such low-frequency sounds ($F_{\max} < 200$ Hz). However, since we prioritized the attachment of the tag with the 3D accelerometer sampled at 400 Hz on mothers,

we could not confirm the production of low-frequency sounds by calves. Our next step is to confirm the production of LF sounds in females using accelerometer data.

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**CHAPTER 2: Determining the source of low-frequency sounds
and individual vocal signatures in social calls of humpback whale
females and calves**



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Determining the source of low-frequency sounds and individual vocal signatures in social calls of humpback whale females and calves.

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ABSTRACT

For marine mammals, acoustic signalling is critical for many biological and social functions, and vocalizations convey important information about the emitter. Being able to accurately assign vocalizations to individual whales is fundamental for understanding the biological function and role of these vocalizations. Humpback whale mother-calf pairs use social calls in a context of mother-offspring interactions as well as in social interactions with other conspecifics. Using the methodology for identifying the calling individual based on high-resolution accelerometers on acoustic tags, we investigated the source-detection of four given low-frequency calls suggested to be produced by 5 mothers. Then, we investigated the individual vocal signatures for 17 mother-calf groups by analysing the five most frequent calls (low-frequency and amplitude modulated calls) suggested to be produced by mothers and the most frequent call (a mid-frequency call) from calves' vocal repertoire. Among the 4 low-frequency calls attributed to mothers, there was only one call type for which 97% were detected on accelerometer data, which confirms that this call type is indeed produced by the mothers. Using different acoustic variables measured from the six studied call types, we found that they are individual-specific, and thus could be involved in individual identification. The investigation of individual vocal signatures in vocalisations could be an alternative method to identify the call-source, especially when accelerometer data are not applicable or efficient.

INTRODUCTION

Humpback whales are born in low latitude warm waters where courtship behaviours take place. In their breeding and calving grounds, social behaviours are very pronounced and vocalizations play an important role in their mating system. Males are well known for displaying their long, continuous complex songs which are assumed to play several different roles such as females' attractions, male-male interactions as well as in the organization of lek mating system (Herman 2016). In addition to these songs, each individual (males, females and calves) produces non-song vocalizations during social interactions (Dunlop *et al.* 2008; Silber 1986; Zoidis *et al.* 2008; Simao & Moreira 2005). Several catalogues of their social calls have been described from their feeding and breeding ground, as well as their migratory routes (Silber 1986; Dunlop *et al.* 2007; Zoidis *et al.* 2008; Rekdahl *et al.* 2013; Rekdahl *et al.* 2015; Fournet *et al.* 2015; Stimpert *et al.* 2011; Jurasz & Jurasz 1979; Cerchio & Dahlheim 2001; D'Vincent *et al.* 1985). Despite these described studies, documentation is lacking on assessing the identity of callers, which limits the knowledge on the function and the biological significance of their vocal production. Passive acoustic monitoring using two-hydrophone arrays have been used to determine humpback whale calves vocalizations based on measured time delays of recordings between the two hydrophones (Zoidis *et al.* 2008). The use of multi-sensor tags (equipped with hydrophones and sensors for orientation, depth and acceleration) attached to given individual animals has greatly increased the knowledge of cetaceans' vocal communication coupled with their underwater behaviours. However, one of the major challenges is still the determination of the source of an acoustic signal and the assignment of the emitted sound to an individual. Studies performed on Odontocete species, such as Blainville's beaked whales and Sperm whales, showed that sounds could just as easily be assigned to the tagged whale itself as to nearby conspecifics based on the angle of arrival (Oliveira *et al.* 2013; Madsen *et al.* 2013). In

studies performed on Mysticetes such as right whales, calls produced by tagged whale, as opposed to other nearby animals, were identified by a combination of high reception levels with a greater signal-to-noise ratio (SNR >10 dB), and visual observations, confirming that the calling whale was alone at the time of the detected call (Parks *et al.* 2011). For fin whales, low-frequency vocalizations (i.e., 20 Hz calls) were detected on the individual producing the call by using high-sample rate accelerometer data (Goldbogen *et al.* 2014), however all calls could still not be identified. Identifying call-emitter is particularly challenging for humpback whales, especially during the breeding and calving period during which animals evolve in an environment full of other conspecifics social vocalizations (i.e., both male songs and social sounds). Humpback whales' social calls include low-frequency calls (Dunlop *et al.* 2007; Fournet *et al.* 2015), and it has been suggested that females accompanied by their newborns produce such low-frequency signals to interact with their newborns (Saloma *et al.* in rev). The first part of this study will aim to detect the low-frequency social sounds suggested to be produced by mothers (i.e., 100 Hz, *bass*, *boom*, and *wop*). This is assessed by using high-resolution accelerometer data from Acousondes attached to females in mother-calf pairs, following the methods described by Goldbogen *et al.* (2014).

Social vocalizations contain important information about the emitter such as individual identity, sex, age-class or motivation (Halliday & Slater 1983). Recognizing and maintaining contact with specific individuals is important for social and gregarious species, especially in parent-offspring association (Halliday & Slater 1983). The individual recognition process starts by the production of individual-specific signals by the sender (i.e., the individual vocal signature), then is followed by the ability to perceive signal differences (by the receiver) and to choose the right individual (the decision) and finally to respond accordingly (Loesche, Stoddard, Higgins, & Beecher, 1991). One of the first works on cetaceans' vocal signatures was performed on

bottlenose dolphin (*Tursiops truncatus*) whistles, and authors observed great inter-individual variation and intra-individual consistency in the spectrogram contours (Caldwell & Caldwell 1965; Caldwell & Caldwell 1968). Since then, individual vocal signatures have been investigated in many marine mammals species (Nousek *et al.* 2006; Renata S. *et al.* 2002; McCowan & Reiss 1995; Sayigh *et al.* 1999; Charrier *et al.* 2003; Charrier *et al.* 2017) but none yet on baleen whale species. According to Jones *et al.* (1987), the development of individual vocal signatures occurs in species where mother and offspring are often separated or when individuals form large groups or aggregations during breeding season. For humpback whales that use vocalizations as an important part of their social behaviours, we can emit the hypothesis that social sounds are used to maintain contact among specific individuals, especially those involved in mother-calf interactions. Based on this, social sounds might contain information about individual identity. The second part of this study will thus focus on the investigation of individual vocal signatures on 5 selected call types likely produced by mothers and on 1 call type (the most represented call) from the calves' vocal repertoire.

METHODS

Study site

Acoustic recordings were collected in 2013, 2014, 2016 and 2017 during breeding season in Sainte-Marie Channel, North-East of Madagascar (49°50' E-50°10' E, 16°60'S-17°55' S). Sainte-Marie channel is a relatively shallow water, showing a maximum depth of 60 meters and an average depth between 25 and 35 meters (Trudelle *et al.* 2018).

Tagging procedures

We used two Acousonde 3B (www.acousonde.com) tags that were deployed on females and/or calves using a non-invasive suction cups attachment system. All methods were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by the Fisheries Resources Ministry, Madagascar (national research permit n° 44/13, 44/14, 46/15, 28/16, 26/17 MRHP/DGPRH). To deploy the tags, we used a rigid boat TM 21 model, 6 m long and 2.3m wide. Acousonde deployment trips were organized when the Beaufort reading was ≤ 3 corresponding to gentle breeze, a maximum wind speed of 12 km/h, wave height varying from 0.2-0.5 m. The team consisted of 4 persons on board: one operator, one photographer, one note taker and one person identified to tag. Safety procedures were conducted prior to each deployment to ensure the safety people on board and the safety of whales. The major roles (tagging and operator) were only performed by highly experienced people possessing more than 6 years of experience on whale behaviours. This configuration permitted optimization of all the approaches we performed and increased the chance of tagging success, while reducing the time spent with the targeted group.

Tags were attached to a grip at the end of a 5-m rigid handheld carbon fiber pole. The grip we used during our tagging procedure was modified to attach the Acousonde tag to the side of the whale and not on its back. The tag was then placed on the lateral side of the whale, as low as possible, to ensure it permanently stayed under water, even if the tagged individual performed long surfacing activity with the upper back out of the water. As we did not follow the groups after tagging, we did not require VHF signal for tracking purposes, preferring continuous acoustic recordings, especially as mother-calf groups often remain at the surface for long periods of time.

When mother-calf, accompanied or not by escort, were spotted (blows were usually seen at 1-2 km distance from boat), we performed approaches similar to tourist boats, in order to follow Madagascar's Code of Conduct for whale watching activities (inter-ministerial decree March 8th, 2000): the speed of the boat was gradually reduced at an 800 m distance from spotted group. The observation area for mother-calf groups is set at a 200 m radius around them; this distance was used to observe the groups' behaviours and we noted group composition at the same time: mother-calf alone (MC) or accompanied by one escort (MCE) or two or more escorts (MCEs). Behavioural observations and photo-identification were obtained concurrently for each group to avoid double sampling during the same season, and the calf's relative age was estimated by using the inclination of the dorsal fin, as the dorsal fin in humpback whale calves straightens with age (Cartwright & Sullivan 2009). Three age classes were considered by measuring the inclination of their dorsal fins: C1: newborns present some folds and scars and their skin colour tends to be light grey dorsally and white ventrally (Faria *et al.* 2013) with the angle of dorsal fin less than 45°, C2: calves having dorsal fins furled more than 45° but less than 72°, and C3: older calves that have unfurled dorsal fins (> 72°).

A total of 62 deployments, of which 10 were simultaneous tagging (two Acousonde tags were deployed on the same mother-calf pair), were performed during the 4 years of data sampling. In total, 35 calves and 27 mothers were tagged. Among the 62 deployments, 14 could not be used for various reasons: 2 deployments were sampled with a 0 dB or +10 dB gain, and neither social sounds nor songs were recorded, 6 deployments were too short (< 15 min) for further analysis, 3 deployments did not record sounds (due to technical issues with the tag) and 3 deployments presented recordings but showed a high level of background noise or male songs, thus no social calls could be extracted for further analysis. Thus, a total of 48 deployments resulting in 185 hours of recordings were used throughout this study.

Data collection and acoustic analysis

Acoustic recordings were recorded at a 24453 Hz frequency sampling rate. Two Acousondes were used, one from 2013 to 2015, and a second one for 2016 and 2017 seasons. For the first one, auxiliary sensors (pressure, 3D accelerometers, 3D magnetometer and temperature) were sampled at a 10 Hz frequency sampling rate, and for the second one, all sensors were sampled at 10 Hz except the 3D accelerometer sampled at 400 Hz.

Audio files were converted from .MT file format to .WAV using Goldwave Software and were analysed using Avisoft SASLab Pro (R. Spetch, version 5.207, Avisoft Bioacoustics, Berlin, Germany). Spectrograms of social calls were produced using 1024-point Fast Fourier Transform, 75% overlap and Hamming window. All social calls were labelled and only clearly audible calls, with no visible overlap, and presenting a signal-to-noise ratio (SNR) greater than 10 dB were selected for acoustic analysis.

A first aural-visual qualitative classification based on spectrographic characteristics was performed (Dunlop *et al.* 2007; Rekdahl *et al.* 2013; Fournet *et al.* 2015) and for each selected call, temporal and spectral characteristics were measured. The following acoustic parameters were considered: start and end times (s) of each social call on the oscillogram (cursor precision: 1ms) to determine the total duration of the call (Dur, s). Automatic measurements were performed on the average spectrum, such as fundamental frequency (F0, Hz), peak frequency (F1max, Hz), energy quartiles (Q, Hz) where the frequency below which 25% (Q25), 50% (Q50) and 75% (Q75) of the total energy occurred, and the frequency bandwidth in which the energy falls was within 12 dB of the first peak (Bdw, Hz).

We focused our analysis on 6 selected social calls from the 26 social calls described from mother-calf acoustic recordings in 2013-2014. We selected a limited number of identified social

calls according to several criteria. In addition of having SNR > 10 dB and no call overlap, calls had to be present in at least 5 groups from the 16 studied groups in 2013-2014 and calls had to be part of a suggested mother-calf vocal interactions from recordings in 2013-2014. Thus, we selected *100 Hz*, *bass*, *boom*, *wop* belonging to the low-frequency harmonic sound category and *trills* belonging to the amplitude modulated sound category for suggested mothers' vocalizations. We only selected *heek* belonging to mid-frequency harmonic sounds, which is the most common call found in calves' vocal repertoire (Saloma *et al.* in rev). Among these selected calls, *100 Hz*, *bass* and *boom* were specific to our vocal repertoire from Madagascar's breeding ground, while *trill* and *wop* are social calls also described in other breeding areas. *Wop* and *trill* was described by Dunlop *et al.* 2008 and *wop* was the predominant call in mother-calf groups, suggesting the use of this call as a mother-offspring contact call, while *trill* was also a social call and part of song units in the Australian waters.

These selected calls were then labelled and measured on recordings from 2016 and 2017 in addition to those measured from 2013 and 2014. In order to avoid double measurements of the same calls for data obtained from simultaneous mother-calf tagging, we analysed both recordings and each call present in both recordings was counted and analysed only once. In our analysis, we did not consider whether the calf or the mother was tagged. As long as one of the targeted call types was detected in the recording, it was considered as produced by either the mother or the calf. Indeed, social calls are produced at a very low amplitude level, and it is thus unlikely that targeted social calls come from an individual other than the mother-calf pair. Thus, for each studied group, *100 Hz*, *bass*, *boom*, *wop* and *trill* in the recordings were considered in a first step as mother's calls and *heek* as calf's call (Table 2).

Sound-source identification

The sound source identification was only carried out on deployments performed on mothers from mother-calf groups and for which the Acousonde tag in which the 3D accelerometer was sampled at 400 Hz. Analyses were performed on 5 deployments from 2016 season (among these, 3 were simultaneous deployments, i.e, both the mother and her calf were tagged with two different Acousonde tags and the Acousonde sampled at 400 Hz was attached to the mother) (Table 1).

Table 1: Details of the tagging analysed: date, group number, tagged individual ID, duration of tag deployment on the animal, and number of measured calls per call type.

Date (m-d-y)	Group #	Tagged Ind. ID	Duration (hr-min-sec)	Number of detectable calls			
				100 Hz	Bass	Boom	Wop
08/02/2016 Sim. Tagging*	1	Mother 13	01:13:56		44		
		Calf 13					
08/10/2016	2	Mother 14	02:06:40		61		9
08/13/2016	3	Mother 16	06:55:08	60	10	157	1
08/18/2016 Sim. Tagging*	4	Mother 18	10:14:04	14	7	81	
		Calf 18					
09/05/2016 Sim. Tagging*	5	Mother 19	07:46:08	46	15	13	
		Calf 19					
Total			28:15:56	120	137	251	10

*simultaneous tagging

Among the selected call types in this study, 4 of them (*100 Hz*, *bas*, *boom* and *wop*) have an $F_{\max} < 160$ Hz (Table 3) and were selected for source-detection using accelerometer data. To examine accelerometer signals associated with these acoustic signals, we followed the methods described by Goldbogen *et al.* 2004. Using a custom-routine in MATLAB, synchronized audio spectrogram and 3D-accelerometer spectrograms were visually compared and we could then determine if a call was produced by the tagged whale when the call could be visualized on the audio-spectrogram and at least one-axis accelerometer spectrogram.

Individual vocal signatures

Among the 48 deployments, 21 (13 on mothers and 9 on calves) from the 17 mother-calf groups contained the selected social calls that followed our criteria (Table 2). We used a total of 990 social calls for our statistical analysis. Since all measured acoustic variables showed non-normal distribution and unequal variances, Kruskal-Wallis tests were carried out to assess significant differences among individuals (either among females or among calves). For each call type, and for each measured acoustic variable, we calculated the between-individual coefficient of variation CV_b and within-individual CV_i . All variation coefficients were calculated using small sample size correction: $CV = (SD / \bar{x}) [1 + (1 / 4n)]$, where SD is standard deviation, \bar{x} is the mean of the given individual and n is the number of calls of a given individual (Sokal & Rohlf 1981). For every acoustic variable of each call type, we calculated the potential for individual coding (PIC). This was obtained with the ratio CV_b / CV_i , where CV_i is the average of all within-individual CV_{is} (Robisson *et al.* 1993). A PIC value > 1 indicates that the inter-individual variability is greater than the intra-individual variability, thus the variable is individual-specific (Robisson *et al.* 1993).

Finally, a permuted discriminant function analysis (pDFA) with a cross-validation was used to assess correct individual classification rate (Mundry & Sommer 2007). To optimize the discrimination among individuals, we used only acoustic variables presenting PIC values > 1 and significant differences among individuals (Kruskal-Wallis tests significant at $p = 0.01$). For this analysis, 5 calls per individual were chosen randomly by permutation ($n = 1000$) to build the model, and the remaining calls were classified to a given individual and defined the correct classification rate. This process was repeated 100 times. Statistical analyses were performed with R Studio version 1.1.414 © (R Development Core Team 2014). The pDFA was

performed by using R script written by Roger Mundry, based on the “lda” function, package MASS (Venables & Ripley 2002).

In this second step, if we are able to identify an individual vocal signature in a given call type, we could indirectly prove that the selected calls came from the tagged animal. If no individual signature was found, we would not be able to conclude if a call type was not individual-specific or if the selected calls potentially came from different individuals around the tagged animal.

Table 2: Details of the tagging analysed: date, group number, tagged individual ID, duration of tag deployment on the animal, and number of measured calls per call type.

Date (m-d-y)	Group #	Tagged Ind. ID	Duration (hr-min-sec)	Number of measured calls					
				100 Hz	Bass	Boom	Wop	Trill	Heek
08/05/2013	1	Mother 1	05:15:17	17		6			
09/07/2013	2	Mother 2	04:05:39	8				6	
09/12/2013	3	Mother 5	03:14:00			7		6	
08/26/2014	4	Mother 8	14:23:31		9			16	
09/08/2014	5	Mother 9	03:27:04	7					
09/10/2014	6	Mother 11	02:15:47	7	38	8			
09/10/2014	7	Calf 11	02:15:47						20
08/02/2016	8	Mother 13	01:13:56		74				
Sim. Tagging*		Calf 13	01:13:56						
08/10/2016	9	Mother 14	02:06:40		134	6	6		
08/11/2016	10	Calf 15	05:38:19						51
08/13/2016	11	Mother 16	06:55:08	6	7	6		22	
08/17/2016	12	Calf 17	02:46:08		7	38	6	177	10
Sim. Tagging*		Mother 17	07:19:02						
08/18/2016	13	Mother 18	10:14:04	18	10		47	26	
Sim. Tagging*		Calf 18	01:07:02						
09/05/2016	14	Mother 19	07:46:08		32		12	37	
Sim. Tagging*		Calf 19	09:04:02						
08/10/2017	15	Calf 20	01:20:00				6		
Sim. Tagging*		Mother 20	01:18:38						
08/28/2017	16	Calf 28	05:32:11						90
09/01/2017	17	Calf 29	02:30:47						7
Total			101:03:06	63	311	71	77	290	178

*simultaneous tagging

RESULTS

Sound source detection

From the 28h15min of combined tag recordings, 566 calls were detectable and analysed. *Booms* were the most represented calls ($n = 251$), followed by *bass* ($n = 137$) and *100 Hz* ($n = 120$). *Wops* ($n = 10$) were only detectable in two groups and thus they were the least represented.

We visually examined if at least one axis accelerometer spectrogram matched the audio spectrogram. If so, we concluded that the call was indeed produced by the tagged mother. Among the detectable call types, only *bass* were detected on both audio and accelerometer spectrograms. For instance, 97% of *bass* detectable were source-identified, thus produced by the 5 studied mothers (Figure 1). The other low-frequency calls such as *booms*, *100 Hz* and *wops* were not detectable on accelerometer spectrograms.

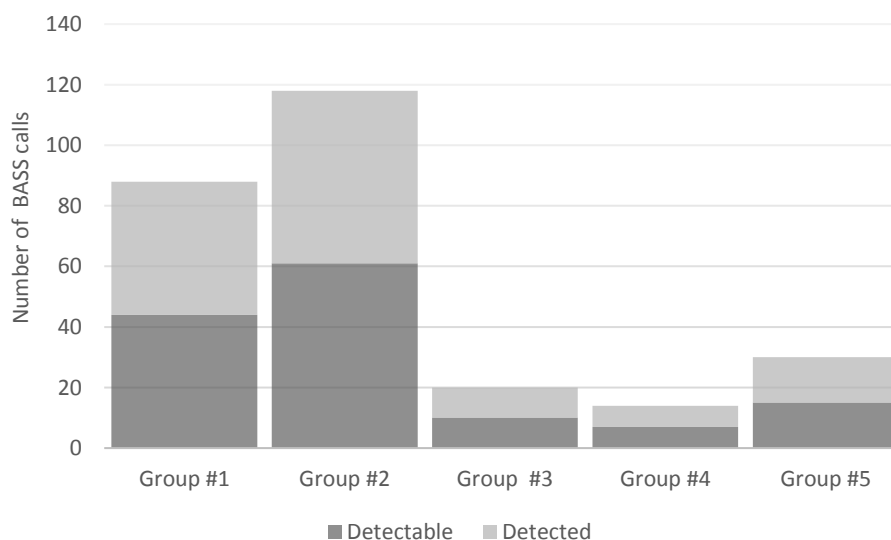


Figure 1: Number of bass detectable on audio recording, and detected on both audio and accelerometer spectrograms for each studied mother.

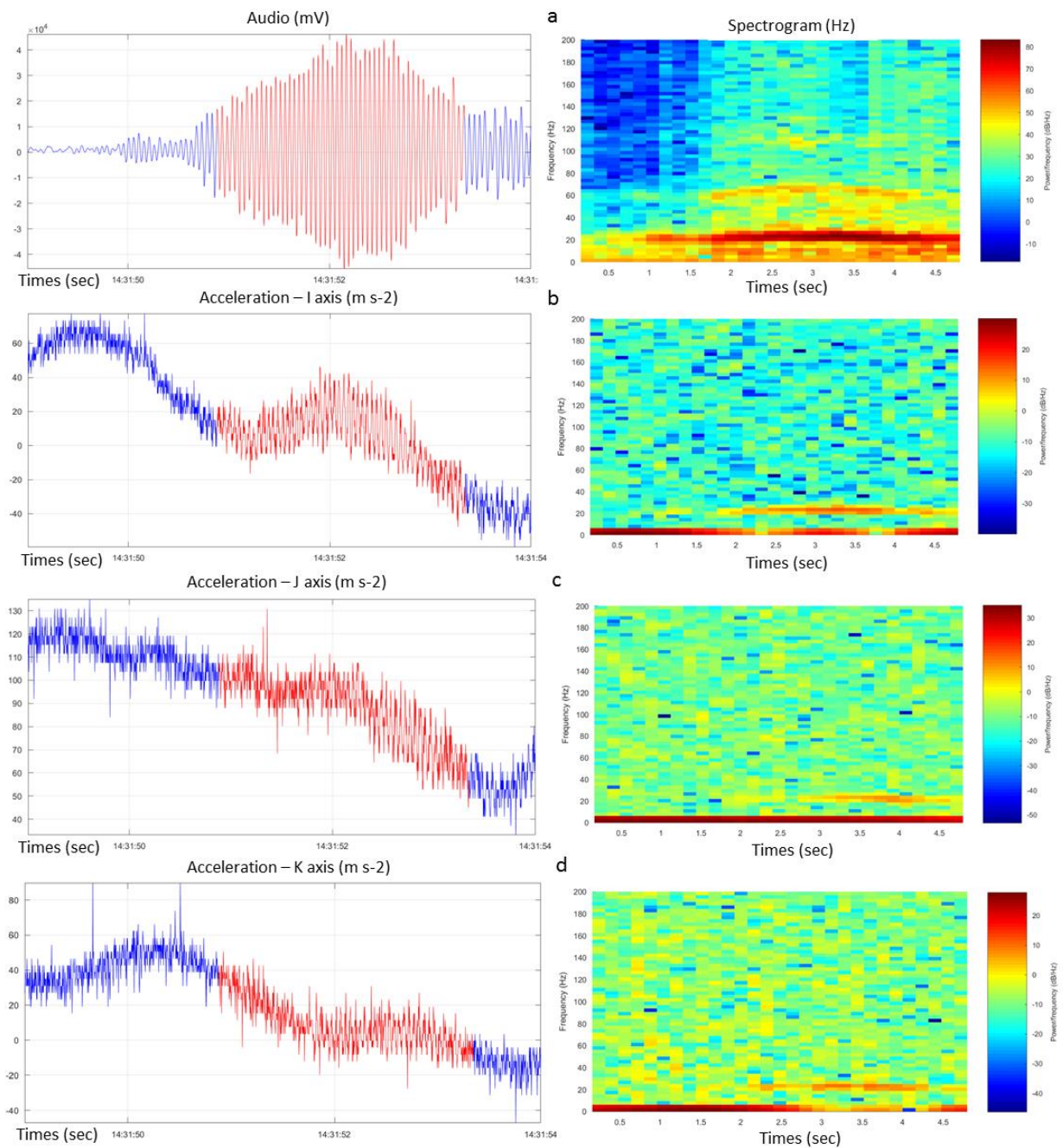


Figure 2: Bass on the audio file and tri-axial accelerometer: (a) Waveform and spectrograms of bass from the audio file (a) and from the 3D accelerometer, (b, c, d) I, J, K represent the 3 orthogonal axes (Group #1, Mother 13).

Individual vocal signatures

In the second step, we investigated the 4 selected social call types (*100 Hz*, *bass*, *boom*, *wop* and *trill*), the occurrence of an individual vocal signatures, and 812 calls were analysed. Each individual group had a minimum of 6 replicates for each call type. For the call *heek*, suggested to be produced by calves, 178 calls from 5 different groups were used for the analysis and each group had a minimum of 6 replicates of this call type.

Table 3: Mean and standard deviation of each measured acoustic variables for the 6 selected social calls (100 Hz, bass, boom, wop and trill suggested to be produced by mothers and heek suggested to be produced by calves).

Call types	N (calls)	Dur (ms)	Fmax (Hz)	Q25 (Hz)	Q50 (Hz)	Q75 (Hz)	Bdw (Hz)
<i>100 Hz</i>	63	523 ± 208	131 ± 28	172 ± 69	486 ± 316	1408 ± 851	18 ± 12
<i>Bass</i>	311	949 ± 889	40 ± 15	40 ± 17	95 ± 103	365 ± 418	7 ± 6
<i>Boom</i>	71	525 ± 244	72 ± 28	142 ± 111	667 ± 360	1833 ± 702	18 ± 8
<i>Wop</i>	77	224 ± 70	152 ± 111	165 ± 77	316 ± 225	747 ± 543	32 ± 27
<i>Trill</i>	290	980 ± 399	332 ± 47	341 ± 41	602 ± 224	1644 ± 585	8 ± 5
<i>Heek</i>	178	386 ± 214	410 ± 447	469 ± 367	1019 ± 617	1868 ± 873	37 ± 28

Intra-individual coefficients of variation (CV_i) were lower than inter-individual ones (CV_b) for all acoustic variables measured, except for the duration of *wop*, resulting in PIC values > 1 for most parameters (Table 3). The six measured variables (Dur, Fmax, Q25, Q50, Q75 and Bdw) can thus be used to differentiate the various individuals. Kruskal-Wallis tests revealed that some acoustic variables do not show a significant difference among groups: Q25 and Bdw for *100 Hz* and *heek*; Bdw for *boom* as well as Dur, Q75 and the Bdw for *wop* (Table 4) and these variables were then not included in the pDFA.

Table 4: Values of the potential for individual coding (PIC) for each acoustic variable measured on each call type (100 Hz, bass, boom, wop and trill suggested to be produced by mothers and on heek suggested to be produced by calves) as well as results of Kruskal-Wallis tests (X^2 and p-values). Values indicated in grey correspond to variables for which the KW test was not significant and/ or the PIC < 1.

	Dur (ms)	Fmax (Hz)	Q25 (Hz)	Q50 (Hz)	Q75 (Hz)	Bdw (Hz)
100 Hz						
PIC	1.41	1.47	1.23	1.36	1.58	1.21
χ^2 value	28.43	34.69	7.84	18.49	23.41	10.14
p-value	< 0.001	< 0.001	0.165	0.002	< 0.001	0.071
Bass						
PIC	1.42	1.46	1.03	1.59	1.08	1.37
χ^2 value	127.75	97.37	50.62	137.04	64.87	98.47
p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Boom						
PIC	2.32	2.61	1.82	1.1	1.33	1.13
χ^2 value	54.09	43.22	38.09	19.95	36.77	9.09
p-value	< 0.001	< 0.001	< 0.001	0.001	< 0.001	0.106
Wop						
PIC	0.89	1.5	1.29	1.59	1.06	1.05
χ^2 value	13.358	21.36	36.81	23.97	5.66	5.9
p-value	0.001	< 0.001	< 0.001	< 0.001	0.226	0.206
Trill						
PIC	1.56	1.11	1.06	1.21	1.01	1.13
χ^2 value	77.85	98	67.49	20.99	40	38.65
p-value	< 0.001	< 0.001	< 0.001	0.002	< 0.001	< 0.001
Heek						
PIC	1.26	1.13	1.42	1.48	1.07	1.03
χ^2 value	40.75	22.35	14.673	32.52	55.43	11.01
p-value	< 0.001	0.001	0.023	< 0.001	< 0.001	0.088

Except for *bass* of the mother from group 12, all correct classification rates were greater than those expected by chance. In 78.4% of the cases, correct classification rates were greater or equal to twice the rates expected by chance. The nested pDFA provides robust results with a small number of calls per individual as the analysis was repeated 100 times (Mundry & Sommer 2007). The correct classification rate does not seem to correlate directly with the number of calls (Table 5). *Booms* showed the highest averaged correct classification rate, *trill* and *100 Hz* also showed high correct classification rates. Even if *bass*, *wops* and *heeks* have lower correct

classification rates compared to other social call types, they were at least twice higher than chance.

Table 5: Values of the correct classification percentages for each call type of each group compared to the correct classification percentages expected by chance from nested pDFAs with cross-validation (% of correct classification rate obtained /% of correct classification expected by chance and (number of cross-validated calls)).

Group #	Tagged Ind. ID	100 Hz	Bass	Boom	Wop	Trill	Heek
1	Mother 1	48 / 16.67 (12)		48 / 16.67 (1)			
2	Mother 2	43 / 16.67 (3)				100 / 14.29 (1)	
3	Mother 5			23 / 16.67 (2)		56 / 14.29 (1)	
4	Mother 8		32 / 12.5 (4)			50 / 14.29 (11)	
5	Mother 9	100 / 16.67 (2)					
6	Mother 11	50 / 16.67 (2)	20 / 12.5 (33)	96 / 16.67 (3)			
7	Calf 11						46 / 20 (20)
8	Mother 13		44 / 12.5 (69)				
9	Mother 14		40 / 12.5 (129)		58 / 20 (1)		
10	Calf 15						47 / 20 (46)
11	Mother 16	46 / 16.67 (1)	21 / 12.5 (2)	87 / 16.67 (1)		33 / 14.29 (17)	
12	Mother 17		9 / 12.5 (2)	98 / 16.67 (1)	51 / 20 (1)	35 / 14.29 (172)	69 / 20 (5)
	Calf 17						
13	Mother 18	50 / 16.67 (13)	39 / 12.5 (5)	90 / 16.67 (33)	40 / 20 (42)	38 / 14.29 (21)	
	Calf 18						
14	Mother 19		18 / 12.5 (27)		46 / 20 (7)	70 / 14.29 (32)	
	Calf 19						
15	Mother 20				39 / 20 (1)		
	Calf 20						
16	Calf 28						28 / 20 (85)
17	Calf 29						70 / 20 (2)
		56.17%	27.9%	73.7%	46.8%	54.5%	52%

Within a social call type, classification rates varied among the studied groups (Table 4). For instance, the *booms* from mothers in groups 3 and 6 have correct classification rates of 23% and 96% respectively, whereas the number of cross-validated calls is much greater in group 6 (2 versus 33, respectively). In a similar manner, within an individual, the correct classification rates vary among call types: the mothers in groups 11, 12 and 13 have high rates for the *boom*, medium rates for the *100 Hz*, the *trill* and *wop*, and lower rates for *bass*. In contrast, the mother of group 2 has a low rate for the *boom* and a medium rate for the *trill*. For calves, *heeks* showed high correct classification rates, all greater than expected by chance, except for group #16, calf 28 (Table 5).

DISCUSSION

Source of low-frequency sounds

We suggested that low-frequency sounds were produced by females accompanied with their newborns. These vocalizations could be used in the context of vocal communication between the pairs as well as in a context of social communication with other conspecifics. Here we performed our analysis with the most frequent low-frequency calls detected in mother-calf recordings from Acousonde tag with high-resolution accelerometers. Among the 4 low-frequency calls selected, only *bass* was also detected on accelerometer spectrograms. Among the detectable low-frequency calls, *bass* had the longest duration (949 ± 889 ms), the lowest frequency (40 ± 15 Hz) and the highest amplitude level (154 ± 6 dB re $1\mu\text{Pa}$ RMS, Saloma *et al.* in revisions). For these studied mothers (except for group #2), all the detectable *bass* were detected, thus reliably shown to be produced by the tagged animal itself. Only 3% of *bass* could not be detected, and such proportion is consistent with previous studies (i.e the same call type recorded by the tag from one individual are not all detectable (Goldbogen *et al.* 2014; Saddler *et al.* 2017)).

The other detectable call types, *100 Hz*, *boom*, and *wop*, could not be detected on accelerometer data. Compared to *bass*, these calls showed higher peak frequencies (*100 Hz* = 131 ± 28 Hz, *boom* = 72 ± 28 Hz and *wop* = 72 ± 28 Hz; this study), were also shorter (*100 Hz*: 523 ± 208 ms, *boom*: 525 ± 244 ms and *wop*: 224 ± 70 ms respectively; this study), and were of lower amplitude (*100 Hz*: 141 ± 4 dB; *boom*: 135 ± 3 , *wop*: 141 ± 3 dB; Saloma *et al.* in revisions). The short duration and the low amplitude of these calls could explain why they could have not been detected on accelerometer data, due to the noise induced by body movements. One of the most complicating factors in detecting low-frequency signals in humpback whales is the variation of the source

level of generated sounds (Au *et al.* 2006; Chen *et al.* 2016). Indeed, these non-source identified sounds were produced at 20 to 15 dB lower than *bass*. Such low amplitude could also have explained why they could not be detected with accelerometer data, since they were likely covered by the background noise from the whale's movements. Although accelerometers sampled at high-resolution permitted confirmation caller ID, this method is limited by tag sensor capacity and resolution (Goldbogen *et al.* 2014) and calls from a source with a constant relative orientation would generate similar acceleration signals on the three axes of the accelerometers (Saddler *et al.* 2017). The detection is also dependent on the tag's placement on the whale during the duration of deployment. From our field experiences, the tag can slide along the animal's body changing its location during recordings. Thus, depending on body location, sound-induced vibration of the whale tissues can fluctuate, especially for low-amplitude calls that do not generate enough vibration. According to Saddler *et al.* (2017), the tag also vibrates differently depending on the direction of the sound source, and the author also suggests that vocalization from nearby conspecifics are also capable of registering accelerometer signals in the tagged whales' recording. Based on these findings, further investigations are needed to improve the identification of the source of these low-frequency calls.

Individual vocal signatures

Our results represent the first attempt on investigating individual vocal signatures in a Mysticetes species. Using different acoustic variables measured on different social call types, we found that the six studied call types are individual-specific, and thus could be involved in individual identification. Indeed, in nearly 80% of cases, correct classification rates obtained for all studied groups are either greater or equal to twice the rates expected by chance. These findings support our hypothesis that the studied call types are indeed produced by an individual in the targeted group, namely the mother for *bass*, *boom*, *trill* and *100 Hz*, or the calf for *heek*

in each studied mother-calf group. For instance, if the selected social call types were not produced by the mothers or the calves but from another conspecific at close proximity (i.e. escorts or another mother-calf groups), we would have obtained much lower correct classification rates, lower still than those expected by chance. Another explanation would have been that all selected calls came from another conspecific, and not the tagged animal, which is quite unlikely in our opinion. The occurrence of individual signature in these social call types might be an alternative method of identifying the sound source when other methods are not conclusive.

The acoustic variables that most contributed to distinguishing individuals are related to spectral features such as F_{\max} , and Q50, but also to temporal cues such as duration. Our study also shows that individual stereotypy varies among call types produced by mothers. Indeed, *booms* showed the highest classification rates, followed by *trills* and *100 Hz* whereas *bass* and *wops* had lower values, though still at least twice greater than chance. These findings suggest that depending on their biological functions, certain call types might exhibit higher individuality levels than others. In other words, *booms* as well as *trills* and *100 Hz* are more likely to be involved in individual identification processes than *bass* and *wops*. In a previous study, we found that mothers produced *bass* and *wops* mostly during surface activities with their calf. In contrast, *trills* were produced during shallow dives (around 10 m), and, *booms* and *100 Hz* were produced during deeper dives (20 m on average) (Saloma *et al.* in revision). So, call types produced during diving activities might have the biological function of maintaining contact with the calf when visual contacts might not be reliable due to the distance between the mother and her calf and/or to visibility of the water. Thus, the need for an individual identification might be important when mother-calf pairs are accompanied by conspecifics (either escorts during the breeding season, or by congeners during migration routes or on feeding grounds). When the mother and

her calf keep a visual contact at the surface, calls produced during their interactions might not need be individual-specific, as the biological functions of these surface calls are to reinforce the mother-calf social bonds and thus does not involve individual identification. The occurrence of individual vocal signatures in social sounds could be used as a tool for the long-term monitoring of individuals on their breeding ground. Photo-identification is usually used to match individuals over breeding seasons, but the use of vocal-identification could also be used as a confirmation or validation process when acoustic data is available. Further investigation on other social call types produced in social contexts other than mother-calf interactions to assess whether other call types also show individual vocal signatures is thus needed.

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CHAPTER 3: Vocal and diving activity in mother-calf humpback whales



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Vocal and diving activities of mother-calf humpback whales during the breeding season.

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ABSTRACT

For humpback whale species, the mother-calf pair is the only stable social unit. As in all mammal species, the social bond between the mother and her calf is very strong, and is at least partially maintained by an exchange of vocalisations. Using acoustic tags, we recorded mother-calf vocal interactions as well as their diving activities. From the vocal repertoire of social calls, we investigated the behavioural context of 5 calls suggested to be produced by mothers (*100 Hz*, *bass*, *boom*, *trill* and *wop*), and 1 call type (*heek*) suggested to be produced by calves. This allowed us to determine if these calls are emitted in a particular circumstance (surface or bottom activity, descending or ascending phase of the dive). Having the opportunity to tag calves of 3 different age-classes (C1: calves with dorsal fins angle $< 45^\circ$ C2: calves with dorsal fins angle $> 45^\circ$ but less than 72° , and C3:calves with unfurled dorsal fins with an angle $>72^\circ$), we also studied the development of their diving behaviour. Here, we showed that *heeks* are mainly produced during surface activities. Calls attributed to the mothers: *bass*, *wops* and *trills* are produced as well during surface activities, whereas *booms* and *100 Hz* sounds were produced during diving activities and mostly during the ascending phases. From 21 deployments on calves, we extracted diving profiles for two newborns C1, six C2 calves and thirteen C3 calves. On the 12 dive metrics measured, only maximal and mean dive durations and bottom time were significantly different between age classes, with newborns (C1) being mostly different from older calves (C3). Finally, simultaneous deployments on mothers and calves in 2016 revealed highly synchronised dives, with females leading most of the diving pattern.

INTRODUCTION

In marine environment, different sensory modalities can be used for social interactions between individuals, groups and population; among these, vocal signalling remains the most effective for close and long distance communication (Morton 1977). For marine mammals and particularly for cetaceans, vocal signals are used for many communal activities including vital activities. For instance, humpback whales which undertake annual migration between high latitude feeding grounds and low latitude breeding grounds, are well known to use vocalizations as an important part of their behaviours in both areas, as well as in the migration routes (Dunlop *et al.* 2008; Herman 2016; Rekdahl *et al.* 2015). One of the best studied acoustic communication are humpback whale males' songs, which are an asynchronous complex chorusing, highly structured and heard throughout the winter grounds, along the migration routes (Winn & Winn 1978; Clapham & Mattila 1990; Noad & Cato 2007; Smith *et al.* 2008) and in the feeding grounds, mainly in late spring and late autumn (Mattila *et al.* 1987; Clark & Clapham 2004; A. K. Stimpert *et al.* 2012; Vu *et al.* 2012). These songs appear to play role in females' attraction for mating purposes (Clapham *et al.* 1992; Herman 2016) and in male-male interactions whether for dominance or cooperation (Darling and Berube 2001; Darling *et al.* 2006; Herman 2016). In addition to male songs, humpback whales (males, females and calves) produce non-song vocalizations known as social calls (Dunlop *et al.* 2008; Silber 1986; Zoidis *et al.* 2008). Such as songs, social calls are also present in the breeding and feeding areas, as well as in the migratory routes (Dunlop *et al.* 2007; Fournet *et al.* 2015; Rekdahl *et al.* 2015; Silber 1986; Zoidis *et al.* 2008). Unlike songs, social calls are isolated simple or unstructured vocal sounds (Dunlop *et al.* 2007; Fournet *et al.* 2015) that could be produced alone or in bouts (Rekdahl *et al.* 2015). Frequency and temporal characteristics of humpback whales social calls of Australian migrating population, North Atlantic population and Southeast Alaskan

population have been recently described (Dunlop *et al.* 2007; Fournet *et al.* 2015; Stimpert *et al.* 2011). These studies allowed us to assess if social calls from these different areas show similar structures, and thus suggests some inter-population similarities on social calls among populations. Investigations on humpback whale social calls have increased these last years, and efforts are now focused on the understanding of the behavioural context of their vocal production. In most studies, the behavioural context of whales' vocal production was determined by initially observing their natural interactions among conspecifics. Vocalisations were thus assigned to surfacing behaviour according to an observer. For instance, it was described that humpback whales in a large competitive group produce acoustic threats concurrently and the overall production of these agonistic sounds were positively correlated with the size of the competitive group (Silber 1986). Playback experiments performed on southern right whales (*Eubalaena australis*) have shown an approach response to conspecific vocalizations broadcast by an underwater speaker but no approaching behaviour while humpback whales' songs or sounds were being broadcast (Clark and Clark 1980). Clark (1982) provided the evidence of the use of a frequency modulated upsweep between 0.5-1.5 sec duration and 50-200 Hz maximum frequency by single individuals or swimming groups that join other single or groups of individuals producing such contact calls in southern right whales. More recent studies on humpback whales sound source level have been performed to determine the social context of sound emission with regard to the acoustic properties of each social sounds. The source level is an important parameter determining active space communication on an individual or group scale. For instance, lone humpback whales are more likely to use intense vocalizations for long-distance communication with other- whales in the area, while whales within a group may use low-amplitude signals when communicating with each other (Dunlop *et al.* 2013). In Hawaiian waters, the measurements of song received level to a tag attached on humpback whale calf allowed to estimate the distance of the singer from the pair (Chen, Pack,

et al. 2016). The development of multi-sensor tags attached to animals has opened new avenues for in situ observations and research, and it has allowed researchers to investigate their behaviour in their natural environment. For marine mammals, it is now possible to record their vocal behaviours as well as their movements and diving behaviour at the same time, giving thus unprecedented information on the behavioural context of their vocal production. Recent studies using such suction-cup acoustic tags have shown vocal activity among foraging humpback whales with the production of “paired bursts” sounds produced during bottom feeding (Parks *et al.* 2014).

Here, we use suction-cup acoustic tags (Acousonde) attached to mother-calf pairs to investigate Humpback whale mother-calf pairs’ vocal production as well as their diving behaviour. The aims of this present study are manifold. We first describe the diving context of their vocal production by focussing on 6 selected social sounds: *100 Hz*, *bass*, *boom*, *trill*, and *wop* suggested to be produced by females and *heeks* suggested to be produced by calves. Secondly, we investigate the diving activities of calves at different age-classes to assess if calves show variable diving patterns with age. Finally, we investigate the mother-calf pair diving pattern during simultaneous tagging sessions to better understand the diving dynamics of the pairs. An understanding of mother-calf diving behaviour and vocal production during early stage is biologically important, as this is a critical period during which the calf develops a strong bond with its mother. Moreover, such knowledge is essential for the protection and conservation of humpback whales, especially for mother-calf pairs occurring in shallow and coastal areas, where they are more likely to be exposed to anthropogenic activities.

METHODS

Study site

Acoustic and diving data were collected during 4 successive winters from 2013 to 2016 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), known as one of the most important breeding areas in the south western part of the Indian Ocean. Sainte-Marie channel is a relatively shallow channel showing a maximal depth of 60 meters and an average depth between 25 to 35 meters (Trudelle *et al.* 2018).

Tagging procedure

We used two Acousonde 3B (www.acousonde.com) that were deployed on females and/or calves using a non-invasive attachment system (suction cups). All methods were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by the Fisheries Resources Ministry, Madagascar (national research permit n° 44/13, 44/14, 46/15, 28/16 MRHP/DGPRH). To deploy the tag, we used a rigid boat TM 21 model, 6 m long and 2.3m width. Acousonde deployment trips were organized when the Beaufort scale was ≤ 3 corresponding to gentle breeze, wind speed of 12 km/h, wave height varying from 0.2-0.5 m. The team consisted of 4 persons on board: one operator, one photographer, one note taker and one person identified to tag. Safety procedures were conducted prior to each deployment to ensure the safety people on board and the safety of whales. The major roles (tagging and operator) were only performed by highly experienced people possessing years of experience on whale behaviour. This configuration allowed us to optimise all the approaches we performed and increase the chance of tagging success while reducing the time spent with the targeted group.

Tags were attached to a grip at the end of a 5-m rigid handheld carbon fiber pole. The grip we used during our tagging procedure was modified to attach the Acousonde tag to the side of the whale and not on its back. The tag was then placed on the lateral side of the whale, as low as possible, to ensure it permanently stayed underwater, even if tagged individual performed long surfacing activity with the upper back out of the water. As we did not follow the groups after tagging, we did not require VHF signal for tracking purpose, preferring continuous acoustic recordings, especially as MC groups often remain at the surface for long periods of time.

When mother-calf accompanied or not by escort were spotted (blows were usually seen at 1-2 km distance from boat), we performed similar approaches as touristic boats, in order to follow Madagascar's Code of Conduct for whale watching activities (inter-ministerial decree March 8th, 2000): the speed of the boat was reduced gradually at 800 m distance from spotted group. The observation area for mother-calf groups is set at a 200 m radius around them; this distance was used to observe the groups' behaviours and we noted group composition at the same time: mother-calf alone (MC) or accompanied by one escort (MCE) or more than two escorts (MCEs). Behavioural observations and photo-identification were obtained concurrently for each group to avoid double sampling during the same season and the calf's relative age was estimated by using the inclination of the dorsal fin, as the dorsal fin in humpback whale calves straightens with age (Cartwright and Sullivan 2009b). Three age classes were considered by measuring the inclination of their dorsal fins: C1: newborns present some folds and scars and their skin colour tends to be light grey dorsally and white ventrally with the angle of dorsal fin less than 45° (Faria *et al.* 2013), C2: calves having furled dorsal fins more than 45° but less than 72°, and C3: older calves that have unfurled dorsal fins (> 72°).

The duration of attachment on the animal varies greatly among individuals from 30 minutes to up to 35 hours.

Data collection

Acoustic recordings were performed at a 24453 kHz frequency sampling rate and auxiliary sensors (pressure, 3D accelerometers, 3D magnetometer and temperature) were sampled at a 10 Hz frequency sampling rate. In 2016, we used a second Acousonde 3B that allowed us to tag both the mother and the calf of a given pair. The same settings were used for this second acoustic tag, except that the 3D accelerometer was sampled at 400 Hz.

Acoustic data were extracted and analysed using Avisoft SASLab Pro, and the vocal repertoire of social calls was thus described from the data collected in 2013 and 2014. In order to investigate the behavioural context of social call production, we focused our analysis on call types suggested to be produced by females such as *100 Hz*, *bass*, *boom trill* and *wop* (both low-frequency and amplitude modulated sounds) and by the calves such as *heek* sound.

Diving profiles were extracted from the pressure data using a custom routine in Matlab version r2016b. To compare with previous studies on diving behaviour of humpback whale calves (Stimpert *et al.* 2012), we considered a dive as any excursion below 10m, or about 2 calves' body lengths. The same criterion was used for both mothers and calves diving profiles to enable comparison.

To link vocal production with diving context, we extracted dive metrics at the time of call production at which these calls were produced: mean dive depth (meanDep, in m), if produced during a dive (> 10 m). We also calculated the percentage of calls produced during dives' descending and ascending phases, the percentage of calls produced during diving, and the percentage of calls produced at the surface (Table 2). As both females' and calves' vocalizations could have been recorded by the acoustic tag deployed either on females or calves, analyses were performed separately.

To characterize the dive, we chose some of the dive metrics proposed by Hooker and Baird 2001 (Hooker and Baird 2001) to describe cetacean dive behaviour and previously used for humpback whale calves (A. Stimpert *et al.* 2012). We thus extracted the following dive parameters: number of dives per hour (Dhour, in nb.h⁻¹), maximum dive duration (maxDur, in sec), mean dive duration (meanDur, in sec), maximum dive depth (maxDep, in m), modal dive depth (modDep, in m), bottom time (BotDur, in sec), post-dive surface interval (PostDSI, in sec), mean ascent slope (AscSlope, in m.s⁻¹), mean descent slope (DesSlope, in m.s⁻¹), surface time ratio (SurfaceR, in %). The bottom time was defined as the time spent at >85% of the maximal dive depth for each dive.

Finally, during the 2016 breeding season, as we had the opportunity to tag both mother and calf of a given pair, we investigated their diving patterns, and assessed whether there are similarities in diving profiles, synchrony, and if one of the two protagonists lead the dive. We also assessed the mother-calf vertical proximity and thus the relative position of the calf in relation to its mother, by calculating the pairs' difference in depth at each specific time of their diving profiles.

Statistical analysis

From the dive metrics obtained during the 4 successive breeding seasons, we investigated if the dive characteristics for calves differed among the 3 different age classes (C1, C2, and C3) and adult females. We performed Welch ANOVAs on the different dive variables, and when significant, we used Games Howell post-hoc tests to assess pairwise differences.

To analyse recordings obtained from simultaneous deployments, we jointly plotted the diving profiles of the mother with her calf to assess visual similarities in diving profiles. We then performed two cross-correlation tests between mothers' and calves' diving profiles. These correlations were performed on diving profiles for which we have data for both mothers and

their respective calf (i.e., common diving sections, as mother and calf could not be tagged at the same time). An initial correlation coefficient was measured with a sliding time-window to assess the maximal correlation between the two diving profiles. The time lag corresponding to this maximal correlation allowed to assess the leader of the dive (i.e., the mother follows her calf or vice versa). A second coefficient was measured without time sliding to assess the correlation between the two diving profiles with their original time axes. Normalized cross-correlations were computed using the “xcorr” function in Matlab (the sequences were normalized so that the autocorrelations at zero-lag equal to 1). Finally, we compared the different dive metrics between the mothers and their calves using Wilcoxon rank sum tests. All statistical analyses were performed in R (Version 3.2.5).

RESULTS

During the 4 successive breeding seasons, we performed a total of 45 deployments (21 females and 24 calves), but collected diving data for 39 deployments: 18 on mothers and 21 on calves. Among these 39 deployments, 7 simultaneous mother-calf deployments were performed in 2016 (see Table 1 for details), but simultaneous diving data collected for both mother and calf were obtained for 5 pairs only. For the 2 remaining simultaneous deployments, one of the tag has detached ~ 15 after it was deployed and did not allowed to extract consistent diving profile.

Table 1: Description of the data collection including year, type of group (MB: mother-calf pair, MBE: mother calf with one escort, MBES: mother-calf pair with several escorts), tagged individual (mother or calf), age class (C1: newborn, C2: 7-15 days old, C3: >15 day old, see text for details), and duration of tag attachment on the animal (in hours).

Deployment #	Group type	Tagged Ind.	Age class	Deployment duration (h)
2013_1	MC	mother	adult	5.25
2013_2	MCES	mother	adult	4.10
2013_3	MCE	mother	adult	1.37
2013_5	MC	mother	adult	1.44
2013_6	MCE	mother	adult	0.65
2013_7	MC	calf	C3	3.23
2014_10	MC	mother	adult	0.17
2014_11	MC	calf	C3	0.47
2014_1	MCE	calf	C2	0.74
2014_2	MC	calf	C3	5.05
2014_3	MC	mother	adult	1.95
2014_4	MCES	mother	adult	14.39
2014_5	MC	calf	C3	0.45
2014_6	MCE	calf	C3	3.45
2014_7	MC	calf	C3	4.94
2014_8	MC	calf	C1	2.26
2014_9	MCES	calf	C2	0.59
2015_1	MCE	calf	C2	0.32
2015_2	MC	calf	C2	35.28
2015_4	MCES	calf	C3	3.23
2015_5	MC	calf	C3	2.24
2015_6	MC	mother	adult	0.26
2015_7	MCES	mother	adult	7.99
2016_1a	MC	mother	adult	0.49
2016_1b	MC	calf	C3	0.12
2016_2a	MC	calf	C2	2.46
2016_2b	MC	mother	adult	1.23
2016_3a	MC	mother	adult	1.82
2016_3b	MC	calf	C2	0.06
2016_4a	MC	calf	C3	1.69
2016_4b	MC	mother	adult	4.37
2016_5	MCE	calf	C2	5.68
2016_6	MC	mother	adult	6.93
2016_7a	MCE	mother	adult	7.32
2016_7b	MCE	calf	C3	2.78
2016_8a	MC	mother	adult	10.24
2016_8b	MC	calf	C1	1.12
2016_9a	MC	mother	adult	7.78
2016_9b	MC	calf	C3	9.07

Diving activity and vocal production

From the 2013 and 2014 seasons, *heek* were recorded on 4 out of 7 deployments on calves, and a total of 38 calls were detected. We found that 92% of *heek* sounds recorded on tags attached to calves were usually recorded when calves were at $6.5\text{m} \pm 4.5$ depth (less than 10m) during surface activity. When produced during a dive, 56% of *heek* were produced during the descending phase of the dive, and thus 44% while returning to the surface (i.e. ascending phase). *Heek* sounds recorded on tags attached to females occurred in one instance only, and the female was also at the surface ($3.19 \pm 0.44\text{m}$, $n=2$ calls).

For the females, we focused our investigations on 4 call types belonging in the low-frequency sound range: *100 Hz*, *bass*, *boom* and *wop*; and 1 call type from the AM sounds: *trill*.

Table 2 summarizes dive depth at which these vocalizations were produced by the mothers (Table 2a), and the dive depth at which the calves' same vocalizations were recorded on the calf tag (Table 2b). *Bass*, *trills* and *wops* were mostly produced by females during surface activities (less than 10 m), with *bass* almost exclusively produced at the surface (95%, Table 2a). When produced during diving, most of these calls were emitted during the ascending phase, in other words, when returning to the surface. In contrast, *100 Hz* and *booms* were produced almost exclusively during diving activities (95 and 94% respectively, Table 2a) and mostly during the descending phase (60 and 53.5% respectively, Table 2a). Recordings on tags attached to calves revealed very similar patterns. Indeed, *bass* and *wops* were mostly detected during calves' surface activities (78 and 94% respectively, Table 2a), and *100 Hz* and *Booms* were detected during calf diving activities (74 and 86% respectively, Table 2b). Only *trills* showed a different pattern as they were mostly produced by the females when at the surface, but mostly detected on the calf tags when calves were diving (78%, Table 2b).

Table 2: Relationship between vocal production and dive characteristics for some female calls recorded on tags attached to a) females and to b) calves. % are marked in bold when great than 60%.

	Main call category	Call type	Mean Depth	% at surface (<10m)	% while dive (>10m)	% during ascending phase	% during desc. phase
		(n calls, n dep)	± SD (m)				
a) on females	LF	100 Hz (n=975, 2 dep)	19.8 ± 7.2	5	95	40.0	60.0
	LF	Bass (n=21, 2 dep)	2.5 ± 1.9	95	5	75.0	25.0
	LF	Boom (1394, 2 dep)	20.1 ± 8.8	6	94	46.5	53.5
	LF	Wop (n=13, 4 dep)	6.7 ± 2.1	77	23	54.2	45.8
	AM	Trill (n=109, 4 dep)	10.0 ± 4.2	56	43	37.4	62.6
b) on calves	LF	100 Hz (n=271, 5 dep)	14.6 ± 8.8	26	74	35.3	64.7
	LF	Bass (n=83, 5 dep)	8.6 ± 5.4	78	22	60.3	39.7
	LF	Boom (n=59, 2 dep)	12.9 ± 5.1	14	86	51.6	48.4
	LF	Wop (n=16, 3 dep)	5.9 ± 4.5	94	6	44.4	55.6
	AM	Trill (n=67, 2 dep)	16.6 ± 5.1	22	78	47.9	52.1

Diving characteristics in calves

Table 3 presents the average diving metrics for adult females and calves of the 3 different age classes. When comparing the different dive characteristics, we found that only 3 out of the 10 variables were significantly different among age classes (adult females and 3 calf age-classes). Indeed, maximal and mean dive duration, as well as time spent at the bottom were found to be significantly different among age classes (Table 3, Welch ANOVA p values <0.003), and posthoc tests revealed significant differences for all 3 dive metrics between newborn calves (C1) and older calves C3 (calves older than 15 days). The only significant difference between females and newborn calves C1 was found for MaxDur (Table 3). Indeed, MeanDur and BotDur were not found to be significant however p values were close to significant level (p-values = 0.07, Table 3). Newborn calves C1 showed shorter time periods spent at the bottom but also shorter mean and max dive durations compared to other age-class calves and females (Figure 1A, B, C).

Figure 1: Dive metrics (*meanDur*, *maxDur*, and *BotDur*) found significantly different among age-classes (C1, C2, C3 and mothers). Horizontal bars indicate posthoc tests found significant (p values < 0.05).

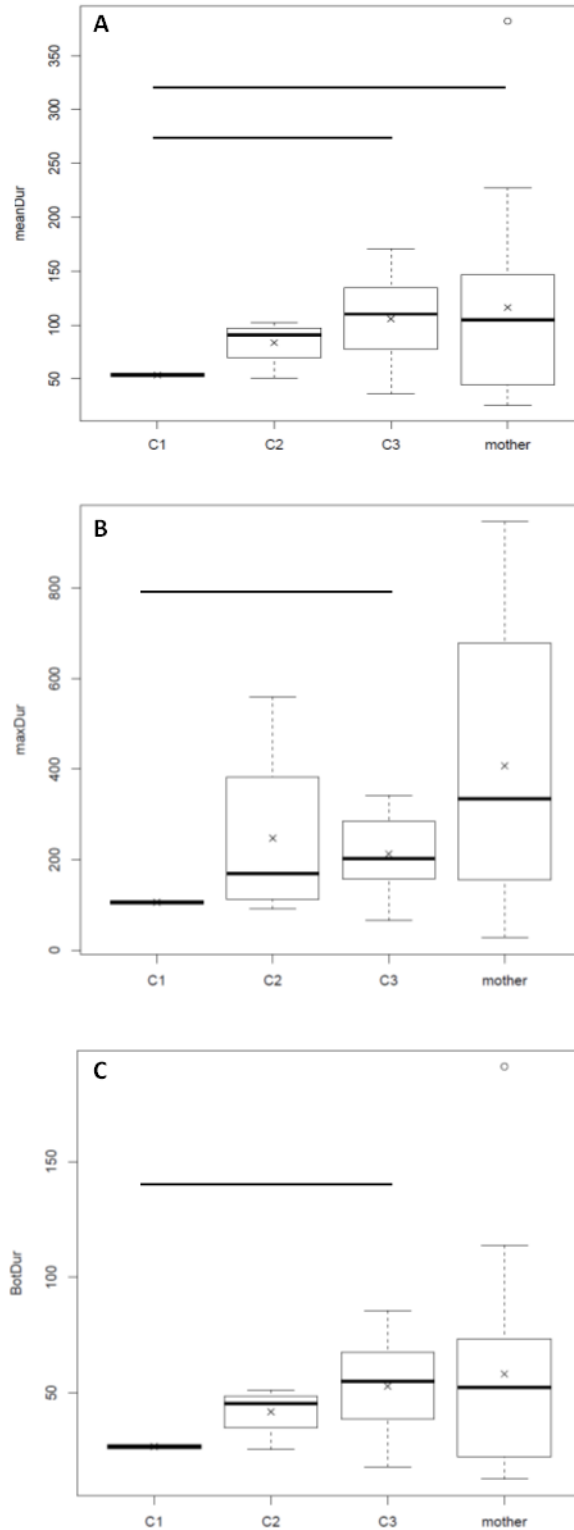


Table 3: Dive metrics for mothers and calves of different age classes. Y values indicate a p -value = 0.07

	Deploy. Dur (h)	maxDur (sec)	meanDur (sec)	maxDep (m)	modDep (m)	BotDur (sec)	Dhour (nb.h ⁻¹)	PostDSI (sec)	AscSlope (m.s ⁻¹)	DesSlope (m.s ⁻¹)	SurfaceR (in %)
Females (F; n=18)											
mean	4.3	407	116	30.3	11.5	58	7.5	276	0.55	-0.47	80
SD	4.1	305	93	9.7	4.6	47	4.4	230	0.35	0.30	20
min	0.2	28	25	12.4	10.0	13	0.0	127	0.22	-1.39	40
max	14.4	946	382	50.8	28.5	191	15.7	1062	1.58	-0.28	100
All calves (n=21)											
mean	4.1	209	95	29.4	12.4	48	9.1	229	0.59	-0.49	80
SD	7.5	122	40	7.2	4.6	20	5.3	111	0.31	0.21	20
min	0.1	66	36	18.2	10.0	18	0.0	100	0.15	-1.16	40
max	35.3	560	171	42.4	25.6	86	17.9	512	1.49	-0.18	100
Calves (C1; n=2)											
mean	1.7	106	54	24.4	10.4	27	13.4	213	0.70	-0.40	80
SD	0.8	6	2	2.3	0.1	1	6.4	93	0.26	0.05	10
min	1.1	102	52	22.8	10.3	26	8.8	147	0.52	-0.44	70
max	2.3	110	55	25.9	10.5	28	17.9	278	0.88	-0.36	90
Calves (C2; n=6)											
mean	7.1	248	84	34.9	13.5	42	6.6	235	0.86	-0.67	80
SD	14.0	214	22	5.1	6.8	11	5.9	94	0.45	0.33	20
min	0.1	92	51	31.3	10.0	26	0.0	139	0.47	-1.16	60
max	35.3	560	102	42.4	23.6	51	14.9	361	1.49	-0.40	100
Calves (C3; n=13)											
mean	3.0	213	106	28.5	12.4	53	9.7	229	0.49	-0.44	70
SD	2.4	90	42	7.4	4.4	21	4.7	125	0.23	0.15	20
min	0.1	66	36	18.2	10.0	18	0.0	100	0.15	-0.69	40
max	9.1	342	171	40.4	25.6	86	15.5	512	0.90	-0.18	100
Welch ANOVA	F = 2.475 P=0.141	F = 9.829 P=0.002	F = 9.261 P=0.0026	F = 3.866 P=0.059	F = 1.174 P=0.367	F = 9.260 P=0.0026	F = 0.725 P=0.588	F=0.171 P=0.911	F = 0.861 P=0.527	F=0.852 P=0.507	F = 0.732 P=0.573
Post hoc tests significant		C1-C3	C1-C3			C1-C3					
		C1-F	C1-F ^Y			C1-F ^Y					

Dive synchrony between calves and mothers

When plotting the dive profiles of the 5 mother-calf pairs, we found that mother and calf show highly synchronized dives (Figure 2, Table 5, Supplementary Figures 1-4 (Appendices Chapter 3)). The dive metrics for mother-calf pairs, as well as correlation coefficients between mother-calf dive profiles are shown in Table 5. We found a very high synchrony between the dive profiles of mothers and calves, with the maximal correlations ranging from 0.8 to 0.98. On several occasions, we observed that the mother stayed at the bottom while her calf returned to the surface to breathe, once or several times (see Figure 2 and Supplementary Figures 1-4 (Appendices Chapter 3)), explaining why the number of dives are greater for some calves compared to mothers (see Table 4). We performed non-parametric tests to compare these dive metrics between mothers and calves, and none was found significantly different. Of the 5 mother-calf pairs, we found that in 4 out of 5 dives females were leading the dive (i.e. negative delta values on Table 5), thus in most cases, calves followed the diving pattern of their mothers. The only case in which the calf led the dive (dep 4, Table 4), the calf systematically dove deeper than its mother (see Supplementary Figure 2 (Appendices Chapter 3)). Mother-calf vertical distances (Table 5, Figure 2, and Supplementary Figures 1-4 (Appendices Chapter 3)) ranged from -38 to 31m, 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 time spent above or below the mother varies greatly among calves (Table 5).

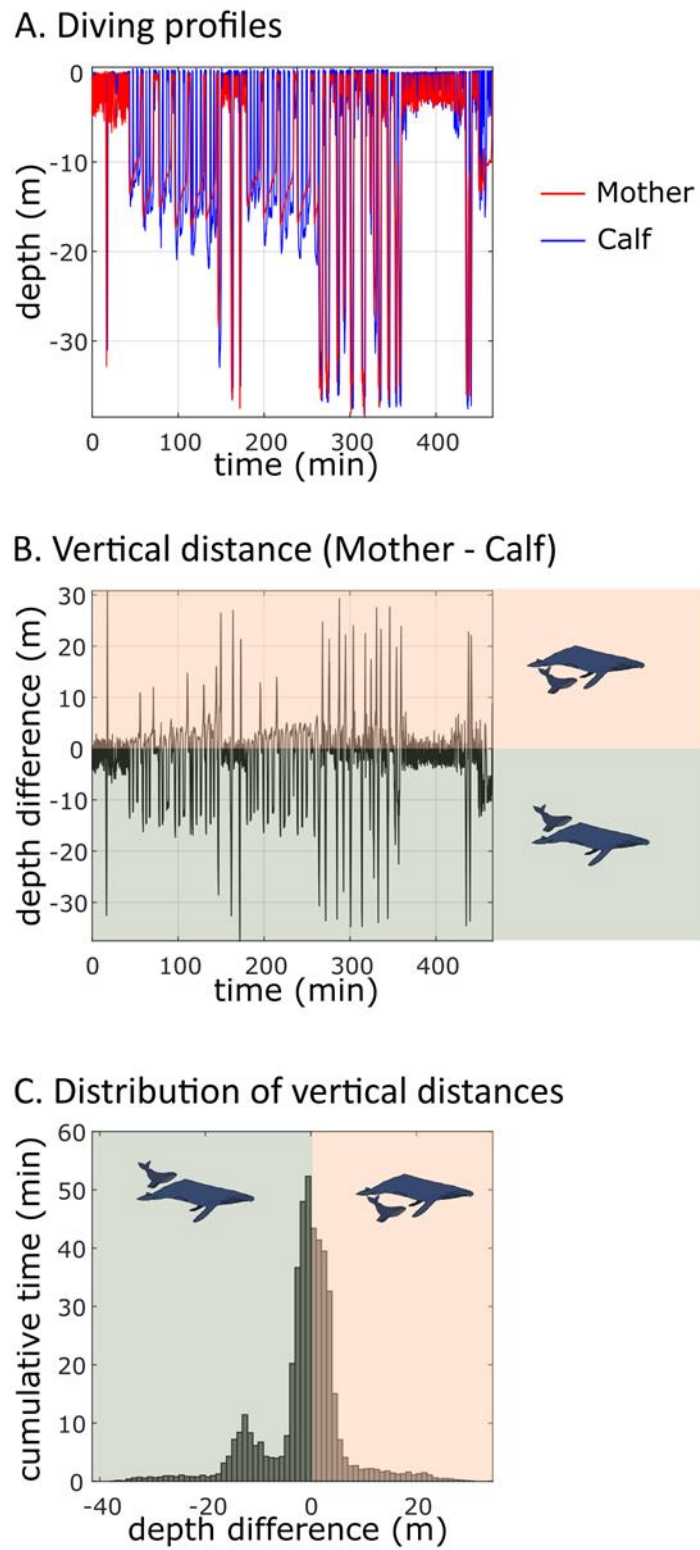
Table 4: Dive metrics for simultaneous deployments on 5 mother-calf pairs.

Dep #	Ind.	Nb dives	maxDur (sec)	meanDur (sec)	maxDep (m)	modDep (m)	BotDur (sec)	Dhour (nb.h ⁻¹)	PostDSI (sec)	AscSlope (m.s ⁻¹)	DesSlope (m.s ⁻¹)	SurfaceR (in %)
2	C	16	160	97	36	7	10	13.0	163	4.16	-3.27	65
2	M	8	650	306	37	11	31	6.5	216	2.22	-2.15	45
4	C	9	120	82	19	13	8	16.4	66	1.30	-1.05	63
4	M	7	370	130	17	12	13	12.7	60	1.34	-0.59	54
7	C	32	230	131	23	13	13	13.3	130	1.21	-1.18	52
7	M	32	240	131	21	10	13	13.3	132	0.79	-1.15	52
8	C	11	110	73	22	13	7	18.7	128	2.71	-1.78	62
8	M	11	160	99	21	14	10	18.7	99	1.80	-1.21	49
9	C	54	280	187	37	12	19	7.0	319	1.67	-1.73	64
9	M	27	970	506	38	13	51	3.5	522	1.55	-1.95	51

Table 5: Correlation coefficients between mothers and calves diving profiles (see text for details), vertical distance (mean, median, range) between the pairs and time percentage calf spends above and below mothers. Delta indicates the time difference between mother-calf dive profiles, a negative value means that the mother dove first, and thus led the dive.

Dep. #	Correl. max	Correl.	Delta (sec)	Mean vertical dist. (meters)	Median vertical dist. (meters)	Range vertical dist. (meters)	Percentage time calf above mother	Percentage time calf below mother
2	0.809	0.812	-11	6	1.8	[-33.5 ; 5.5]	83%	17%
4	0.932	0.855	20	2.3	1.6	[-13.1 ; 5.6]	47%	53%
7	0.978	0.926	-15	4	2.5	[-18.3 ; 20.5]	42%	58%
8	0.909	0.584	-26	3.2	2.1	[-15.8 ; 5.3]	63%	37%
9	0.933	0.784	-28	5.1	2.6	[-37.5 ; 30.8]	54%	46%

Figure 2: Diving profiles, vertical distance and distribution of vertical distances of a given mother-calf pair (Dep9, Table 4).



DISCUSSION

Studying behaviour of cetaceans is challenging. Even if mothers accompanied by their young calves are often visually observed near the water surface, where the young calves breathe easily, rest, swim and feed while staying close to the mother, mother-calf pairs also show diving pattern and thus activity away from the water surface. As calves grow up, the distances between them and their mother tend to increase and most of the time calves can swim alone at the surface while mothers are resting several meters below (Cartwright and Sullivan 2009c; Zoidis 2014). Visual observation provides incomplete information of the pair as soon as they decide to dive even just a few meters, particularly in the case of Sainte-Marie channel water where underwater visibility is poor. The use of non-invasive suction cup tags such as D-tag or Acousonde to understand mother-calf sub-surface activities has recently increased (Chen *et al.* 2016; Stimpert *et al.* 2012; Tyson *et al.* 2012; Videsen *et al.* 2017b) as they permit the extraction of acoustic recordings and their association to diving profiles. Nevertheless, in all aforementioned studies, authors mentioned the difficulty of the tagging process, and the necessity of taking great care while approaching neonate calves. In many studies, tagged animals are followed at a distance. Such proximity could influence the behaviour of the tagged animals. In our study, all tagged animals (mothers, calves or mother-calf pairs) were not followed once tags were deployed on animals, they were left alone, and tags were only retrieved when detached from the animals.

Behavioural context of the vocal production

During breeding season, humpback whale mother-calf pairs evolve in a noisy context. They are exposed to male songs, non-vocal percussive sounds produced by surface active behaviours (tail slapping, pectoral slapping and breaches) as well as non-song social calls produced by conspecifics. This study present the behavioural context of production of selected social calls

suggested to be produced by mother-calf, using acoustic recording and pressure sensors on Acousonde suction cup tag. The *heek* sounds suggested to be produced by calves were present in 4 deployments on calves and 1 deployment on mother. Whether the tag was attached on calves or on mothers, this social call is in 92% of cases produced during surfacing activities and 56% during descending phases and in 44% of cases during ascending phases. In the recordings, *heeks* were most often heard simultaneously with non-vocal social sounds produced during surfacing active behaviours (breach, tail or pectoral slapping) that could be produced by the tagged whale itself or the mother or other whales nearby. Among the 5 calls assigned to females, 2 low-frequency sounds (*bass* and *wop*) were produced mainly during surfacing activities while 2 other low-frequency sounds (*100 Hz* and *boom*) were produced during diving activities (and mostly during descending phases). The same context of production was observed when the tag was attached to calves. In contrast, the *trill*, an amplitude modulated call produced by females, shows a different pattern according to the tagged individual. Indeed, *trills* were heard during surfacing activity when the tag was on females but observed during diving activities when the tag was on calves. Thus, these different contexts of production suggest different functions for these different types of social calls.

It could be suggested from our results, that calves vocalizations happened mainly during surfacing behaviours. Recent knowledge is available on mechanisms of baleen whales sound production. Sounds are produced from their respiratory system and it was suggested that airflows between the lungs and the laryngeal sac passing through the U-fold system produces low-frequency sounds, and the control of air to adjust the internal air pressure, especially inside the laryngeal sac, may affect frequency or amplitude of sounds (Gandilhon *et al.* 2015; Reidenberg and Laitman 2007). It was also suggested that the laryngeal sac could be used for humpback whales buoyancy control in addition to sound production (Gandilhon *et al.* , 2014).

Indeed, singers are well known for their head-down position while singing, suggesting a perfect control of both functions. We found that young calves produce their vocalizations (*heek*) mostly at the surface and rarely while diving. As calves do not yet have great control of their buoyancy (Stimpert *et al.* 2012), this could explain why they vocalize more frequently at the surface, where they do not need to adjust their buoyancy from control of the internal air pressure. When considering results from mothers, some low-frequency sounds were also produced during surfacing activities. Baleen whale mother-calf pairs are well known for having very close relationships resulting in frequent physical contacts. Humpback whales have long pectoral fins that have an important role in maintaining their stability, but mothers also use their pectoral fins to maintain physical contact with their calf. Indeed, calves tend to stay below the rostrum or the pectoral fins during resting behaviour. In addition to this physical proximity, and considering the behavioural pattern of sound production here vocal contact can be used as well, especially when there is a distance separating the pair. Thus, sounds produced during surface active behaviours between the pairs could be used as contact calls mainly during active surfacing behaviours or when other conspecifics (escorts) are nearby. Contact calls between mother-calf pairs have been described for other mysticetes. For instance, Clark 1983 (Clark 1983) have shown the use of “growl-like” call types produced by mother southern right whales (*Eubalaena australis*) when their calves are at a “critical” distance from them; the calf then returns to her side or the mother swims to her calf. The evidence of contact calls between mother-calf bowhead whales (*Baleana mysticetus*) have also been reported, where series of calls were recorded as mother-calf approached each other (Wursig and Clark 1990). Vocal exchanges involving contact calls between mother-calf Bryde’s whales (*Balenopetra edeni*) have been recorded while the mother is feeding with her calf (Edds and Odell 1993). In our study, other social calls studied are produced during diving context, different contexts, and likely serve as well to maintain contact between the mother and her calf. In light of these results, we suggest

that *heeks*, *wops*, *bass* and *trills* could be used as contact calls between humpback whale mother-calf pairs while they are at the surface. In contrast, *100 Hz* and *booms* were exclusively observed while both mothers and calves were diving, and thus they seem to be used to maintain contact during diving activity. Finally, *trills* are produced by the mother while separated from her calf, and are used to maintain contact when they are in different depths/locations (female at bottom and calf at the surface). In such very close relationships as mother-calf bonds, a vocal exchange does not occur exclusively during “active” behaviour. Even though mothers and calves are physically close to each other, they could have an active vocal interaction to maintain contact and also to reinforce the mother-young social bond; as it is also observed in other vertebrate species. For instance, mother-calf social calls are reported to be produced at a low amplitude level (Videsen *et al.* 2017b), thus this could be an additional hypothesis to explain why such low amplitude sound production. .

In our study, we could not investigate whether certain social calls could be used to initiate suckling bouts as we did not have any visual observation of the pairs. Further investigations on the accelerometer data might give us additional information on potential suckling events and thus a link with vocal production.

Diving behaviour of calves

The term “diving behaviour” has been used here to describe any subsurface activity below 10m. Here we described calves diving pattern and mother-calf diving activities during the first three months of the calves’ lives. As some of the tagged calves were newborns, our results present the earliest diving behaviour of baleen whales during their first days, when calves are extremely dependent of their mother, and the maternal proximity ensures calves’ survival. As calves become more autonomous, distance between mother and calf increases (Szabo and Duffus

2008), and calves become more responsible for maintaining proximity to their mother (Tyson *et al.* 2012). Humpback whales as well as other baleen whales are thought to be shallow divers. This holds especially true for mother-calves in breeding areas where they are usually observed very close to shore (Clapham, Mead, and Gray 1999; Whitehead and Moore 1982) especially when calves are newborns (Pack *et al.* 2017). This habitat preference of mother-calf pairs is driven by the presence of aggressive male behaviours in competitive groups, thus staying close to the shore is a way to avoid such competitive groups. Indeed, calves behaviours change when one or many adults males are present in the group (Cartwright and Sullivan 2009a).

Among the 21 calves tagged in our study, there are significant differences in dive durations but not in dive depth among calf age-classes. C1 calves present shorter dives than C3 calves suggesting that newborn calves have limited lung capacity as they are still learning to manage their breathing cycle. In mammals, larger animals have a proportionately greater oxygen storage capacity so greater diving capacity (Schreer and Kovacs 1997). Indeed, diving capacity is among those skills developed gradually by calves (Stimpert *et al.* 2012). For Steller sea lion pups, aerobic dive limit is 0.5 min shorter than juveniles. This is calculated based on their body mass, lower mass-specific oxygen stores and their higher metabolic diving rates (Richmond, Burns, and Rea 2006).

The female humpback whales accompanied by calves reported here present dive metrics that contrast with those available for adults on breeding grounds showing dive durations up to 25.7 min (Baird, Ligon, and Hooker 2000). Our results show no significant difference in depth metrics, C1 calves going as deep as older calves or as their mothers. The shallow waters in Sainte-Marie channel, with an average of 25-35 meters (Trudelle *et al.* 2018), could explain the lack of differences for most dive metrics between calves and adult females. Humpback whales maximum dive depths reported by Hamilton and colleagues (Hamilton, Stone, and

Martin 1997) is 240 m around Bermuda island, and was suggested to be an exploratory foraging dive, however, most breeding areas present shallows water < 00 (Ersts and Rosenbaum 2003; Rasmussen *et al.* 2007; Smith *et al.* 2012; Whitehead and Moore 1982).

Mother-calf synchronized dive

Among the 5 mother-calf pairs tagged simultaneously, 4 out of 5 females were leading the dives. This result confirms that humpback whale calves exhibit a strategy of maternal following previously observed in feeding grounds (Szabo and Duffus 2008; Tyson *et al.* 2012). The only case in which the calf led the dive was for calf 4 (dep4; C3 age-class) where the calf was much older compared to C1 and C2 classes, which may suggest exploratory behaviour. On several occasions, we also found that calves dove 1-3m deeper than their mothers (see Table 4, Figures 2 and Supplementary Figures 1-4 (Appendices Chapter 3)) suggesting that calves might position themselves below their mothers to stay at the bottom as they do not yet properly control their buoyancy (Tyson *et al.* 2012). Our results show that calves may lead the ascendant phase of their dives with mothers following. However reverse behaviour has never been observed, i.e no calves dive alone while mothers remain at the surface. The high level of correlation between diving profiles suggests that the pairs present highly synchronized behaviour, as expected in reference to their behaviour observed at the surface while they are resting or playing. The same highly synchronized behaviour was also observed in mother-calf in their feeding grounds where calves travelled and fed close behind the mother (Tyson *et al.* 2012) even though calves were much older (8- to 12-month old) than in our study. Vertical distance measurements confirm the synchronicity and proximity between the pairs. Even though calves must perform short dives to breathe, distance separating the pairs never exceed ± 5 m. Mother-calf pairs in the breeding ground always stay very close to each other. Similar vertical proximity has been described by Tyson *et al.* (2012) in the feeding ground even though this distance tends to be much greater

($\pm 20\text{m}$) compared to our results where mother-calf are quite close. This supports the increase of vertical distances between the pairs when calves get older (see C3 calves in deployments 4, 7 and 9). However, even if mothers and calves can be separated by up to 30m in some instances, they mostly stay in very close proximity (median vertical distances around 2m, Table 5). Such proximity is likely to evolve with calves' age, and also with the presence of congeners.

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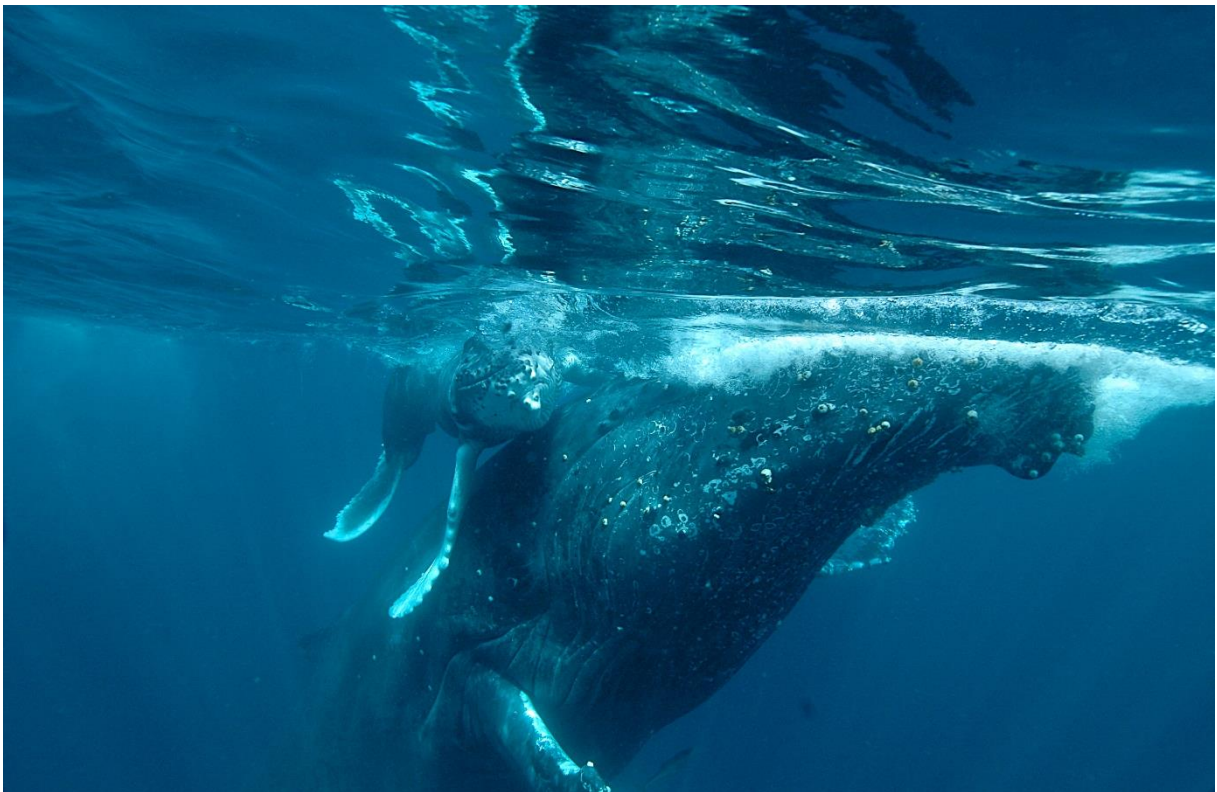
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CHAPTER 4a: Do humpback whales newborn calves have a preference to position themselves to a side of their mother?



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Do humpback whale (*Megaptera novaeangliae*) newborn calves have a preference to position themselves to a side of their mother?

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ABSTRACT

Spatial proximity to mothers is a key factor in offspring survival in group-living mammals. In humpback whales (*Megaptera novaeangliae*), an extreme migrating species, newborn calves stay close to their mothers. This proximity can be modified by the presence of other congeners or other species. The spatial relationship between mother and calf can thus vary with social contexts. We investigated the position of the calf around its mother in different social contexts: alone, with one or several escorts, and in presence of free divers. Using video footages of mother-calf pairs in 3 breeding sites located in Indian and Pacific oceans, we recorded the positions of the calves in the 3D space surrounding their mothers, space methodically divided into ten positions. Calves mainly preferred positions above their mother, either on the right or the left; a strategy allowing the calf to be in an optimal position to breathe and to benefit from the hydrodynamic aspiration flow of its mother. Resting behaviour was significantly related to the below position, involving physical contacts with the mother and thus reinforcing their social bond. Finally, calves in presence of free divers neither approached nor moved away from them suggesting a reduced direct impact on their behaviour.

INTRODUCTION

For large marine mammals that bear a single offspring every two to three years, calf survival is critical for the perpetuation of the species and depends on the mother's ability to both feed and protect the new-born, as well as on calf's abilities to stay close enough to the mother for protection and care. Only females provide care to the young as no paternal care after conception is known (Barlow and Clapham 1997). Humpback whales are born in sub-tropical areas where they spend their first months in a place filled with males displaying aggressive behaviours, which occur within "competitive groups" composed of multiple males competing for proximity to a female, with or without calf (Baker and Herman 1984; Tyack 1981; Tyack and Whitehead 1982). Mother-calf pairs must deal with the presence of other individuals surrounding them, and calves must be able to follow their mother, and their time budgets vary according to the number of males associated to the group (Cartwright and Sullivan 2009a).

Spatial relationship and behaviour between mother-calf pairs in mysticetes present three distinctive phases that have also been observed in Southern Right whale (*Eubalaena australis*) (Taber and Thomas 1982). The youngest calves spend most of their time travelling and breathing while maintaining proximity to their mothers. This spatial relationship becomes more distant as calves get older and allocate most of their time playing and circling at the surface, while mothers stay a few meters underneath (Cartwright and Sullivan 2009b; Zoidis 2014). During movement, the young reduce their proximity to the mother and synchronize their movements and breathing, especially for long displacements such as migration routes (Zoidis, 2014). When they grow up calves acquire new skills but still remain energetically-dependent on their mother (Cartwright and Sullivan 2009b; Zoidis 2014).

Depending on social and maternal context, different sensory modalities are used to maintain such spatial proximity between mothers and new-borns, and the initiative can come either from mothers or calves. In a wide variety of vertebrates including odontocetes, the right-hemisphere of the brain, dedicated to social interactions obtains information from the left eye, thus, a right-side social lateralization pattern has been observed in mother and infant positioning (Damerose and Vauclair 1973; Manning and Chamberlain 1990). In belugas, continuous visual contacts are more important in mother-calf interactions than tactile contacts, and these are initiated by calves (Karenina *et al.* 2010). In wild belugas, calves present a highly significant right-side swimming position preference with their mothers (Hill *et al.* 2017; Karenina *et al.* 2010; Yeater *et al.* 2014). Much like in belugas, dolphin mother-calf pairs maintain right-side visual contact and the mothers seem to be partially responsible for maintaining proximity to their calves (Lyamin *et al.* 2007; Mann and Smuts 1999). The same right-side infant position preference has been observed in wild orcas (Karenina, Giljov, Ivkovich, *et al.* 2013). All these examples of cetaceans include only odontocetes species, but nothing is known for mysticetes.

In the present study, we quantify, in a mysticetes species, the prevalent spatial positions chosen by humpback whale calves around their mother, considering static and traveling behaviours, and their behaviour in presence of free divers.

METHODS

Videos recordings

Opportunistic video data were obtained from different sources: 186 videos from snorkelers (using GOPRO Hero 3 camera), 2 videos from drone (DJI Phantom 3 model) and 26 videos from immersed GOPRO Hero 4 camera using one-meter rigid pole from a boat or from a kayak.

Videos were obtained from different geographic areas in the Indian Ocean (149 videos from Reunion Island, France and 64 from Sainte-Marie Island, Madagascar) and in the Pacific Ocean (1 video from Polynesia). From these 214 video files, a total of 91 mother-calf groups have been scored, and this represented a total observation time of 04 hours and 56 minutes. The mean duration of video files was $00:01:28 \pm 00:00:06$. The sex of the calves was identified when possible, and it resulted in a sample of 20 female calves, 9 male calves and 62 sex-undetermined calves.

Determination of calf position

For consistent interpretation of the results, only spatial positions initiated by calves were considered in the analysis, performed in two different ways. First, at a group level, all 91 mother-calf pairs were considered and the duration of each calf's position around the mother was noted, and we obtained average values for each position and for each calf. In a second part, all video files (214 videos) were considered without focussing on individual mother-calf pairs, an average duration for each position of the calves was obtained. Calves' position were defined by using 8 grid positions around the mother in addition to the position "in front (F)" and "behind (BH)" the mother: above (AB), above right (ABR), above left (ABL), right (R), left (L), below (BL), below right (BLR), below left (BLL) (Figure 1). To compare the duration of each position among the 10 possible positions of the calf around its mother, we used Wilcoxon tests, and we corrected the p-values for multiple comparisons using Bonferroni correction. To detect any possible effect of side preference by the calves, we pooled positions « AR », « R », and « BR » as "Right side" and « AL », « L », and « BL » as «Left side». Chi-squared tests were then carried out to compare the distribution of positions. Comparison between male and female calves could not be investigated due to the low number of sex-identified calves and an unbalanced number (9 males versus 20 females).

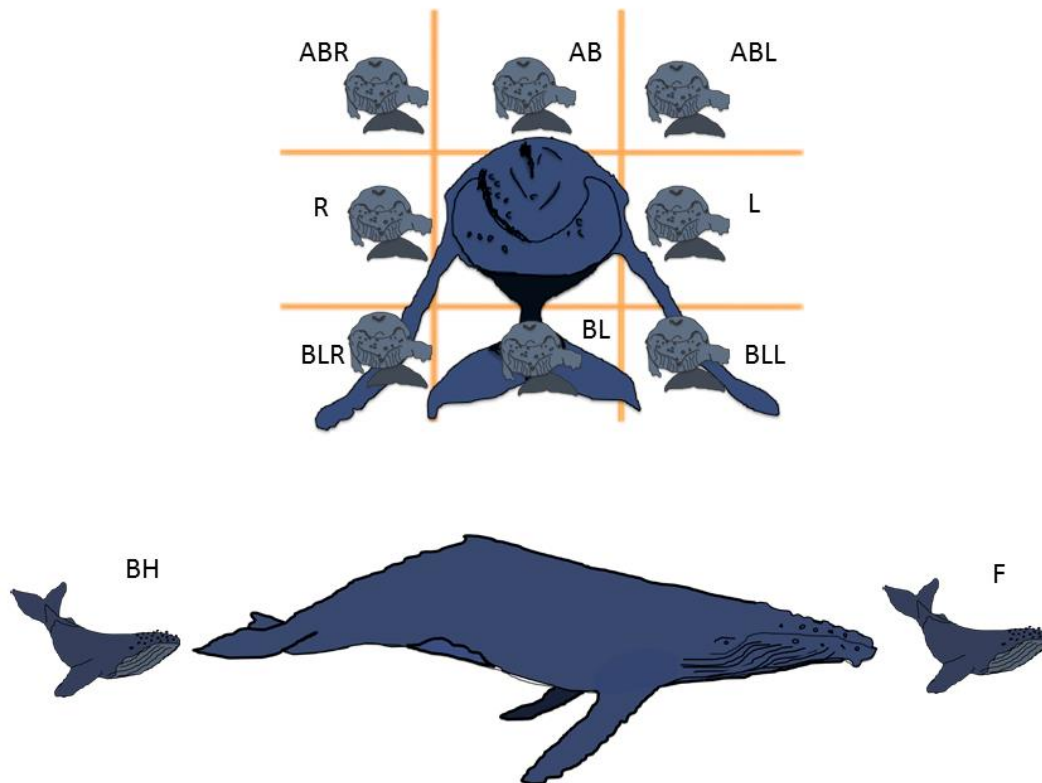


Figure 1: Schematic presentation of calf's position (AB: above, ABR: above right, ABL: above left, R: right, L: left, BL: below, BLR: below right, BLL: below left, BH: behind, F: in front)

Finally, to ensure that the position of the free divers' video-recording underwater did not influence the calf's choices, we also assessed the impact of the free divers' position on the calf's position. The lateral position of calves compared to the free divers' positions were observed and categorized as « opposite side », « same side » or « others » when calves and divers were not in a lateral position (Figure 2). In this analysis, only the position initiated by the calf itself was considered. Moreover, as the free divers did not present the same behaviour with respect to the calf, we divided the diver's behaviour in two categories: « interaction behaviour » when the free divers aimed at interacting with the calf (e.g., proximity, attempt of physical contact), and « neutral » when free divers kept their distance from the calf.

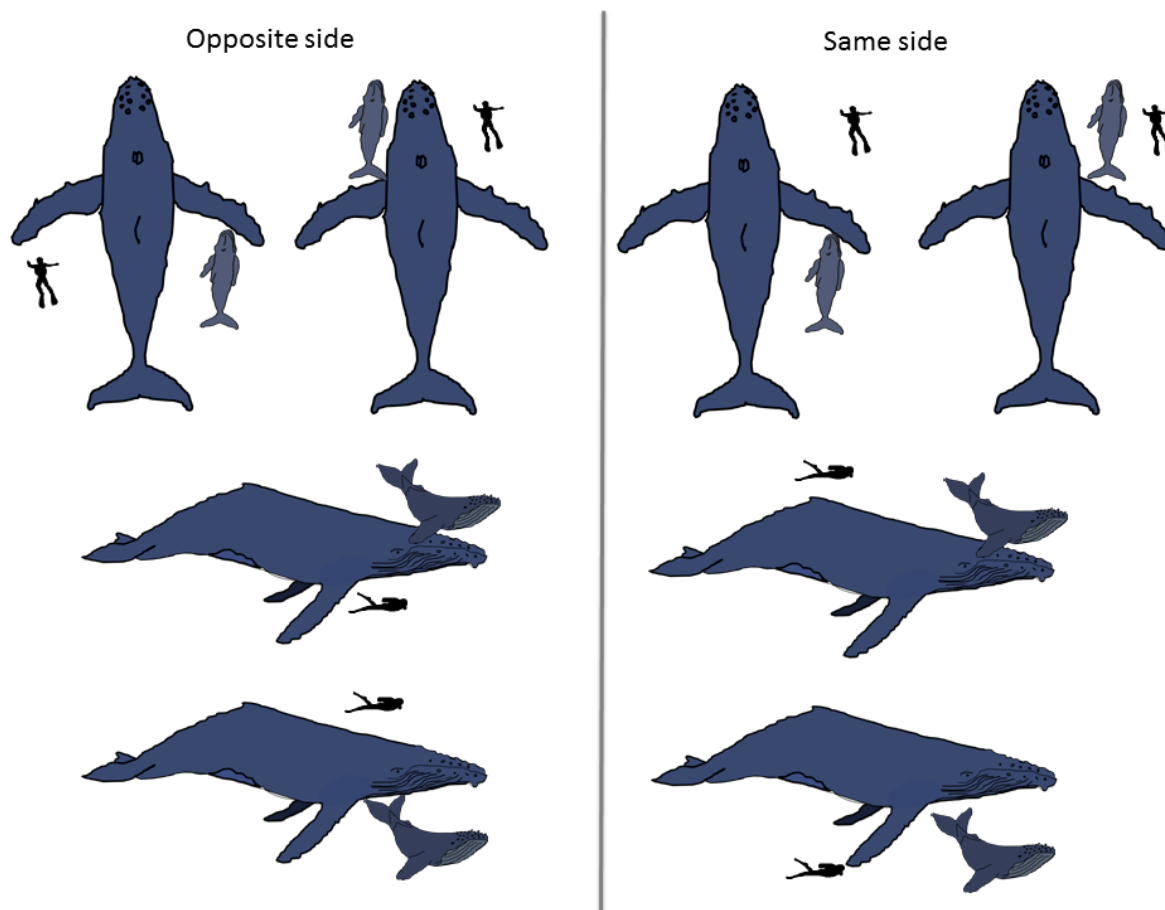


Figure 2: A schematic representation of free divers based on calf's position (same or opposite side).

RESULTS

Calves' position

Analysis on all groups pooled together

Our analysis performed on 91 mother-calf pairs showed that the positions cumulating the longest durations were « Above Right » (ABR=01:16:48) and « Above Left » (ABL=01:21:52). Wilcoxon tests performed for each category showed that the durations for “Above” positions were significantly different from all others (see supplementary Table 1, Chapter 4a). However,

there was no significant difference between “Above Right” and “Above Left” positions (test χ^2 , $ddl=1$, $\chi^2=0.16$, $p=0.68$).

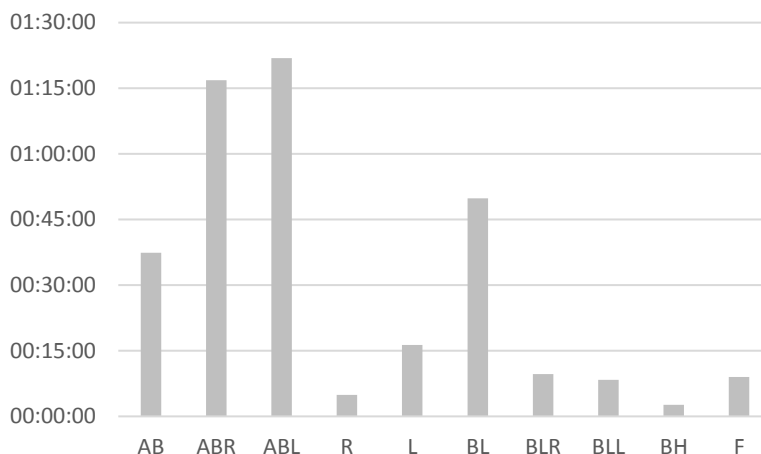


Figure 3: Sum durations for each of the 10 positions for all groups (AB: above, ABR: above right, ABL: above left, R: right, L: left, BL: below, BLR: below right, BLL: below left, BH: behind, F: in front).

Positions “Above” (AB= 00:37:22) and “Below” (BL= 00:49:50) were chosen secondly by calves. No significance difference between these 2 categories was found (test χ^2 , $ddl=1$, $\chi^2=1.74$, $p=0.18$). Right and left positions showed similar average durations and there was no significant difference (test χ^2 , $ddl=1$, $\chi^2=3.39$, $p=0.06$).

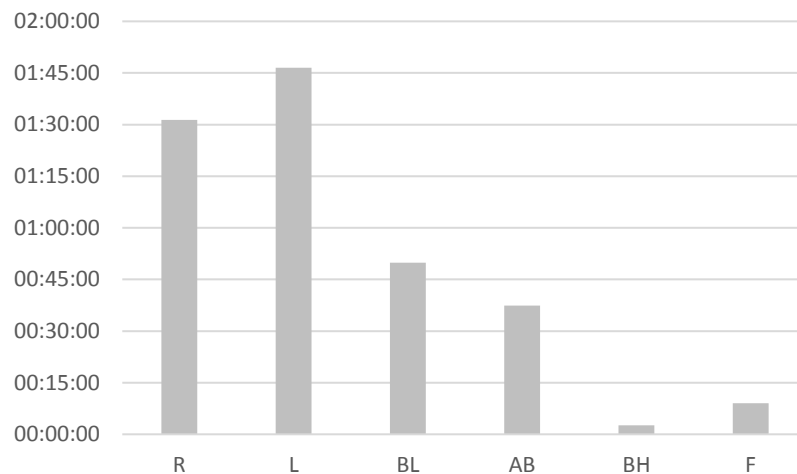


Figure 4: Sum durations for the 6 main positions: pooled right positions (R), pooled left (L), below (BL), Above (AB), behind (BH) and in front (F) for all group together.

Analysis at the group level

At a group level, we now considered the 91 different groups. When a given group presented several videos, an average of the position duration was calculated. Through this prism, the same pattern was found (see supplementary Table 2, Chapter 4a). Considering means per group of the position durations, the main calf's position choices around the mother were "Above left" (00:47:30) and "Above right" (00:44:27); followed by "Below" (00:30:36) and "Above" positions (00:18:41).

However, as for the summation per group, main position durations "Above left" vs. "Above right" were not significantly different, as well as for the second choices "Below" vs. "Above" (respectively, test χ^2 , $ddl=1$, $\chi^2=0.10$, $p=0.75$ and test χ^2 , $ddl=1$, $\chi^2=2.93$, $p=0.08$). Similarly, when pooling all right positions together as well as the left positions, no significant difference was found in their durations (test χ^2 , $ddl=1$, $\chi^2=1.32$, $p=0.24$) (Figure 5).

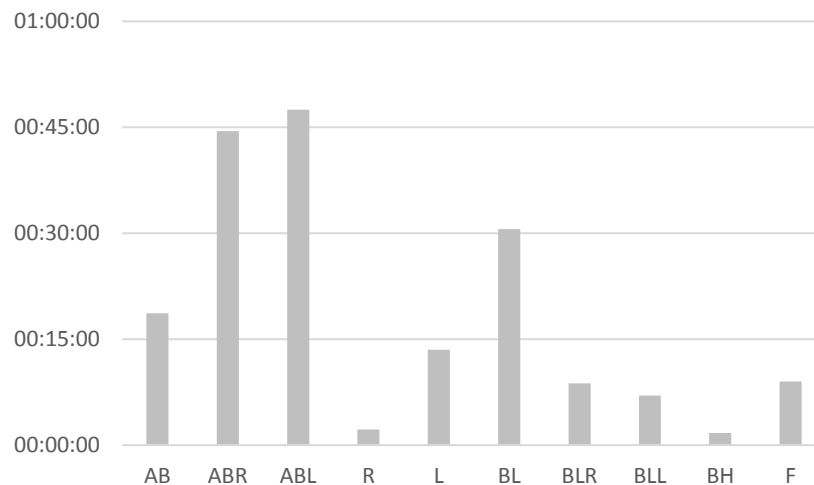


Figure 5: Average durations per observed group for the 10 studied positions (AB: above, ABR: above right, ABL: above left, R: right, L: left, BL: below, BLR: below right, BLL: below left, BH: behind, F: in front).

Impact of diver's position on calves' positioning

Results show that free divers position did not influence the position of the calf. Besides, the position durations where calves and free divers were on the same side of the mother (Same Side= 01:13:07) and those where the mother was between them (Opposite Side= 00:55:17) did not show any significant difference (test χ^2 , ddl=1, $\chi^2=2.50$, $p=0.11$). Calf-diver configurations that placed them on the same axis ("Same Side" and "Opposite Side") were significantly less frequent than all the other configurations (test χ^2 , ddl=2, $\chi^2=74.72$, $p=5.93E-17$). We did not find any effect of the freediver's position on the calf positioning around the mother. Indeed, whatever the behaviour of the freediver, either willing to interact with the calf or keeping distance from the calf, no significant differences between the position durations between "Same side" and "opposite Side" were found (test χ^2 , ddl=1, $\chi^2=0,00053$, $p=0,98$ and test χ^2 , ddl=1, $\chi^2=3.43$, $p=0.06$, for interaction or neutral behaviour respectively) (Figure 6). Regarding the behaviour of free divers towards the calves there was mostly a motivation to interact with the calf (test χ^2 , ddl=1, $\chi^2=101.57$, $p=6.87E-24$).

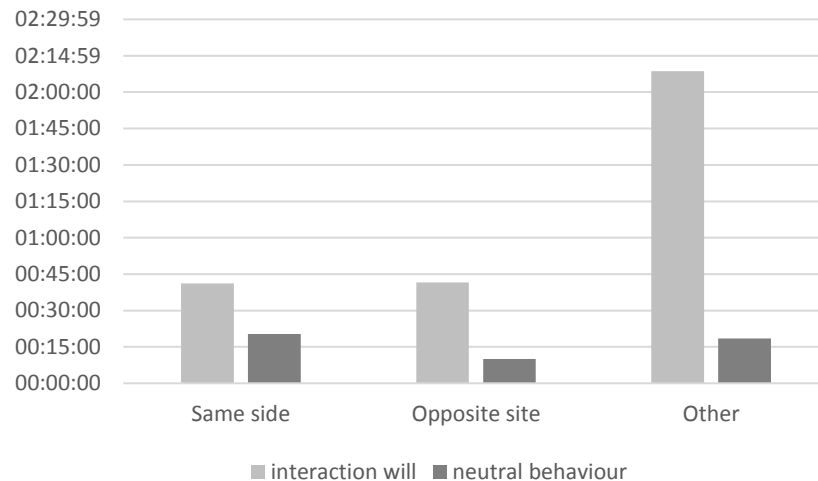


Figure 6: Position durations of the diver-calf dyad in 2 different freediver contexts (i.e., freediver willing to interact with the calf: “interaction will” or the free divers keeping distant from the calf “neutral behaviour”).

DISCUSSION

This study investigates initiative and preferential position of the young calves (i.e., less than 3-month old) around the mother during surface activities. Only two calves were new-borns with one being 2-hours old. Mother-calf dyad position is critical during calves early ages, as proximity must be maintained during travelling, surfacing and diving activities. In other cetacean species such as bottlenose dolphins, it has been demonstrated that some calves’ positions provide locomotor advantages (Noren and Edwards 2011). Here, calves prevailing positions were “Above Right” and “Above Left” during static and traveling behaviour. Being above the mother near the rostrum allowed the mother-calf pair to keep visual contact during static behaviour. While traveling, these positions could be explained as a strategy used to benefit from the aspiration flow or “drafting effect of swimming” (Chatard and Wilson 2003) produced by the mother’s movement which creates a pressure wave around her while diving or traveling. This drafting effect is beneficial to the calves only if they stay close enough to their mother. Calves back-riding have been reported recently in blue, fin and Gray whales, and this supports

the hypothesis of adaptive benefits of locomotion energy savings for calves (Smultea *et al.* 2017). For humpback whales that have a large and mobile lek mating system (Clapham 1996), females accompanied by their calf are exposed to breeding males. Association with groups of multiple males increase mother-calf traveling behaviour and thus energy expenditure (Cartwright and Sullivan 2009a). In the case of a very large lek such as population migrating along Madagascar's breeding area (Cerchio *et al.* 2016), humpback whales travel long distances during the breeding season and females accompanied by their young calf can travel up to 100 km in 24 hours (Dulau *et al.* 2017; Trudelle *et al.* 2016). Keeping a position above and close to the mother allows calves to move securely, controlling their space orientation and reducing energetic expenditure while having the same swim performance level as their mother. The second main position observed is below (rostrum and flipper) that corresponds mostly to calves resting behaviour and occasionally below caudal peduncle although there was no nursing behaviour observed. Humpback whales are well known for their ability to maintain perfect floatability during resting and singing behaviours, showing a head-down position (Adam *et al.* 2013). Controlling their floatability is one skill that calves must acquire during their early stage of life. Thus, staying below the mother provides a secure place to rest and pause when calf's floatability is not yet well controlled, but it also allows the pair to maintain physical contact.

In contrast to what was described in the literature for odontocetes species, calves' lateralization regarding their position around the mother appears to be absent in humpback whales. Even though lateralization has been observed in humpback whales for some active surface behaviours such as flippering (Clapham *et al.* 1995) and potentially for nursing (Zoidis and Lomac-macnair 2017), our results should be considered with caution as further work with larger sample size is required to confirm these results.

The assessment of simultaneous calf and free diver positions revealed no significant impact on the calf positioning to get close or away from free divers. The presence of free divers seems to not have an effect of attraction or repulsion on the calf. This suggests that the free diver presence does not have direct and visible impact on the calf positioning. But this does not mean that other non-behavioural impacts could not occur such as physiological stress. Furthermore, it has been shown that in interaction with divers, the mother was moving closer to her calf when the calf produced a series of *grunt* sounds considered as an alarm signal (Zoidis *et al.* 2008). In the present study, only one scream (a mid-frequency harmonic sound) has been heard while free divers were very close to the calf. We could not assess the behaviour of the mother following this calf's sound production as the mother was not in the visual field of the camera. From our sample, we did not observe other calves producing such alarm calls, so it suggests that in general free divers did not have an impact on the calves' behaviour. However, our sampling method did not allow us to observe all mothers' behaviours and their sound production (especially low-frequency sounds, Saloma *et al.* in revision), so further investigations are needed to explore laterality in mother-calf interactions.

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CHAPTER 4b: Mother-calf spatial relationships in humpback whales



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Left or right, near or far? Mother-calf spatial relationships in humpback whales.

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In preparation for Animal Cognition

ABSTRACT

Humpback whale females accompanied by their neonates are rarely distant from one to another and close relationships link the pairs. Here, we analysed aerial video recordings to define their spatial relationship during the calf's early stage of life in the Sainte-Marie channel breeding ground. We investigated lateralization behaviour between pairs, considering spatial positioning initiated by calves during static and slow travel behaviours, in presence or absence of escorts. By using photogrammetric methods, we measured both mother and calf body lengths, and defined the spatial range of the calf around its mother. Analyses performed on 65 groups showed that when the pairs were alone, calves were evenly situated to the right or left side of their mothers, whereas in presence of escorts, calves showed a right-biased positioning towards their mother. Using photogrammetric, we measured mother-calf body lengths for 25 pairs. Mothers' lengths were an average of 13.9 meters and calves 5.7 meters; these measures were similar to that observed from another breeding area. Finally, the measure of calves' spatial range around their mothers provides more information on their close relationship. The mean distance between the pair was about 7 m and rarely exceeds 20 m. Newborn calves spend much time lying on or close to their mothers' rostrum.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan species performing annual migrations between low latitude breeding grounds and high latitude feeding grounds. Humpback whales are known to exhibit social behaviours in both areas. One of the most organized social behaviours is their cooperative lunge feeding behaviour, in which many individuals display synchronized behaviour coupled with vocal production (Jurasz & Jurasz 1979; Cerchio & Dahlheim 2001; Stimpert *et al.* 2012). Humpback whales do not live in stable social groups (Clapham 1996). On breeding grounds, their group composition consist of an ephemeral cluster ranging from two individuals to large groups of whales which are most of the time characterized by males' aggressive behaviours for access to a female (Baker & Herman 1984; Tyack & Whitehead 1982; Baker *et al.* 1985). Whether on breeding or feeding grounds, the only stable social association is the mother accompanied by her own calf. This pair generally lasts for almost a year and half (Baker *et al.* 2000; Clapham & Mayo 1987; Straley *et al.* 1994). As in many gregarious terrestrial mammals, humpback whale mothers use the “follower strategy” (Lent 1974; Taber & Thomas 1982; Szabo & Duffus 2008; Tyson *et al.* 2012) in which females and their dependent calves move side-by-side in their environment. Animals presenting laterally placed eyes (or relatively little binocular overlap) express brain lateralization through pronounced one-sided behavioural biases (Vallortigara *et al.* 1999). Cerebral lateralization requires simultaneous but separate use of both hemispheres, which enhances brain efficiency in cognitive tasks (Rogers *et al.* 2004). In many mammal species including marine mammals, the right-hemisphere of the brain plays an important role in social processing, thus a right-side social lateralization pattern has been observed in mother-offspring interactions (Damerose & Vauclair 1973; Manning & Chamberlain 1990).

In captive belugas, continuous visual contact is more important in mother-calf interactions than tactile ones, and these contacts are initiated by calves (Karenina *et al.* 2010). In wild belugas, calves present a highly significant right-side swimming position preference with their mothers (Karenina *et al.* 2010; Yeater *et al.* 2014; Hill *et al.* 2017). As in belugas, dolphin mother-calf pairs maintain right-side visual contacts and mothers seem to be partially responsible for maintaining proximity to their calves (Mann & Smuts 1999; Lyamin *et al.* 2007). The same right-side infant position preference has been observed in wild orcas (Karenina, Giljov, Ivkovich, *et al.* 2013). In contrast, sperm whale (*Physeter microcephalus*) calves do not follow this rule and show a bias to mothers' left side, a distinction that could be explained by the unique blowhole displaced to the left side, and a probable calves nasal suckling (Karenina *et al.* 2010).

Both mother and infant potentially influence lateralisation behaviours (Scola *et al.* 2013), however, in most studied Odontocetes species, the positional asymmetry in a mother-calf pair results from the choice made by the calf (Karenina *et al.* 2010). Lateralized behaviours in mysticetes have been poorly investigated and thus no conclusion has been drawn. Adults humpback whales were reported to exhibit behavioural asymmetry during bottom-feeding behaviours using a right-biased turning position (Clapham *et al.* 1995). The same right-bias was reported in humpback whale calves suckling behaviours (Zoidis & Lomac-macnair 2017), and southern right whale (*Eubalaena australis*) calves were described to be right-biased positioned regarding their mothers (right whale data was only obtained from photographs) (Karenina *et al.* 2017). As in terrestrial followers, humpback whale mother-calf pairs maintain a very close spatial proximity. For instance, they exhibit very well synchronised dives on both feeding and breeding grounds (Szabo & Duffus 2008; Tyson *et al.* 2012). The mother-calf proximity seems to change over time, and as calves get older, the distance between them increases (Szabo & Duffus 2008). On feeding grounds, it has been reported that mothers and calves stay within a

maximum of 50m (Tyson *et al.* 2012). On breeding grounds, it can therefore be important to relate the mother-calf proximity distance with the size of the calf. Humpback whales at birth were reported to be one third the size of their mothers (Ferreira *et al.* 2011; Faria *et al.* 2013) and a mean body length at birth of 4.5 m was stated by (Chittleborough 1958). Calves increase both their body length and weight during the first months, and an estimation of their size using body length can be important to better interpret their general behaviour.

Certain difficulties in studying large whales' behaviour have been resolved recently by the use of new technologies, which facilitate learning about their diving activities or surfacing behaviours. Different cutting-edge devices have recently been made available to reduce the impacts of observers on the behaviour of wild animals. Here, we use aerial drones to observe humpback whale mother-calf surfacing behaviour on their breeding ground. Videos were analysed to define if humpback whale calves present lateralized behaviour toward their mothers. By using photogrammetric methods, we also measured mother-calf body length and we estimated the horizontal space used by calves around their mothers at the early stage of their live.

METHODS

Study site and data collection

This study was conducted in Sainte-Marie channel, Madagascar during humpback whale breeding season from July to September 2017. Video footage was obtained using 3 different models of drones: DJI Phantom 3, DJI Phantom 4 and the DJI Mavic pro. For each drone a dual battery was used to increase sampling effort as they have an autonomy of ~25 min. To approach

mother-calf pairs, a rigid boat TM 21 model (2.35 m width and 6.5 m long) equipped with a 115 HP engine was used. A day-trip was organised when the weather allowed us to use the drones (Beaufort scale ≤ 3 corresponding to gentle breeze, wind speed of 12 km/h, wave height varying from 0.2-0.5 m). At least 2 drone pilots were present on the boat. When a static or slow traveling mother-calf group (accompanied or not by single or more than 2 individuals) was spotted, the boat started to reduce speed at an 800 m distance from the group and a slow approach was performed until the boat was at about 300 m distance from the targeted group. Prior to drone deployment, the behaviour of the mother-calf group was observed for 10 to 15 min and the target group composition was noted: MC for lone mother-calf, MCE for mother-calf accompanied by one escort and MCES for mother-calf accompanied by 2 escorts or more. Drones were only deployed when groups did not change their behaviour towards the approaching boat. The boat was kept less than 300 m from the mother-calf group to provide clear sight of drones and to facilitate positioning over the pairs. The altitude of the drones varied from 6 to 30 m with an average of 16 m. Altitude was chosen depending on behavioural context, needed details on the whales and environmental parameters (wind direction).

Data were collected under national permit n° 26/17-MRPH/SG/DGRHP delivered by the Ministry of Fisheries Resources Madagascar.

Lateralised behaviour in calves

Video file analysis

A total of 20 trips were performed and allowed us to obtain video recordings from 65 groups. Each group was filmed several times as the drones had limited battery life. An average of 3 videos per group were analysed, and we considered only the sequences in which the group was visible. Thus, we analysed sequences of a total duration of 19:48:15 (mean duration 00:05:17

± 00:04:10). The analysis started the moment the group was sighted and ended when the group dove and we lost them or when the recording ended (no more battery). Video recordings were analysed by using GOM Player© version 2.3.26.5283. This software provides precise temporal analysis of each recorded video (i.e., 1-sec step video analysis). For consistent interpretation of results, only spatial positions initiated by calves towards their mother were considered in the present study. The position of the calf in regards to the mother was defined using 10 grid positions: AB (above) when calf is located above the rostrum or the back of its mother, BL (below) when calf is located below the mother, whether below the rostrum or the ventral part of its mother, IF (in front) when calf is located in front of the rostrum, BH (behind) when calf is behind the caudal fin, R1-R2-R3 when calf is located on the right side of its mother and next to the rostrum, pectoral fin or caudal fin respectively, and L1-L2-L3 when calf is on the left side of its mother and next to the rostrum pectoral fin and caudal fin respectively (Figure 1). The duration of these 10 positions were measured for each studied calf.

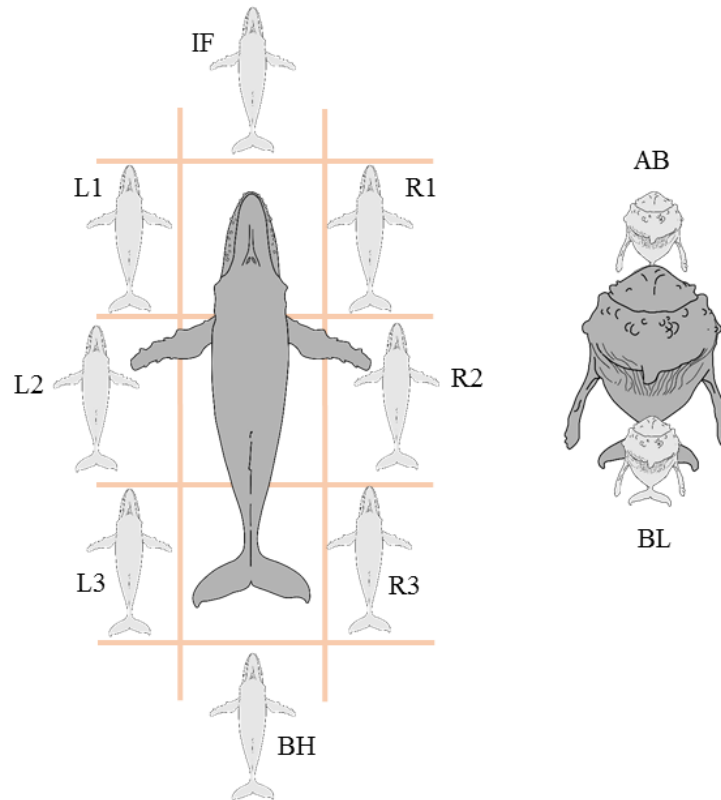


Figure 1: Schematic presentation of the 10 potential positions of the calf around its mother (AB: above, BL: below, IF: in front, BH: behind, R1-R2-R3: mother's right side and L1-L2-L3: mother's left side).

We also measured the duration of mother-calf's other behaviours in the analysed sequences and noted DB (dive both) when both the mother and the calf dove together and thus were not visible on the surface, DC (dive calf) when the calf dove (not visible at the surface) and its mother was still visible at the surface, DM (Dive mother) when the mother dove and only her calf was still visible at the surface.

Statistical Analysis

For statistical analysis, the duration of all positions were standardized and transformed to percentages. We performed Kruskal-Wallis tests to compare percentages among the different positions, and if significant, this was followed by multiple pairwise comparisons using Mann-

Whitney U-tests to detect significant differences between calves' positions and others behaviours. P-values were corrected using Bonferroni correction. To detect any side preferences in calves, we performed our analysis in two different ways. In the first analysis, we pooled all data without focussing on mother-calf groups (i.e., MC, MCE, and MCEs). We pooled the durations for R1+R2+R3 positions to calculate a total duration for "right side" and L1+L2+L3 for a total duration for "left side". Chi-squared tests were then carried out to compare left and right proportions.

A second analysis was performed on each separate video file and for each mother-calf group, to assess the lateralization behaviour at a group level. Chi-squared tests were carried out to categorize each video in 3 different classes: class L (left) when left side duration was significantly longer than right side, class R (right) when right side duration was significantly longer than left side, and class N (neither left nor right) when no difference between left and right positions durations was found. We compared the number of video files showing these 3 classes (L, R and N) using chi-squared tests. Finally, to assess if the number of videos presenting lateralized behaviour (right and left) is influenced by mother-calf group composition (MC, MCE and MCEs), we performed Kruskal-Wallis tests.

Calf spatial range around the mother

Data quality

To measure mother-calf body length and calves' spatial positioning, a photogrammetric method was used to analyse photographs extracted from drone video footage. To obtain accurate measurements, groups in which we could not obtain at least 2 completely vertical images with the contour of the animal's body in the water clearly visible in the photographs were excluded

from the analysis. Each photograph in which measurements were performed was measured twice, by two independent researchers.

Image calibration

Image calibration was made from images of known-sized objects, following the method described by (Jaquet 2006). The reference used here was the TM 21 rigid boat used during data collection. The 6.5-m boat (we consider only the length of the hull of the boat, without the engine) was photographed with the drone positioned in a vertical position above the middle of the boat and pictures were taken at different altitudes 6, 10, 15, 20, 25 and 30 m. Viewing the photographs in Inkscape© version 0.92.2 and using the measuring tool we performed pixel measurements of the boat from end to end, using all six altitudes. The number of pixels in the photographs per meter, was obtained as follows:

$$\text{Meter/pixel (m/px)} = \text{boat real length} / \text{length in pixel in the photograph}$$

A Pearson correlation test carried out between altitudes and the number of meters/pixels, and a correlation coefficient of 0.9981 was found. From the linear regression, we obtained the relation between altitude and meter/pixel as follows in equation 1:

$$m/px = 0,0008103 * \text{Altitude} + 0,0002335$$

Real length in the picture was thus obtained from equation 2:

$$\text{Real length} = (0,0008103 * \text{Altitude} + 0,0002335) * \text{number of pixels}$$

Table 1: Boat measurements in m/px corresponding to defined altitudes

Altitude(m)	Mesure 1 (px)	Mesure 2 (px)	Mean (px)	Boat real length (m)	m/px
6	1353	1354	1354	6.5	0.0048
10	675	674	674	6.5	0.0096
15	467	468	467	6.5	0.0138
20	369	369	369	6.5	0.0175
25	292	291	291	6.5	0.0222
30	246	246	246	6.5	0.0263

The measurement of the boat at different altitudes shows an average difference of 29.1 cm with respect to the boat's actual size. Thus, the variation is about 4.5 % and the measures were more precise between altitudes of 20 to 30 m (Figure 2).

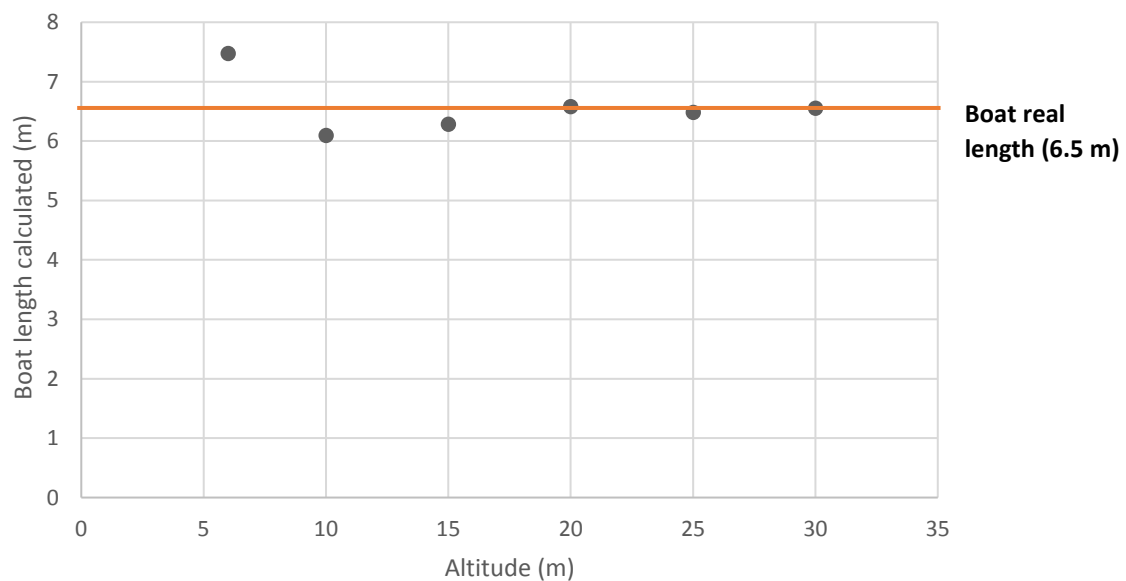


Figure 2: Relationship between the altitudes (m), the length calculated (m) and the boat real length (m).

Body length measurements

For each group, we used both the vertical photographs in which mother-calf were straight and their contours clearly visible. For each photograph, relative length (in pixels) of the mother and her calf were measured twice, and again by two independent researchers and the mean of all 4 measurements was used as the relative length estimate. Whales' absolute measurements (in meters) were obtained by following the same meters/pixel measurements described above. For each group we measured mother's total length (TL), and calf's total length (tl) by measuring the distance from the rostrum tip of the snout to the notch in the fluke (Figure 3).

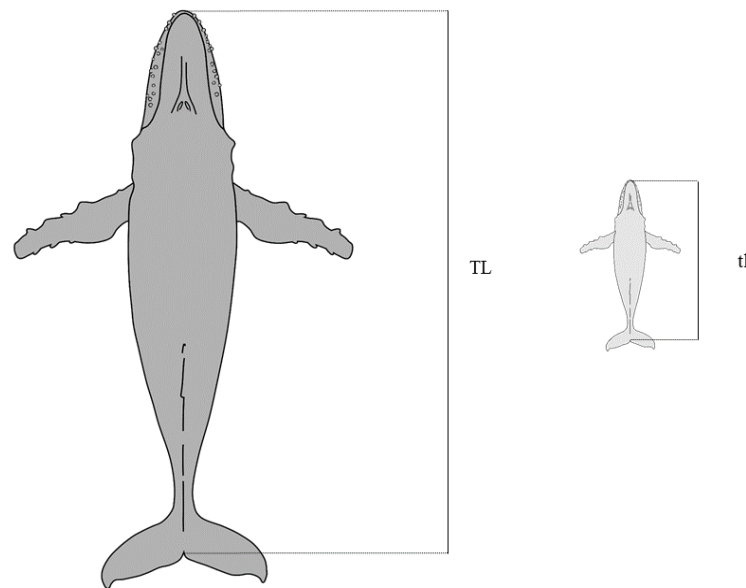


Figure 3: Schematic presentation of mother-calf measurements (TL: mother's total length, tl: calf's total length)

Surface used by the calf around the mother

From the total duration of the analysed video sequences of each group, image captures were taken every 30 seconds, as from field experiences it has been noticed that calves rarely exhibit fast moving behaviours, especially during static or slow travelling of the pair.

We used Autodesk Autocad 2014 SP1© Software to estimate mother-calf distance measurements. We scaled each image captured by using the following equation:

$$\text{Meter/pixel} = \text{mothers real TL} / \text{mothers TL in the photography}$$

These m/px values were used to perform Autocad measurements: we converted pixel measures in meters to obtain Autocad unit (1 meter = 1 Autocad unit). To obtain calves' spatial location around their mothers, we created points in Autocad related to calves' dorsal fins and placed them individually for each photo and for each group. Then, we placed the mothers in a (x, y) axis plan; mothers' dorsal fins were considered as point 0 (x_0, y_0) and the rostrums was turned to +y axis (Figure 3). Photos of groups that did not match this configuration were then rotated to turn the rostrum into the +y axis. Then, we placed all calves' points (that correspond to calves' dorsal fins) around their respective mothers. Finally, x and y coordinates for each calf's position, generated automatically from Autocad, were extracted into an Excel file which allowed us to measure distance $R = \sqrt{(x^2 + y^2)}$ (Figure 4). To obtain a final representation of calves' positions around their mothers, we polled all calves' position and related them to one mother measuring 14 m (mothers mean length in our study).

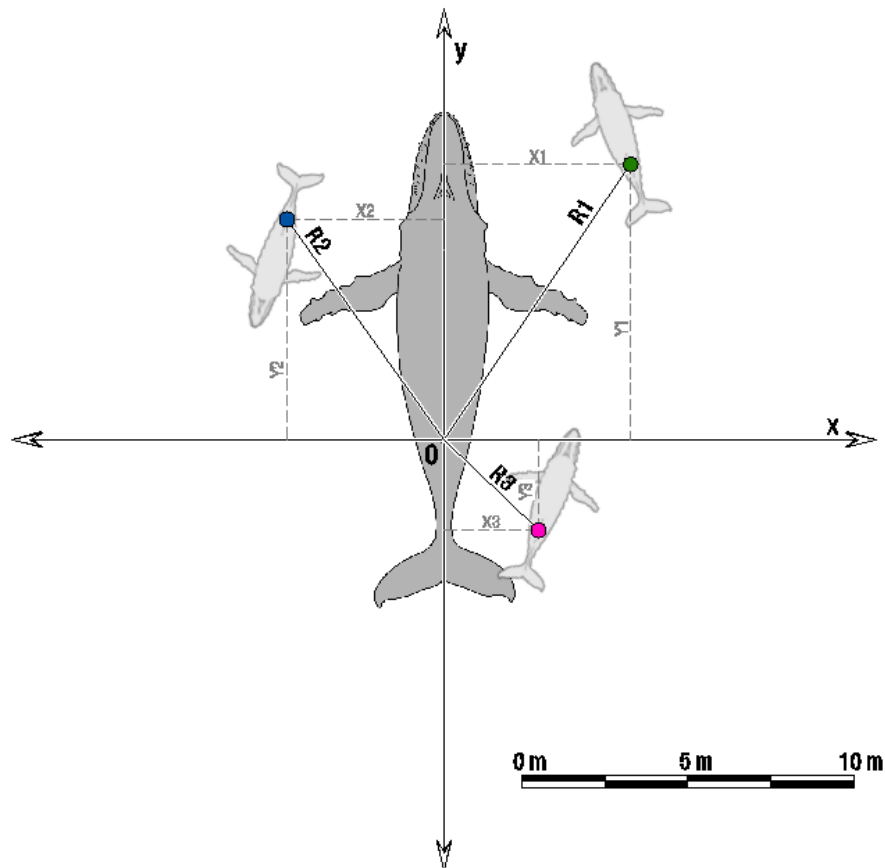


Figure 4: Measurements performed in Autodesk Autocad 2014 SP1 ©. Mothers' dorsal fin placed at (x_0, y_0) and rostrum oriented to $+y$ axis; points placed on calves' dorsal fin allowing to obtain (x, y) values to calculate radius of calves' positioning.

Statistical analysis

The body sizes of calves were classified into two classes: class 1 represented calves less than 6 m long, and class 2 included calves longer than 6 m. We thus performed Kruskal-Wallis tests to assess if the surface used by calves around the mother varies with calf body length.

The mean value of the radius of each calf's positioning towards their mother was obtained and Kruskal-Wallis tests were used to assess the variation of spaces used by calves according to their lengths (class 1 and class 2).

With all calves' positions around the mother pooled together, we divided space around the mother in 4 parts: S1= in front left, S2= in front right, S3=back left and S4=back right (Figure 9). Chi-squared tests were used to compare the number of calves' position located in these predefined surfaces around their mothers.

RESULTS

Lateralsised behaviour in calves

For each noted position adopted by calves and behaviour adopted by pairs (whether the calf or the mother or both were diving), we obtained the following mean repartition in percentages: DC=6.66, DM=10.85, DB=14.47, AB= 6.19, BL=3.20, IF=0.98, BH=0.08, L1=12.59, L2=12.23, L3=1.09, R1=15.35, R2=15.95 and R3=0.36 (Supplementary Table 1 and Figure 5). Calves prevalent positions around their mothers were R2, R1 and L1, L2 and there was no significant difference among these four main positions (χ^2 test: ddl=3; $\chi^2= 0.76567$; $p = 0.8577$).

When we pooled the L1+L2+L3 positions to constitute the "left side" and R1+R2+R2 to constitute "right side" on all videos, the percentages for left side and right durations were 31.65% and 25.91% respectively (Figure 5), and no significant difference was found between these two positions (χ^2 test, ddl=1, $\chi^2=0.5724$, p-value = 0.449).

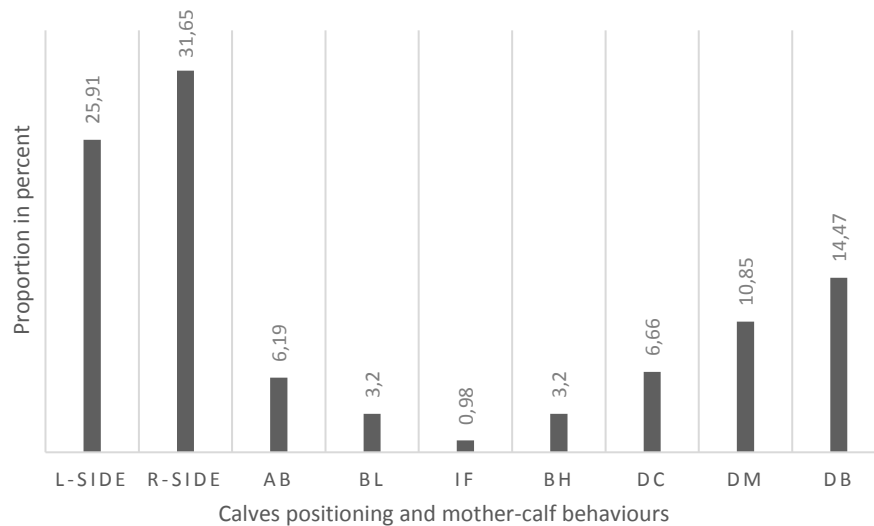


Figure 5: Calves' positioning duration (L-side: L1+L2+L3, R-side: R1+R2+R3, AB: above, BL: below, IF: in front and BH: behind) and mother-calf behaviours (DC: Dive calf, DM: Dive mother and DB: dive both) in percentage for all pooled video files.

Taking positions “left side” (L1+L2+L3) and “right side” (R1+R2+R2) into account when we analysed each video separately, 70 videos were categorised as L class (left side significantly longer than right side), 95 videos as R class (right side significantly longer than left side) and 47 videos as N class (no significant difference in duration between left and right side). When we compared these three classes, the number of videos with lateralisation (either L or R) was greater than the number of video without (N class) (test χ^2 , ddl=1, $\chi^2=65.67$, p-value < 0.00001). Then, when comparing the number of videos with L and R class, the difference was not significant (test χ^2 , ddl=1, $\chi^2=3.78$, p-value = 0.05163).

When we compared the number of videos of L and R classes taking group composition into account the group type (Figure 6), we found that for MC groups, L and R positions showed similar proportions (test χ^2 , ddl=1, $\chi^2=0.65$, p-value = 0.419); for MCE groups, R class showed a greater proportion than L class (test χ^2 , ddl=1, $\chi^2=11.364$, p-value = 0.000749); and finally for MCEs groups, R class also had greater proportion than L class (test χ^2 , ddl=1, $\chi^2=5.33$, p-value = 0.0209).

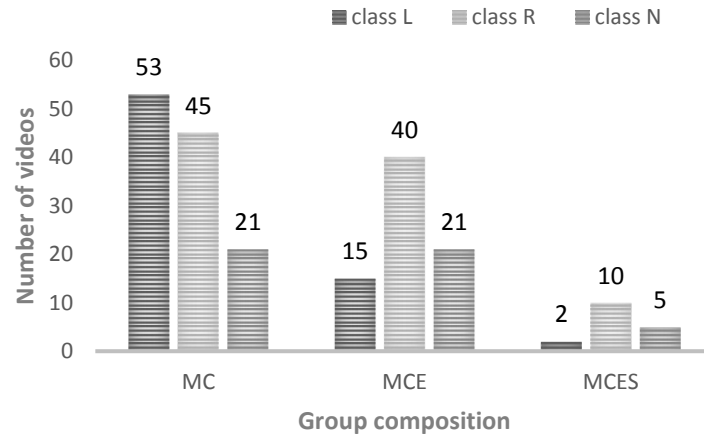


Figure 6: Number of videos in class L (*left*), R (*right*) and N (*no lateralization*) according to group composition (MC: mother and calf, MCE: mother-calf accompanied by one escort, MCEs: mother and calf accompanied by two to three escorts).

Moreover, we found that group composition has a significant effect on calf position, with calves tending to stay on the right side of their mothers when they are accompanied by one or several escorts (Kruskal-Wallis tests for the right side proportions: $\chi^2 = 30.43$, $df = 2$, $p\text{-value} = 0.00001$; and left side proportions: $\chi^2 = 1.94$, $df = 2$, $p\text{-value} = 0.3777$; Figure 7).

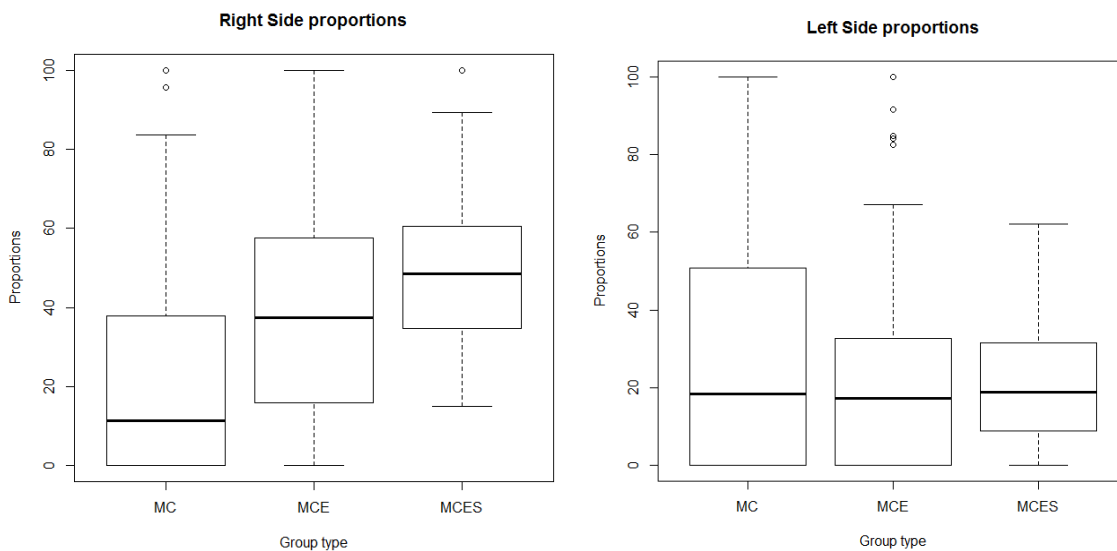


Figure 7: Proportion of right and left side position in calves depending on group composition (MC: mother and calf, MCE: mother-calf accompanied by one escort, MCEs: mother and calf accompanied by two to three escorts).

Mother-calf body lengths

Over the 65 groups recorded, only 25 met our criteria and were measured. We extracted 2 totally vertical photos of each mother-calf pair and measured the body lengths of these 25 females accompanied by their calves. Females body lengths ranged from 10.58 m to 18.3 m (mean 13.88 ± 0.75 m) (Figure 8a). Calves body lengths ranged from 4.46 m to 7.06 m, (mean 5.75 ± 0.25 m) (Figure 8b). Among the 25 measured calves, 16 belonged to class 1 (< 6 m) and 9 to class 2 (> 6 m).

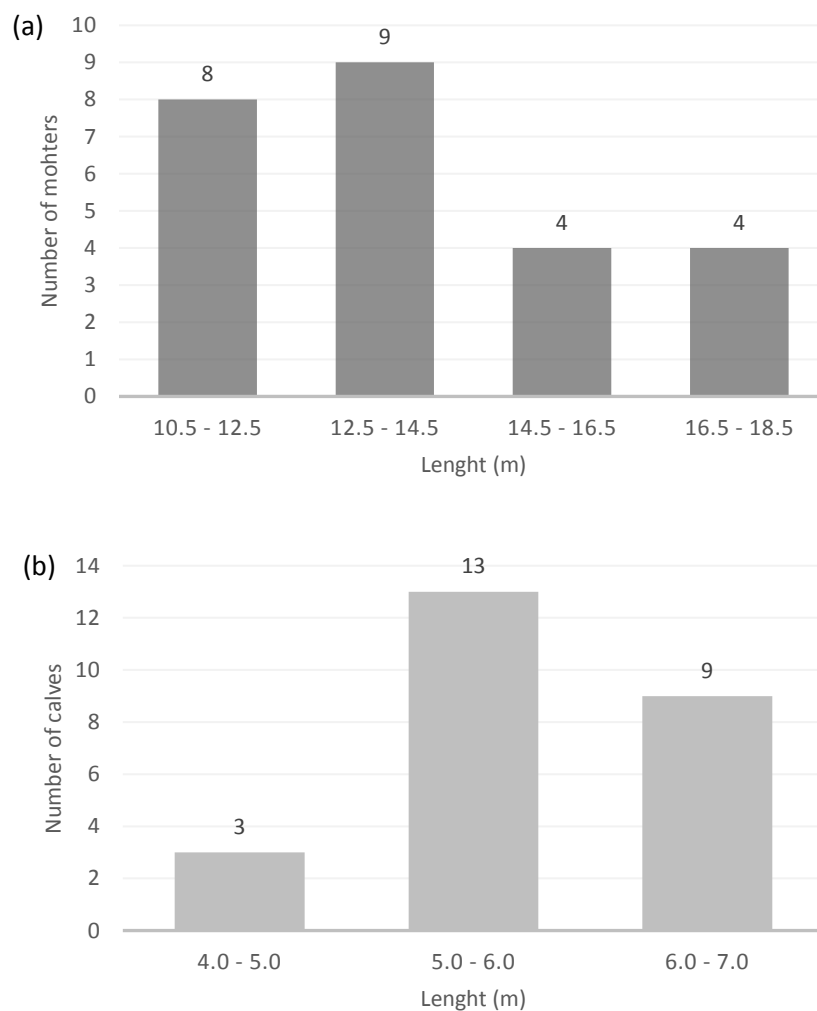


Figure 8: Length distributions of measured mother-calf pairs. (a) mothers ($n=25$) and (b) calves ($n=25$).

Calves' spatial range around their mothers

When we calculated the radius starting from mothers' dorsal fins to calves dorsal fins for each mother-calf group, the mean distance measured was 7.21 ± 3.20 m, with a minimum of 0.98 m and a maximum of 20.05 m. The surface around the mother used by calves in this study is ~ 345 m². When we polled all calves' positioning around their mothers, and considered the space around the mothers divided in 4 parts (S1, S2, S3 and S4), calves significantly used S1 and S2 locations (in front positions) more than S3 and S4 (behind positions) (χ^2 test; $\chi^2=486.29$ df =3, p-value < 0.00001) (Figure 9).

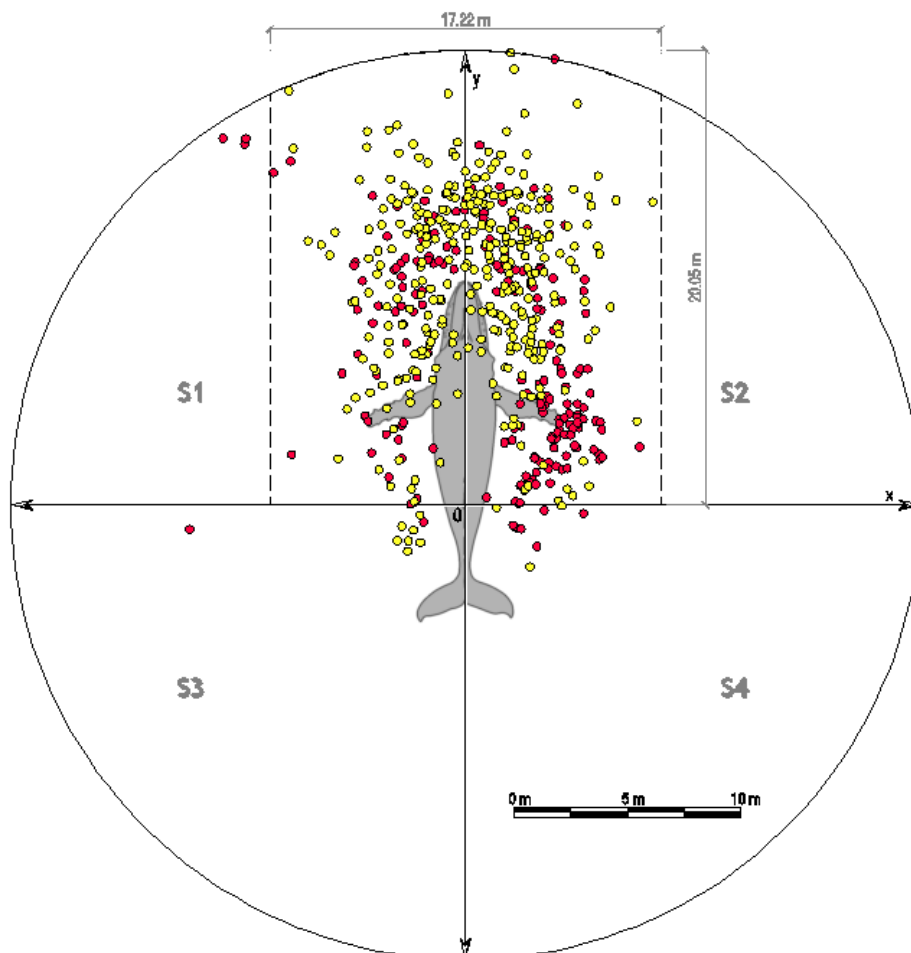


Figure 9: Presentation of the space around the mother used by calves; calves < 6 m positioning are shown in yellow and calves > 6 m positioning are shown in red.

Statistical analysis shows that spatial range used by calves around their mothers varies with calf's class (Kruskal-Wallis tests $\chi^2 = 3.968$, $df = 1$, $p\text{-value} = 0.0463$). The difference obtained here is nearly meaningless especially with the limited number of samples.

DISCUSSION

The aim of this study was to investigate humpback whales' mother-calf surface behaviours. Our data sampling was focused on static and slow travelling behaviours and analysis was mainly oriented toward calves' initiatives. One limiting factor in using UAVs is their limited autonomy. For the 3 drones we used here, autonomy was about 25 min, and during data collection, we spent about 5 to 7 min to start and position the drone vertically above the studied group, 5 – 7 min more to bring the drone back to the boat, so finally only 10 – 15 min could be dedicated to recording whales' behaviours. This explains why the mean duration of the analysed sequences was 5 min.

We filmed the studied groups from altitudes ranging from 6 to 30 m with an average of 16 m. Even though we had only 4 cases in which the drones were less than 10 m, we did not detect any behavioural responses of the animals toward the UAVs. Other studies from other areas and another species of large whales also report similar observations (Christiansen *et al.* 2016; Nowacek *et al.* 2016; Christiansen *et al.* 2014).

Left or right?

Behavioural lateralization resulting from brain asymmetry is shared by many species (Vallortigara *et al.* 2011; Salva *et al.* 2012). For mammals that have laterally placed eyes such as cetaceans, the expression of brain lateralisation through one-sided behavioural biases is especially pronounced. Our findings show spatial lateralization behaviour in a young baleen

whale. In this study focused on behaviours performed by calves, we found that calves did not exhibit left or right biased behaviour when the pairs were alone during static or slow traveling behaviour. However, in presence of one or several conspecifics (i.e., escorts), calves presented a right-biased lateralized behaviour towards their mothers. In many non-human mammals, the right hemisphere exhibits a dominant role in the monitoring of conspecifics (Bourne & Todd 2004; Salva *et al.* 2012) and highly lateralized behaviours were described in animals living in social groups. For instance, for many Odontocetes species living in social groups, right-biased lateralized behaviour has been observed in mother-calf association (Karenina *et al.* 2010; Karenina, Giljov, Glazov, *et al.* 2013; Blois-Heulin *et al.* 2012; Karenina, Giljov, Ivkovich, *et al.* 2013). For species evolving in a social group, conformity to lateralized behaviours provides enhanced escape performance (Lippolis *et al.* 2005) and calves usually initiate changes in position in relation to their mothers and are responsible for maintenance of the spatial asymmetry (Karenina, Giljov, Glazov, *et al.* 2013). Female mysticetes raise their calves alone, not within a social group as odontocetes usually do. Mother-calf pairs spend much of their time at the surface, with the mother adopting a static behaviour and the calf moving around her. We found that though calves did not show a biased positioning when the pair is alone, in presence of conspecifics especially several males displaying aggressive behaviours, the pairs fall within a social group configuration. Thus, the necessity for calves to conform to right-biased behaviour enhances their ability to follow their mother as when the number of male associates increases, the pair spends more time travelling than resting, (Cartwright & Sullivan 2009). The left eye-brain hemisphere system may benefit calves when facing challenging circumstances and thus increase calves' ability to recognise familiar individuals and facilitate a rapid reunion if separation between the mother and the calf occurs. From visual observations in the field, when a mother-calf pair is surrounded by several competing escorts, females usually place themselves between the calf and the aggressive males. In such circumstances, the decision to place the calf

either on her left or right side is suggested to be exclusively the choice of the female. In wild orcas, an approaching boat appears to have an influence on calf positioning with the calf moving from the right to the left side of its mother when the vessel was close to the group (Karenina, Giljov, Ivkovich, *et al.* 2013). Thus, it seems that depending on the social context, both mother and calf can influence spatial lateralization behaviours.

Mother-calf body lengths

All measurements performed here were based on the measurement of a known-length straight object (the boat) photographed at different altitudes. We chose rigorous selection criteria, and groups that did not allow to obtain two completely vertical photos were removed, and the measurements were performed, as much as possible, when the whales in the photo were straight. Thus, our sample size was reduced from 65 to 25 groups. However, it is worth noting that images analysed here are obtained from video capture, thus potential measurement errors related to measurement precision or whales' arches and curves that are difficult to detect could have tended to underestimate the relative measurements obtained in this study. Image calibrations we performed were more precise at higher altitudes (20 – 30 m).

As in other mysticetes, females' humpback whales are 1-1.5 m longer than males (Chittleborough 1965). Females' lengths measured during the whaling period varied widely among populations. Matthews LH (1937) reported female lengths from Antarctic to be 14.9 m and True (1904) reported a size of 14.2 m from Newfoundland. Chittleborough (1965), reported females from whaling data measuring 16.2 m, but this value was from unpublished measurements from southern hemisphere Australia, New Zealand and Norfolk Island. Females measured from Moss Landing and Trinidad, California between 1919 and 1926 were the largest females, measuring 18.6 m (Clapham *et al.* 1997). In our results, females had a mean size of

~14 m, which is consistent with the mean length reported in literature. Females' minimum length was 10.58 m and 8 females measured were less than 12.5 m, corresponding to females' approximate length reaching sexual maturity at 5 years (Chittleborough 1965; Pack *et al.* 2012). Among the 25 females measured, 9 females with calves ranged between 12.5 – 14.5 m, which is also consistent with measurements performed by videogrammetric methods from other breeding areas (Pack *et al.* 2009; Nolan *et al.* 2000; Pack *et al.* 2017). Finally, 4 females measured between 14.5 – 16.5 and 4 more between 16.5 – 18.5 m with one female with the largest size of 18.3 m, so categorized as larger than the largest female body size reported from whaling data. The measurements of these longest lengths were performed at an altitude ranging from 20 to 30 m, thus, more precise. Clapham *et al.* (1999) emphasizes the improbability of females measuring 18 m according to our current knowledge. They also indicated that most of the measurements reported in the literature were recorded from heavily exploited populations from which the largest individuals had been removed. Although videogrammetric and photogrammetric methods from other breeding areas did not report such large sizes for females, as 16% of females measured here present lengths greater than 16 m, we can suggest that it is conceivable to find large females in some populations.

Calves minimum length measured was 4.5 m, which is consistent compared to estimated length at birth of 4.5 m by Chittleborough (1958). The maximum length reported here is 7.1 m, approximately the length of an older but not yet weaned calf reported by (Clapham *et al.* 1999) and close to calves' maximal lengths measured in Hawaiian waters (Pack *et al.* 2017). Humpback whale calves' growth rate has not yet been studied and could be investigated to estimate the approximate length of calves when their mothers decide to leave their breeding grounds.

Near or far?

To estimate the space used by calves around their mothers, the measurements we performed take into account the distance from mother's dorsal fin to calf's dorsal fin. It gave an approximate distance between the pair and allowed to estimate calves' spatial range around their mothers. Our results showed that all calves followed a well-defined location around their mother. This is consistent with our previous findings showing that calves usually stay at mothers' left and right side but preferably next to the pectoral fins and the rostrum (i.e., frontal positions). This positioning supports the hypothesis that calves evolve in their mothers' field of vision of and were rarely behind them. For instance, calves usually used the space on their lateral side as well as in their mothers' frontal position. We did not see obvious nursing events throughout the analysed groups. This could be explained by the poor visibility of the waters of the Sainte-Marie channel, and when calves were not bellow their mothers' rostrum, we were not able to state exactly whether they were diving or bellow mothers ventral part. Calves' nursing behaviours were therefore not considered in order to avoid misinterpretations, as we only considered behaviours of calves whose dorsal fins were visible at the surface of the water. Nursing is suggested to be brief and happens when the mother is stationary or swimming very slowly at a depth of 10-15 m (Glockner-Ferrari & Ferrari 1985) and occasionally at the surface with the mother's tail fluke extended into the air (Morete *et al.* 2003). Calves are usually positioned at an angle of approximately 30° to the midline of mother's body with rostrum up and tail down (Zoidis & Lomac-macnair 2017). The observation of nursing bouts is rare and infrequent even though humpback whale mother-calf pairs are widely observed (Zoidis & Lomac-macnair 2017) which could imply that nursing bouts are brief and could mostly happen at depth where observations are rare.

Calves measured in this study were predominantly between 5 to 6 m in length. At this stage of calves' lives, mothers and calves are almost continuously in physical contact with each other and calves usually place themselves on their mother's rostrum. When the mothers are static, calves usually evolve around their mother and touch them as often as possible. This behaviour seems to be part of calves functional behaviour as it was also observed in Right whales (Taber *et al.* 1982). These results support visual observations of very close proximity between the pair, especially during the early stage. Calves rarely exceeded a 20 m distance from their mothers, and usually stayed within a distance of less than 10 m from them. On feeding grounds, in approximately 94% of all simultaneous surface observations of humpback whale mother-calf pairs, they were within 50 m (Szabo & Duffus 2008). Calves studied here were less than 3 months old and when investigating the distance between the pairs according to calves' sizes (less or more than 6 m) there was no really obvious difference. This results can be criticised, as our sample size did not allow to detect a noticeable difference. However, when comparing the distance separating the pairs here to distance (calves less than 3 months) in the feeding ground, performed with older calves (calves older than 7 months), we can state that calves spatial range increase with age. As soon as the calf is born, mother-calf humpback whales also exhibit a synchronized behaviour (Saloma *et al.* in revision) and this synchrony is maintained until calves reached 8 – 12 months (Tyson *et al.* 2012). It appears that when the calf is moving around the mother while the mother is static, the calf seems to be the one that re-establish their proximity; and when the mother starts moving, the calf always follows, the mother appears to always initiate the movements. This supports the hypothesis that the spatial association between female humpback whales and their offspring is similar to that observed in terrestrial followers: neonates accompany their mother soon after parturition and are rarely distant from the mother until their permanent separation or weaning (Lent 1974).

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SYNTHESIS



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The overall purpose of my PhD was to fill the gap of knowledge on mother-calf interactions in humpback whales. Different methods were used, first to describe their vocal production and their vocal interactions, then the diving pattern of their sound production, the ontogeny of calves' diving behaviour, and finally their spatial relationships.

Tagging procedures

Since the first report by Stimpert *et al.* (2012) describing approaches to be performed for tagging mother-calf pairs, other studies have followed their methods and their suggested approach has been applied in other breeding areas (Videsen *et al.* 2017a; Chen *et al.* 2016) and in a feeding area (Tyson *et al.* 2012). Our team tagged mother-calf pairs during 5 consecutive years, starting in 2013. Protocol described by Stimpert *et al.* (2012) was followed during all our fieldwork seasons, but was adapted to the context of our study area (the great number of humpback whale mother-calves staying in one area in the Sainte-Marie channel), and therefore the behaviour adopted by whales in this area. Whale observation regulations in Madagascar's coastal areas are among the most restricted and respectful to animals, and the guidelines were well-followed by the tagging team. The scientific boat worked collaboratively with tourist boats, which enhances the chance of working with static groups. Prior to each tagging process, safety procedures were checked to ensure crew's security, and for all approaches, the engine was always left on for safety reasons, as suggested by Stimpert *et al.* (2012). All attempted tagging were performed with great care and were conservative towards the studied animals. Calves in this study were separated into 3 different classes: C1 class grouped those with neonate traits and colours and with the angle of their dorsal fins $< 45^\circ$, C2 grouped those with no apparent neonate traits but still furled dorsal fins $< 72^\circ$ and C3 which grouped older calves, and the angle of their dorsal fins were unfurled $> 72^\circ$ (Cartwright & Sullivan 2009).

Of the 51 groups successfully tagged in this study, 16 groups were with calves that had furred dorsal fins, thus belonging to C1 and C2 classes.

Two important factors made this study particularly specific. The first was the possibility to approach and tag newborn calves. Newborns (i.e., few days old calves) are sighted each year in Sainte-Marie channel. Several groups often remain static in the same area and are often ~200 m apart. This advantage allowed us to easily perform the drifting approach in order to tag calves belonging to C1 and C2 classes (calves with furred dorsal fins). Active approaches were generally performed on groups with C3 class calves and the boat was placed parallel to the targeted group to follow the group's slow travel speed. Tagging was aborted when the group's swimming speed accelerated. No more than 3 approaches or 3 tagging attempts per group were performed, and the maximum time spent with each group never exceeded 30 min. The tagging process was also aborted at the first sign of avoidance response by the group towards the boat. The easiest approaches were achieved on groups with calves belonging to C1 class. The success of these attempts was enhanced by the tendency of calves from this class to approach the boat, allowing our team to tag them without apparent stress from the pair. Indeed, in three cases, the groups did not move away from the boat after tagging, and the boat had to wait and use sea surface current to drift away before leaving the group. Simultaneous tagging (two acoustic tags deployed at the same time on the same mother-calf pair) was performed on 10 groups. In such cases, two people on board each tagged one whale from the same mother-calf pair. This allowed us to place tags simultaneously on both mother and calf, reducing the time spent with the pair even though two animals were tagged.

The second specific factor of this study was the modification of the grip attached to the end of the tagging pole. The grip's launch mechanism was made static and horizontal, to permit placing of tags on the lateral side of the animals. The usual configuration is to place acoustic

tags on the back of animals, near the dorsal fin (Nowacek *et al.* 2004; Friedlaender *et al.* 2009; Hazen *et al.* 2009; Tyson *et al.* 2012; A. Stimpert *et al.* 2012; Chen *et al.* 2016; Videsen *et al.* 2017b). This modified configuration was chosen as researchers usually follow the tagged whale and thus detect the VHF signal when the animal is at the surface. For our study, the Acousonde tags were placed on the lateral side, as low as possible. This alternate configuration assured the tags would almost always be submerged, thus enhancing acoustic recordings, as mother-calf pairs spend a lot of time at the surface, especially during calves' first months. Recordings in which tags were placed on the back of the calves were saturated by surfacing background noises and generally, during these surfacing periods, no analysable sounds appeared on recordings. Placing tags on the lateral side requires the boat be well placed parallel to the targeted group, which gives the added advantage of being in the mother's field of vision. We noted from field experience, that being seen by the mothers allowed us to perform better approaches. On the other hand, having the tag as low as possible on the lateral side of the animal does not allow the use of radio-tracking (the HF emitter was always submerged), but as we did not follow the groups after tagging, this had no impact on our protocol, and the Acousonde tag was retrieved only after it was detached from the animal.

Tagging humpback whale mother-calf pairs requires a specialized approach and should be conducted by expert on whale behaviours. For instance, the high success rate of our tagging was enhanced by the experienced team. Over 68 deployments, 60% of tagging were successful on the first approached groups, 30% on the second group approached and 10% on third group approached.

Mother-calf social calls and their context of production

For nearly fifty years, researchers have debated the complexity of humpback whales' (*Megaptera novaeangliae*) vocal communication. Humpback whale male songs are one of the most studied forms of Mysticetes communication. Songs from several regions and different latitudes have been described, and multiple and complex functions have been ascribed to these songs. (Payne & McVay 1971; Payne & Payne 1985; Darling *et al.* 2006; Bank *et al.* 1990; Noad *et al.* 2000; Au *et al.* 2006; Smith *et al.* 2008; Parsons *et al.* 2008; Garland *et al.* 2011; Mercado *et al.* 2005; A. K. Stimpert *et al.* 2012; Vu *et al.* 2012; Maeda *et al.* 2000; Garland *et al.* 2017; Oviedo *et al.* 2008; Herman 2016). Meanwhile, humpback's non-song vocalizations from the breeding and feeding grounds, generally known as social calls, were also first described by Silber (1986) and Thompson *et al.* (1986), but they have not been as widely studied as songs. More recent studies have given detailed descriptions of these social calls from migrating population of east Australia and feeding population from Alaska (Dunlop *et al.* 2007; Fournet *et al.* 2015). These studies have shown that social calls have been recorded for all group compositions containing males and females, as well as calves (Dunlop *et al.* 2008; Dunlop *et al.* 2007; Zoidis *et al.* 2008; Simao & Moreira 2005; Rekdahl *et al.* 2013; Rekdahl *et al.* 2015; Fournet *et al.* 2015). However, little is known about the social calls assigned to males or females, and only limited information is available on calves' vocalizations.

An interesting challenge in describing and understanding mother-calf vocal production has been in pinpointing the identification of the call-emitter. For instance, social calls were present in all analysed recordings and some presented similar patterns of production. However, call attribution to a specific tagged whale was complex. Available literature suggests that several methods have been used to identify call-emitters in cetaceans (Oliveira *et al.* 2013; Madsen *et al.* 2013; Parks *et al.* 2011; Goldbogen *et al.* 2014). However, detection of humpback whales'

vocal activity is particularly difficult as they are acoustically masked in part or fully by conspecifics songs and social sounds. In addition, the lack of information on females' vocalizations does not permit comparison. In this study of the production patterns of certain social sounds, social calls attributed to mothers were mostly low-frequency sounds and females were suggested to have a relatively large vocal repertoire. As song units can be also used as social calls (Dunlop *et al.* 2007), some were partly detected in recordings of mother-calf pairs. Previous literature also suggests that calves produce vocalizations ranging from low to mid-frequency, amplitude modulated calls as well as pulsed calls. These calls are short and simple in structure (Zoidis *et al.* 2008). In our dataset, the most frequent of these described calls (predominantly low-frequency sounds for calls attributed to mothers and mid-frequency sounds for call attributed to calves) were selected and a series of analyses were performed. We demonstrated that one call type, which showed the lowest frequency among all social calls and the highest amplitude level, was detected by the accelerometer sampled at 400 Hz, following the method described by Goldbogen *et al.* (2014), confirming that it was emitted by the tagged whale itself (i.e., mother). The same analysis could not be performed for other low-frequency calls attributed to mothers or calves in this study. Mother-calf social calls are mostly produced at a low amplitude level (Chen *et al.* 2016; Videsen *et al.* 2017b), which made their detection difficult or impossible, even though most are low-frequency calls.

Methods for detecting low-frequency sounds allowed attribution of a vocalization to the tagged animal. However, in similar call types of recordings from the same individual, all detectable calls could not always be reliably detected, as seen in previous studies performed on other species (Goldbogen *et al.* 2014; Saddler *et al.* 2017; Stimpert *et al.* 2015). For instance, this method is limited by several conditions: tag sensors capacity and resolution, orientation of the tag, and therefore the three axes of the accelerometers, tag positioning on the animal which had

an impact on the direction and vibration of the tag (Goldbogen *et al.* 2014; Saddler *et al.* 2017). Further investigation is needed to improve this method and additional methods need to be developed to better understand and pinpoint call emitters in large whales, especially in humpback whales.

Calves' vocalizations were produced in a frequency range undetectable by the 3D accelerometer of the Acousonde tag (peak frequency > 200 Hz). Source identification was thus only possible from simultaneous tagging (2 Acousonde tags deployed on the mother and its calf), based on time or received level differences. Such methods were however also challenging, since synchronous high-quality calls present on both tags, with apparent isolation of the tagged animal, have rarely been observed. This complicated measurement. Nonetheless, some calves' calls described in this study presented similarities to calves' vocalizations described in another breeding area (Zoidis *et al.* 2008), enabling comparison.

One highly original aspect of this work is the investigation and occurrence of individual vocal signatures in selected mother-calf calls. Indeed, this is the first study showing individual vocal signatures in Mysticetes. Even if we cannot ascertain that calls were emitted by the tagged animal, the occurrence of a clear individual signature in their calls provides proof that they are indeed produced by a specific individual. In addition, these selected calls were part of a mother-calf "vocal interactions" as they were detected in both mother-calf recordings and were found to be synchronously produced or overlapping, constituting a kind of call and answer between the pair.

Further investigation is still needed to identify the actual source of other social sounds. One of the critical gaps hindering the understanding of humpback whales' vocal communication is the lack of knowledge on the biological function of their vocalizations. This gap is especially

important as researchers had difficulty identifying the call-emitter and behaviour linked to such sound production. Very few hypotheses have been made on the possible function of certain calls produced (Thompson *et al.* 1986; Zoidis *et al.* 2008; Dunlop *et al.* 2008; Silber 1986). Still, basing our analysis on the selected calls from the most representative social calls of mother-calf recordings and linking them to the diving profile, we were able to demonstrate that they present a well-defined pattern of production: produced either during surfacing activities or during diving activities. Calves mainly vocalized during active behaviours while surfacing, as their calls were simultaneously heard with social sounds such as slapping of tail or pectoral fins. We hypothesized that as calves do not yet control buoyancy very well (Stimpert *et al.* 2012), this could explain the reason they vocalize more frequently at the surface. Indeed, when at the surface, they do not need to adjust internal air pressure in their respiratory system in order to control their buoyancy. The production of calls at the surface by mothers suggests the occurrence of vocal interactions between the pair during active behaviours while surfacing, or in presence of other conspecifics exhibiting active behaviours. This finding is consistent with Dunlop *et al.* (2008) suggesting the use of a call type in mother-offspring vocal exchanges.

Mother-calf behaviours: diving and surfacing activities

One goal of this study was to understand mother-calf diving behaviour and to define distance between individuals of the pairs. The development of new technologies has significantly improved the understanding of cetaceans' behaviours. Attaching a multi-sensor tag to an animal allows recording of both vocal activities coupled with diving behaviours. More recently, the use of unmanned aerial vehicle (UAV) commonly known as aerial drones to record their surfacing or subsurface activities helps provide better information. The main advantage of these tools is that they open the possibility of studying cetaceans' behaviours by reducing anthropogenic presence which can impact the studied individual's behaviours. By deploying

Acousonde tags over 5 successive years, this work provided unprecedented information on mother-calf diving behaviour during calves' first months. Studied calves were separated into three age-classes. Results permitted us to document the diving pattern of the youngest humpback whale calves ever tagged. One of the most interesting findings of our results is the lack of difference in depth metrics between younger and older calves, as well as between calves and their mothers. Results from simultaneous data recordings show that calves are able to dive as deep as their mothers quite soon after birth. However, our result can be criticized due to the depth limitations of the Sainte-Marie channel, averaging close to 25-35 m (Trudelle *et al.* 2018) and given that maximum dive depth recorded by humpback whale calves (C3 class calf) from another breeding area was 78 m (Stimpert *et al.* 2012) and the maximum depth performed by one calf in its feeding area was 250 m (Tyson *et al.* 2012). Thus, we cannot confirm whether newborn calves could dive more than 40 m if their mothers did. Though we can hypothesize that they are able to dive relatively deep soon after birth, as C1 and C3 class calves approximately have a 30-day age difference (Cartwright & Sullivan 2009) and C3 calves are usually no older than 90 days. Our results show that mothers lead the dive during the critical stage, but as calves grow, they become more responsible for maintaining proximity to their mothers (Tyson *et al.* 2012). Moreover, in terms of dive duration, younger calves present shorter dive times compared to older calves and mothers. This result is therefore consistent with previous reports suggesting that calves' lung capacity increases with body mass, giving greater diving capacity as they grow (Schreer & Kovacs 1997; A. Stimpert *et al.* 2012; Tyson *et al.* 2012). In addition, we have been able to calculate vertical distance between mothers and their newborn. Mean vertical separation was ~ 2 m (in calves less than 3 months old), showing they remain quite close to one another and exhibit synchronized behaviours. In the feeding group, they show similar synchronization even during feeding behaviours, and their vertical distance was ~20m (calf was between 8 to 12 months old) (Tyson *et al.* 2012). All these findings support the hypothesis that the distance

between the pair increases as calves become more secure and confident, and more responsible to maintain proximity with their mothers (Taber *et al.* 1982; Tyson *et al.* 2012; A. Stimpert *et al.* 2012).

Aerial video obtained from drones allowed us to observe their surface behaviour from vertical view. However, video footage from UAVs requires rigorous protocols to provide reliable data analysis and especially when using photogrammetric methods. In measurements of horizontal distance between the pair, newborn calves stay within a mean distance of < 10 m around their mothers and this distance increases as they get older. Distances were shown to be within 50 m in the feeding ground (Szabo & Duffus 2008). One interesting information obtained from aerial videos was calves positioning towards their mothers. Lateralized behaviour in mother-offspring has mostly been observed in individuals belonging to social groups (Karenina *et al.* 2013; Karenina, Giljov, Glazov, *et al.* 2013; Karenina *et al.* 2010; Karenina *et al.* 2017) Here we performed a series of analyses which allowed to conclude that humpback whale calves exhibit the same right-biased lateralized behaviour when in presence of conspecifics as that observed in odontocetes (when they were escorted by one or more than two individuals). However, this tendency was not conclusively observed when the pair was alone (i.e., no escort). Calves were moving to both left and right sides of their mothers, and were rarely behind or far from their mothers (maximum distance ~20 m). Humpback whale mother-calf pairs' behaviours reported here are consistent with previous studies stating that humpback whale mother-calf spatial association is similar to terrestrial followers (Lent 1974; Szabo & Duffus 2008; Tyson *et al.* 2012).

Photogrammetric methods have been used by many researchers to measure cetaceans body conditions and length (Huang *et al.* 2009; Christiansen *et al.* 2014; Christiansen, Dujon, *et al.* 2016). Results presented in this study are consistent with previous studies performed on

humpback whales' measurements from other breeding grounds (Elliot 2000; Pack *et al.* 2009, 2017). In remaining within the objectives of this study, we performed only length measurements. Additional measurements such as mothers' and calves' width could have been obtained to define calves' growth rates and females weight loss rates, and more clearly estimate body condition.

Impact of the study on humpback-whale conservation

Rapid growth of whale-watching as a tourism activity has been observed worldwide over the past twenty years (Hoyt 2001; Hoyt 2005; Hoyt & Iñíguez 2008). These activities generate an estimated ~2.1 billion USD (2009) in revenues and supports about 13,000 jobs (O'Connor *et al.* 2009). Whale-watching also has ecological benefits (Cisneros-Montemayor *et al.* 2010) as it is an effective tool for raising awareness for ocean conservation. However, authors have stated the necessity to establish well-managed whale-watching to avoid potential negative impacts on marine mammals (Curtin 2003). Protection of large whale species, especially mother-calf pairs is critical for population recovery. Typical regulations restrict the number of vessels, divers, swimmers and aircrafts that may observe a given group of whales or dolphins, and their proximity to the animals. The most adopted approach is the limitation of the number of boats with a maximum of 3 vessels within 300 m of any whale and a minimum approach distance of 100 m (e.g the state of Queensland Australia and Madagascar). However, management of whale-watching varies considerably around the world and depends on the local context, some areas being stricter than others. Understanding whales' behaviours, especially their acoustic communications, which are most greatly exposed to anthropogenic activities helps improve the implementation of effective regulation policies towards human activities.

Humpback whales are presumably the most observed worldwide coastal baleen whales. Females accompanied by their newborns are well known to stay in shallow waters, close to shore (Pack *et al.* 2017; Trudelle *et al.* 2016) they are therefore more exposed to whale-watching activities. Our findings which show that mother-calf pair use low- and mid-frequency calls emitted at a low amplitude level to interact with each other, reinforce the idea that both distance and duration of observations must be limited. The example of Madagascar's code of conduct limiting mother-calf observations to 30 min at 200 m is interesting. Also, gradual reduction of engine speed at 800 m from the groups allows the whale watching boat to perform a slow and quiet approach towards the group. This certainly makes sense, given that mother-calf pairs are mostly static and at the surface. The number of boats observing them also plays an important role, as noise could be critical in reproductive success and calf survival. For instance, limiting ambient noise levels in breeding grounds should be mandatory for their preservation, especially at this critical, early stage of life.

Some countries (such as Madagascar) have forbidden swimming with wild cetaceans some have not. When analysing calves behaviours in presence of free divers in this study, they did not seem to have a direct and visible impact on calf positioning towards their mothers. However, the absence of apparent behavioural stress does not mean that whales were not stressed. Indeed, increase in heart rate and stress hormone levels such as cortisol have been observed in other mammal species (Martin & Réale 2008; Ropert-Coudert *et al.* 2009) and these are undetectable from visual observation. It is worth noting that mother-calf spatial behaviours described here report behaviours from aerial view, thus in absence of free divers, and with the boat situated at > 200 m from the recorded groups. We did not detect any behavioural responses of the animals toward the UAVs while filming, and other studies from other areas and another species of large whales also report similar observations (Christiansen, Rojano-Doñate, *et al.* 2016; Nowacek *et*

al. 2016; Christiansen *et al.* 2014). We can therefore consider that behaviours described here are close to natural behaviours and could be used as a basis for more advanced study of the possible effects of touristic boats or free divers.

Whale watching is an industry that generates socio-economic and ecological benefits to countries or areas. With proper and duly respected guidelines in place, continued protection of marine mammals can only be beneficial, sustainable and an invaluable tool to promote education and awareness of ocean conservation at large.

Direction for future research

Collectively, the data analysed from this study strongly suggest that vocalizations are an important part of mother-calf interactions, as important as visual and physical contact. Pairs show synchronous behaviours, whether in breeding or in feeding grounds (Tyson *et al.* 2012), and multiple sensory modalities are certainly involved in maintaining their synchrony as well as their proximity. This study provides a knowledge base on females' vocal production and the use of these vocalizations in a context of interaction with their offspring. Clearly, the most critical gap and limiting factor in all studies is the lack of conclusive information on call-emitter, even though humpback whales produce low-frequency vocalizations such as other Mysticetes. Simultaneous deployment of acoustic tags on escorts and mother-calf pairs is recommended, as this will allow to identify social calls present in males' recordings and thus perform comparisons with those present in mothers, especially in regards to the amplitude levels of sound production. Further investigation could focus on examining the intensities and frequencies of non-song sounds relative to humpback whale songs in order to determine whether there is any evidence of a "frequency partitioning" performed by mother-calf pairs to minimize masking from conspecifics, especially singing males.

It is worth noting that a comparison of humpback whales' social sounds described from different parts of the world, and recorded by different research groups, would be interesting but challenging. It is difficult to find a consensus when naming and categorizing these calls based only on numbers describing acoustic parameters and published spectral images. Social calls described in this study were named with the previously described call names when they seemed similar and the spectrograms were made as clear as possible.

Only a few calls have been studied here. Further investigation, taking into account all possible females vocalizations could provide more information on the function and biological significance of these calls. Comparison with another breeding area would help to better understand the biological significance of vocalizations produced by humpback calves and mothers, and how it may change depending on social structure, environmental cues, calves' ontogeny, and the pair's behaviour. Sharing acoustic recordings or at least examples of social call types would also help in describing social calls worldwide, and would avoid multiple names for each particular call type. Finally, the comparison of social calls among geographic areas would also determine if geographical vocal variations occur.

Calves' calls reported in this study represent the basics of their vocalization. It would be interesting to understand the differences between male and female vocalizations and to know how it evolves according to the calf's sex. Also understanding the ontogeny of calves' vocal repertoire could be further investigated by studying how it evolves in the breeding areas, on migration routes and even in their feeding grounds. To go further still, the study of juveniles could also be interesting as it could help determine when they start singing, and thus better understand the ontogeny of male songs.

The Acousonde Tag provides different data from tagged individuals, as it contains different sensors in addition to the hydrophone. Throughout this study, we focused analysis on acoustic recordings and pressure sensors that gave information on diving profiles. Data from accelerometers were only used to detect low-frequency sound production by females. It is worth noting that this data could be further investigated to understand mother-calf's underwater behaviours, especially calves nursing events coupled with vocal production. And these results could be compared to results from other breeding areas (Videsen *et al.* 2017a).

In the future, using an acoustic tag coupled with video camera (e.g., CATS camera) should be the best configuration to understand the behavioural context of a vocal production. Such devices would be also quite useful in describing the behavioural response of humpback whale groups to “playback experiment,” and may also improve our understanding of the function of conspecifics vocalizations (i.e., social sounds or male songs or song units).

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APPENDICES



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CHAPTER 1a

Supplementary figures

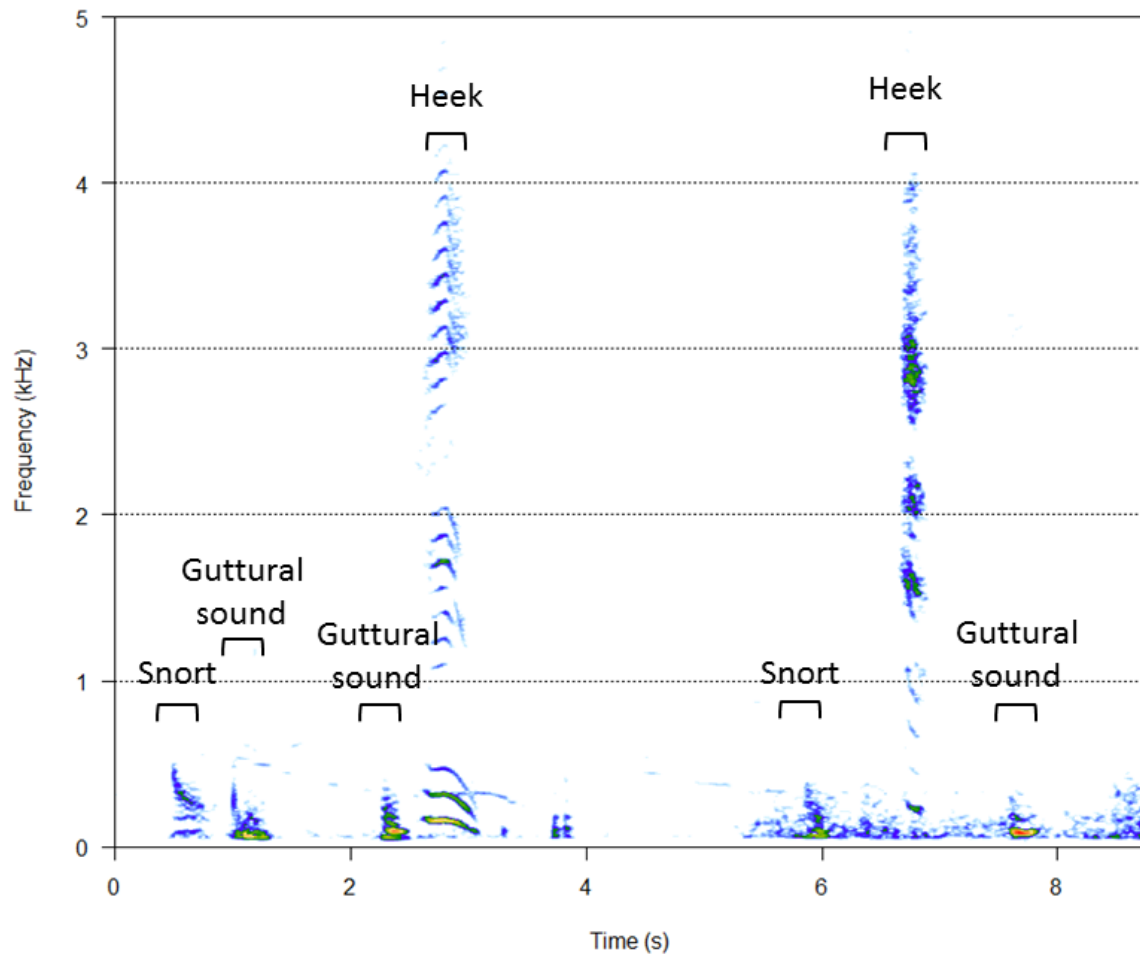


Figure 1: Spectrogram of a suggested mother-calf vocal interaction (snort, gru and heek) [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap – performed using Seewave (Sueur et al. 2008)]



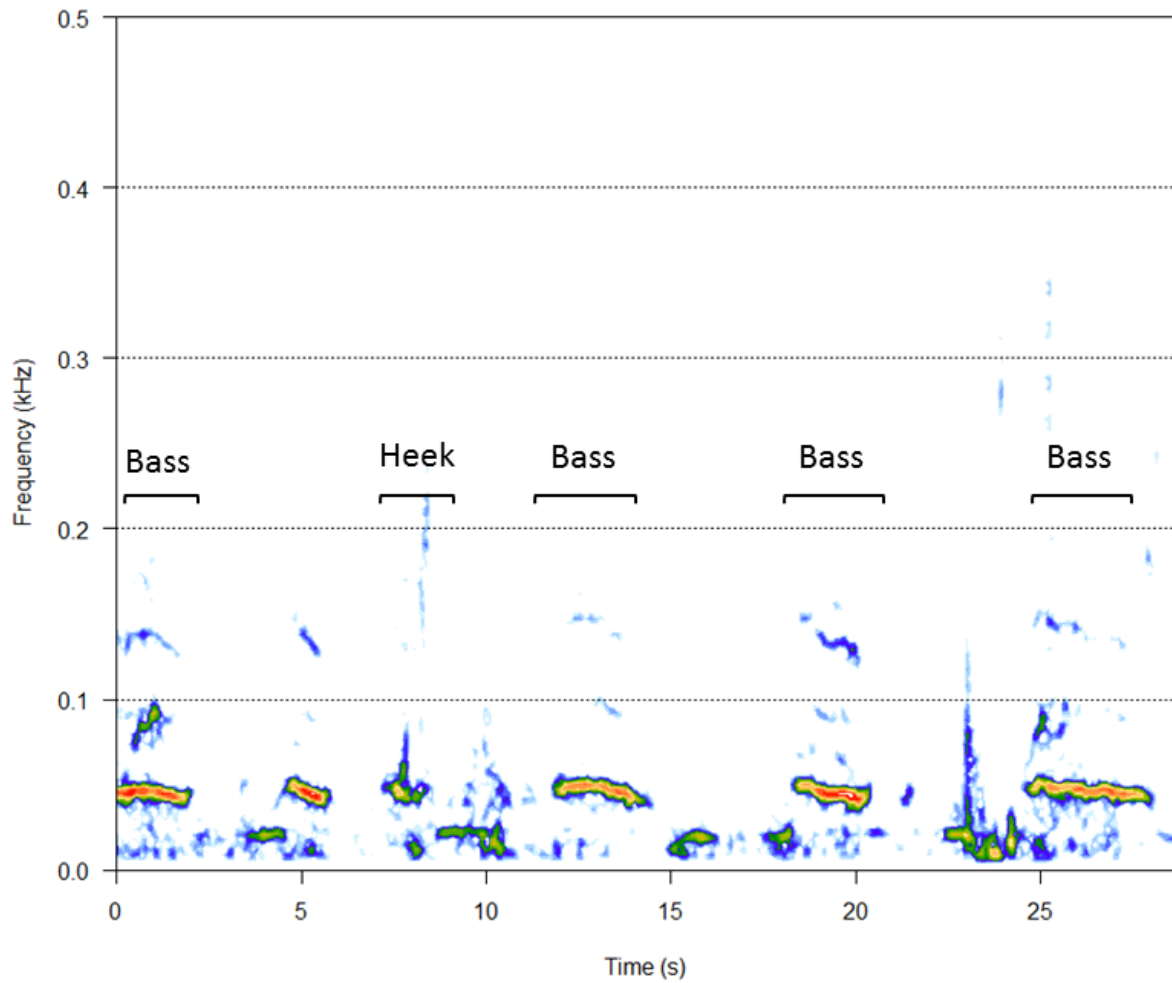


Figure 2: Spectrogram of a suggested mother-calf vocal interaction (bass and heek) [Spectrogram parameters: Hamming window, FFT window size: 512 pts, 90% overlap – performed using Seewave (Sueur et al. 2008)]



Supplementary table

Table 1: Descriptive data (N, mean, SD, Min and Max values) of each sub-categories of social calls included in the 5 main call categories (high frequency, mid frequency, low-frequency, amplitude modulated and pulsed sounds), as well as the number of groups in which they were produced.

LOW-FREQUENCY SOUNDS						
100 Hz	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	7	303	0.52	0.26	0.1	1.76
Start Freq (Hz)	7	244	95.66	16.90	50	190
End Freq (Hz)	7	244	158.69	23.11	110	360
Exc. Freq	7	240	63.00	14.87	30	170
Fmax 1 (Hz)	7	177	131.58	24.34	93	187
Fmax 2 (Hz)	7	41	260.98	175.34	43	979
Fmax 3 (Hz)	5	21	618.38	313.33	240	1348
Peak Freq(Hz)	6	151	131.06	25.30	93	186
Q25%	6	151	129.43	39.25	71.7	350
Q50%	6	151	198.04	228.34	93.7	1798
Q75%	6	151	384.81	701.46	98.8	3936
Bandwidth	6	151	17.02	11.16	2.5	64
Bass	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	8	84	1.22	0.79	0.015	3.626
Fmax 1 (Hz)	8	72	47.44	11.22	21	131
Fmax 2 (Hz)	8	60	112.23	23.59	59	170
Fmax 3 (Hz)	7	46	132.72	34.86	84	246
Peak Freq(Hz)	7	59	44.77	8.78	5	55.2
Q25%	8	62	39.18	9.99	12.4	50.5
Q50%	8	62	59.10	26.03	16.8	153
Q75%	8	62	280.67	412.05	49	2733
Bandwidth	8	62	11.20	26.95	0.949	156
F0	7	40	13.82	15.07	1.9	60

LOW-FREQUENCY SOUNDS

<i>Boom</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	4	210	0.27	0.08	0.104	0.563
Start Freq (Hz)	4	210	54.00	23.64	30	140
End Freq (Hz)	4	210	103.24	26.63	70	180
Exc. Freq	4	202	49.31	11.00	20	90
Fmax 1 (Hz)	4	186	85.08	30.72	50	314
Fmax 2 (Hz)	4	106	157.27	114.30	55	1070
Fmax 3 (Hz)	3	35	286.89	194.15	109	844
Peak Freq(Hz)	3	156	84.51	25.25	52	150
Q25%	3	156	95.96	60.63	54.9	461
Q50%	3	156	177.17	302.90	60.7	2084
Q75%	3	156	353.41	771.40	70.3	3897
Bandwidth	3	156	16.74	6.94	2.9	46
F0	3	102	49.08	37.85	4	134
<i>Boom2</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	2	0.17	0.04	0.139	0.201
Start Freq (Hz)	1	2	105.00	7.07	100	110
End Freq (Hz)	1	2	165.00	7.07	160	170
Exc. Freq	1	2	60.00	0.00	60	60
<i>Snort</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	12	0.16	0.06	0.06	0.276
Fmax 1 (KHz)	1	9	107.44	58.23	16	186
Fmax 2 (KHz)	1	8	140.13	106.00	46	365
Fmax 3 (KHz)	1	8	299.50	343.83	89	1121
Peak Freq(Hz)	1	10	101.40	60.75	17	190
Q 25%	1	10	111.00	45.23	46	181
Q50%	1	10	231.00	93.19	105	427
Q75%	1	10	772.20	338.16	257	1142
Bandwidth	1	10	48.80	53.82	5	180
F0	1	2	90.50	0.71	90	91
Pulse rate	1	9	44.35	9.02	32.4	58.9
Bandwidth	1	3	13.13	5.80	8.7	19.7



LOW-FREQUENCY SOUNDS

<i>Gru</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	17	0.25	0.08	0.139	0.48
Start Freq (Hz)	1	2	125.00	77.78	70	180
End Freq (Hz)	1	2	175.00	106.07	100	250
Exc. Freq	1	2	50.00	28.28	30	70
Fmax 1 (Hz)	1	14	52.29	20.83	16	89
Fmax 2 (Hz)	1	12	118.42	62.63	21	225
Fmax 3 (Hz)	1	5	151.80	77.90	17	212
Peak Freq(Hz)	1	12	44.25	25.71	10	87
Q25%	1	12	48.75	19.59	20	76
Q50%	1	12	222.75	485.27	43	1751
Q75%	1	12	1053.83	1047.67	17	3058
Bandwidth	1	12	20.25	9.28	5	39
<i>Burp</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	2	18	0.47	0.21	0.177	0.82
Fmax 1 (Hz)	2	15	31.00	10.01	21	63
Fmax 2 (Hz)	1	15	64.00	17.44	34	93
Fmax 3 (Hz)	1	15	90.33	15.98	59	119
Peak Freq(Hz)	2	15	27.69	12.35	8	64
Q25%	2	15	32.84	8.57	21.9	60
Q50%	2	15	76.84	15.77	58.5	114
Q75%	2	15	226.69	116.46	117	445.3
Bandwidth	2	15	9.72	5.28	4	20
F0	2	2		5.66	27	35
<i>Guttural sound</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	6	0.69	0.10	0.546	0.812
Fmax 1 (Hz)	1	6	90.00	18.92	72	116
Fmax 2 (Hz)	1	5	121.74	57.76	50	190
Fmax 3 (Hz)	1	2	188.55	159.03	76.1	301
Peak Freq(Hz)	1	4	75.50	46.11	7	106.9
Q25%	1	4	114.65	87.85	55.6	245.3
Q50%	1	4	427.85	712.01	13.1	1494
Q75%	1	4	796.55	1230.93	10.6	2630

LOW-FREQUENCY SOUNDS

<i>Thowp</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	7	35	0.72	0.44	0.107	1.627
Fmax 1 (Hz)	4	17	63.71	29.15	21	114
Fmax 2 (Hz)	3	14	99.64	42.81	42	170
Fmax 3 (Hz)	3	9	174.89	56.24	85	246
Peak Freq(Hz)	3	12	45.36	35.71	7	105
Q25%	3	12	50.53	21.02	23.4	96
Q50%	3	12	113.82	60.46	57	246
Q75%	3	12	362.19	305.81	128	1218
Bandwidth	3	12	16.29	13.86	4.3	52
F0	1	2	17.50	16.26	6	29
<i>Wop</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	8	25	0.30	0.18	0.103	0.851
Fmax 1 (Hz)	8	19	77.53	94.18	21	411
Fmax 2 (Hz)	6	17	95.65	43.05	29	201
Fmax 3 (Hz)	5	12	240.25	236.43	89	900
Peak Freq(Hz)	7	13	70.86	104.57	6.5	413
Q25%	7	13	65.51	56.29	38	251
Q50%	7	13	130.32	96.98	49.8	439
Q75%	7	13	434.01	466.22	57.8	1751
Bandwidth	7	13	26.12	15.93	8	55
F0	1	1	41.00	NA	41	41

MID-FREQUENCY SOUNDS

<i>Groan</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	1	2	5.01	2.05	3.556	6.46
Start Freq (Hz)	1	2	135.00	21.21	120	150
End Freq (Hz)	1	2	460.00	70.71	410	510
Exc. Freq	1	2	325.00	49.50	290	360
<i>Downsweep</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	5	140	0.67	0.32	0.185	1.7
Start Freq (Hz)	5	128	306.95	188.54	110	2060
End Freq (Hz)	5	128	736.17	218.12	250	2780
Exc. Freq	5	128	429.22	130.44	80	790
Fmax 1 (Hz)	3	47	410.49	292.19	209	2091
Fmax 2 (Hz)	3	46	805.54	385.48	106	2160
Fmax 3 (Hz)	2	35	1361.26	666.51	114	4330
Peak Freq (Hz)	3	44	392.33	303.81	11.7	2089.5
Q25%	2	43	428.46	278.22	216.7	2044.5
Q50%	2	43	654.20	315.15	339.1	2254.7
Q75%	2	43	1608.22	602.18	563.9	3026
Bandwidth	2	43	43.28	59.06	0.7	287.1
F0	1	8	134.81	63.63	104	291.5
<i>Woohoo</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	5	141	0.93	0.50	0.285	2.565
Start Freq (Hz)	4	108	229.81	52.45	90	370
End Freq (Hz)	4	108	312.69	59.96	160	440
Exc. Freq	4	108	82.87	39.22	10	280
Fmax 1 (Hz)	3	31	286.39	61.41	201	432
Fmax 2 (Hz)	2	23	656.83	260.18	402	1431
Fmax 3 (Hz)	3	14	1010.57	332.90	432	1487
Peak Freq (Hz)	4	28	287.60	64.02	203.6	431.3
Q25%	4	28	330.85	63.01	214.9	435.4
Q50%	4	28	728.40	369.84	319.3	1495.6
Q75%	4	28	2157.64	457.36	1037	2921.2
Bandwidth	4	28	23.01	63.46	2.5	344.2
F0	3	5	246.00	82.50	201	393.3

MID-FREQUENCY SOUNDS

<i>Trumpet call</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	3	28	1.63	0.39	0.709	2.257
Start Freq (Hz)	3	24	214.17	88.36	100	430
End Freq (Hz)	3	24	293.75	108.78	210	580
Exc. Freq	3	24	79.58	33.94	40	150
Fmax 1 (Hz)	2	17	365.94	133.30	201	570
Fmax 2 (Hz)	2	16	465.94	296.82	203	1163
Fmax 3 (Hz)	2	14	1179.14	511.71	424	2245
Peak Freq(Hz)	2	13	371.84	130.36	204.3	504.6
Q25%	2	16	509.20	173.05	218.6	925.4
Q50%	2	16	1024.34	510.43	485.2	1801
Q75%	2	16	2011.51	705.88	889.8	2828.2
<i>Heek</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	3	28	0.43	0.22	0.199	0.945
Start Freq (Hz)	1	10	99.00	29.61	50	150
End Freq (Hz)	1	10	177.00	31.99	120	220
Exc. Freq	1	10	78.00	19.89	30	100
Fmax 1 (Hz)	3	21	529.14	899.23	42	3024
Fmax 2 (Hz)	3	20	751.35	1092.31	93	3451
Fmax 3 (Hz)	2	16	1285.50	1083.37	84	3646
Peak Freq (Hz)	2	16	479.89	780.17	60	2797
Q25%	2	16	703.88	739.76	153	2588
Q50%	2	16	1625.71	875.31	276	3232
Q75%	2	16	2745.57	865.18	348	3928
Bandwidth	2	16	24.79	17.71	5.8	71
F0	1	2	160.70	7.50	155.4	166

MID-FREQUENCY SOUNDS

Whoop	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	7	112	0.78	0.34	0.192	1.433
Start Freq (Hz)	7	94	430.96	136.54	110	720
End Freq (Hz)	7	94	656.49	176.11	350	970
Exc. Freq	7	58	205.86	94.83	60	470
Fmax 1 (Hz)	6	82	505.12	137.21	139	742
Fmax 2 (Hz)	5	56	741.51	488.78	106	1793
Fmax 3 (Hz)	5	36	1148.72	445.61	366	2088
Peak Freq(Hz)	6	77	498.94	138.03	140.6	707.8
Q25%	6	77	514.58	178.62	150.8	1557.1
Q50%	6	77	681.92	216.16	8	1261.2
Q75%	6	76	1700.90	595.71	536.1	3382.3
Bandwidth	6	76	38.39	64.51	2.1	292
F0	4	17	318.82	199.27	0	703.1



HIGH FREQUENCY SOUNDS

<i>Squeak</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	7	160	0.29	0.14	0.102	1.134
Start Freq (Hz)	7	156	1051.73	160.17	390	1600
End Freq (Hz)	7	156	1282.95	117.59	990	1830
Exc. Freq	7	156	231.22	136.79	70	770
Fmax 1 (Hz)	6	85	1200.65	334.05	56	3673
Fmax 2 (Hz)	6	73	2200.25	594.88	398	3584
Fmax 3 (Hz)	6	54	3072.70	846.90	590	5642
Peak Freq (Hz)	6	77	1186.69	376.16	0.7	3676
Q25%	6	77	1158.30	203.27	875	2712.1
Q50%	6	77	1431.91	366.86	984	3544.9
Q75%	6	77	2626.37	479.55	1751	3759.5
Bandwidth	6	77	26.92	19.15	2.1	124
F0	4	23	606.00	418.88	62	1384
<i>Ascending shriek</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	4	42	1.27	0.81	0.206	4.106
Start Freq (Hz)	4	40	968.50	669.76	260	2020
End Freq (Hz)	4	40	1701.75	499.28	1190	3010
Exc. Freq	4	40	733.25	470.36	70	1550
Fmax 1 (Hz)	3	23	1634.22	434.85	1164	2419
Fmax 2 (Hz)	2	17	2232.88	993.36	1041	4439
Fmax 3 (Hz)	2	16	3325.56	1718.07	249	5113
Peak Freq (Hz)	2	18	1753.41	417.84	1179.1	2418.4
Q25%	2	18	1644.93	394.93	889.1	2067.9
Q50%	2	18	2088.75	356.77	1309.5	2511.8
Q75%	2	18	3024.56	688.01	2285.8	4208.4
Bandwidth	2	18	21.68	24.02	3.2	104

AMPLITUDE MODULATED SOUNDS

<i>Door</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration (s)	1	5	3.39	0.35	2.83	3.775
<i>Whine</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	1	5	2.41	0.87	1.049	3.061
Start Freq (Hz)	1	5	160	40.00	120	220
End Freq (Hz)	1	5	242	43.24	200	310
Exc. Freq	1	5	82	16.43	60	100
Fmax 1 (Hz)	1	5	319	68.01	216	380
Fmax 2 (Hz)	1	5	498	401.85	169	1148
Fmax 3 (Hz)	1	4	630.5	94.83	545	756
Peak Freq(Hz)	1	5	320.18	67.63	216.4	379.5
Q25%	1	5	301.46	50.99	225.5	362.3
Q50%	1	5	482.46	115.15	390	675.2
Q75%	1	5	1190.12	104.07	1063.8	1277.7
Bandwidth	1	5	5.5	2.88	2.5	10.2
<i>Trill</i>	<i>N (groups)</i>	<i>N (sounds)</i>	<i>Mean</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Duration	5	104	2.29	0.91	0.984	5.02
Start Freq (Hz)	4	18	275.00	85.49	100	430
End Freq (Hz)	4	18	409.44	85.51	300	580
Exc. Freq	4	18	134.44	76.87	40	270
Fmax 1 (Hz)	5	53	352.62	93.82	224	651
Fmax 2 (Hz)	3	29	686.10	243.02	352	1192
Fmax 3 (Hz)	3	8	1522.88	392.93	878	2213
Peak Freq(Hz)	3	23	332.93	74.45	232.9	487.4
Q25%	3	25	353.13	95.94	243.1	641.4
Q50%	3	25	609.39	176.79	345.3	936.9
Q75%	3	25	1771.38	634.26	921.3	3828.3

AMPLITUDE MODULATED SOUNDS

<i>Bug sound</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	20	3.08	0.63	1.092	4.2
Start Freq (Hz)	1	10	244.00	67.86	110	310
End Freq (Hz)	1	10	363.00	71.66	260	490
Exc. Freq	1	10	119.00	43.32	70	190
Fmax 1 (Hz)	1	7	304.43	58.25	232	398
Fmax 2 (Hz)	1	7	537.29	413.50	104	1055
Fmax 3 (Hz)	1	6	939.83	259.57	695	1200
Peak Freq(Hz)	1	7	198.47	181.55	6.7	400.6
Q25%	1	7	370.42	76.43	280.5	498.77
Q50%	1	7	652.58	250.12	368.9	1020.35
Q75%	1	7	1289.75	324.92	880.3	1700.8

PULSED SOUNDS

<i>Fry</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	2	11	0.78	0.30	0.446	1.43
Peak Freq(Hz)	2	11	31.02	14.02	19.7	65.9
Q 25%	2	11	69.51	41.09	29.2	155.2
Q50%	2	11	320.25	206.24	57.8	600.5
Q75%	2	11	1051.05	658.89	258.5	2523.9
Bandwidth	2	11	9.89	4.45	4.3	20.5
Pulse rate	2	11	23.35	2.58	19.6	26.7
<i>Bubble sound</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	2	0.75	0.23	0.594	0.914
Peak Freq(Hz)	1	2	39.10	1.56	38	40.2
Q 25%	1	2	62.50	12.02	54	71
Q50%	1	2	199.65	80.12	143	256.3
Q75%	1	2	498.95	281.36	300	697.9
Bandwidth	1	2	10.25	5.30	6.5	14
Pulse rate	1	2	23.76	1.27	22.8	24.6
<i>Moped</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	4	3.80	1.42	2.912	5.898
Peak Freq(Hz)	1	4	402.55	36.87	353	439.2
Q 25%	1	4	305.58	102.40	209.6	403
Q50%	1	4	639.25	177.78	422.9	802.3
Q75%	1	4	1456.83	230.83	1120.4	1639.5
Bandwidth	1	4	1.53	0.57	1	2.3
F0	1	4	192.50	19.57	170	217
Pulse rate	1	4	6.13	0.33	5.9	6.6
<i>Gloop</i>	N (groups)	N (sounds)	Mean	SD	Min	Max
Duration	1	4	3.02	1.46	1.081	4.585
Peak Freq(Hz)	1	4	471.63	238.31	314.5	826.7
Q25%	1	4	315.58	32.26	286.5	358.1
Q50%	1	4	486.98	122.54	407.4	667.7
Q75%	1	4	821.45	62.05	752.7	903.4
Bandwidth	1	4	2.63	2.19	1	5.8
Pulse rate	1	4	11.00	1.63	8.9	12.8

CHAPTER 3

Supplementary figures

Figure 1: Diving profiles, vertical distance and distribution of vertical distances of a given mother-calf pairs (dep2).

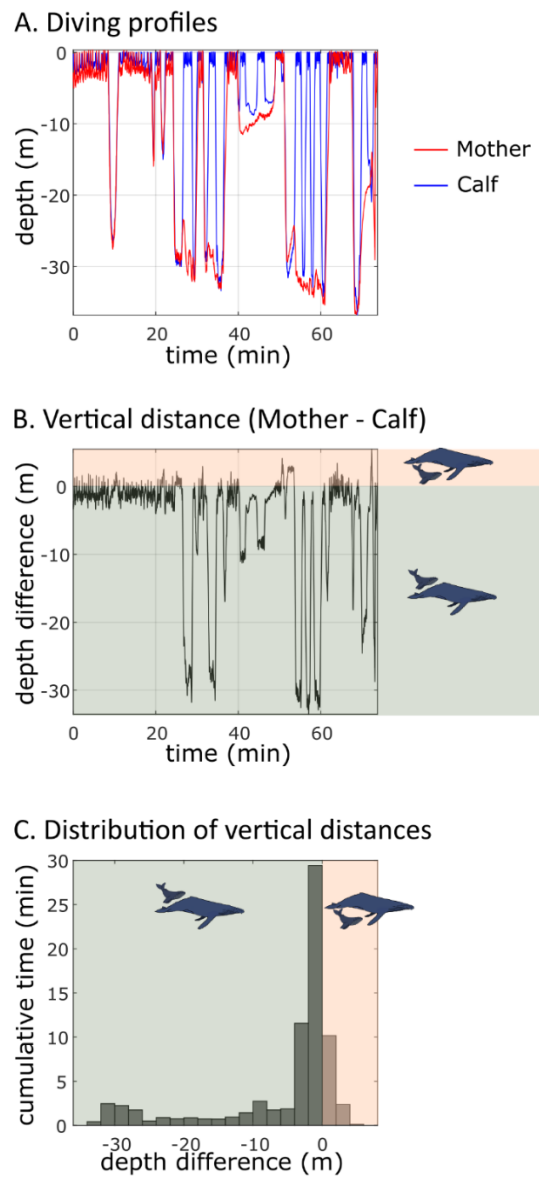
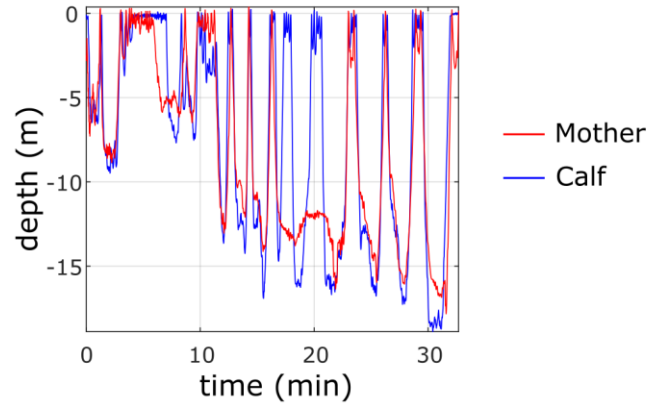
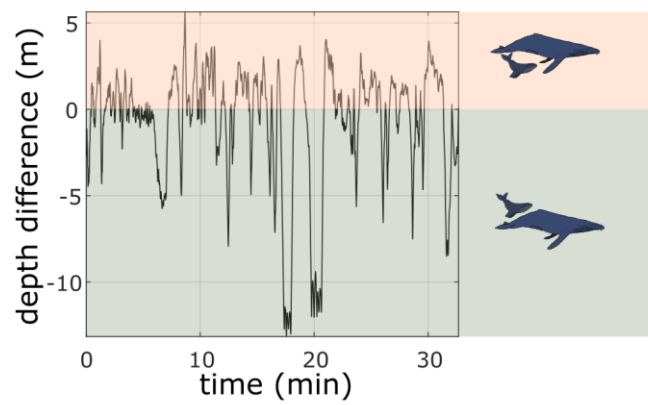


Figure 2: Diving profiles, vertical distance and distribution of vertical distances of a given mother-calf pairs (dep4).

A. Diving profiles



B. Vertical distance (Mother - Calf)



C. Distribution of vertical distances

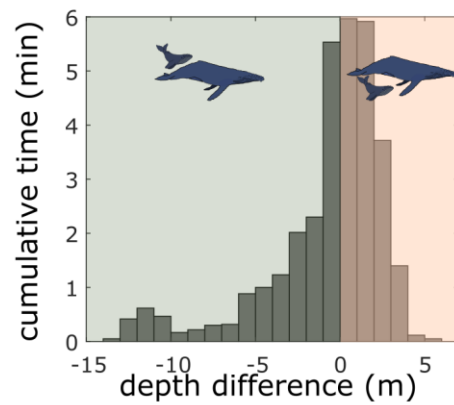
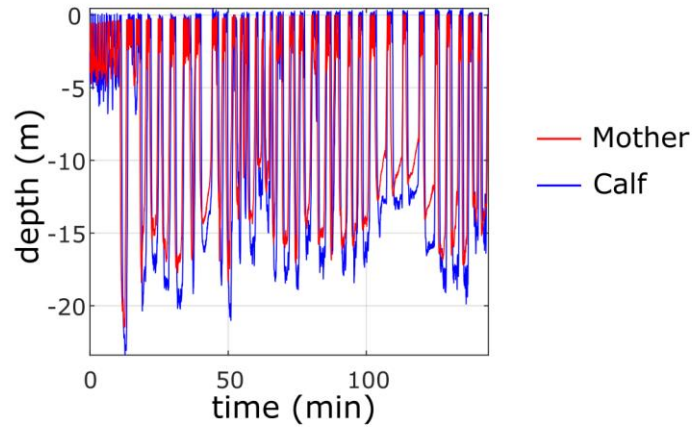
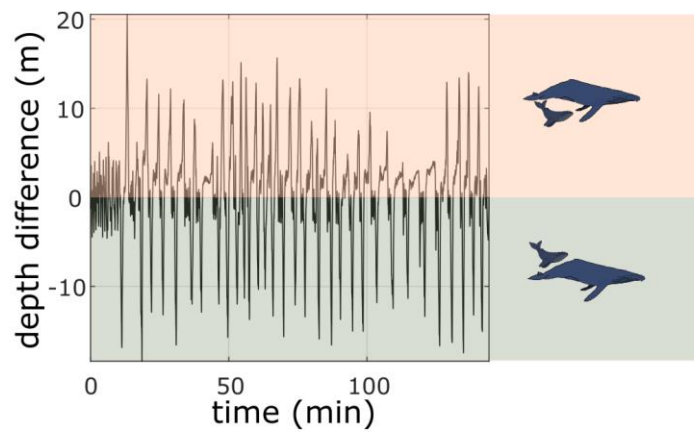


Figure 3: Diving profiles, vertical distance and distribution of vertical distances of a given mother-calf pairs (dep7).

A. Diving profiles



B. Vertical distance (Mother - Calf)



C. Distribution of vertical distances

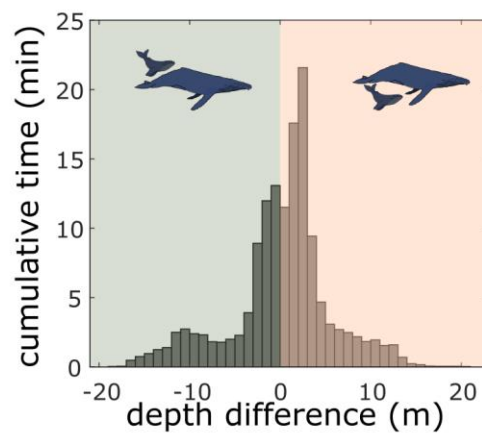
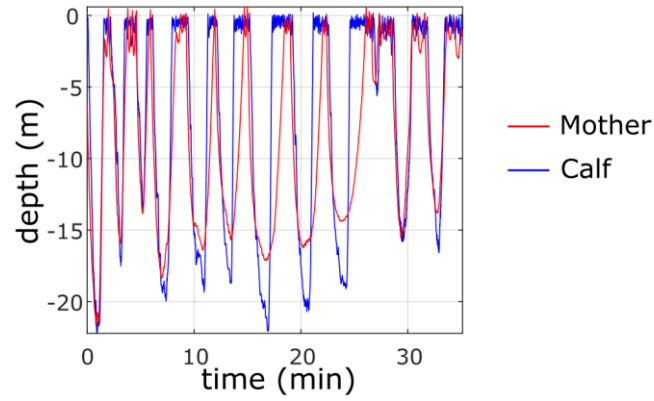
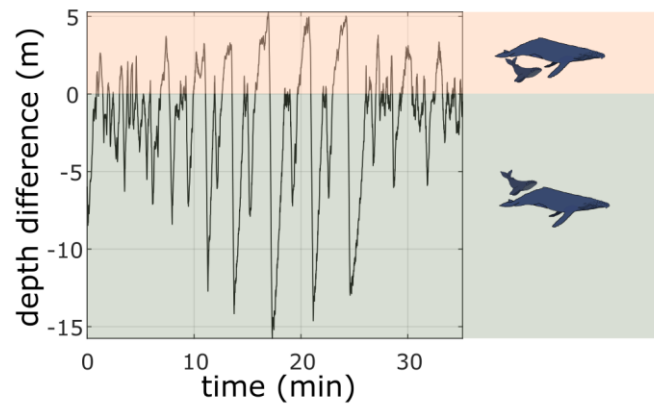


Figure 4: Diving profiles, vertical distance and distribution of vertical distances of a given mother-calf pairs (dep8).

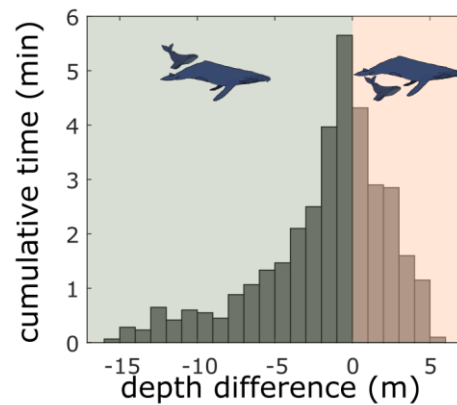
A. Diving profiles



B. Vertical distance (Mother - Calf)



C. Distribution of vertical distances



CHAPTER 4a

Supplementary table

Table 1: Comparison of sum durations for each of the 10 calf positions around the mother. P values were assessed using pairwise Wilcoxon tests and a Bonferroni correction for multiple comparisons was applied

	AB	ABR	ABL	R	L	BL	BLR	BLL	IF	BH
AB										
ABR	4.75E-06									
ABL	6.48E-05	1.65E+01								
R	1.27E-02	< 9.90E-15	< 9.90E-15							
L	5.24E+00	4.23E-11	1.68E-09	1.16E+00						
BL	1.46E+01	4.59E-04	4.03E-03	2.04E-04	4.01E-01					
BLR	3.00E-02	9.90E-15	1.09E-13	4.18E+01	1.97E+00	6.61E-04				
BLL	2.99E-01	1.60E-13	< 9.90E-15	1.47E+01	1.04E+01	1.08E-02	1.85E+01			
F	3.00E-02	3.30E-13	1.22E-11	1.75E+01	9.98E+00	7.61E-03	2.37E+01	4.25E+01		
BH	2.02E-06	< 9.90E-15	< 9.90E-15	3.05E-01	4.43E-04	1.30E-08	2.89E-01	3.12E-02	5.41E-02	

Table 2: Comparison of mean durations for each of the 10 calf positions around the mother. P values were assessed using Wilcoxon tests and a Bonferroni correction for multiple comparisons.

	AB	ABR	ABL	R	L	BL	BLR	BLL	IF	BH
AB										
ABR	3.92E-06									
ABL	2.78E-04	1.39E+01								
R	4.22E-03	< 9.90E-15	< 9.90E-15							
L	4.14E+00	6.05E-11	1.43E-08	9.06E-01						
BL	1.22E+01	1.53E-03	3.16E-02	6.56E-05	2.76E-01					
BLR	1.66E-02	< 9.90E-15	4.62E-13	4.18E+01	1.66E+00	3.31E-04				
BLL	1.65E-01	2.36E-13	4.09E-11	1.68E+01	8.22E+00	4.83E-03	2.23E+01			
F	3.28E-01	4.77E-12	5.18E-10	1.48E+01	1.17E+01	7.70E-03	2.07E+01	4.06E+01		
BH	1.10E-06	< 9.90E-15	< 9.90E-15	3.17E-01	4.73E-04	6.74E-09	2.84E-01	5.51E-02	4.90E-02	



CHAPTER 4b

Supplementary table

Table 1: Comparison of mean durations (in percentage) for the 10 calf's positions around the mother (AB: above, BH: behind, BL: below, IF: in front, L1: left rostrum, L2: left pectoral fin, L3: left caudal fin, R1: left rostrum, R2: left pectoral fin, R3: left caudal fin), and the 3 behaviours described (DB: dive both, DC: Dive calf, DM: Dive mother). P-values were assessed using pairwise Wilcoxon tests and a Bonferroni correction for multiple comparisons was applied.

	AB	BH	BL	DB	DC	DM	IF	L1	L2	L3	R1	R2
BH	<2e-16	-	-	-	-	-	-	-	-	-	-	-
BL	0.00017	4.7e-08	-	-	-	-	-	-	-	-	-	-
DB	1.00000	<2e-16	1.6e-07	-	-	-	-	-	-	-	-	-
DC	1.00000	<2e-16	0.00553	0.76730	-	-	-	-	-	-	-	-
DM	1.00000	2e-160.0002	1.00000	1.00000	-	-	-	-	-	-	-	-
IF	1.8e-10	0.00064	1.00000	2.6e-13	4.1e-08	1.1e-09	-	-	-	-	-	-
L1	0.21696	<2e-16	9.6e-11	1.00000	0.03547	1.00000	<2e-16	-	-	-	-	-
L2	1.00000	<2e-16	7.8e-09	1.00000	0.36719	1.00000	1.4e-15	1.00000	-	-	-	-
L3	7.5e-16	0.83625	0.00253	<2e-16	4.9e-13	1.0e-14	1.00000	<2e-16	<2e-16	-	-	-
R1	0.00071	<2e-16	7.7e-15	1.00000	8.1e-05	0.01564	<2e-16	1.00000	1.00000	<2e-16	-	-
R2	0.00158	<2e-16	7.4e-15	1.00000	0.00016	0.01391	<2e-16	1.00000	1.00000	<2e-16	1.00000	-
R3	1.2e-15	0.33651	0.00535	<2e-16	8.6e-13	1.8e-14	1.00000	<2e-16	<2e-16	1.00000	<2e-16	<2e-16

Titre : Interactions mère-baleineau chez la baleine à bosse (*Megaptera novaeangliae*).

Mots clés : baleine à bosse, baleineau, communication acoustique, sons sociaux, comportement spatial

Résumé : Chez les baleines à bosse (*Megaptera novaeangliae*), le maintien des liens sociaux entre les femelles et leurs nouveau-nés implique différentes modalités sensorielles telles que l'ouïe, le toucher et la vision. Si la communication acoustique chez les mâles chanteurs de cette espèce a été largement étudiée, les sons sociaux, en particulier ceux produits par les femelles et leurs nouveau-nés, ont été peu reportés. Cette étude décrit les sons sociaux présents dans les enregistrements acoustiques axés sur les groupes mère-baleineau et discute des vocalisations produites par les femelles et les baleineaux dans les interactions mère-jeune. En considérant les sons les plus fréquents de ce répertoire vocal, une analyse centrée sur la détermination de la source des sons de *bass* fréquence produits par la mère a été effectuée et des analyses ont été réalisées pour mettre en évidence l'individualité de

certaines vocalisations appartenant à la mère et à son petit. Une description du contexte comportemental de leur production vocale a été réalisée et parallèlement, les profils de plongée des mères et de leurs nouveau-nés ont été décrits. En outre, les femelles et leurs petits passent beaucoup de temps à la surface de l'eau. Les mères sont souvent statiques à la surface tandis que les baleineaux évoluent autour d'elles. Cette étude est également consacrée à la compréhension de leurs comportements de surface, en tenant compte des comportements initiés par les baleineaux. Des séries d'analyses ont été réalisées pour déterminer si les baleineaux présentaient des comportements de latéralisation par rapport à leur mère. Enfin, en utilisant la méthode de photogrammétrie, les tailles des femelles et des nouveau-nés ont été mesurées, ainsi que l'espace utilisée par les baleineaux autour de leur mère.

Title: Humpback whales (*Megaptera novaeangliae*) mother-calf interactions.

Keywords: humpback whale, calf, acoustic communication, social calls, spatial behaviour

Abstract: In humpback whales (*Megaptera novaeangliae*), maintaining social bonds between females and their newborns involves different sensory modalities such as hearing, touching and vision. While acoustic communication in male singers of this species has been extensively studied, social sounds, especially those produced by the females and their newborns have been poorly documented. This study describes the social sounds present in acoustic recordings focused on mother-calf groups and discusses the vocalizations used by females and calves in mother-offspring interactions. By considering the most frequent sounds from their vocal repertoire, an analysis focused on the determination of the source of the low-frequency sounds produced by the mother have been carried out and analyses were

performed to investigate the individuality of some vocalizations belonging to the mothers and the calves. A description of the behavioural context of their vocal production was performed and the diving profiles of mother-calf pairs were described. Moreover, females with their calves spend a lot of time on the water surface. Mothers are often static at the surface while calves move around them. This study is also dedicated to the understanding of their surface behaviours, considering the behaviours initiated by calves. A series of analyses were carried out to determine whether calves exhibited lateralization behaviours in relation to their mothers. Finally, by using photogrammetry method, mother-calf lengths were measured, and calves spatial range around their mothers was investigated.