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Humpback whale mother-calf interactions : investigating nursing, swimming, and vocal behaviors

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Humpback whale mother-calf interactions: investigating nursing, swimming, and vocal behaviors

*Interactions mère-baleineau chez la baleine à bosse : étude des comportements
d'allaitement, de nage, et de production vocale*

Thèse de doctorat de l'université Paris-Saclay et de l'université d'Antananarivo

École doctorale n° 568 Signalisations et Réseaux intégratifs en Biologie (BIOSIGNE)

Spécialité de doctorat : Sciences de la vie et de la santé

Graduate School : Life and Health Sciences. Référent : Faculté de médecine

Thèse préparée à l'**Institut des Neurosciences Paris-Saclay (Université Paris-Saclay, CNRS)** et au sein de la **Mention Zoologie et Biodiversité Animale (Université d'Antananarivo)**, sous la direction d'**Isabelle CHARRIER**, Directrice de Recherche CNRS, et la co-direction d'**Aristide ANDRIANARIMISA** et **Olivier ADAM**, Professeurs

Thèse soutenue à Paris-Saclay, le 08 novembre 2023, par

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« I believe that awe-inspiring life-forms like whales can focus human minds on the urgency of ceasing our destruction of the wild world. Many of humanity's most intractable problems are caused by disregarding the voices of the Other—including non-humans.

Just imagine what would be possible if we understood what animals are saying to each other; what occupies their thoughts; what they love, fear, desire, avoid, hate, are intrigued by, and treasure. »

Roger Payne (1935 –2023)

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Extended summary

Mammals exhibit particularly sophisticated forms of parental care, mainly provided by the female (maternal care). From the birth of the young until they become independent, the mother provides them with essential nutrition in the form of maternal milk, ensures their protection, and assists in their development. Maternal strategies, and thus the characteristics of mother-offspring relationships, vary significantly from one species to another and are related to biological traits and environmental characteristics. Various aspects, such as nursing, movements, and communication, differ depending on the maternal strategy used.

Among mammals, cetaceans (baleen whales and toothed whales) have the unique feature of living exclusively in aquatic environments (obligate swimmers). They have retained several mammalian traits inherited from their terrestrial ancestors; however, they have also evolved several unique traits related to the challenges they have had to adapt to in the context of life underwater. The aspects of maternal care in cetaceans have long interested researchers. Studies have been conducted to understand nursing behavior, swimming, and acoustic communication in females and their calves. However, these studies were limited by the technical and logistical means available at the time, which did not allow for comprehensive observation and tracking of cetaceans in their natural habitat. Thus, most studies were limited to captive animals or partial observations at the surface or subsurface.

In this thesis, I took the recent opportunity offered by the development of animal-borne multi-sensor tags to understand better mother-offspring interactions in free-ranging aquatic mammals. I focused on the humpback whale (*Megaptera novaeangliae*), one of the most popular, extensively studied, and accessible baleen whale species. I used data from tags equipped with or without a camera (CATS cam and Acousonde tags) placed on young calves (<3 months old) and their mothers off Sainte Marie, Madagascar.

I examined nursing behavior in the first part (Chapters 1 and 2). In Chapter 1, I developed a method to study nursing behavior even with data lacking videos and presented an initial detailed description. Starting from Chapter 1, which allowed the combination of data with and without videos to create a larger dataset, details about the nursing pattern in humpback whales were obtained (Chapter 2). In these first two chapters, I showed that nursing behavior is highly stereotyped, and nursing sessions are segmented into several successive series occurring approximately every two hours. Furthermore, I documented that nursing can occur at night. I suggested that some characteristics, such as the nursing intensity and the depth of occurrence of nursing, change as the calf grows.

In the second part (Chapters 3 and 4), I focused on the swimming behavior of mother-calf pairs. I demonstrated that the mother-calf pairs' swimming activities change with the calf's age, particularly the time engaged in slow swimming (milling) and that the mother mainly drives some of the activities. In contrast, other activities are initiated by the calf (Chapter 3). I concluded that the time budget, especially the time spent resting and milling, is a balance between the mother's need to conserve energy for the upcoming migration and caring for the calf (humpback whales being capital breeders) and the calf's need to optimize its growth and rapidly improve its swimming performance. In Chapter 4, I demonstrated for the first time that adult humpback whales can control their buoyancy and exploit it to optimize swimming efforts during vertical movements. In contrast, calves cannot do so and rely on their mothers, especially to remain stationary at a given depth.

In the third part (Chapters 5 and 6), I studied the context of social calls in mother-calf pairs to understand their biological functions better. I began by finding a method to identify and separate the mother's calls from those of the calf, a significant challenge in studying cetacean vocalizations from animal-borne tags for several years. With this problem solved, I found that the calf is primarily responsible for maintaining acoustic contact during vertical separations (e.g. when the calf goes to the surface to breathe), and the mother rarely responds vocally. I also showed that the acoustic characteristics of calf calls differ significantly from those of adults and thus could facilitate maternal responses. In Chapter 6, I explored the relationships between calf behaviors and the calls. I found that some behaviors, such as suckling, are associated with a high call rate and a homogeneous set of calls (calls of more or less the same type). In contrast, others, like synchronized traveling of the mother and calf and resting, are associated with silence.

These findings provide new and crucial insights for a better understanding of the maternal care dynamics, the development of young whales, and the importance of acoustic signals in mother-young communication in a relatively challenging aquatic environment. They constitute a novel knowledge that could motivate and guide conservation measures and serve as the foundation for further studies.

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Résumé étendu

Les mammifères présentent des formes de soins parentaux particulièrement sophistiquées qui sont principalement dispensées par la femelle (soin maternel). La mère, à partir de la naissance des jeunes et jusqu'à leur indépendance, approvisionne obligatoirement les jeunes en nourriture sous forme de lait maternel, assure leur protection, et les assiste dans leur développement. Les stratégies maternelles, et donc les caractéristiques des relations mères-jeune, sont très diversifiées et en relation avec les traits biologiques et les caractéristiques de l'environnement. Selon la stratégie maternelle utilisée, divers aspects tels que l'allaitement, le déplacement, et la communication vont être différents.

Parmi les mammifères, les cétacés (baleines à fanons et baleines à dents) ont la particularité de vivre exclusivement en milieu aquatique (nageurs obligés). Ils ont conservé plusieurs caractéristiques mammaliennes héritées de leurs ancêtres terrestres, mais ils ont également acquis plusieurs traits uniques liés aux défis auxquels ils ont dû s'adapter dans le contexte de la vie sous l'eau. Les aspects du soin maternel chez les cétacés ont intéressé les chercheurs depuis longtemps déjà. Des études ont été conduites pour comprendre le comportement d'allaitement, la nage et la communication acoustique chez les femelles et leurs petits. Ces études ont toutefois été limitées par les moyens techniques et logistiques disponibles à l'époque qui ne permettaient pas d'observer et de suivre intégralement les cétacés dans leur milieu naturel. Ainsi, la plupart des études se sont limitées à des animaux en captivité ou à des observations partielles en surface ou en subsurface.

Dans cette thèse, j'ai saisi l'opportunité récente offerte par le développement de balises multi-capteurs embarquées pour mieux comprendre les interactions mère-jeune des mammifères aquatiques dans leur milieu naturel. Je me suis focalisé sur la baleine à bosse (*Megaptera novaeangliae*), une des espèces de baleine à fanons les plus populaires, les plus étudiées et les plus accessibles. J'ai utilisé des données issues de balises équipées ou non de caméra (balises CATS cam et Acousonde) posées sur des jeunes baleineaux (<3 mois) et leurs mères dans les eaux côtières de Sainte Marie, Madagascar.

Dans la première partie (Chapitres 1 et 2), je me suis consacré à l'étude du comportement d'allaitement. Dans le Chapitre 1, j'ai développé une méthode pour étudier le comportement d'allaitement même avec des données sans vidéos et en présente une première description détaillée. A partir du Chapitre 1 qui a permis la combinaison de données avec et sans vidéos pour avoir un jeu de données plus grand, des détails sur le schéma d'allaitement chez la baleine à bosse ont été obtenus (Chapitre 2). J'ai montré, dans ces deux premiers chapitres, que le comportement d'allaitement est très stéréotypé et que les sessions d'allaitement sont segmentées en plusieurs séries et se font toutes les deux heures environ. De plus, j'ai établi que

l'allaitement peut également se faire la nuit, et suggéré que certaines caractéristiques telles que l'intensité d'allaitement et la profondeur à laquelle l'allaitement se passe changent à mesure que le baleineau grandit.

Dans la deuxième partie (Chapitres 3 et 4), je me suis focalisé sur la nage des couples mère baleineau. J'ai montré que les activités de nage des couples mère baleineau changent avec l'âge du baleineau (notamment le temps passé à faire des nages lentes) et que certaines activités sont surtout imposées par la mère et d'autres sont entreprises par le baleineau (Chapitre 3). J'ai conclu que le budget temps, notamment le temps passé à se reposer et à nager de manière erratique, est une balance entre le besoin pour la mère de conserver de l'énergie pour la migration à venir et pour prendre soin du baleineau (la baleine à bosse étant un reproducteur capital) et le besoin du baleineau à optimiser sa croissance et à améliorer rapidement sa performance de nage. Dans le Chapitre 4, j'ai démontré pour la première fois que les baleines à bosse adultes sont capables de contrôler leur flottabilité et l'exploiter pour optimiser les efforts de nage lors des mouvements verticaux, alors que les baleineaux n'en sont pas capables et se font alors aider par leur mère, notamment pour se maintenir à une profondeur donnée.

Dans la troisième partie (Chapitres 5 et 6), j'ai étudié le contexte des cris sociaux des couples mère-baleineau pour mieux comprendre leurs fonctions biologiques. J'ai commencé par trouver un moyen pour identifier et séparer les cris de la mère de ceux du baleineau, un problème majeur depuis plusieurs années dans l'étude des vocalisations des cétacés à partir de balises embarquées. Ce problème résolu, j'ai pu trouver que le baleineau est le principal responsable du contact acoustique lors des séparations verticales (e.g., quand le baleineau part respirer à la surface) et que la mère ne répond vocalement que rarement. J'ai aussi montré que les caractéristiques acoustiques des cris des baleineaux diffèrent suffisamment de celles des adultes et pourraient faciliter les réponses maternelles. Dans le Chapitre 6, j'ai exploré les relations entre les comportements du baleineau et les cris qu'il utilise. J'ai trouvé que certains comportements comme l'allaitement sont associés à un taux de vocalisation élevé et sont associés à un lot homogène de cris (cris plus ou moins du même type), alors que d'autres comportements comme les déplacements synchronisés de la mère et le baleineau et le repos sont associés à un silence.

Ces résultats constituent des éléments nouveaux et déterminants pour une meilleure compréhension de la dynamique des soins maternels, du développement des jeunes, et de l'importance des signaux acoustiques dans le contexte de la communication mère-jeune dans un environnement aquatique relativement contraignant. Ils constituent une base de connaissance inédite qui pourrait motiver et guider la mise en place de mesures de conservation et qui pourrait servir de fondement pour des études complémentaires

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General introduction



1. Parental care in mammals

From an organismal point of view, each organism aims to maximize its fitness and, in the long term, to preserve its genes, in particular through its descendants (Gould, 2002). In this sense, Smiseth et al. (2012) defined parental care as any parental trait that improves the fitness of the descendants and favors the preservation of the parental genes. In most animal species, parental care is mainly limited to choosing a safe and adequate place for the eggs and providing eggs with a reserve to feed the young until they can live independently. In other species, like mammals and birds, the parents will go as far as providing care even after birth/hatching. Such post-natal/post-hatching care may be provided exclusively by one parent (mother or father) or both (Balshine, 2012). Since parental care represents a form of reproductive investment, it usually involves targeted allocations to prevent spending resources on non-filial offspring and investing in other's reproductive success (Clutton-Brock, 1991).

In most mammals, only the mother usually provides post-natal care (Gubernick & Klopfer, 1981; Maestriperi & Mateo, 2009; Nowak et al., 2000; Rosenblatt et al., 1985). Biparental and cooperative care (where several adults of a group provide care to the young) are uncommon (Kleiman & Malcolm, 1981; König, 1997; A. F. Russell, 2004; West & Capellini, 2016). The most striking form of maternal care is food provisioning, water provisioning, and immunity support through maternal milk (Nowak et al., 2000; Oftedal, 2012). Maternal milk is a nutritive substance produced by mammary glands, a unique feature of mammals from which their name was derived (Gregory, 1910). As maternal milk is the only food source for young mammals during the first stage of their life, at least a minimum of maternal attendance is compulsory in mammals. Milk production by male mammals remains rare and mostly anecdotal (Daly, 1979; Kunz & Hosken, 2009).

Along with providing food to their young, female mammals can provide them warmth (thermal assistance), protect them from predators, assist their locomotion, etc. Thermal assistance can be a direct action, such as embracing the young (e.g., in bats; Sano, 2000) or providing them with an adequately chosen 'nest' (or shelter/burrow/den). Protection against predators is achieved through behaviors such as discouraging predators, assisting escape, or creating barriers/hides to prevent predators from reaching the young (Ford & Reeves, 2008; Hamel & Côté, 2009; Pitman et al., 2015; Smith, 1987). Regarding locomotory assistance, a classic example is the case of primates carrying their young (Ross, 2001).

2. Pattern of maternal care in mammals

How maternal care is provided in mammals varies from one species to another, depending on its life history and environment. Among the notable correlates are the neonates' developmental status and the litter's size. In species that give birth to underdeveloped young (limited sensory, locomotor, and thermal regulation capacities

at birth – 'altricial' species) and in large litters, the mother uses a nest where all mother-young interactions happen. These species include canids, felids, several rodents, and lagomorphs (Benedek et al., 2020; Denenberg et al., 1969; Fernández et al., 2002; Naaktgeboren, 1968; Nowak et al., 2000). Conversely, 'precocial' species (as opposed to altricial species) that produce only small litter, like most ungulates, typically do not nest (Fisher et al., 2002; Lent, 1974; Nowak et al., 2000). On the other hand, intermediate species (relatively well-developed senses but with insufficient locomotory and thermoregulatory abilities at birth), such as primates, may nest or not, mainly depending on the litter size (Ross, 2001).

The mother has to look after several young gathered and isolated in the same place in the case of nesting species. The nest provides litter both protection from cold and predators. The remaining main task of the mother is to provide food. Non-nesting species, on the other hand, have the particularity of being delivered at birth to the environment where they will spend their adult life. The young are directly exposed to environmental hazards and challenges, including predators and potentially aggressive conspecifics. In addition to providing food, the mother must thus immediately provide warmth if needed, defend their offspring from predators and other conspecifics, and eventually assist them in their locomotion.

Along with young developmental status and litter size, a notable correlate related to the maternal care pattern concerns habitat structure. This aspect has been particularly well documented in terrestrial ungulates. Terrestrial ungulates are generally precocial, produce only one young at a time (with a few exceptions), and are non-nesters exposed to predation. However, depending on the structure of their habitat, a variation in the pattern of maternal care can be observed. For those living in closed habitats, the young remain hidden in the vegetation, safe from predators, while the mother engages in various vital activities, such as foraging. This strategy is commonly referred to as the 'hiding' anti-predator strategy (Fisher et al., 2002; Lent, 1974). The difference with nester species is that the hiding place can change regularly, and, in many cases, the young choose the exact hiding spot (Blank, 2017; Grovenburg et al., 2010; Lent, 1974). The young choosing the hiding spot is made possible by its great autonomy soon after birth.

For terrestrial ungulates living in open environments, the young follow the mother wherever she goes. Indeed, the environment does not offer any cover for the young as it does for the hidiers; thus, the young must rely on continuous protection from their mother. This strategy is known as the 'following' anti-predator strategy (Fisher et al., 2002; Lent, 1974) and may also be favored by the mother's size (Fisher et al., 2002). Large females are naturally better able to protect an offspring that is constantly next to them and are less vulnerable to predators that may take advantage of the reduced mobility and ease of detection caused by the presence of a youngster.

Various aspects of mother-offspring interactions are closely linked to the patterns above. The following sections will introduce three essential components: the nursing behavior, the movements, and the communication.

3. Nursing and suckling behavior

It is essential to clarify some terminologies used to discuss nursing behavior first. The literature often confuses different vocabularies, notably between lactation, suckling, sucking, and nursing (Hall et al., 1988). Lactation refers to the physiological state associated with milk production or, more generally, the period during which an individual produces milk. Suckling refers to the behavior of the young to obtain milk from a lactating individual. Generally speaking, nursing and suckling correspond to the same mother-young behavior, the transfer of milk from a lactating individual to the young, but from two different perspectives: from the lactating individual's perspective (the mother) and the young's perspective, respectively. The term suckling is to be distinguished from sucking, a component of suckling. Sucking refers specifically to the action of exerting negative pressure on the nipples or teats to obtain the milk.

In 'monotremes' (platypuses and echidnas), milk beads from the milk patch on the mother's abdomen (Oftedal, 2002, 2012; Stead et al., 2022). Their nursing is, therefore, relatively simple. The mother lets the young lick the milk patch to feed them. In 'metatherians' (represented by marsupials) and 'eutherians' ('modern' mammals), the milk is expelled via nipples or teats (Oftedal, 2012; Stead et al., 2022). In metatherians, the young directly crawl towards the nipple at birth and attach themselves to it continuously to obtain milk during the first stage of their development (Hunsaker & Shupe, 1977; Stead et al., 2022). After that, suckling becomes intermittent. For eutherians, nursing is intermittent rather than continuous (Stead et al., 2022).

The nursing pattern throughout the day is closely linked to the maternal strategy employed by the mother-offspring group. This link has been well explored in terrestrial ungulates, where there is a marked contrast between the nursing pattern of the hider and follower species (Gloneková et al., 2017; Lent, 1974; Rosenblatt et al., 1985). In nesting species, nursing is reduced to infrequent periods corresponding to when the mother returns to the nest (Nowak et al., 2000; Zarrow et al., 1965). In hider species, a similar pattern has been observed. Nursing is limited to a few moments during the day when the mother-offspring pair meets and is often prolonged. With follower species, nursing is frequent but in short sessions, as the pair is always together (Gloneková et al., 2017; Lent, 1974; Rosenblatt et al., 1985).

Nursing is, by nature, costly because producing sufficiently rich milk requires a lot of energy from mothers (Braithwaite et al., 2015; Oftedal et al., 1987; Speakman, 2008). However, depending on whether it is performed in a nest or not, it may also incur additional costs for the mother. For example, the mother and the young may need to stop their movements or at least slow down to facilitate suckling, which, in turn, may

inadvertently facilitate predator attacks.

The duration of lactation varies significantly from one species to another. It can last several years in some species, such as great apes (Carvajal & Schuppli, 2022), elephants (Lee & Moss, 2011), some pinniped species (Riedman, 1990), and toothed whales (Chivers, 2009). In others, it can last just a few days. The most striking example is the hooded seal, whose lactation lasts only four days (Bowen et al., 1985). The lactation length is linked to different constraints and needs in different species (Hayssen, 1993; Lee, 1996). For instance, more prolonged lactation may be associated with sophisticated social learning requirements for the young (Brodie, 1969). Short lactation may be linked to constraints pushing the mother to leave her young rapidly. An example is the need for the mother to feed after fasting in hooded seals (Oftedal, 1993).

The nursing intensity varies from birth to weaning (Fiialkovskyi et al., 2023; Nowak et al., 2000; Skok, 2022). In several species, neonates suckle intensively during the first period following birth. This first milk is crucial because, at this stage, the milk contains immunoglobulins essential for building initial immunity ('colostrum'). Afterward, suckling intensity decreases and eventually stabilizes until the weaning period approaches. As the weaning period nears, suckling intensity rapidly declines, and eventually, nursing ceases. The decrease in nursing intensity may be associated with a reduction in the milk requirement of the young as they begin to eat solid food, either on their own or by eating what their mother brings. Increased mother-offspring conflict may also explain this decrease. As the young grow, their energy demands increase, exceeding what the mother can offer without severely affecting her future reproductive success (Trivers, 1974). As a result, the mother starts to restrict milk access.

4. Mother-offspring locomotion and movements

The provision of maternal care implies the mother's presence at the offspring's side, at least for nursing. However, the mother must also ensure her needs are met to survive. She must thus move from one place to another, for example, to forage and sustain herself. In nesting species, the young have no locomotory ability to leave the nest; thus, the mother forages outside the nest unaccompanied. There is no notion of mother and young moving together to join another place. She may only move with her young when forced to because of a disturbance or increased predation risk (Boonstra & Craine, 1986; Galef Jr, 1981; Laack et al., 2005). For instance, in such forced situations, the mother simply carries the young to the new nest using her mouth. Otariids can also be compared to nesters. Although otariid pups are sensorially and thermally autonomous on land, their fur is not adapted to water yet, and they have limited swimming ability (Donohue et al., 2000). Thus, otariid pups stay in one place (on the beach) while their mother feeds at sea. Hider species also show similar characteristics to nesting species. The mother moves alone while the young wait in their hiding place (Fisher et al., 2002; Lent, 1974).

Other species, such as marsupials and several primates, are constantly moving with their young; however, the young do not need to deploy any locomotion effort. For marsupials, the young remain in the mother's ventral pouch for most of their early life stage (Hunsaker & Shupe, 1977). In the case of primates, the young cling to their mother's abdomen or back (Ross, 2001). These strategies imply that the mother is not restricted to staying in or returning to the same place and can freely explore her environment to meet her needs.

For follower species, the young move alongside their mother without being carried. As with mothers who carry their young, the following strategy enables the mother to continue her vital activities and the young to benefit from continuous maternal care (Fisher et al., 2002; Lent, 1974). However, it presents specific challenges, such as the fact that the offspring, even if very precocious, may have more limited locomotor skills than the mother (Noren et al., 2006). The offspring must manage to keep up with the mother, and the mother must adjust her movements to allow the offspring to follow her. The offspring must, for instance, quickly improve their locomotor performance. In the case of terrestrial ungulates, this means significantly practicing running and walking. As for the mother, she must accommodate her pace to her offspring's performance to reduce the risk of separation (Huetz et al., 2022; Lent, 1974; Szabo & Duffus, 2008). Such accommodation includes allocating sufficient time for resting. She can also occasionally provide direct assistance, like pushing or dragging the young (Ford & Reeves, 2008; Noren et al., 2008; Noren & Edwards, 2011; Pitman et al., 2015). As both the mother and the young are independent in their movements, there must be some coordination, including communicating (when and where to move) and maintaining track of each other's position. The aspect of communication will be developed in the next section.

5. Mother-offspring communication

Animal communication refers to the transmission of information or signals, whether acoustic, visual, chemical, or tactile, between individuals of the same or different species (Bradbury et al., 1998). It involves at least two protagonists: the sender, who transmits coded information in a given channel, and the receiver, who decodes and interprets it. Communication implies signals and cues. Signals are intentional and benefit both the sender and the receiver. In contrast, cues are sent unintentionally by a sender to a receiver and benefit only the receiver. Both give some information that can be interpreted by the receiver to adjust its behavioral state and adapt its behavior. A typical example of the use of cues is the case of predators attentive to information transmitted by their prey (Roberts et al., 2007).

The mother-young relationships usually involve a two-way information exchange between the young and the mother. From the young's point of view, maternal care is a matter of individual survival (Trivers, 1974). Therefore, they must ensure they get the

maximum benefit from maternal care. As a result, they seek to influence their mother's behavior, notably by sending signals to her about their needs (Gubernick & Klopfer, 1981; Lent, 1974; Nowak et al., 2000). Returning to the earlier points, young animals may, for example, communicate with their mother to beg for milk. They may also call the mother in the event of separation. Since maternal care is a way for the mother to secure her reproductive success, she remains attentive to these signals from her young. She responds accordingly, as long as the cost does not negatively affect her long-term reproductive success (Trivers, 1974).

Another vital point that must involve some form of information exchange concerns the identification of the young by the mother to ensure that the care is only provided to filial offspring and the identification of the mother by the young for cases where other potentially aggressive conspecifics may be present. For nesting mammals, the mother only needs to recognize her litter identity and(or) remember her nest location. Individual recognition of the young is thus optional (Nowak et al., 2000); hence, at most, only signals containing litter identity from the young are needed. The young's individual recognition of the mother is not necessary either, as no other individual than the mother is expected to enter the nest (Nowak et al., 2000). Thus, the mother does not necessarily have to transmit information about her identity. For non-nesting mammals, there is a strong need for mother-young individual recognition (mutual or unidirectional). Indeed, the mother may be surrounded by offspring from other females, and the young must avoid aggressive conspecifics (Clutton-Brock, 1991; Lent, 1974; Martin et al., 2022; Nowak et al., 2000).

Depending on the information to be transmitted and the conditions in the environment, the mother and her young may employ different communication modalities or combine several (Higham & Hebets, 2013) to ensure the information reaches the receiver reliably. Indeed, the environmental conditions and the type of signal impose various transmission constraints. Acoustic signals, for example, can be effective over long distances and for rapid communication (McComb et al., 2003; Rosenthal & Ryan, 2000; Zuberbühler et al., 1997), enabling mother and young to communicate at a distance. However, their propagation can be altered by physical obstacles or noise. For instance, in dense forests, the vegetation can attenuate or distort sound (Michelsen & Larsen, 1983; Wells & Schwartz, 1982). Visual signals can be effective at short and medium distances and also allow immediate communication but largely depend on light or weather conditions restricting visibility (Rosenthal & Ryan, 2000). Chemical signals can be especially effective at short distances but are highly sensitive to local conditions such as wind direction, wind speed, humidity, etc. (Alberts, 1992). Finally, tactile communication only works at very short distances (Langbauer Jr, 2000).

6. Mother-offspring interactions in cetaceans

Cetaceans (whales, including dolphins and porpoises), along with sirenians, are the only mammal groups that are entirely aquatic or obligate swimmers (Ballance, 2018; Jefferson et al., 1993; Thewissen et al., 2009). The vast majority are exclusively marine. Cetaceans are divided into two distinct groups: baleen whales (mysticetes) and toothed whales (odontocetes). They descended from a terrestrial mammalian ancestor they share with all modern ungulates (Fordyce, 2018; Thewissen et al., 2009). While they have retained most of the main features of mammals, including the fact that they breathe air and that the females lactate and take care of the young, they have undergone several physiological, anatomical, and behavioral transformations in the course of evolution to adapt to this exclusively aquatic life. Such transformations include their exceptional diving ability, the evolution of unique sound production systems, the switch to a mainly sound-based lifestyle, the disappearance of the hind limbs, the transformation of the tail into a flipper, etc. (Thewissen et al., 2009).

Cetaceans are similar to their terrestrial relatives in that they give birth to unique and highly precocial offspring and are often compared to follower species concerning the mother-calf spatial relationships (Huetz et al., 2022; Rendell et al., 2019; Szabo & Duffus, 2008; Taber & Thomas, 1982; Thomas & Taber, 1984; Tyson et al., 2012). Cetacean mother-calf pairs, however, face distinct challenges related to the unique nature of the aquatic environment. Firstly, cetaceans move in a three-dimensional space. Moreover, there is a separation between where they spend most of their life (underwater) and where they get oxygen (at the surface). In the case of mother-calf pairs, both the mother and the calf must, therefore, manage their movements in this three-dimensional environment, balancing the need to breathe at the surface – which may differ between adults and calves (Cartwright & Sullivan, 2009; Huetz et al., 2022; Szabo & Duffus, 2008) – and the need to stay underwater, ideally together.

Secondly, cetaceans live in an environment where sounds propagate very well (Au & Hastings, 2008; Ladich & Winkler, 2017). It is not surprising, therefore, if this is their primary means of communication (Dudzinski et al., 2009). Unfortunately, while sound efficiency in an underwater context can be advantageous for optimizing maternal care (long-range and rapid communication, good acoustic vigilance), it can also be a disadvantage. Indeed, the background sound is highly variable under water and diverse (surface vs. deep, anthropized vs. non-anthropized areas, presence of singing males, etc.) (Hildebrand, 2004; Richardson et al., 2013), making it potentially challenging to extract information from acoustic signals, and predators or unsolicited conspecifics can also easily exploit sound to detect communicating mother-calf pairs (Dabelsteen, 2005; Haskell, 1994).

General introduction

Cetaceans also generally rely on resources extending to vast areas, meaning the mother and their calf must cover substantial distances. Such need for extensive travel is especially pronounced among most baleen whale species, which rely on a seasonal food resource in a well-defined geographical area, different and far from the habitat favorable to breeding and calving (Bannister, 2018; Corkeron & Connor, 1999; Lockyer, 1984). Baleen whale mothers thus often rely on a limited energy reserve to care for the calf, and the calf must be prepared to undertake the travel to join the area where the food resource is abundant.

Although the aquatic environment is very different from the terrestrial environment, other environmental conditions experienced by cetaceans are also comparable and potentially homologous to some of the conditions experienced by terrestrial and semi-aquatic mammals. For example, cetaceans live in an environment that can be considered open and are exposed to predators, similar to terrestrial mammals that use the following strategy (Szabo & Duffus, 2008; Tyson et al., 2012). Like some seals, baleen whales rely on their reserves to reproduce (capital breeders) (Oftedal, 1993).

Nursing and suckling behavior

Toothed whale calves generally remain with their mothers for approximately two years, while baleen whale calves depend on their mothers for only one year (Chivers, 2009). The frequency of nursing during these periods of dependence and details on how the calves suckle remain poorly documented. Nursing has been mainly studied in captive toothed whales. It has been shown that captive toothed whale calves suckle by remaining attached to their mother's teats for only a brief period (less than 10 s) but repetitively (Clark & Odell, 1999a; J. M. Russell et al., 1997; Triossi et al., 1998). The intensity of nursing peaks at birth and then decreases as the calf grows (Clark & Odell, 1999a, 1999b; J. M. Russell et al., 1997; Triossi et al., 1998). After a few months, however, there may be an upturn in nursing intensity, but the reason for this is unclear (Triossi et al., 1998). In all cases, the approaching weaning was suggested to be always associated with a progressive decline in nursing intensity (Clark & Odell, 1999a, 1999b; J. M. Russell et al., 1997; Triossi et al., 1998). In natural environments, the most accurate descriptions of cetacean nursing behavior have been obtained from underwater videos recorded by divers (e.g., Sarano et al., 2023; Zoidis & Lomac-MacNair, 2017) or by placing cameras on calves (Tackaberry et al., 2020). These studies (on sperm and humpback whales) have highlighted two crucial points: the calves remain continuously attached to their mother's teat for an average of 20-40 s, and suckling occurs at depth, not at the surface.

Mother-calf swimming behavior

The cetacean mother-calf pair's swimming behavior is highly synchronized (Fellner et al., 2013; Huetz et al., 2022; Noren et al., 2008; Noren & Edwards, 2011; Rendell et al.,

2019; Smultea et al., 2017; Szabo & Duffus, 2008; Taber & Thomas, 1982; Thomas & Taber, 1984; Tyson et al., 2012). The pair usually adopts an elaborate swimming configuration known for providing energetic benefits for the calf to accommodate its limited swimming capabilities (Noren, 2008; Noren et al., 2008; Noren & Edwards, 2011; Ratsimbazafindranahaka, 2019; Smultea et al., 2017). These energetic advantages have been particularly well quantified in dolphins (Noren, 2008; Noren et al., 2008; Noren & Edwards, 2011; Weihs, 2004). By moving in echelon relative to its mother, the calf is pushed towards the mother, and the effort needed to swim is considerably reduced. Mothers also tend to display modified swimming behavior adapted to the calf's performance. In humpback whales, for example, it has been shown that mothers reduce their dive time (Szabo & Duffus, 2008). These behavioral adaptations are likely one of several strategies mother-calf pairs employ to facilitate the calf's ability to stay close to the mother.

Mother-calf acoustic communication

Acoustic recordings in the wild have shown that like most cetacean social groups, cetacean mother-calf pairs produce diverse sounds (in addition to echolocation clicks for toothed whales), commonly called 'social' sounds (Ames et al., 2021; Cusano et al., 2022; Hill, 2023; Indeck et al., 2021, 2022; S. L. King et al., 2016; Nielsen et al., 2019; Parks et al., 2019; Saloma et al., 2022; Sayigh et al., 2023; Videsen et al., 2017; Zoidis et al., 2008). These sounds include non-vocal sounds, such as the percussive sounds produced by hitting the sea surface with either the caudal, pectoral fins, or the head, and vocal sounds produced by specialized vocal apparatus (Dudzinski et al., 2009; Edds-Walton, 1997). The functions of these social sounds, however, remain to be determined. In dolphins, studies have suggested that signature whistles facilitate the reunion and mutual recognition of mother-calf pairs (S. L. King et al., 2016). In baleen whales, vocalizations have mainly been associated with mother-calf contact (Indeck et al., 2022; Videsen et al., 2017; Zoidis et al., 2008). To date, no sound type has been clearly associated with a particular mother-calf behavior. More recently, several studies focused on how mother-calf vocalizations adapt to the presence of predators. In particular, cryptic communication has been highlighted: mothers and calves communicate discreetly (i.e., low amplitude level and low call rate) to avoid predators and unsolicited males who may seek to mate with the mother (Indeck et al., 2022; Nielsen et al., 2019; Parks et al., 2019; Videsen et al., 2017).

7. Why our knowledge of the mother-offspring interactions in cetaceans remained very limited?

The above information depicts a relatively limited knowledge of mother-young interactions in cetaceans. Observations from animals in captivity (mainly toothed whales) form much of the current knowledge. The extent of their validity in the natural environment remains uncertain since life in the aquarium is very different from natural conditions and, therefore, far from the natural challenges faced by animals. The focus on captive animals was mainly motivated by the fact that, by nature, cetaceans are challenging to access in their natural environment. Some species are very cryptic and difficult to detect, others do not specifically stay in a given area, and as already stated above, they all spend most of their time underwater (Ballance, 2018). Studies of larger species in their natural habitat, particularly baleen whales, have begun to develop, but most studies have been based on surface and subsurface observations. The main drawbacks of these observations are that they do not allow precise identification of behaviors and only represent cetacean's life at the surface. The most relevant example of this is the description of nursing behavior, which is almost impossible to confirm from the surface (Tackaberry et al., 2020). Regarding acoustic communication studies in the wild, the available technology has also limited many observations. Many studies have relied on moored, towed, or diver-carried hydrophones and, thus, have been limited to recordings at a fixed or relatively immobile point. They were unable to follow the whales as they moved or dove.

The development of animal-borne multi-sensor tags has opened up a new way of overcoming these problems. Their integrated pressure sensor, triaxial accelerometer, and integrated hydrophone can remotely record whale behavior and vocalizations accurately and at a fine scale (Goldbogen et al., 2006; Johnson & Tyack, 2003). More recent models are even equipped with a camera, enabling further characterizations (Goldbogen et al., 2017; Tackaberry et al., 2020). Unfortunately, many studies focusing on these new techniques have suffered from the difficulty in placing the tags on the whales, which has largely restricted the sample size. Furthermore, in attempts to associate behaviors with vocalizations, the interpretations remained limited in the case of mother-calf pair studies because of the uncertainty in the identity of the emitters. Indeed, a tag placed on an individual may record both the vocalizations of the tagged individual and any surrounding individual and the methods proposed to separate them are still debated (Goldbogen et al., 2014; Saddler et al., 2017).

8. Towards understanding mother-offspring interactions in an exclusively aquatic environment: the humpback whale as a model

Understanding the mother-offspring interactions in a given environmental context can provide insight into how the environmental and social challenges have shaped the maternal strategies mammals use. It also helps comprehend the role of maternal care

in multiple aspects of young mammal development, such as locomotor, cognitive abilities, social, and communication skills development. In this scope, the humpback whale, a mysticete species, can be a good model for investigating mother-calf interaction in cetaceans in their natural environment and, on a larger scale, understanding mother-calf interactions in the complex context of the aquatic environment.

The humpback whale is one of the most popular and most studied cetaceans in its natural environment (Clapham, 2018). This abundant species can be found in all the world's oceans, often along the coasts. Like most mysticetes, most humpback whales undertake long seasonal migrations. The summer is spent feeding in high latitudes' rich, productive, cold waters. In winter, the majority move to warmer tropical waters and stop feeding. More adequate for reproduction, they stay there to mate and give birth. Humpback whales mostly occupy shallow coastal waters and continental shelves (Dawbin, 1966).

The species is polygamous, i.e., it does not form fixed couples (Clapham, 1996; Clapham & Mayo, 1987, 1990; Glockner-Ferrari & Ferrari, 1985). During the same season, the males may mate with several females, and the females may mate with several males. The breeding season is usually characterized by intense competition between males for access to the females. This intense competition gives rise to behavioral displays visible from the surface, such as breaching, pectoral slaps, caudal slaps, etc. (Silber, 1986). Males are also known to sing during the breeding season, probably to attract females (Dudzinski et al., 2009; Edds-Walton, 1997; Payne & McVay, 1971; Tyack, 1981, 1998, 1999). Adults are about 14–15 m long, and females are usually longer than males. They can weigh up to 40 tons. Sexual maturity is reached around five years old, but males generally do not mate until later, around seven years old, as they often cannot compete with older males (Chittleborough, 1955; Clapham, 1992, 2018). Females give birth to their first calf at around five to eight years old and produce a calf on average every two years (Chittleborough, 1955, 1958; Clapham, 2018).

Gestation lasts about 10 to 12 months and is well synchronized with the migration timing (Chittleborough, 1958; Clapham, 2018). The calf measures 4–4.5 m long at birth (Chittleborough, 1965; Clapham, 2018). It stays with its mother until it is one year old (Chittleborough, 1958; Clapham, 2018). The first three months of the calf's life are spent in the breeding area. Then, the calf leaves the breeding area alongside its mother to reach the feeding area. The calf feeds on prey for the first time in the feeding area at around six or seven months old (Clapham, 2018). Weaning occurs during the trip back to the breeding area or while still in the feeding area (Baraff & Weinrich, 1993; Steiger & Calambokidis, 2000).

With all the studies on the species, the location of humpback whales at any given time and their behaviors can be easily anticipated. This predictability helps streamline the

planning of data acquisition campaigns and facilitates the allocation of resources for research purposes. Moreover, since they are easy to find and spot because of their remarkable abundance and their visually conspicuous surface active behaviors, challenges associated with locating them are minimized. The advanced knowledge of their ecology and life history also means that observations can be better contextualized for interpreting mother-calf interactions within a broader ecological and behavioral framework.

9. Research objectives

Motivated by the compelling attributes of the species, I investigated in the present thesis the mother-calf interactions in free-ranging humpback whales using innovative methods to acquire novel perspectives for understanding mammalian mother-calf interactions in an aquatic environment.

I focused on three facets of the mother-young interactions in mother-calf pairs with calves less than three months old: the nursing/suckling behavior, the swimming behavior, and the acoustic communication. The aim was to answer the following questions:

- ❖ *How, where, and when is the nursing performed?*
- ❖ *Does the nursing pattern change as the calf grows?*
- ❖ *How are the swimming and resting activities of mother-calf pairs organized in time?*
- ❖ *Are there swimming skills that the adult has but the calf does not? If any, how do mother-calf pairs cope with it?*
- ❖ *In which context do the mother and the calf use vocalizations, and what functions do the vocalizations potentially have?*

In order to answer these questions, I conducted various studies using existing data from animal-borne multi-sensor tags with or without a camera (collected from 2013 to 2019) as well as new data that I collected during the period of my thesis. I have organized the presentation of the studies into three parts, corresponding to the three main aspects of interest of the dissertation:

Part I: On the suckling and nursing behavior of humpback whales

In this first part, in two chapters, I present two studies that have addressed the first two questions of my thesis regarding the nursing and suckling behavior of the humpback whale in a breeding area. Nursing is challenging to observe, and acquiring animal-borne tag data is complex, time-consuming, and expensive. Two central problems had thus to be solved first: (1) the practical limit of animal-borne tags equipped with a camera in some instances (inappropriate camera orientation, limited field of view, insufficient light, water turbidity, video data gaps, etc.), and (2) the limited sample size of available data collected from animal-borne tags equipped with a camera. Thus, through the study presented in Chapter 1, I developed a method to address these issues. Thanks to this method, I have been able to describe the frequency, duration, posture, depth, and temporal distribution of the nursing behavior with satisfactory data constituting the largest sample collected to date to study nursing/suckling behavior in baleen whales (Chapter 2). Chapters 1 and 2 provide the foundation for understanding the nursing behavior of humpback whales, one of the most crucial and decisive components of mother-calf interactions.

Part II: Keeping up with mom: the swimming behavior of humpback whale mother-calf pairs

The second part dealt with my thesis's third and fourth questions on the movements and locomotion of mother-calf pairs. In Chapter 3, I present a study in which I established the time budget for the mother-calf pair's activities to understand better the extent of time spent moving and how they are organized. Then, in Chapter 4, I introduce a study addressing the often-forgotten yet critical topic in most aquatic animals: buoyancy control. I showed that mysticete species can manage their buoyancy and investigated the ontogeny of such ability. For the calf, an inability to control its buoyancy has implications at the behavioral level (spatial configuration of the mother-calf pair, depth preference when engaging in certain activities, required learning) and at the energetic level for vertical movements (diving and breaching). This Part II delivers essential elements to understand the strategies used by mother-calf pairs to evolve in their aquatic environment.

Part III: Mother-calf vocalizations: from who, what, when, why?

My thesis's third and last part is dedicated to my last research question and includes two chapters: Chapters 5 and 6. In Chapter 5, I present how I explored a new possibility of differentiating the calls emitted by the mother and the calf and gave results on the spatial context of call production and the occurrence of vocal exchanges. The results presented in Chapter 5 served as a basis for the investigations developed in Chapter 6 on the behavioral context of the calf's calls. Part III highlights the use of specific acoustic

signals to maintain social bonds and to coordinate mother-calf pairs' activities.

Each chapter in the present work corresponds to an article published, submitted, or targeted for publication in a scientific journal. The formats have been preserved as in the published, submitted, or prepared versions, allowing them to be read independently. The chapters serve as self-contained contributions to the broader interest of the dissertation.

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Materials & Methods



As the present work has been organized into chapters corresponding to an article, each chapter already contains all the details concerning the corresponding materials and methods. The present section focuses only on an overview to provide a global perspective without going into the specific details already addressed in each chapter.

1. Study site and population

The animal-borne multi-sensor tag data used for the present dissertation were collected off Sainte Marie, Madagascar, during southern humpback whales' breeding seasons (southern winter) in 2013-2019 and 2021-2022. The Sainte Marie Island is located in the northeast of the mainland of Madagascar, less than 30 km away from the coast, between latitudes $17^{\circ} 19'$ and $16^{\circ} 42'$ South and longitudes $49^{\circ} 48'$ and $50^{\circ} 01'$ East (Figure 1). The coastal waters around Sainte Marie are relatively shallow. They are known to be an important calving ground where several female humpback whales with their calves can be encountered between July and September (Trudelle et al., 2016, 2018). The humpback whales in the zone are part of the southwestern Indian Ocean humpback whale population. They feed in Antarctica, mainly between longitudes 10° and 70° East (Fossette et al., 2014).

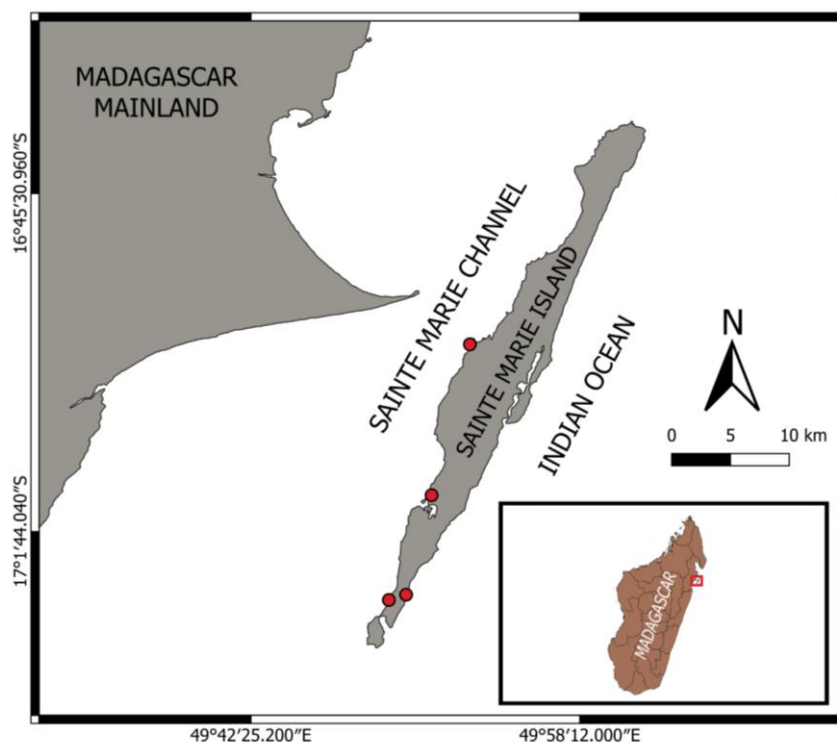


Figure 1. Map of the study site. Red points indicate the various boat departure locations between 2013 and 2022

All of the studies conducted on the site were approved by the Ministry of Fisheries Resources, Madagascar, under the Malagasy national research permits #44/13-MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #46/15-MRHP/SG/DGRHP, #28/16-MRHP/SG/DGRHP, #26/17-MRHP/SG/DGRHP and #28/18-MRHP/SG/DGRHP, #36/19-MAEP/SG/DGPA, #30/21-MAEP/SG/DGPA, and #54/22-MPEB/SG/DGPA and complied with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU).

2. Using animal-borne multi-sensor tags to study humpback whale mother-calf pairs

As highlighted, animal-borne multi-sensor tags can be a powerful tool for studying whales in their natural environment. Indeed, they enable continuous recording of data on the individual, even when they are at depth. Tags can also be used to collect data on the whale's environment. Moreover, the tags enable researchers to stay outside the vicinity of the studied individuals, which can significantly limit disturbances. Therefore, it is evident that multi-sensor tags are particularly useful for studying groups susceptible to disturbance, such as mother-calf pairs, and especially for investigating cryptic behaviors, such as nursing underwater.

For my thesis, I used Acousonde tags (Acousonde 3B) and CATS cam tags attached to whales via four suction cups (Figure 2). Suction-cup tags have the advantage of being minimally invasive regarding their attachment system. They are also very lightweight and small, minimizing the impact on animal behaviors. Their weight in the air represents less than 0.1% of that of a newborn humpback whale calf. The Acousonde tag measures 23 cm long, 8 cm wide, and 3 cm high, with a weight in air of around 400 g, and the CATS cam tag measures 25 cm long, 13 cm wide, and 4 cm high, with a weight of around 500 g. The Acousonde and CATS cam tags are fairly comparable: both feature a 3-axis accelerometer, a 3-axis magnetometer, a pressure sensor, a temperature sensor, a light sensor (auxiliary sensors), and a hydrophone. The major difference is that the CATS cam tag has a camera, a significant asset for the present work. When used at sea, a VHF emitter was attached to the tags to enable them to be tracked and found.

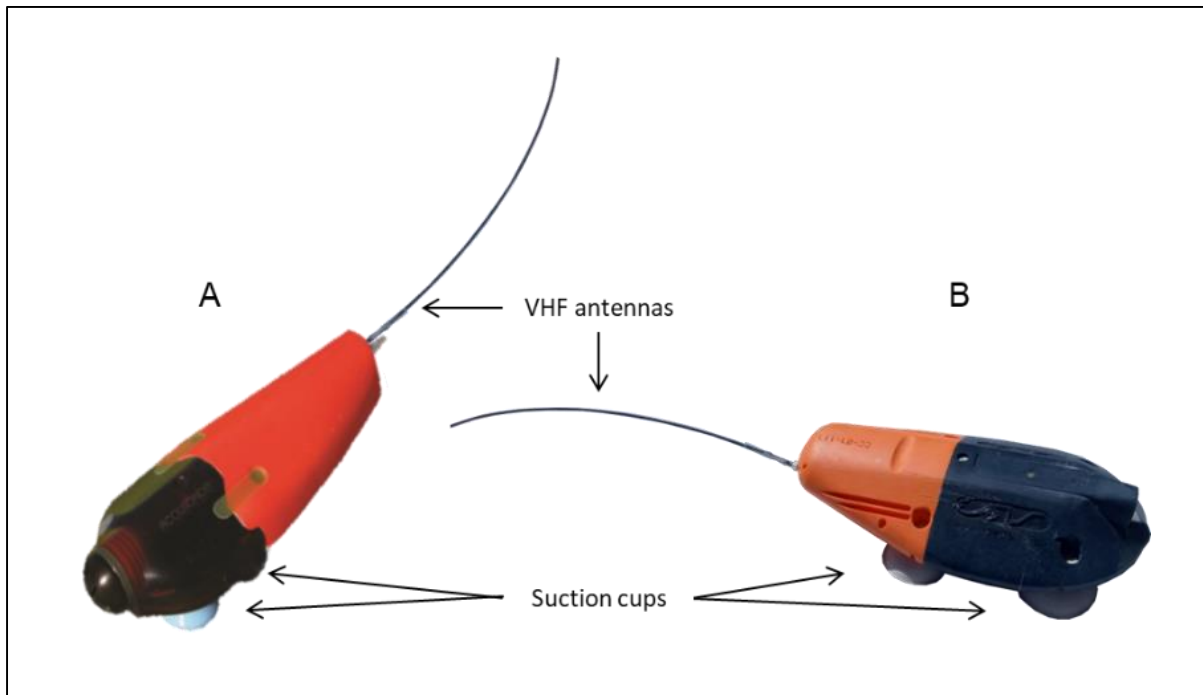


Figure 2. Acousonde 3B tag (A) and CATS cam tag (B)

Sensor sampling frequencies can be set as required. For my thesis, the sampling frequencies chosen were a compromise between power savings, the need for sufficiently high-resolution data, storage management, and anticipation of data processing speed. Thus, from year to year, settings may vary somewhat. However, I have always ensured that the data were uniform for each analysis. So, I have, on several occasions, downsampled the data to match the sampling frequencies. I created MATLAB (Mathworks) code routines, which also use open-source codes widely used by the scientific community working on multi-sensor tags (CATS Matlab toolkit, <https://github.com/wgough/CATS-Methods-Materials>; Cade et al., 2021; Animal Tag toolbox, <http://www.animaltags.org>), to standardize the Acousonde and CATS cam data.

An important step when working with multi-sensor tags is to produce 'intuitively interpretable' measurements. For my purposes, I mainly focused on the computation of the following parameters from the raw data: depth, depth rate, posture, fluke strokes, forward speed, and overall dynamic body acceleration (ODBA).

The depth (in meters) was obtained from the pressure data. It represents the depth at which the animal is located, although strictly speaking, it measures the depth at which the tag is located. The depth was the primary data for almost all the studies presented in this manuscript, as it allows the establishment of the whale's dive profile. The depth rate (in meters/second) was obtained from the depth data and allowed the investigation of the speed at which the animal ascends or descends and whether the animal remains at a given depth.

Postures represented by the pitch and roll (and heading, although not used in the present study; in degrees) (Johnson & Tyack, 2003) and fluke strokes (pitch corresponding to the dorsoventral body undulations; in degree) (López et al., 2016) were obtained from the acceleration data. Indeed, the accelerometer measures the dynamic acceleration and the acceleration of gravity in the three axes of the tag, making it possible to deduce the tag's orientation relative to the gravity vector and changes in tag velocity. By correcting this orientation to take account of the orientation of the tag relative to the animal (the axis of the tag and the animal do not generally coincide), the animal's orientation is obtained (Figure 3; Johnson & Tyack, 2003). A filter is then applied to isolate posture (frequencies <0.2 Hz) from rapid, cyclical movements linked to the body undulations and rapid movements (frequencies $0.2-1$ Hz) (Simon et al., 2012). The postures were particularly valuable for identifying, describing, and understanding the suckling/nursing behaviors (Chapters 1 and 2) and deriving other measures (see below, Chapters 1 and 4). The fluke stroke data was useful for quantifying the swimming effort (Chapters 1 and 4).

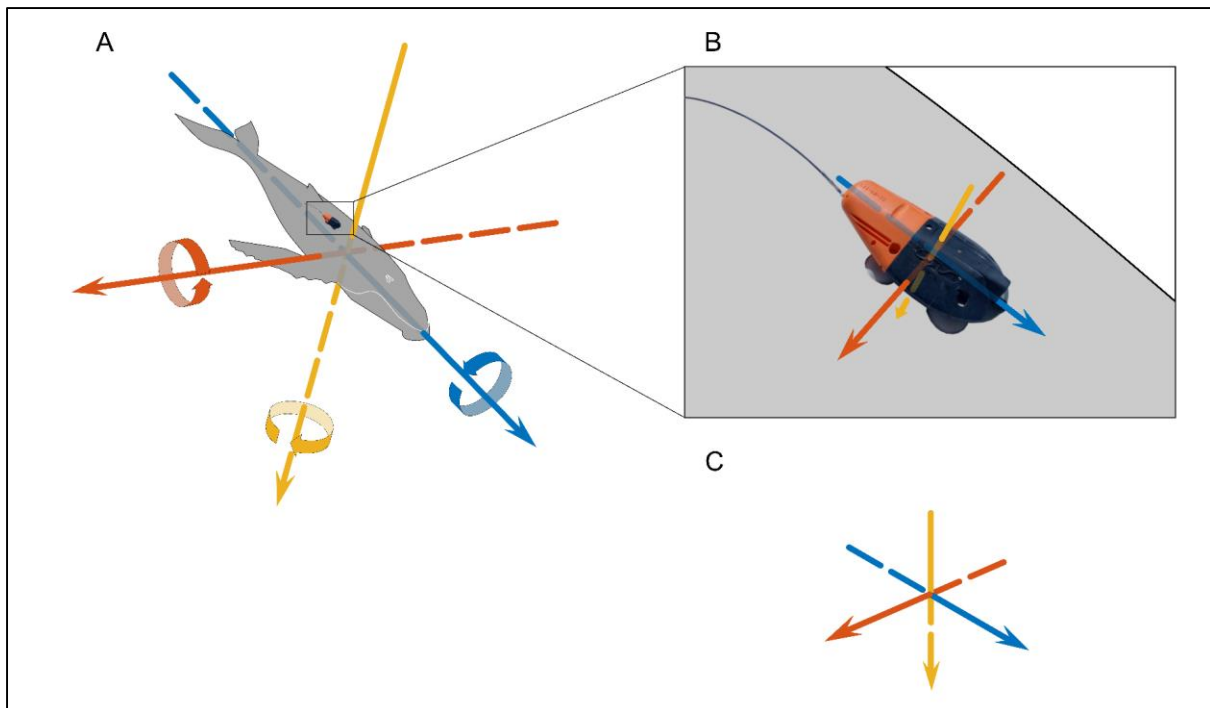


Figure 3. Diagram showing the frame of references for computing the whale orientation from 3-axis accelerometer data. (A) whale frame, (B) tag frame, (C) earth frame. Blue, red, and yellow correspond to the x, y, and z axes. Pitch, roll, and heading correspond to the rotation around the y, x, and z-axis, respectively, as represented in (A) for the whale

The forward speed (often simply referred to as speed, in meters/second) represents the speed at which the animal moves in its 3D environment. As the tags I used did not contain a speed sensor, I had to rely on various speed estimation techniques based on the available data. Each had its advantages and limitations, which I detailed at each mention of their use in the chapters of this thesis. First was the orientation corrected depth rate (OCDR), the speed estimated from the pitch and vertical speed (depth rate) with the formula $OCDR = \Delta\text{depth}/\sin(\text{pitch})$ (Cade et al., 2021; Miller et al., 2004; Chapters 1 and 4). It was only calculated when the pitch was sufficiently high ($>30^\circ$ or $<-30^\circ$) because the estimation error is significant at a lower pitch (Narazaki et al., 2018). In order to obtain the speed for the rest of the data, the technique consisted of regressing the OCDR on the flow noise recorded by the hydrophone or the vibration of the tag (tag jiggle) recorded by the accelerometer (if the latter samples at frequency >100 Hz) and using the regression to predict the speed (Cade et al., 2017). Indeed, the animal's speed is correlated to the flow noise and vibration of the tag (Cade et al., 2017; Finger et al., 1979; Izadi et al., 2018). I have named these speed estimations the absolute speed, as they are estimated directly in meters/second. Second was the relative speed, e.g., relative to the mean or the min and max, estimated from the flow noise recorded by the hydrophone. This technique has been particularly useful in cases where some deployments did not have sufficient data points for regressing the OCDR on the flow noise or tag jiggle (Chapters 2, 3, 4, and 6).

The ODBA represents the animal's effort and complements the fluke stroke data (Chapters 1 and 2). It was calculated as the sum of the absolute dynamic accelerations on the three axes. This measurement can be particularly sensitive to variations in tag placement, especially from one individual to another. So, in some experimental designs, I had to normalize the measurements by dividing the ODBA by the median calculated for each individual (Chapter 2).

3. The tagging

It goes without saying that, to obtain the data mentioned above, one must first succeed in placing the tags on the whales. The tags were deployed from a 6.40 m rigid boat using a long carbon-fiber pole. The whole process required experimented operators because it was necessary to know both the animals' behavior to get close to them and the safety measures for the security of the participants and the animals. The crew on the boat was always comprised of at least three persons and did not exceed five. One person was in charge of the tagging, one operated the boat, and one or two persons were in charge of the note-taking and the photo identification.

For every deployment, we followed the same strict approach. Once we had detected a mother-calf group, we took the time to observe them closely, keeping a parallel distance of 200 m between the boat and the group. This observation was performed to ensure that the group was new (based on the shape of the dorsal fin, the

pigmentation on the fluke, the markings on the body, etc., and with the help of any photos already taken) and avoid double sampling. It was also performed to assess the group's behavior and decide whether an approach could be attempted (only relatively calm groups with consistent behavior were targeted). The first observation phase also allowed the note taker to record information about the group, in particular, the presence of escort(s) (accompanying male(s) trying to access the female) and the relative age of the calf: C1, C2, or C3. C1 refers to newborn calves (neonates). C1 calves have noticeable folds and scars, possibly caused during birth by the barnacles near the mother's genital slit, have predominantly light grey dorsal and white ventral skin coloration, and have a dorsal fin furl angle of approximately 45° or less. C2 describes calves that are still relatively young but no longer considered neonates. They display a dorsal fin furl angle of more than 45° but less than approximately 70° . C3 refers to older calves under three months old with an unfurled dorsal fin, typically exceeding an angle of approximately 70° (Cartwright & Sullivan, 2009; Faria et al., 2013; Huetz et al., 2022).

The tagging approach was initiated after all needed data on the individuals had been taken, if and only if the behavior was judged appropriate. The group was approached from three-quarters rear (Figure 4). The tagger always aimed the back in the case of CATS cam tags for a better camera view and the flank for Acousonde tags to minimize periods during which the tag is out of the water (for optimized sound recordings, see Chapter 5). Depending on the opportunity, the targeted individual can be the mother or the calf, except for the CATS cam tags, which were prioritized for the calf. The two were targeted one after another whenever the opportunity arose to tag them sequentially.

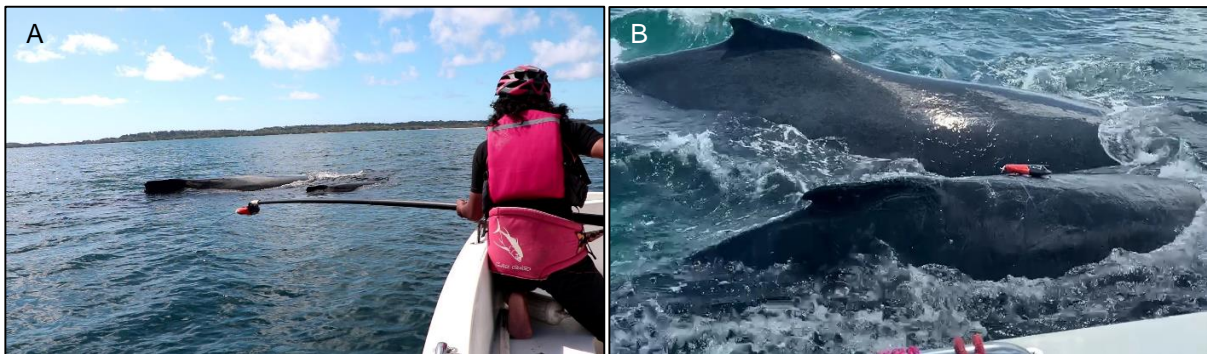


Figure 4. Approach for tagging an individual in a mother-calf pair (A) and example of successful CATS cam tag deployment on a calf (B)

The whales were never followed after tagging to avoid further disturbance. The tags were recovered by tracking the VHF signal emitted by the transmitter using a radio antenna. The retrievals were initiated after confirming that the tags already detached. A periodic loss of the VHF signal generally indicated that the tag was still attached to the animal. Indeed, the VHF signal can only be received when the VHF antenna is out of the water, which only happens when the animal surfaces (causing the signal to be

received periodically) or when the tag is no longer attached to the animal (continuous signal). The tags usually detached from the animals after 4–6 hours, but in some cases, they remained for up to 20 hours. The tag recovery is imperative; otherwise, the recorded data are lost.

In total, a multi-sensor tag dataset from 50 mother-calf pairs was considered in the present study. The dataset consisted of data from 31 single tag deployments on calves (12 CATS cam tag and 19 Acousonde tag deployments), 14 single deployments on mothers (all with Acousonde tags), and six simultaneous deployments (i.e., both the mother and the calf were equipped with a tag – Acousonde tags only) (Table 1). This dataset was the culmination of a decade-long sampling effort in Sainte Marie, representing up to 4 to 8 hours of outings per day spanning 10 to 30 days per two to three months of fieldwork campaign per year.

4. Data analysis

With the depth, depth rate, posture, fluke stroke, speed, ODBA, sound, and video data, I conducted various analyses and statistical tests to answer my different research questions. However, before getting to this stage, I had to identify and define the different behaviors of interest. One of the challenges was, of course, to identify nursing events when there were no images to identify them visually. I developed and adopted an approach based on supervised machine learning (AdaBoostM1) (Chapters 1 and 2). I used visually confirmed nursing features to train the machine learning model to automatically detect nursing in data lacking video. I have dedicated an entire chapter to discussing this method's various stages and testing its performance (Chapter 1). To identify the sequences of behavioral states, such as resting and traveling, I used an unsupervised machine learning technique that considers the temporal sequence and switching patterns of behaviors: the hidden Markov model (HMM) (Chapters 3 and 6).

Concerning the acoustic analyses, it was necessary to identify the types of social calls and their sources (i.e., the caller identity) (Chapters 5 and 6). To identify the call types, I used two approaches. The first approach was based on qualitatively comparing the calls to those from a catalog we established for the study population beforehand (Appendix I) and relied purely on aural and visual identification (Chapter 5). The second approach used an unsupervised automatic classification method (Hierarchical Clustering on Principal Components, HCPC) to separate the calls into relatively homogeneous clusters (Chapter 6). To identify the emitter, I used the data from simultaneous deployments and a machine learning technique (Random Forest algorithm – RF) (Chapter 5). I compared the calls recorded only on the mother's tag with those recorded only on the calf's tag. The comparison allowed me to perform automated classification to assign an identity to each call. I then used the result of Chapter 5 to conclude which individual emitted the calls studied in Chapter 6.

I used classic statistical analyses such as linear mixed-effects models (LMMs) followed by Tukey's post-hoc test, for example, to compare the means of several groups of data or to analyze the relationship between several variables while controlling for individual variations. For instance, I used these approaches to compare nursing and non-nursing periods (Chapters 1 and 2), to test the variation of nursing characteristics and time budget with age (Chapters 2, 3), or to investigate the relationship between swimming behavior, depth, and age (Chapter 4). When I used statistical models, I always made sure that the model's assumptions were respected (homoscedasticity, independence, and normality of the residuals) using a graphical approach. To compare observation frequencies, I used tests like the χ^2 and the exact multinomial test (Chapters 2 and 5). I used a threshold $\alpha = 0.05$ for statistical significance.

As traditional statistical analyses often rely on very specific and restrictive assumptions about the data to be analyzed, their application on complex and heterogeneous data can sometimes be difficult or even impossible. So, in some instances, I adopted analysis techniques based on machine learning instead to extract biological knowledge from the data. In particular, I used this approach to analyze the link between vocalizations and the involved activity (Chapter 6). In this example, the analysis question was formulated as follows: *To what extent can the recorded vocalizations predict the behavioral state in which the animal is involved or will be involved?*

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Table 1. Summary of the deployments used for studying the mother-calf interactions in humpback whales off Sainte Marie, Madagascar

Raw deployment ID	Pair ID	Age (a)	Category	Tag on date (local)	Tag off date (local)	Duration (h): all data	Duration (h): data with 'good' video	Tag model (b)
dep1_5aout2013_Mother	G001	A	Mother	05-Aug-2013 12:17	05-Aug-2013 17:12	4.91	0	Acousonde
dep2_7aout2013_Mother	G002	A	Mother	07-Aug-2013 12:12	07-Aug-2013 16:13	4.03	0	Acousonde
dep5_5sept2013_Mother	G003	A	Mother	05-Sep-2013 08:37	05-Sep-2013 10:02	1.42	0	Acousonde
dep6_9sept2013_Mother	G004	A	Mother	09-Sep-2013 10:02	09-Sep-2013 10:36	0.56	0	Acousonde
dep7_12sept2013_Calf	G005	C3	Calf	12-Sep-2013 09:44	12-Sep-2013 12:56	3.21	0	Acousonde
dep1_20aout2014_Calf	G006	C2	Calf	20-Aug-2014 11:08	20-Aug-2014 11:52	0.73	0	Acousonde
dep2_22aout2014_Calf	G007	C3	Calf	22-Aug-2014 09:52	22-Aug-2014 14:53	5.01	0	Acousonde
dep3_24aout2014_Mother	G008	A	Mother	24-Aug-2014 11:29	24-Aug-2014 14:04	2.57	0	Acousonde
dep4_26aout2014_Mother	G009	A	Mother	26-Aug-2014 08:26	26-Aug-2014 22:48	14.37	0	Acousonde
dep5_29aout2014_Calf	G010	C3	Calf	29-Aug-2014 07:57	29-Aug-2014 08:24	0.45	0	Acousonde
dep6_08sept2014_Calf	G011	C3	Calf	08-Sep-2014 09:29	08-Sep-2014 12:50	3.34	0	Acousonde
dep7_09sept2014_Calf	G012	C3	Calf	09-Sep-2014 14:40	09-Sep-2014 19:32	4.87	0	Acousonde
dep8_10sept2014_Calf	G013	C1	Calf	10-Sep-2014 13:51	10-Sep-2014 15:44	1.89	0	Acousonde
dep9_11sept2014_Calf	G014	C2	Calf	11-Sep-2014 12:22	11-Sep-2014 12:54	0.54	0	Acousonde
dep11_17sept2014_Calf	G015	C3	Calf	17-Sep-2014 12:28	17-Sep-2014 12:56	0.46	0	Acousonde
dep1_01aout2016_Calf	G016	C3	Calf	01-Aug-2016 09:40	01-Aug-2016 10:09	0.48	0	Acousonde
dep2_02aout2016_Calf	G017	C3	Calf	02-Aug-2016 14:37	02-Aug-2016 16:51	2.24	0	Acousonde
dep2_02aout2016_Mother	G017	A	Mother	02-Aug-2016 14:40	02-Aug-2016 15:51	1.18	0	Acousonde

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dep3_09aout2016_Mother	G018	A	Mother	09-Aug-2016 13:08	09-Aug-2016 14:56	1.79	0	Acousonde
dep4_10aout2016_Mother	G019	A	Mother	10-Aug-2016 13:26	10-Aug-2016 14:58	1.53	0	Acousonde
dep5_11aout2016_Mother	G020	A	Mother	11-Aug-2016 08:58	11-Aug-2016 14:35	5.61	0	Acousonde
dep6_13aout2016_Mother	G021	A	Mother	13-Aug-2016 14:38	13-Aug-2016 21:26	6.81	0	Acousonde
dep7_17aout2016_Calf	G022	C3	Calf	17-Aug-2016 11:20	17-Aug-2016 13:52	2.53	0	Acousonde
dep7_17aout2016_Mother	G022	A	Mother	17-Aug-2016 11:28	17-Aug-2016 18:01	6.55	0	Acousonde
dep8_18aout2016_Calf	G023	C1	Calf	18-Aug-2016 13:13	18-Aug-2016 14:19	1.1	0	Acousonde
dep8_18aout2016_Mother	G023	A	Mother	18-Aug-2016 13:44	18-Aug-2016 23:58	10.24	0	Acousonde
dep9_05sept2016_Calf	G024	C3	Calf	05-Sep-2016 13:54	05-Sep-2016 22:54	9.01	0	Acousonde
dep9_05sept2016_Mother	G024	A	Mother	05-Sep-2016 13:53	05-Sep-2016 21:40	7.78	0	Acousonde
dep2-04.08.2017_Calf	G025	C3	Calf	04-Aug-2017 14:04	04-Aug-2017 15:02	0.96	0	Acousonde
dep4-10.08.2017_Calf	G026	C3	Calf	10-Aug-2017 12:30	10-Aug-2017 13:48	1.3	0	Acousonde
dep4-10.08.2017_Mother	G026	A	Mother	10-Aug-2017 12:26	10-Aug-2017 13:44	1.31	0	Acousonde
dep5-11.08.2017_Calf	G027	C3	Calf	11-Aug-2017 11:39	11-Aug-2017 16:47	5.13	0	Acousonde
dep6-13.08.2017_Calf	G028	C2	Calf	13-Aug-2017 11:52	13-Aug-2017 14:39	2.78	0	Acousonde
dep7-15.08.2017_Calf	G029	C2	Calf	15-Aug-2017 15:22	15-Aug-2017 15:46	0.39	0	Acousonde
dep7-15.08.2017_Mother	G029	A	Mother	15-Aug-2017 16:00	15-Aug-2017 16:29	0.48	0	Acousonde
dep8-16.08.2017_Calf	G030	C2	Calf	16-Aug-2017 09:03	16-Aug-2017 16:18	7.25	0	Acousonde
dep9-21.08.2017_Calf	G031	C2	Calf	21-Aug-2017 12:13	21-Aug-2017 15:28	3.26	0	Acousonde
dep10-22.08.2017_Mother	G032	A	Mother	22-Aug-2017 12:58	22-Aug-2017 16:22	3.41	0	Acousonde
dep12-26.08.2017_Calf	G033	C3	Calf	26-Aug-2017 14:57	27-Aug-2017 08:19	17.36	0	Acousonde
dep13-28.08.2017_Calf	G034	C3	Calf	28-Aug-2017 10:25	28-Aug-2017 15:53	5.46	0	Acousonde

dep13-28.08.2017_Mother	G035	A	Mother	28-Aug-2017 12:48	28-Aug-2017 16:48	4	0	Acousonde
dep14-01.09.2017_Calf	G036	C3	Calf	01-Sep-2017 09:15	01-Sep-2017 11:42	2.45	0	Acousonde
dep14-01.09.2017_Mother	G037	A	Mother	01-Sep-2017 10:57	01-Sep-2017 14:12	3.24	0	Acousonde
dep15-03.09.2017_Calf	G038	C2	Calf	03-Sep-2017 10:30	03-Sep-2017 10:59	0.48	0	Acousonde
dep15-03.09.2017_Mother	G038	A	Mother	03-Sep-2017 10:08	03-Sep-2017 12:36	2.47	0	Acousonde
Orange_01Sept2022_Calf	G039	C2	Calf	01-Sep-2022 09:56	01-Sep-2022 18:09	8.21	6.7	CATS cam
Orange_05Sept2022_Calf	G040	C2	Calf	05-Sep-2022 09:02	05-Sep-2022 15:14	6.19	5.62	CATS cam
Orange_07Aout2022_Calf	G041	C2	Calf	07-Aug-2022 10:57	07-Aug-2022 14:14	3.27	2.88	CATS cam
Orange_13Sept2022_Calf	G042	C2	Calf	13-Sep-2022 13:42	13-Sep-2022 16:15	2.56	2.56	CATS cam
Orange_15Aout2022_Calf	G043	C2	Calf	15-Aug-2022 11:00	15-Aug-2022 11:57	0.95	0.95	CATS cam
Orange_19Aout2022_Calf	G044	C3	Calf	19-Aug-2022 09:35	19-Aug-2022 15:29	5.88	5.88	CATS cam
Orange_26Aout2022_Calf	G045	C3	Calf	26-Aug-2022 09:26	26-Aug-2022 11:12	1.78	1.07	CATS cam
Orange_30Aout2022_Calf	G046	C2	Calf	30-Aug-2022 14:48	30-Aug-2022 18:34	3.77	2.97	CATS cam
Orange_31July2022_Calf	G047	C2	Calf	31-Jul-2022 10:52	31-Jul-2022 13:02	2.15	0	CATS cam
Jaune_06aout2019_Calf	G048	C3	Calf	06-Aug-2019 10:56	06-Aug-2019 12:34	1.61	1.61	CATS cam
Jaune_14sept2018_Calf	G049	C3	Calf	14-Sep-2018 11:34	14-Sep-2018 14:18	2.48	2.48	CATS cam
Orange_09aout2019_Calf	G050	C3	Calf	09-Aug-2019 10:03	09-Aug-2019 18:44	7.95	6.42	CATS cam

(a) relative age. For the calves, the relative age was estimated based on the coloration, skinfolds, and angle of furling of the dorsal fin. C1: neonate, C2: very young but non-neonate, C3: older calves (but <3 months old), A: adult.

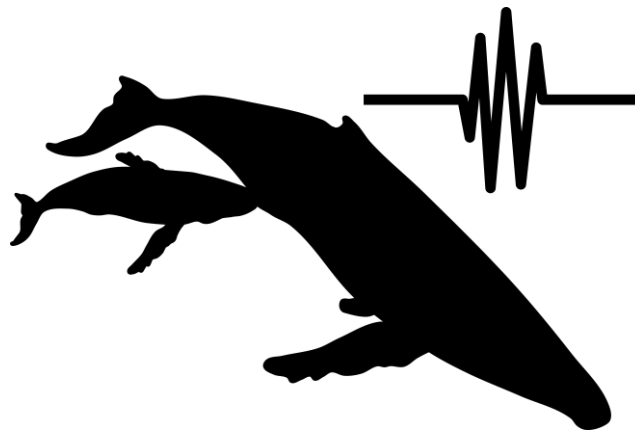
(b) Acousonde: animal-borne multi-sensor tag not equipped with a camera. CATS cam: animal-borne multi-sensor tag equipped with a camera.

Part I: On the suckling and nursing behavior of humpback whales



Chapter 1. Characterizing the suckling behavior by video and 3D-accelerometry in humpback whale calves on a breeding ground

Maevatiana N. Ratsimbazafindranahaka, Chloé Huetz, Aristide Andrianarimisa, Joy S. Reidenberg, Anjara Saloma, Olivier Adam, Isabelle Charrier



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Synthesis

How, where, and when is the nursing performed? Preliminary results from the calf's perspective and test of a new detection method

Methods

The data from the first three successful CATS cam tag deployments on calves (2018–2019) were used to obtain a preliminary detailed characterization of the suckling behavior and to identify and test the appropriate supervised machine learning algorithm for automatically detecting suckling events based on acceleration and depth-derived data. The suckling events were visually identified on the videos, and their characteristics were extracted from the accelerometer and depth sensor data and then compared to the characteristics of non-suckling periods using LMMs. The summary statistics of several measured characteristics were used as features fed to supervised machine learning candidate algorithms in a design where data from two calves were used as a training set for detecting the suckling events of the remaining calf.

Findings

Suckling events are relatively short (less than 30 s) and primarily occur during dives. During suckling, the calf maintains a pitch angle of about 30–45° relative to the midline of its mother's body, always rolls either the right or left depending on the suckled teat, and uses its tongue. For her part, the mother leans slightly downward. The calf usually performs successive 2–6 suckling events and alternates between the two teats.

The suckling events have very distinctive kinematic signatures. They are associated with a higher average absolute roll, often a higher effort level (high average fluke stroke rate), and a lower average speed than non-suckling periods. When the data are divided into non-overlapping 2 s blocks, the AdaBoostM1, an ensemble classifier that performed the best among several candidate algorithms, can find at least about 40% of the blocks corresponding to suckling with a detection precision of at least 60% based solely on the acceleration and depth-derived data.

Characterizing the suckling behavior by video and 3D-accelerometry in humpback whale calves on a breeding ground

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ABSTRACT

Getting maternal milk through nursing is vital for all newborn mammals. Despite its importance, nursing has been poorly documented in humpback whales (*Megaptera novaeangliae*). Nursing is difficult to observe underwater without disturbing the whales and is usually impossible to observe from a ship. We attempted to observe nursing from the calf's perspective by placing CATS cam tags on three humpback whale calves in the Sainte Marie channel, Madagascar, Indian Ocean, during the breeding seasons. CATS cam tags are animal-borne multi-sensor tags equipped with a video camera, a hydrophone, and several auxiliary sensors (including a 3-axis accelerometer, a 3-axis magnetometer, and a depth sensor). The use of multi-sensor tags minimized potential disturbance from human presence. A total of 10.52 h of video recordings were collected with the corresponding auxiliary data. Video recordings were manually analyzed and correlated with the auxiliary data, allowing us to extract different kinematic features including the depth rate, speed, Fluke Stroke Rate (FSR), Overall Body Dynamic Acceleration (ODBA), pitch, roll, and roll rate. We found that suckling events lasted 18.8 ± 8.8 s on average ($N = 34$) and were performed mostly during dives. Suckling events represented 1.7% of the total observation time. During suckling, the calves were visually estimated to be at a 30–45° pitch angle relative to the midline of their mother's body and were always observed rolling either to the right or to the left. In our auxiliary dataset, we confirmed that suckling behavior was primarily characterized by a high average absolute roll and additionally we also found that it was likely characterized by a high average FSR and a low average speed. Kinematic features were used for supervised machine learning in order to subsequently detect suckling behavior automatically. Our study is a proof of method on which future investigations can build upon. It opens new opportunities for further investigation of suckling behavior in humpback whales and the baleen whale species.

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INTRODUCTION

Female mammals feed their offspring with maternal milk to ensure their progeny's development and survival during the early dependent life stages of the young (Pond, 1977; Smith, 1977; Daly, 1979; Gittleman & Thompson, 1988; Balshine, 2012). The maternal behavior associated to the transfer of milk to the offspring is referred to as 'nursing.' From the offspring's perspective, this behavior can be referred to as 'suckling,' *i.e.*, to obtain milk from the mammary gland (breast) through the mammary papilla (nipple or teat) (Hall, Hudson & Brake, 1988). Suckling can involve an active role of mouth movements from the young to stimulate nipple erection, compress the breast's lactiferous sinuses, and generate negative pressure (suction) along with a pulling motion on the teat in order to withdraw the milk. Alternatively, suckling can involve a passive role in which milk is squirted into the open mouth with no stimulating movements of the offspring's mouth.

Nursing behavior is an integral part of mammalian reproductive behavior (Gittleman & Thompson, 1988). The duration of lactation (the period of time during which milk can be produced; Hall, Hudson & Brake, 1988) and the frequency of nursing vary greatly among mammals and are related to the developmental characteristics of the young and their environmental constraints (Ofstedal, Boness & Tedman, 1987; Ofstedal, 1993).

Whale breasts are positioned ventro-laterally on either side of the midline genital slit (opening of the vestibule vagina). The location of each breast is marked by a short mammary slit in the overlying blubber through which the nipple can be extruded for nursing. The mammary glandular tissue is located deep to the overlying blubber layer, thus providing a hydrodynamically streamlined outline even when the whale's breasts are engorged with milk during lactation. Lactation in baleen whales typically occurs initially in the winter, when calves are born (Lockyer, 1984; Ofstedal, 1993; Bannister, 2018). As most baleen whales migrate, lactation that begins on the calving area continues during the migration to the feeding area (Lockyer, 1984; Ofstedal, 1993; Bannister, 2018).

Humpback whales (*Megaptera novaeangliae*), the subject of this study, are migratory cetaceans. They move between high-latitude (closer to the poles) feeding grounds and low-latitude (closer to the equator) breeding/calving grounds (Clapham, 2018). Similar to other baleen whales, their nursing strategy is constrained by a prolonged fasting of the mother during lactating period, related to the migratory pattern (Ofstedal, 1993). A young humpback whale (calf) feeds exclusively on maternal milk during its first six months of life (Clapham, 2018). The energy intake from the milk is crucial in ensuring rapid growth (Lockyer, 1984) and therefore allowing the calf to migrate to the feeding area in cold waters alongside its mother (Lockyer, 1984; Corkeron & Connor, 1999; Braithwaite, Meeuwig & Hipsey, 2015). Mother-calf pairs make slower progress compared to groups not accompanied by calf in part due to presumed slower swimming or frequent pauses that allow the calf to suckle (Noad & Cato, 2007). After its first six months of life, the calf starts to feed on prey but continues to get nutrition from milk until complete weaning at 10 to 12 months old (Chittleborough, 1958; Clapham, 2018). The weaning coincides with the mother returning to the calving area. Although early weaning on the feeding grounds may also occur (Baraff & Weinrich, 1993; Steiger & Calambokidis, 2000).

Despite its importance, nursing (and suckling) behavior has been poorly documented in humpback whales because it is difficult to observe with accuracy and certainty. Indeed, nursing can occur at varying depths from the sub-surface (<5 m) to deep dives (up to 64 m) as suggested by camera-observed nursing events in feeding areas ([Tackaberry et al., 2020](#)). The earlier descriptions of nursing behavior in humpback whales were mostly based on limited surface and sub-surface observations of stationary or slow moving whales and relied mainly on the positioning of the calf ([Glockner & Venus, 1983](#); [Glockner-Ferrari & Ferrari, 1985](#); [Clapham & Mayo, 1987](#); [Morete et al., 2003](#); [Videsen et al., 2017](#)). [Clapham & Mayo \(1987\)](#) for example described nursing as an event between two calf's successive breaths on either sides of the mother's caudal peduncle when the mother is stationary at the surface and during which the calf is beneath the mother. [Videsen et al. \(2017\)](#) defined nursing events by associating them with the occurrence of 'peduncle dives,' defined as repeated dives during which the calf remained submerged beneath the mother's caudal peduncle.

Nevertheless, from these different studies, various nursing modalities have been advanced. While nursing, the mother is either stationary or swimming very slowly at a depth around 10–15 m ([Glockner-Ferrari & Ferrari, 1985](#)), or occasionally at the surface with her tail in the air ([Morete et al., 2003](#)). The calf is typically positioned vertically (head up, tail down) beneath the mother ([Glockner & Venus, 1983](#)). [Videsen et al. \(2017\)](#) suggested that to initiate suckling, the calf uses tactile stimuli on the mother rather than vocalizations. Tactile stimulation likely results in an autonomic reflex causing extrusion of the nipple. The calf can then grasp the nipple with its tongue. From an underwater video footage of suckling humpback whale calf recorded in the tropical waters of Tonga, South Pacific Ocean, by Scott Portelli, 2021, pers. comm., it has been observed that the whale calf has an unusual tongue that is lined with lingual papillae (fringes) that may help the tongue grasp the nipple, and may even seal the tongue into a tube that facilitates transferring milk into the mouth.

Underwater video is the best method for studying the nursing and suckling behaviors of whales. Various solutions are possible. One option is to use a video camera from a surface platform (boat or kayak) but it has two major drawbacks: (1) it is necessary to get very close to the whales and potentially interfere with their behavior (harassment); (2) visual contact is lost when the whales dive deeply, even when the water is very clear. Another option is to use an underwater drone (Remotely Operated underwater Vehicle—ROV or Autonomous Underwater Vehicle—AUV, [Butcher et al., 2021](#)). ROVs and AUVs have potential but presently vehicles are not yet agile enough to track whales. They are too slow and difficult to manoeuvre, with ROVs also being limited by cable length. Alternatively, underwater video can be obtained during close approaches by breath-holding or scuba divers. However, this is only possible when the whales are stationary or swimming very slowly as it would be impossible for a diver to keep pace with traveling whales. Additionally, the presence of divers in close proximity may disturb the whales and habituation is not a desirable tactic. Scott Portelli, 2021, pers. comm., [Zoidis & Lomac-MacNair \(2017\)](#) successfully video documented humpback whale suckling behavior thanks to breath-holding divers. In [Zoidis & Lomac-MacNair \(2017\)](#), the recording of milk clouds in the water column

allowed the confirmation of the occurrence of suckling. However, only few events could be recorded ($N = 5$ from four mother-calf pairs).

The development of animal-borne multi-sensor tags such as Customized Animal Tracking Solutions (CATS) cam tags provided a way for remote and accurate recording of whale behavior (Cade *et al.*, 2016). Bio-loggers can be equipped with a suite of sensors including cameras, accelerometers, gyroscopes, magnetometers, pressure (depth) sensor, temperature sensor, light sensor, and hydrophone. CATS cam tags are particularly well suited to study suckling behavior since in addition to kinematic sensors they also allow the recording of video directly from the calf's perspective and thus allow confident confirmation of suckling events. Such devices were used by Tackaberry *et al.* (2020) to accurately describe the suckling behavior of humpback whale calves on feeding areas. One disadvantage of using an animal-borne tag is the potential stress generated during the tag attachment phase. The deployment must be done by experienced operators following a strict protocol (slow speed approach, brief deployment time, *etc.*) to minimize the disturbance (Stimpert *et al.*, 2012; Saloma, 2018).

In this study, we characterized the suckling behavior of <3 months old humpback whale calves on their calving ground using CATS cam tags. We aimed to describe in detail: (1) how and at what depth the suckling is performed, its duration, and its frequency; (2) the behavioral signatures of suckling events using accelerometry and depth data; and (3) whether the different kinematic features extracted from only two sensors (*i.e.*, 3-axis accelerometer and depth sensor) among all the available sensors in the CATS cam tags were sufficient for a supervised machine learning algorithm to automatically detect suckling behavior. Supervised machine learning is a type of machine learning in which an algorithm learns from labelled datasets to classify unforeseen data. Such classification technique would open the opportunity to detect suckling events from data collected by tags without video camera such as Acousonde or Dtags or when visual observations are not good enough (*e.g.*, during night time or in water with poor visibility).

MATERIALS & METHODS

Study area

The study occurred in the Indian Ocean along coast of Madagascar, specifically in the Sainte Marie channel. The channel is located between the Sainte Marie Island (between latitudes 17°19' and 16°42'South, and longitudes 49°48' and 50°01'East) and the east coast of Madagascar's mainland. The channel is approximately 60 km long and 7–30 km wide. It is relatively shallow: its average depth is about 35 m and the maximal depth is 60 m (Trudelle *et al.*, 2016). The tag deployments were conducted as part of an ongoing study on humpback whale mother-calf interactions during the calving season and occurred between August and September of 2018 and 2019.

Tag specifications

We used CATS cam tags to investigate humpback whale suckling behavior. CATS cam tags are small and lightweight (~500 g) non-invasive animal-borne multi-sensor tags attached *via* suction cups. They contain six auxiliary sensors (3-axis accelerometer, 3-axis

gyroscope, 3-axis magnetometer, pressure/depth sensor, temperature sensor, and light sensor), a hydrophone, and an HD video camera (100° Field of view). A VHF transmitter (ATS F1835B) attached on the tag allows tracking for tag retrieval. The sampling frequency was set at 10 Hz for the magnetometer, gyroscope, depth, and temperature sensors. Accelerometer sampling rate was set at 400 Hz in 2018 and at 800 Hz in 2019. Accelerometer data from 2019 were however always downsampled to 400 Hz in subsequent analyses for a matter of consistency. The camera recorded videos with a 1,280 × 720-pixel resolution at 30 frames per second in 2018 and with a 1,920 × 1,072-pixel resolution at 30 frames per second in 2019. The hydrophone recorded sound at a 48 kHz sampling rate in 2018 and at a 24 kHz sampling rate in 2019 (16-bit resolution). Two individual CATS cam tags were used in our study (designated as Cats1 and Cats2 hereafter).

Tagging procedures

CATS cam tags were deployed on calves accompanied by their mother from a 6.40 m rigid motor boat using a 5-m carbon-fiber pole. Deployment were performed by researchers experienced in successfully approaching mother-calf pairs with minimal disturbance. The tags were placed on the back, near the dorsal fin of the animal. Calves were tagged using one of the two approaches described in [Stimpert et al. \(2012\)](#) and in [Saloma \(2018\)](#) in order to minimize disturbance to the mother-calf pair. Tagging efforts were terminated if the pair displayed avoidance behavior or if the calf was not successfully tagged within 30 min. Immediate behavioral response of the animals to tagging was recorded as in [Stimpert et al. \(2012\)](#). All mother-calf pairs were photo-identified to avoid double-sampling within the calving season. We attributed a relative age to each tagged calf depending on the angle of furl of the dorsal fin (neonate *versus* non-neonate, [Cartwright & Sullivan, 2009](#); [Faria et al., 2013](#); [Saloma, 2018](#)).

Tagged animals were not followed after tag deployment to avoid any further disturbance of their behavior. After tag deployment or an aborted attempt, the boat slowly moved away in the opposite direction of the mother-calf pair. The tag was retrieved after few hours or the following day, when it detached itself from the animal (usually as a consequence of rubbing against the mother, surface active behavior, *etc.*). The VHF tag emitted a continuous signal, facilitating retrieval. All methods and approaches were carried out in accordance with relevant guidelines and regulations in force in Madagascar and were approved by the Ministry of Fisheries Resources, Madagascar, under the national research and collect permits #28/18-MRHP/SG/DGRHP and #36/19-MAEP/SG/DGPA. This present study complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU) and also with current Malagasy laws.

Sensor data processing

Data from all sensors were downloaded as CSV files and imported into MATLAB (Mathworks) using dedicated scripts (*CATS Matlab toolkit*, <https://github.com/wgough/CATS-Methods-Materials>, [Cade et al., 2021](#)). Raw accelerometer data were downsampled to obtain a common sampling rate of 10 Hz across all sensors and depth data (in meters) was smoothed with a 0.5 s running median filter. In all computation described hereafter

the output sampling frequency was of 10 Hz. Sensors reading were rotated to match the calf's orientation frame using established methods and raw animal pitch and roll (in degree) were then calculated (*Johnson & Tyack, 2003; Cade et al., 2016; Tackaberry et al., 2020; Cade et al., 2021*). To obtain pitch and roll data representing only the body posture and without fluke stroke signal, we low-pass filtered the raw pitch and roll data (0.2 Hz low-pass filter) as in *Simon, Johnson & Madsen (2012)*. On the other hand, we used band-pass filtered raw pitch (0.2–1 Hz band-pass filter) to obtain the fluke stroke pattern, similar to *Simon, Johnson & Madsen (2012)*. Stroking was identified when the band-pass filtered pitch passed from below -3° to above $+3^\circ$ or vice versa within 6.5 s. The used thresholds were determined by visual inspection of the accelerometry plots (*Iwata et al., 2021*). From the identified fluke strokes, the Fluke Stroke Rate (FSR, in Hertz) was calculated on the basis of half-strokes (*López et al., 2015*). Animal forward speed (speed hereafter, in meter/second) was determined using the tag jiggle recorded in the original high frequency accelerometer data (*Cade et al., 2017*). Speed was smoothed with a 0.5 s running mean filter. In addition, we calculated the Overall Dynamic Body Acceleration (ODBA, in G and converted to meter/second²) as in *Wilson et al. (2006)*, the roll rate (in degree/second), and the depth rate (in meter/second) using custom scripts and the *Animal Tag* toolbox (<http://www.animaltags.org>).

Depth data helped determine various diving or surface activity phases. We defined diving as any submergence to a depth of >10 m (*Stimpert et al., 2012; Saloma, 2018*). Dives were further divided into three phases: descent, bottom, and ascent phase. As individual dives could include stops at various depths, the bottom phase was defined as the segment at $>85\%$ of the maximal dive depth for a dive (*Stimpert et al., 2012*). The descent phase was defined as the segment starting at the surface that immediately preceded the bottom phase. Inversely, the ascent phase was defined as the segment that follows directly the bottom phase and ends at the surface.

Video data analysis and suckling data extraction

We identified and labelled suckling events from the video files using the Behavioral Observation Research Interactive Software (BORIS; *Friard & Gamba, 2016*). The corresponding depth data was displayed concurrent with the video. We defined a suckling event as a period during which the tip of the calf's snout continuously touched (>2 s) the mammary slit of the mother and a milk cloud (see video clip in <https://www.youtube.com/watch?v=UcyCgiCieFk>), even in low density, was observed in the water during the event or upon release of contact (*Tackaberry et al., 2020*). For each suckling event, we calculated its duration and extracted its corresponding activity phase (descent, bottom, ascent, or surface), together with the average depth, depth rate, speed, FSR, ODBA pitch, roll, and roll rate. In addition to suckling events identification, we estimated the proportion of time each calf was in close proximity under its mother (mother visible above the calf) without suckling. Furthermore, we also counted the number of suckling dives during which one or several confirmed suckling events were recorded and the number of non-suckling dives during which the calf is observed staying at least 5 s under the mother, in close proximity and without any suckling event.

Comparison of suckling with non-suckling segments

A reference data set for comparison is needed to contrast and identify the behavioral signatures unique to suckling events. To generate such comparison data, we divided our dataset from each deployment into non-overlapping segments of 20 s (duration comparable to suckling events). Then we selected 10 random segments that did not match to any suckling event for each activity phase in which suckling occurred, similar to [Tackaberry et al. \(2020\)](#). These selected segments, referred as ‘non-suckling segments,’ were analyzed for the same characteristics as suckling events (see above). To assess if there was a significant difference between suckling events and non-suckling segments, we used a linear mixed-effects models (LMMs) estimated in R using REML (Restricted Maximum Likelihood) that included the suckling status (suckling *versus* non-suckling) and the activity phase as fixed effects, and individuals as random effect ([Tackaberry et al., 2020](#)). In the models, we considered the following response variables: average depth rate, average speed, average FSR, average ODBA, average pitch, absolute average roll, and average roll rate. Absolute value has been used for roll to emphasize any deviation from zero. The model’s reference levels (intercept) corresponded to bottom non-suckling (non-suckling segment occurring at the bottom phase of dive). The LMMs were followed by Tukey’s post-hoc multiple comparison test using the R package *emmeans* ([Lenth et al., 2018](#)). Statistical significance level was set to $\alpha = 0.05$.

Testing automatic identification of suckling behavior using supervised machine learning

Data preparation

For the supervised machine learning process, as the goal was to identify automatically suckling in non-labelled data, the entire dataset was included in the analysis (*i.e.*, data with video from tag on to tag off). For each deployment, we split the dataset into 2 s non-overlapping blocks (windows) and then determined which behavioral period each block fell under (suckling or non-suckling period). Two classes were thus considered: (1) ‘suckling’ and (2) ‘non-suckling.’ Each block falling under both suckling and non-suckling period (*i.e.*, transition to or from a suckling period) was labelled as ‘suckling’ only if 3/5 of its duration fell under suckling period. Otherwise, it was labelled as ‘non-suckling.’ For each block, we computed 43 features: mean, minimum, maximum, variance, skewness and kurtosis for depth, depth rate, speed, ODBA, pitch, roll, and roll rate, and finally mean for FSR. Indeed, as suggested in [Ladds et al. \(2016\)](#), a great number of summary statistics may help in detecting subtle differences between classes.

Similar to [Jeantet et al. \(2020\)](#), we segmented the data prior to machine learning implementation. We excluded blocks too close to the surface (<1.5 m depth) or of high speed activities (>2 m s⁻¹). This exclusion helped in partially removing noise from the data and also in reducing class imbalance. As suggested by observations on a feeding ground, suckling events occur mostly at depth ([Tackaberry et al., 2020](#)). Also, given the size of the mothers (>11 m in length and >2 m diameter at the umbilical section level in adult whales, as determined by estimates in the field), the generally observed nursing configuration (calf generally below the mother), and speed during nursing

(Zoidis & Lomac-MacNair, 2017; Tackaberry et al., 2020), we were confident that no suckling events would be recorded at <1.5 m depth or at >2 m s^{-1} speed. We checked the validity of these threshold assumptions in our data to ensure that indeed no suckling events were removed partially or entirely. Validating these parameters ensured that this segmentation could be automatically performed on unknown data, with a very low probability to remove suckling events.

Identification of the adequate classifier

In order to define an appropriate classification model (machine learning model) for associating the suckling status of the calf with the corresponding patterns of different kinematic features, we trained four types of supervised machine learning algorithms —(i) K-Nearest Neighbors (KNN), (ii) Decision tree, (iii) Ensemble classifiers, and (iv) Support Vector Machine (SVM)—using the MATLAB toolbox *Statistics and Machine Learning*. We repeatedly performed a 60:40 holdout splits on our data (*i.e.*, 60% of the data as training set and 40% of the data as testing set) while maintaining class ratios (30 runs): the training set was used for training and the classifier's efficiency was evaluated on the remaining unseen data. The holdout split is a commonly used approach for evaluating general model performance in many machine-learning applications (*e.g.*, Nathan et al., 2012; Carroll et al., 2014; Ladds et al., 2016). Preliminary model selection and hyperparameter tuning for each classifier type were performed using a Bayesian Optimization approach with 5-fold cross-validation. We followed the workflow described in the associated documentation (<https://fr.mathworks.com/help/stats/bayesian-optimization-workflow>). With the *Statistics and Machine Learning* toolbox's Bayesian Optimization algorithm, we optimized the different types of supervised machine learning algorithms across a selection of classification models and hyperparameter values in order to pre-select the best classification models that were suitable for our dataset. An optimization run pre-selected one model as the best one by seeking to minimize classification error. For Ensemble classifiers, the selection of classification models included Bootstrap Aggregation (Bagging), Random Forest (Bag), Random Subspace (Subspace), Adaptive Boosting for Binary Classification (AdaBoostM1), Adaptive Boosting for Multiclass Classification (AdaBoostM2), Gentle Adaptive Boosting (GentleBoost), Adaptive Logistic Regression (LogitBoost), Linear Programming Boosting (LPBoost), Least-Squares Boosting (LSBoost), Robust Boosting (RobustBoost), Random Undersampling Boosting (RUSBoost), and Totally Corrective Boosting (TotalBoost). For KNN classifiers, it included Cityblock, Chebyshev, Correlation, Cosine, Euclidean, Hamming, Jaccard, Mahalanobis, Minkowski, Seclidean, and Spearman metrics-based KNN. For Decision trees, it included classifiers that are based on Gini's diversity index (Gdi), twoing rule, and deviance splitting criterion. For SVM, it included SVM with Gaussian, linear, and polynomial kernels. These different models are detailed in the aforementioned documentation. The number of runs we used for the data splitting (30 runs) and for the Bayesian optimization (100 runs per split per classifier type) were chosen to optimize results stability and processing speed.

For each trial and each class, we calculated five evaluation metrics for making a final decision on the classification model to be retained: Sensitivity (True Positive Rate, Hit Rate

or Recall), Precision (Positive Predictive Value), False Positive Rate (FPR), *F*-score, and Global accuracy. These metrics were calculated as follows and used to select the best and most adapted classification model (definitions as in [Jeantet et al., 2020](#)):

The Sensitivity measures the ability to detect one behavior among other behaviors:

$$\text{Sensitivity} = \frac{TP}{TP + FN}. \quad (1)$$

The Precision measures the ability to correctly identify a behavior:

$$\text{Precision} = \frac{TP}{TP + FP}. \quad (2)$$

The FPR measures the rate of wrongly considering other behaviors as the behavior of interest. It is related to the Specificity, which is the ability to avoid wrongly considering other behaviors as the behavior of interest:

$$\text{FPR} = 1 - \text{Specificity} \quad \text{with} \quad \text{Specificity} = \frac{TN}{TN + FP} \quad (3)$$

The *F*-score measures the accuracy in classifying a behavior. It is the harmonic mean of precision and sensitivity:

$$\text{F-score} = \frac{2TP}{2TP + FP + FN} \quad (4)$$

The Global accuracy measures the ability to correctly identify all behaviors as a whole:

$$\text{Global accuracy} = \frac{TP + TN}{TP + TN + FP + FN}. \quad (5)$$

These formulas use the following abbreviations: TP–True Positive, TN–True Negative, FN–False Negative), and FP–False Positive.

To assess the potential influence of training set size reduction on the performance of the elected model, we tested whether changing the training set size changed the performance. We ran a series of trainings with different holdout splitting of the data (training-testing): 60:40 as in the original model selection process, 50:50, 40:60, 30:70, 20:80, and 10:90. The process was repeated 30 times for each splitting. A general workflow of the whole machine learning process we followed is presented in [Fig. S1](#).

Generalization across individuals

To assess whether the model can generalize across different individual whale calves, we also tested a leave-one-out split, similar to [Ladds et al. \(2016\)](#). We trained the model with the highest performance on two calves' data. We then tested its performance on the unseen remaining calf data, establishing if the tag data obtained from individuals could be used to identify the suckling behavior of a different individual. We repeated this analysis three times, leaving out a different calf's data each time following the same machine learning workflow outlined in [Fig. S1](#).

Aside from possible influence of training set size (e.g., the recorded data from the individuals used for training is relatively small), lack of generalization ability across

individuals may result from a dataset with high inter-individual variability of suckling behavior characteristics. To address this potential issue, we tested whether excluding features that contribute most to inter-individual difference (if any) in the suckling blocks would improve the performance of the supervised machine learning. To identify the features that contribute most to inter-individual difference, we trained a Random Forest algorithm to classify individuals based only on the suckling blocks using the R software package *randomForest* (Liaw & Wiener, 2002). Features that contributed the most to the differentiation by individual were identified as those that had a high Gini index in the Random Forest. We re-ran the leave-one-out design, as described above, but excluding the features identified by using the Gini index. We confirmed the reduction of the inter-individual difference of the suckling blocks by examining the error rate (Out-of-the-bag error rate) of the Random Forest algorithm trained to classify individuals. A reduction of inter-individual difference would result in an increase of the error rate. A low error rate indicated that the inter-individual difference is evident enough and thus the Random Forest algorithm is able to make very good classifications.

RESULTS

Tag deployments

Four calves were tagged with CATS cam tag in the Sainte Marie channel: one during the calving season of 2018 (identified as Calf1) and three during the calving season of 2019 (identified as Calf2, Calf3, and Calf4). Calf1 and Calf2 were tagged with Cats1 while Calf3 and Calf4 were tagged with Cats2. Their immediate reaction to tagging was a slow evasive swimming, which corresponded to a mild reaction (Stimpert et al., 2012). All of them had unfurled dorsal fins, indicating that they were not neonate calves (Cartwright & Sullivan, 2009). The deployment on Calf4 was not suitable for our study as the tag (thus the camera) was pointing toward the side of the calf (i.e., away from the mouth) and was thus excluded from our analyses. For Calf3, the data towards the end of the deployment was not usable and thus not analyzed due to lack of visibility on the corresponding video recording as the night approached. Deployment information including date and time is indicated in Table 1. The three deployments provided a total of 10.52 h of usable video and auxiliary data.

General description of suckling

In all our video recordings, a milk cloud could be observed during or after contact each time the calf's snout continuously touched (>2 s) the mammary slit. All these events appeared to be intentional and were all defined as suckling. We detected 34 suckling events, which lasted on average 18.8 ± 8.8 s and represented 1.7% of the total video deployment (Fig. S2). Detailed summary statistics per individual are presented in Table 1. Most suckling events were clustered in a series of 2–6 suckling events occurring less than a minute apart (Fig. S2). Eighty-eight percent of the suckling events (30 suckling events) were recorded during ten different clusters of suckling events. The global temporal distribution of the suckling events through the duration of each deployment are presented in Fig. S3. There was no evidence of increasing trends in suckling frequency through the duration of the

Table 1 Characteristics of all suckling events for each calf. Date-times are presented in the format DD/MM/YYYY hhmm-hhmm and corresponds to deployment date, data start time, and data end time. Data start time also corresponds to tag attachment time. Data end time corresponds to tag detachment time, except for Calf3 since the data towards the end of the deployment on Calf3 was not usable due to lack of visibility on the video recording as the evening approached (the tag detached at 1845). The letters R/L indicate the rolling sides of the calf as observed on the video recordings: Right/Left. Budget represents the proportion of time the animal was observed suckling. The remaining values are presented following the format mean \pm SD (min; max). Note the use of absolute value for roll to emphasize the roll deviation from zero (regardless of the side). No suckling events were observed during ascent phase of dives.

ID	Date-time	Occurrence	R/L	Duration (s)	Budget (%)	Depth (m)	Depth rate (m s ⁻¹)	Speed (m s ⁻¹)	Averages				
									FSR (Hz)	Pitch (°)	Roll (°)	Roll rate (° s ⁻¹)	ODBA (m s ⁻²)
Calf1	14/09/2018 1134- 1418	During dive (descent) N = 2	1/1	23.3 \pm 1.5 (22.2; 24.3)	0.5	24.6 \pm 3.3 (22.3; 26.9)	0.2 \pm 0.1 (0.1; 0.2)	1.5 \pm 0.1 (1.4; 1.5)	0.3 (0.3; 0.3)	-13 \pm 12 (-22; -5)	39 \pm 13 (30; 48)	3.6 \pm 1.9 (2.2; 4.9)	0.4 (0.3; 0.4)
			2/1	22.2 \pm 12.8 (8.8; 34.2)	0.7	30.6 \pm 1.2 (29.3; 31.8)	0.1 \pm 0.3 (-0.2; 0.4)	1.4 \pm 0.1 (1.4; 1.5)	0.2 (0.1; 0.2)	-5 \pm 14 (-15; 12)	37 \pm 15 (20; 49)	4.1 \pm 0.8 (3.5; 5.1)	0.4 \pm 0.1 (0.3; 0.5)
Calf2	06/08/2019 1057- 1234	During dive (bottom) N = 3	0/1	44.9	0.8	22.2	0.1	1.6	0.1	25	63	3.5	0.4
			3/0	18.4 \pm 12.3 (6.2; 30.9)	0.9	26.1 \pm 6.7 (19.3; 32.6)	0 \pm 0.2 (-0.1; 0.3)	1.7 \pm 0.1 (1.6; 1.8)	0.2 (0.2; 0.2)	11 \pm 7 (3; 16)	47 \pm 3 (44; 48)	3.7 \pm 0.9 (3.1; 4.8)	0.5 \pm 0.1 (0.5; 0.6)
Calf3	09/08/2019 1003- 1802	During dive (descent) N = 6	2/4	10.9 \pm 4.2 (4.8; 15.6)	0.3	12.4 \pm 3.4 (8.9; 17.8)	0.2 \pm 0.1 (0.1; 0.3)	1.3 \pm 0.1 (1.2; 1.5)	0.3 \pm 0.1 (0; 0.4)	3 \pm 10 (-10; 19)	47 \pm 12 (27; 63)	5.8 \pm 2.7 (3.1; 9.9)	0.3 \pm 0.1 (0.2; 0.4)
			8/6	18.9 \pm 4.6 (11.2; 25.5)	1.1	16.8 \pm 3.2 (11.1; 21.1)	0 \pm 0.1 (-0.1; 0.3)	1.3 \pm 0.2 (1.1; 1.7)	0.3 \pm 0.1 (0; 0.4)	10 \pm 7 (0; 25)	51 \pm 9 (25; 61)	4.6 \pm 2.1 (0.5; 8.6)	0.3 \pm 0.1 (0.3; 0.4)
		At surface N = 5	3/2	19.6 \pm 10 (7.9; 35)	0.4	6.2 \pm 2.7 (2; 8.4)	0 \pm 0.1 (-0.1; 0.1)	1.2 (1.2; 1.2)	0.2 \pm 0.1 (0.2; 0.3)	5 \pm 10 (-6; 19)	37 \pm 24 (6; 59)	6.4 \pm 1.9 (4.5; 9)	0.3 \pm 0.1 (0.2; 0.4)

deployments (no indication of a habituation effect, *i.e.*, habituation to tag). Indeed, for the three deployments the first recorded suckling events occurred within the first 90 min of the deployment (within the first 30 min for Calf2) and the periods towards the end of the deployments were not necessarily associated with more frequent suckling events (Fig. S3).

The majority of suckling events occurred while diving, during the descent and the bottom phases ($N = 9$ for descent suckling and $N = 20$ for bottom suckling, Table 1). Suckling during descent and during bottom phases of dives occurred at a mean average depth of 16.2 ± 6.5 m and 20.2 ± 6.6 m respectively (Table 1). Only five suckling events occurred at the surface, at a mean average depth of 6.2 ± 2.7 m (Table 1). No suckling event occurred during ascent phase of dives.

While calves were visually estimated to be at about 30–45° pitch angle relative to the midline of their mother's body during suckling in the videos, the pitch recorded by the tag (pitch angle relative to the horizontal) was fairly lower on average (during descent: mean average = $2 \pm 14^\circ$, bottom: mean average = $8 \pm 10^\circ$, at surface: mean average = $5 \pm 10^\circ$, Table 1). Visual estimation of the calf's pitch assumed that the mother had a relatively straight body during nursing, as we observed no apparent extreme body arching of the mother. In all of the observed events, we could visually tell that the calf was always rolling to one side (to the right or to the left). These rolling periods during suckling were recorded by the tag as a sustained deviation of the roll from zero during the event (Fig. S2). In all but one cluster of suckling events, the calf alternated between suckling with a right roll then rotating to suckle with a left roll or vice-versa (Fig. S2). In eleven suckling events (one for Calf1, four for Calf2 and six for Calf3), we were able to visually confirm that the calf's mouth covered only one mammary teat during a suckling event. In three of these events, the tongue was clearly visible and displayed a rhythmic movement (Fig. 1, see also example footage in <https://www.youtube.com/watch?v=nyqhb9BemYI>). For these events with confirmed covered teat, rolling to the right corresponded to a mouth covering the right teat ($N = 3$) and rolling to the left corresponded to a mouth covering the left teat ($N = 8$, Fig. S2).

Relation between calf's positioning and suckling during dive

During our tag deployments, Calf1, Calf2, and Calf3 spent respectively 11.7%, 12%, and 8.9% of their total video time in close proximity to their mother's ventral side without suckling. Non-suckling dives in which the calf remained beneath the mother for at least consecutive 5 s were more common than suckling dives (Table S1). In other words, using calf proximity to the mother's ventral side alone does not indicate that suckling is occurring. Additional accelerometry cues, which are described below, are thus necessary to determine the occurrence of this behavior.

Behavioral signatures of suckling

The characteristics of suckling events and non-suckling segments are summarized in Fig. 2. Raw data are provided in Data S1. The detailed results of the LMMs are presented in Table S2 and the detailed results of the post-hoc tests are provided in Table S3. Within our model, for the average depth rate, the effect of suckling, surface phase, and the interaction effect

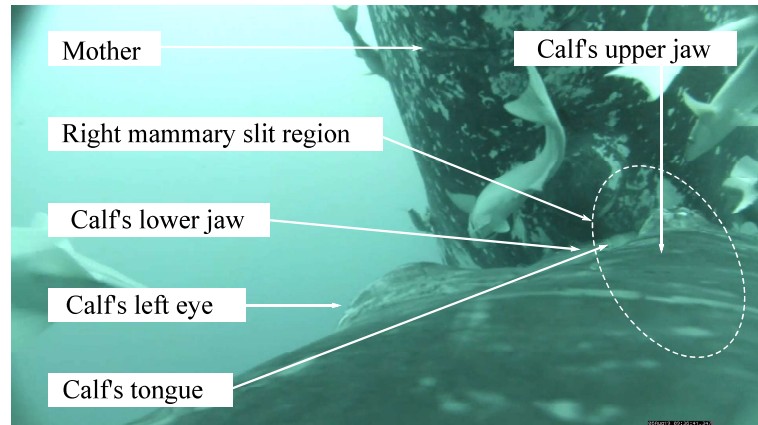


Figure 1 Screen capture of a video footage of humpback whale calf suckling on the right teat of its mother. Photo credit: Isabelle Charrier.

Full-size  DOI: [10.7717/peerj.12945/fig-1](https://doi.org/10.7717/peerj.12945/fig-1)

between surface phase and suckling were all statistically non-significant and close to zero (Suckling: $\beta = -0.01$, $P = 0.85$, Surface: $\beta = -0.02$, $P = 0.849$, Suckling*Surface: $\beta = 0.03$, $P = 0.863$, Table S2). The effect of descent was on the other hand statistically significant, substantial, and positive ($\beta = 0.6$, $P < 0.001$, Table S2). The interaction effect between suckling and descent was also statistically significant and was moderate, although negative ($\beta = -0.44$, $P < 0.001$, Table S2). In other words, descent phase was associated with a significant increase in average depth rate, which is expected, but the increase is significantly attenuated when suckling. Bottom phase and surface phase were associated to comparable low average depth rate and were not significantly influenced by the act of suckling. There was substantial and statistically significant difference in average depth rate between suckling and non-suckling during descent (Tukey's post-hoc test, $\beta = -0.46$, $P < 0.001$, Table S3). The difference in average depth rate between suckling and non-suckling at the bottom of dive and at surface were however weak and statistically non-significant (Tukey's post-hoc test, Bottom suckling - Bottom non-suckling, $\beta = -0.01$, $P = 1$, Surface suckling - Surface non-suckling, $\beta = 0.01$, $P = 1$, Table S3).

With respect to average speed, the effect of descent phase and surface phase were statistically significant and positive (Descent: $\beta = 0.22$, $P = 0.016$, Surface: $\beta = 0.3$, $P = 0.033$, Table S2). The effect of suckling, the interaction effect between descent phase and suckling, and the interaction effect between surface phase and suckling were negative but were statistically non-significant (Suckling: $\beta = -0.1$, $P = 0.363$, Suckling*Descent: $\beta = -0.21$, $P = 0.22$, Suckling*Surface: $\beta = -0.38$, $P = 0.082$, Table S2). To be specific, descent phase and surface phase were associated with a significant increase in average speed irrespective of the suckling state. Globally, post-hoc tests showed that the average speed tended to be lower during suckling compared to non-suckling for all activity phases (Tukey's post hoc test, negative β for all activity phase, Table S3). However, the difference was statistically non-significant (Tukey's post-hoc test, $P > 0.05$, Table S3).

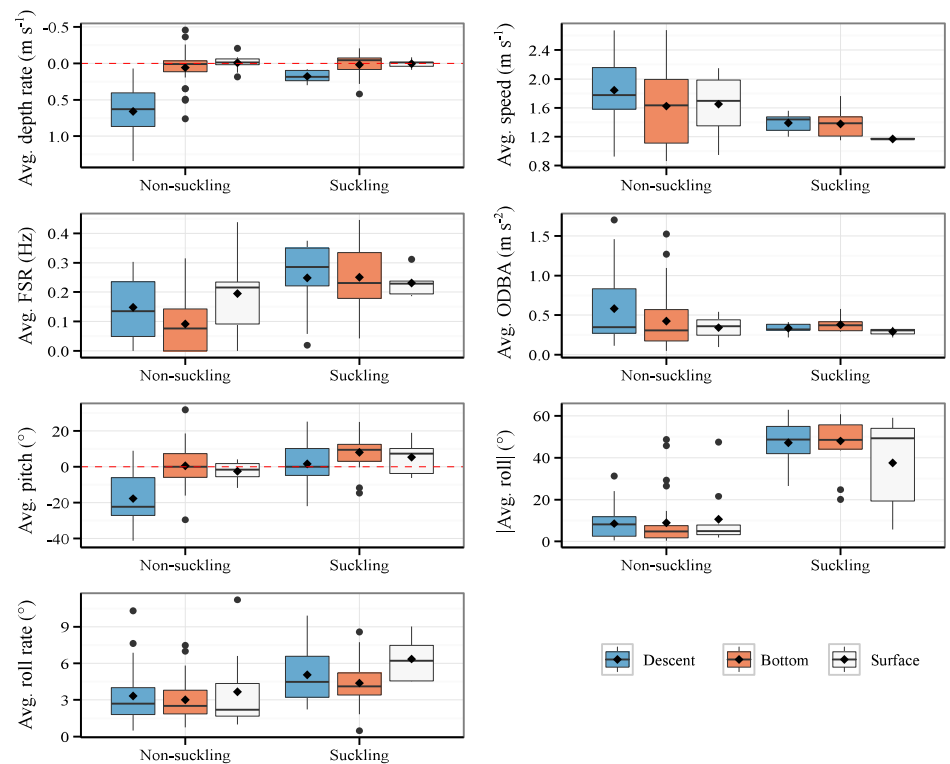


Figure 2 Comparison of suckling events (18.8 s average duration) and non-suckling segments (20 s duration) with respect to activity phases. Avg.: average. Mean and median are indicated by diamond marks and bold horizontal lines respectively. No ascent suckling has been observed.

Full-size [DOI: 10.7717/peerj.12945/fig-2](https://doi.org/10.7717/peerj.12945/fig-2)

Suckling, descent phase and surface phase had moderate and statistically significant positive effect on average Fluke Stroke Rate (FSR) (Suckling: $\beta = 0.16$, $P < 0.001$, Descent: $\beta = 0.06$, $P = 0.04$, Surface: $\beta = 0.1$, $P = 0.016$, Table S2). The interaction of suckling with descent phase and with surface phase had negative but statistically non-significant effect (Suckling*Descent: $\beta = -0.06$, $P = 0.258$, Suckling*Surface: $\beta = -0.12$, $P = 0.073$, Table S2). Specifically, descent phase and surface phase were associated with an increase in average FSR and for all activity phases the act of suckling was associated with an increase in average FSR. Post-hoc tests (Table S3) showed however that there was no statistically significant difference in average FSR between suckling and non-suckling except when at bottom (Tukey's post-hoc test, $\beta = 0.16$, $P < 0.001$).

Regarding the average Overall Dynamic Body Acceleration (ODBA), only descent had statistically significant effect ($\beta = 0.16$, $P = 0.028$, Table S2). Suckling and surface phase had statistically non-significant effect (Suckling: $\beta = 0.05$, $P = 0.522$, Surface: $\beta = 0.1$, $P = 0.377$, Table S2). The interaction of suckling with descent phase and with surface phase also had statistically non-significant effect (Suckling*Descent: $\beta = -0.2$, $P = 0.132$, Suckling*Surface: $\beta = 0.1$, $P = 0.551$, Table S2). In other words, descent phase was

associated with an increase in average ODBA and for all activity phases, the act of suckling did not significantly influence the average ODBA. Overall, there was no statistically significant difference in average ODBA between suckling and non-suckling for all activity phases (Tukey's post-hoc test, $-0.15 \leq \beta \leq 0.05$, $P > 0.05$, Table S3).

For average pitch, the effect of surface phase and the interaction effect between surface phase and suckling were weak and statistically non-significant (Surface: $\beta = -5.05$, $P = 0.222$, Suckling*Surface: $\beta = 1.41$, $P = 0.829$, Table S2). The effect of suckling was weak, yet statistically significant ($\beta = 6.36$, $P = 0.044$, Table S2). The effect of descent phase was on the other hand statistically significant, substantial, and negative ($\beta = -18.26$, $P < 0.001$, Table S2). The interaction effect of suckling on descent phase was also statistically significant and moderate but positive ($\beta = 12.77$, $P = 0.011$, Table S2). Specifically, descent phase was associated with a significant decrease in average pitch, which is expected, but the decrease was significantly attenuated when suckling (posture close to the horizontal when suckling). Bottom phase and surface phase were associated to an average pitch close to zero, positively influenced by the act of suckling (slight upward pitch when suckling). There was substantial and statistically significant difference of average pitch between suckling and non-suckling during descent (Tukey's post-hoc test, $\beta = 19.13$, $P < 0.001$, Table S3). The difference in average pitch between suckling and non-suckling at the bottom of dive and at surface were however weak and statistically non-significant (Tukey's post-hoc test, Bottom suckling - Bottom non-suckling, $\beta = 6.36$, $P = 0.345$, Surface suckling - Surface non-suckling, $\beta = 7.77$, $P = 0.756$, Table S3).

The effect of suckling on average absolute roll was statistically significant and very strong ($\beta = 38.46$, $P < 0.001$, Table S2). All other effects were statistically non-significant and mostly weak (Descent: $\beta = -0.44$, $P = 0.882$, Surface: $\beta = 0.64$, $P = 0.885$, Suckling*Descent: $\beta = -0.25$, $P = 0.965$, Suckling*Surface: $\beta = -11.56$, $P = 0.108$, Table S2). In other words, all activity phases were associated with fairly low average absolute roll and the average absolute roll was positively influenced by suckling, regardless of the activity phase, *i.e.*, the average absolute roll was high during suckling for all activity phases. Post-hoc test indicated a significant difference in average absolute roll between suckling and non-suckling for all activity phases (Tukey's post-hoc test: $26.89 \leq \beta \leq 38.46$, $P < 0.001$, Table S3).

The effect of suckling, descent phase and surface phase, and the interaction effect between descent phase and suckling and between surface phase and suckling on the average roll rate were all low and statistically non-significant (Suckling: $\beta = 1.17$, $P = 0.06$, Descent: $\beta = 0.32$, $P = 0.559$, Surface: $\beta = 0.28$, $P = 0.726$, Suckling*Descent: $\beta = 0.4$, $P = 0.692$, Suckling*Surface: $\beta = 1.51$, $P = 0.249$, Table S2). The average roll rate displayed by calf during bottom phase, descent phase, and surface phase were comparable and the average roll rate was not significantly influenced by suckling. Overall, there was no statistically significant difference of roll rate between suckling and non-suckling for all activity phases (Tukey's post-hoc test: $\beta \leq 2.68$, $P > 0.05$, Table S3).

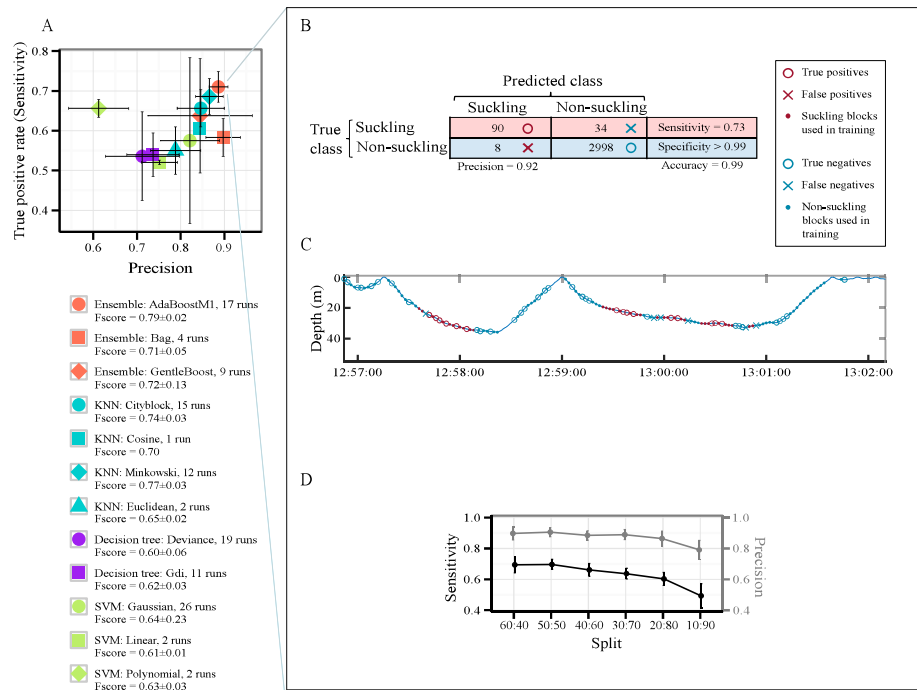


Figure 3 Models' performance in automatically identifying suckling blocks. The data included all three tag deployments on humpback whale calf. A 60:40 holdout training-testing split was used. (A) Sensitivity versus Precision plot of 12 models pre-selected using a Bayesian optimization approach. The symbols show the mean values and the SD. The models were pre-selected in the optimization procedure for each type of classifier over 30 runs. (B) Example of global results from automatic identification of suckling behaviour using the AdaBoostM1 model. (C) Example of results from automatic identification of suckling behaviour using the AdaBoostM1 model for Calf1. (D) Performance of the AdaBoostM1 model when the training set size is reduced. The symbols show the mean values and the SD (30 runs).

Full-size [DOI: 10.7717/peerj.12945/fig-3](https://doi.org/10.7717/peerj.12945/fig-3)

Best classifier for automatic identification of suckling

A total of 7,827 behavioral blocks of 2 s duration (4,697 for training and 3,130 for testing, 60:40 holdout splitting) were obtained from the datasets after removing blocks too close to the surface and those of high speed activities (see Segmentation in the Method section). The raw data used for this part of the study are available in [Data S2](#). No suckling events were affected by our thresholds for removing blocks too close to the surface and those of high speed activities. The class 'suckling' represented 4% of the data and the class 'non-suckling' represented 96%. [Figure 3A](#) presents all models pre-selected by the optimization procedure for identifying automatically suckling in non-labelled data. How often each model was selected over the 30 runs of the optimization procedure for each type of classifier is presented in [Fig. 3A](#), and details are presented in [Table S4](#).

All pre-selected classification models had a mean global accuracy $\geq 96.93\%$ on unseen data ([Table S4](#)). They all identified suckling events with a low False Positive Rate (mean

FPR < 1%) except for SVM with polynomial kernels (mean FPR > 1% but not exceeding 2%, Table S4). The likelihood of misclassifying an event as suckling when it should have been classified as non-suckling is thus extremely low for most of the pre-selected models. As shown in Fig. 3A, the SVM with linear kernel model and all decision trees are more located at the bottom left quadrant of the figure, indicating that they had a lower Precision and Sensitivity with regard to suckling, in contrast to AdaBoostM1, GentleBoost, Minkovski metrics-based KNN, Cityblock metrics-based KNN, and Cosine metrics-based KNN models that lay on the top right of the figure. The SVM with polynomial kernel model lays on the top left of the figure, indicating that it had a high Sensitivity but had a low Precision. On the other hand, the Bag or Random Forest model, the SVM with Gaussian kernel model, and the Euclidean metrics-based KNN model lay on the bottom right, indicating that they had high Precision but had low Sensitivity. The AdaBoostM1, an Ensemble classifier, was the model presenting the highest *F*-score. It had the highest Sensitivity while having at the same time a very good Precision (red circle symbol in Fig. 3A). It was therefore the best model for correctly identifying suckling periods. Examples of classification resulting from the AdaBoostM1 are presented in Figs. 3B and 3C. In these examples, the AdaboostM1 model only misclassified non-suckling blocks as suckling in very rare cases (False Positives, 8 in Fig. 3B and null in Fig. 3C—no red cross). However, it misclassified suckling blocks as non-suckling more often (False Negatives, 34 in Fig. 3B and 6 in Fig. 3C—blue crosses). Nevertheless, it detected most of the real suckling blocks (True Positives, 90 in Fig. 3B and 15 in Fig. 3C—red circles).

As shown in Fig. 3D, while there was typical decrease in the performance of the AdaBoostM1 when we reduced the training set size, the model still detected substantial amount of suckling blocks and had a relatively good precision even when using only 10% of the data as training set (mean at 10:90 split for suckling: sensitivity = 0.49 ± 0.08 , precision = 0.79 ± 0.06 , *F*-score = 0.60 ± 0.06 , *N* = 30). However, the results seemed more variable (high SD) when training set was really small (Fig. 3D).

Generalization of the supervised machine learning across individuals

We evaluated the generalization ability of the AdaBoostM1 model, the best identified classifier in the context of suckling identification, using a leave-one-out design. The goal was to assess whether we can use data from other individuals to detect the suckling behavior of a new individual. Given that we had three individuals, there were only three possible splitting combinations: (1) blocks from Calf2 and Calf3 as training set (5,766 blocks, 4.5% suckling and 95.5% non-suckling) and blocks from Calf1 as testing set (2,061 blocks, 2.6% suckling and 97.4% non-suckling), (2) blocks from Calf1 and Calf3 as training set (7,256 blocks, 3.6% suckling and 96.4% non-suckling) and blocks from Calf2 as testing set (571 blocks, 8.6% suckling and 91.4% non-suckling), and (3) blocks from Calf1 and Calf2 as training set (2,632 blocks, 3.9% suckling and 96.1% non-suckling) and blocks from Calf3 as testing set (5,195 blocks, 4% suckling and 96% non-suckling).

Results of the leave-one-out design are presented in Fig. 4. All combinations were more located at the bottom part of the Sensitivity *versus* Precision plot (open symbols).

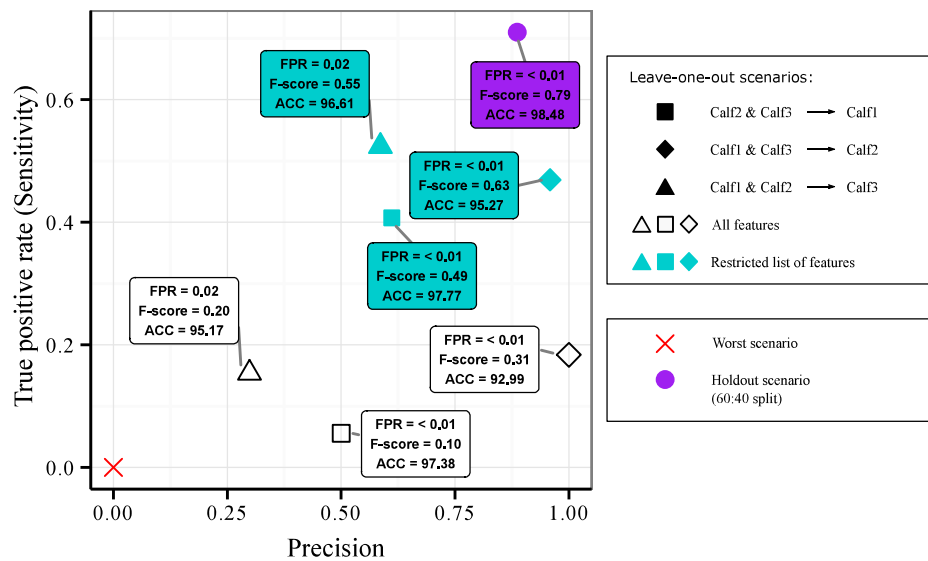


Figure 4 Sensitivity versus precision plot obtained from the AdaBoostM1 model for the suckling class when using leave-one-out splits on data from three humpback whale calves. In a leave-one-out split, data from two individuals were used for training while one individual is kept unseen for testing. The plot shows the classifier's performance when all features were included (open symbols) versus when the features that contributed most to the inter-individual variation in terms of suckling were excluded (blue symbols). For comparison, mean results from 60:40 holdout split (purple symbol) and the worst scenario (red cross symbol) are shown.

Full-size [DOI: 10.7717/peerj.12945/fig-4](https://doi.org/10.7717/peerj.12945/fig-4)

This indicated that the quantity of the detected suckling blocks was low (low Sensitivity) regardless of the combination. The quality was however still good (relatively high Precision) for the first and second combinations (open square and open diamond symbols). The third combination (open triangle symbol) was on the other hand more located at the left of the plot, indicating that the quality of the classification was bad (low Precision). Globally, it can be said that while some good quality classification can be obtained, it still depended on the combination used.

As inter-individual variation of the suckling blocks' kinematic features may have influenced the generalization ability of the AdaBoostM1, we assessed the model's performance when the features that contributed the most to inter-individual difference were excluded. We performed Random Forest classification of the individuals to check the existence of inter-individual differences on suckling blocks, analyzed the features' contribution to the differentiation, and identified a set of features to be excluded in order to reduce the inter-individual difference. The Random Forest algorithm indicated that there was effectively a strong inter-individual difference. Indeed, the classification error rate, indicated by the Out-of-the-bag error rate, was very low (Out-of-the-bag error rate = 3.22%). As shown in the Fig. 5A, the Random Forest algorithm was able to correctly predict to which individual each suckling block belongs to in most of the cases (correspondence between true class and predicted class). The Fig. 5B shows the Gini index of each feature.

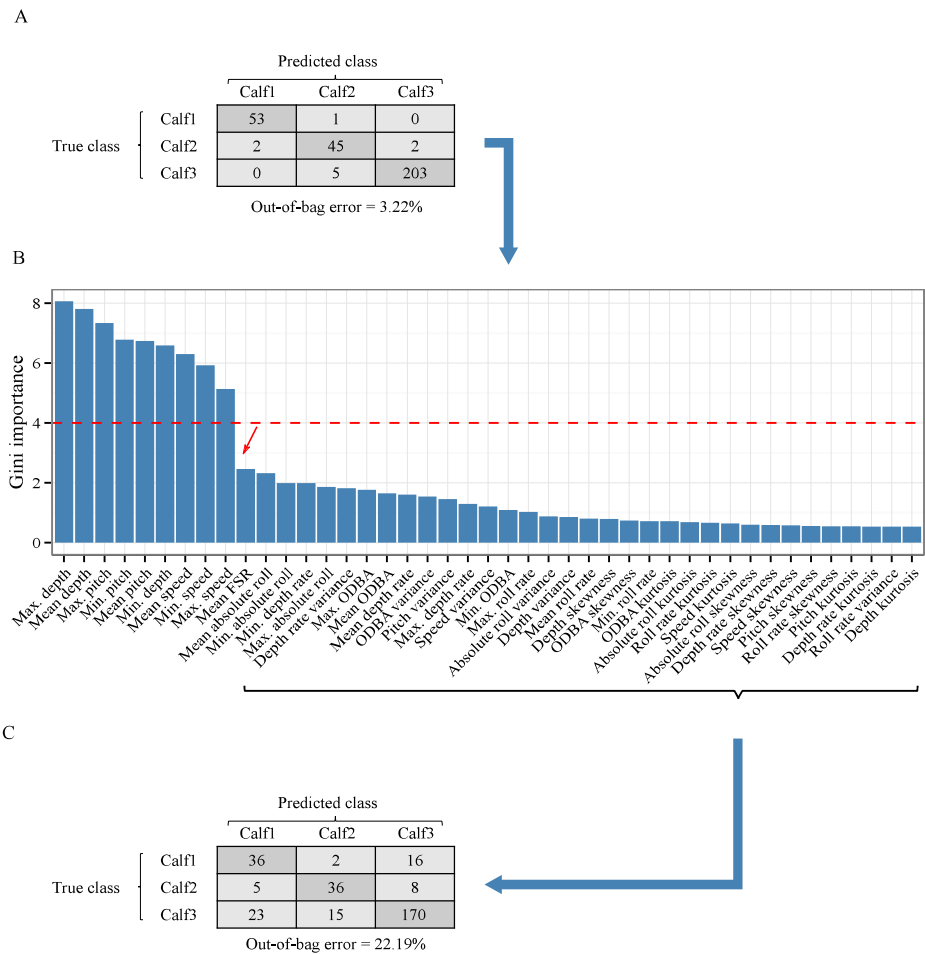


Figure 5 Analysis of the inter-individual difference between the suckling blocks of three humpback whale calves. (A) Result of a Random Forest classification (confusion matrix) of the suckling blocks by individuals when all features were used. (B) Importance of the features in the classification by individuals. A sharp drop of the Gini index is noticeable after the 9th feature (red arrow). (C) Result of a Random Forest classification (confusion matrix) of the suckling blocks by individuals when the first 9 most important features were excluded.

Full-size DOI: [10.7717/peerj.12945/fig-5](https://doi.org/10.7717/peerj.12945/fig-5)

A high Gini index indicated that the feature played great role in the classification (in other words, in the individual differentiation). In the plot, we noticed a sharp drop in importance after the 9th feature. We thus chose to exclude the first 9 features (Gini index > 4): the maximum depth, mean depth, maximum pitch, minimum pitch, mean pitch, minimum depth, mean speed, minimum speed, and the maximum speed. The Fig. 5C shows the new resulting classification of the suckling blocks by individuals when these features were not included. The classification error rate increased notably (Out-of-the-bag error rate = 22.19%). The Random Forest algorithm confused the individual attribution of the suckling

blocks more often (more non-corresponding true class and predicted class), indicating that we successfully reduced partially the inter-individual differences. We observed a substantial increase in performance when we re-ran the leave-one-out design using the restricted list of features (mean FSR, mean absolute roll, minimum absolute roll, minimum depth rate, maximum absolute roll, depth rate variance, maximum ODBA, mean ODBA, mean depth rate, ODBA variance, pitch variance, maximum depth rate, speed variance, minimum ODBA, maximum roll rate, absolute roll variance, depth variance, mean roll rate, depth skewness, ODBA skewness, minimum roll rate, ODBA kurtosis, absolute roll kurtosis, roll rate kurtosis, speed kurtosis, absolute roll skewness, depth rate skewness, speed skewness, pitch skewness, roll rate skewness, pitch kurtosis, depth rate kurtosis, roll rate variance, depth kurtosis) (Fig. 4, blue symbols). Indeed, the Global accuracy was higher than when including all features, and the FPR for suckling blocks decreased. Most importantly, the quantity of detected suckling blocks increased (higher Sensitivity). Also the quality of the classification improved globally (increased Precision), even for the combination that had a very poor Precision at first.

DISCUSSION

Our study characterized the suckling behavior in humpback whale calves less than 3-month old using CATS cam tags on one calving ground in the South Western Indian Ocean. Several important aspects of this vital behavior were investigated: (i) duration and frequency, (ii) occurrence in the water column, (iii) modalities, (iv) behavioral signatures, and (v) the possibility to use only acceleration and depth-derived data (*i.e.*, depth, depth rate, speed, Fluke Stroke Rate (FSR), Overall Dynamic Body Acceleration (ODBA), pitch, roll, roll rate, which were obtained using the data from the depth sensor and/or the 3-axis accelerometer only) to perform an automatic detection of suckling events.

Advantage of using animal-borne camera-equipped multi-sensor tags

Animal-borne multi-sensor tags equipped with video camera are very efficient for studying suckling behavior since they can deliver a view from calf's perspective and thus confirm evidence of suckling. Video from tags allowed differentiation of events in which the calf started to intentionally touch its mother's mammary slit to suckle from events when the calf was only positioning itself under the mother. Such differentiation between suckling and non-suckling periods would not be possible if the visual observations were performed from a different perspective or at distance (*e.g.*, surface ship-based, or aerial drone-based), therefore leading to biased estimations of suckling behavior.

In our study, the view offered by the video camera allowed clear definition of suckling events initiated by physical contact between the calf's snout and the mammary teat. Such contact did not happen every time the calf was under the mother. Suckling behavior was further confirmed by the presence of a milk cloud as in [Tackaberry et al. \(2020\)](#). This method greatly improved describing suckling behavior with confidence.

Previously, positioning and posture of the calves have been used frequently as a proxy for determining the occurrence of nursing or suckling in humpback whales ([Glockner & Venus, 1983](#); [Glockner-Ferrari & Ferrari, 1985](#); [Clapham & Mayo, 1987](#); [Morete et al.,](#)

2003; *Videsen et al., 2017*; *Zoidis & Lomac-MacNair, 2017*). As previously shown by *Tackaberry et al. (2020)* with older calves (studied in their feeding grounds), we found that young calves were also positioned frequently under the mother and in close proximity but they were actually not suckling. Furthermore, suckling dives (*i.e.*, dives during which suckling was visually confirmed by evidence of a milk cloud) appeared to be much rarer in comparison to non-suckling dives during which the calf was observed under the mother. Consequently, great care must be taken when associating calf positioning with suckling or with suckling dives as these are not necessarily associated. The calf, when positioning under the mother while not necessarily suckling may be taking advantage of reduced drag, as shown for dolphin calves (*Noren & Edwards, 2011*).

Duration and frequency of suckling events

Suckling events were brief and rare (18.8 ± 8.8 s on average and $<2\%$ of observation time). They were shorter in duration compared to those observed by divers in another breeding area (30.6 ± 17 s on average, *Zoidis & Lomac-MacNair, 2017*). This difference might be related to the method used, as discussed above. The average suckling duration reported in the feeding area is quite similar to what we observed (23 ± 7 s, *Tackaberry et al., 2020*). The associated suckling frequency was however much lower in the feeding area (0.3% of the time for an observation between 0745 and 1700 local time; (*Tackaberry et al., 2020*) compared to what we observed in the calving area (1.7% between 1000 and 1800 local time). This expected difference suggests suckling rate varies with age (greater for young calves in the breeding grounds *versus* older calves in the feeding grounds), as is the case with several species of pinnipeds (*Oftedal, Boness & Tedman, 1987*).

Occurrences of suckling in the water column

As in *Tackaberry et al. (2020)*, most of the suckling events occurred at depth and during dives. Humpback whales may favor nursing at depth to help the calf in maintaining the suckling posture as the latter would be more buoyant at surface, or for facilitating the thermoregulation of the adult female (*Videsen et al., 2017*). We noticed that the rare surface suckling events only occurred at the end of the day, when the sun was less intense, suggesting a possible link between surface nursing events and thermoregulation behavior. Further investigations on suckling during the night are needed for comparison, as most videos were recorded during daylight only (this study; *Tackaberry et al., 2020*). Nursing behavior might show different patterns at night for the reasons cited above. If indeed suckling at night is more common and is occurring more at the surface, this has implications for the risk of boat-strikes at a time when visual cues are limited (for those at the helm).

The maximum suckling depth we recorded (32.6 m) was much shallower than the maximum reported by *Tackaberry et al. (2020)*. However, this does not necessarily relate to any physical limits of young calves. Rather, this maximum suckling depth might be an effect of the environment. Indeed, the average depth of the Sainte Marie channel is 35 m (*Trudelle et al., 2016*) and in our video recordings it was common to see the seabed when the whales dove to around 30 m depth.

All suckling events during dives occurred during the descent and bottom phases only, unlike in *Tackaberry et al. (2020)* where they also observed suckling events during the

ascent phase. One possible explanation is that very young calves found in breeding grounds have less breath capacities ([Saloma, 2018](#)) than older calves found in feeding areas. Thus, during the ascent phase of their dive, their priority would be to reach the surface to breathe rather than to suckle.

Suckling modalities

With respect to posture, as estimated from the video recordings, the calf positioned itself at 30–45° pitch angle relative to the midline of the mother's body when suckling. This is in agreement with past observations ([Glockner-Ferrari & Ferrari, 1985](#); [Zoidis & Lomac-MacNair, 2017](#)). However, the pitch recorded by the tags (pitch angle relative to the horizontal) during suckling was always relatively low on average (<15°). This suggests that the mother is generally oriented facing slightly downward when nursing its calf even during phases other than the descent (during which the mother does not otherwise have to lean downward).

One of the most innovative findings of our study was the calf's tendency to roll continuously to the side when suckling. Our data confirm the correspondence between the rolling side and the suckled teat in nine events. The calves rolled to the left to suckle on the left teat and rolled to the right to suckle on the right teat. The rolling behavior might be thus related to the anatomy of the mammary gland, in particular the orientation of the nipple as the nipple is extruded from the mammary slit. If each breast is positioned so that the teat is directed at an angle relative to the midsagittal plane, then the calf would be forced to match that angle with its mouth in order to stimulate the nipple to extrude and then grasp the nipple with its tongue. Video recordings showed the calf's tongue is directed laterally, visible in the oral gape of the mouth on one side of the head. The calf must roll to one side in order to align the lateral aspect of its mouth with the mammary slit (rolling left to align its right oral gape against the mother's left breast, and vice versa).

There was also the clear pattern of alternation from one side to the other between successive suckling events. Why then must the calf alternate sides? Perhaps the milk supply of each breast is limited, forcing the calf to suckle both sides in order to obtain a sufficient volume for satiation. This would ensure that the mother's breasts continue to lactate evenly on both sides. Another reason may be related to the milk production/storage/ejection system. It is widely accepted that milk is voluntarily ejected by the mother into the calf's mouth in cetaceans ([Slijper, 1966](#)). It is possible that the amount of milk the mother can continuously eject is limited and the gland may need a refractory period during which it must reset before the next ejection can occur. If so, then alternating which side to suckle maximizes feeding for the calf while increasing milk delivery efficiency for the mother. In this scenario, the currently suckled breast performs milk ejection while the previously suckled breast refills in preparation for the next ejection. This would thus force the calf to alternate between the two mammary glands to get enough milk during the successive nursing bouts. In-depth anatomical investigation is needed to answer this question, as there is scant literature on whale lactation or breast anatomy. The pattern of alternation between the two mammary gland, if indeed necessary and related to the milk

production/storage/ejection system in whales, may have an implication on the post-partum viability of twins in cetaceans.

Regarding the anatomy of suckling, it is important to note that in a few cases, rhythmic movements of the calf's tongue were observed during suckling events. This suggests that the calf actively participates in directing milk into its mouth. It is unclear whether these movements are stimulatory to the mother's 'let down' reflex (nipple erection and milk ejection), serve to 'strip' the nipple (as occurs in many land mammals to squeeze milk out), or create a piston-like suction to draw out milk (perhaps in combination with milk ejection from the mother). The lateral aspect of the calf's rostral tongue is comprised of elongated marginal papillae that may serve to grasp the nipple. This latching-on-nipple function has been proposed for newborn tongues in other whale species ([Kastelein & Dubbeldam, 1990](#); [Shindo et al., 2008](#); [Ferrando et al., 2010](#); [Kienle et al., 2015](#)). These marginal papillae may also 'zipper' together to form a tube for channeling milk into the mouth, compensating for the calf's lack of lips and cheeks to seal and contain the nipple and the extruded milk. Alternatively, the rhythmic movements of the tongue may be only an artefact produced by the calf's swimming movements as the calf undulates its body to maintain its suckling position while the tongue maintains constant contact with the nipple. Further study of the calf tongue may provide additional insights to its function.

Behavioral signatures of suckling events

The comparison of the data derived from accelerometer and depth sensor for suckling and non-suckling events revealed mainly one distinctive characteristic of the suckling behavior: a high absolute roll. Other characteristics, although not obvious, such as high FSR and low speed are also suggested by the results of our comparisons. For suckling occurring during the descent phase, there were additional notable specificities: a low depth rate and a pitch close to zero. This is in sharp contrast with descent non-suckling where calves showed a high descent rate on average and were directed downwards.

To our knowledge, no study to date has highlighted the characteristics of suckling behavior of whales in terms of roll recorded by an accelerometer. The sustained roll deviance from zero during suckling events is directly related to the aforementioned rolling pattern observed in the videos: rolling to the side may facilitate access to a particular mammary teat.

With respect to the kinematics, lower speed while still deploying some physical effort (high FSR) when suckling is consistent with the results of [Tackaberry et al. \(2020\)](#). Even though the pair makes little or no forward movement during suckling, the calf still has to maintain actively the suckling posture to stay in physical contact with the mammary slit. Unlike [Tackaberry et al. \(2020\)](#), we however did not find any specificity of suckling with respect to ODBA. Concerning the descent suckling, the relatively low depth rate may help the calf in maintaining the suckling posture.

Automatic detection of suckling using accelerometer and depth-derived data

In the field of ethology, the advances in machine learning have offered the opportunity to classify behaviors within a complex database ([Valletta et al., 2017](#)). Given the stereotyped

traits of suckling behavior in humpback whale calves, we tested whether it was possible to apply supervised machine learning algorithms on labelled accelerometer and depth sensor data to automatically discern suckling from non-suckling periods. Although accelerometer data have been already largely coupled with supervised machine learning to detect behaviors in various species ([Nathan et al., 2012](#); [Carroll et al., 2014](#); [Ladds et al., 2016](#); [Jeantet et al., 2020](#)), our study is the first attempt to use it for humpback whales and in the framework of a suckling behavior study.

The biggest challenge in the automatic classification of suckling behavior is probably the class imbalance. Indeed, suckling events are naturally rare (this study; [Tackaberry et al., 2020](#)). It is argued that unbalanced data tend to bias predictions in favor of the majority class. This bias is problematic in situations in which missing the minority class case is worse than misclassifying a majority class ([Levy et al., 2018](#)). In the case of suckling *versus* non-suckling classification, this bias is not a significant concern since there is more interest in minimizing the False Positive Rate (FPR) for the targeted behavior (*i.e.*, suckling). Such conservative measure is generally adopted in behavioral detection ([Nathan et al., 2012](#); [Carroll et al., 2014](#); [Tennesen et al., 2019](#)). On the other hand, the best model we found for identifying suckling periods, the AdaBoostM1, is a model suitable for unbalanced binary classifications ([Galar et al., 2011](#); [Levy et al., 2018](#)). Thus, class imbalance is less of a concern. In order to avoid evaluation bias, the evaluation process was guided primarily by the minimization of the FPR rather than the Global accuracy, since the latter does not distinguish between the numbers of correctly classified examples of different classes and can be misleading in the framework of an unbalanced dataset ([Galar et al., 2011](#)). It is important to recall that we also performed a data segmentation (we excluded blocks at <1.5 m depth or at >2 m s^{-1} speed) that helped in reducing data imbalance and in improving the results. While the thresholds we chose for the segmentation works well with our data and are compatible with our current knowledge on the suckling behavior of humpback whale, they may be subject to change and adjustment as our knowledge on humpback whale behavior evolves.

With an initial 60:40 holdout training-testing split, the average Sensitivity and Precision of the AdaBoostM1 model with respect to suckling class were of 0.71 and 0.89 respectively and the mean FPR was $<1\%$. In other words, the model was able to detect the vast majority of suckling blocks and about 9 out of 10 blocks reported as suckling corresponded to visually confirmed suckling periods.

The Leave-one-out design (blocks from two individuals as training set and the one remaining individual as a testing set) allowed testing whether data from two individuals can be used to detect suckling behavior in a novel individual. In this design, it was expected that the performance would drop notably (lower Sensitivity and Precision). Indeed, the inter-individual difference has been shown to generally penalize the performance of automatic classification models ([Vázquez Diosdado et al., 2015](#); [Ladds et al., 2016](#)). When we reduced the inter-individual difference in terms of suckling by excluding features that introduce substantial inter-individual differences, the performance returned to a reasonable level regardless of the combination (*i.e.*, the model generalized better and became more robust). Indeed, out of every 10 blocks reported as suckling, at least about 6 blocks were

confirmed to be correct (lowest Precision = 0.59). The associated Sensitivity was relatively low, indicating that several suckling blocks were not detected. However, detecting only few blocks but with precision is acceptable in the case where the goal is to be sure that a positive result means the identified suckling blocks really correspond to suckling periods. Furthermore, with only few blocks detected with high confidence, complete suckling events (start and end) may be determined by examining the corresponding sustained roll deviations, thus compensating the lack of sensitivity.

We were not able to investigate the effect of individual tag differences due to limited sample. We can however expect that this effect, if any, is relatively small. In the first and second combinations of our leave-one-out experiments, the two calves used for training were tagged with different individual tags (Cats1 and Cats2) and the remaining calf used for testing was tagged with one of the individual tags involved in training (Cats1 or Calf2). However, in the third combination, the two calves used for training were tagged with the same individual tag (Cats1) and the remaining calf used for testing was tagged with a different individual tag (Cats2). The fact that there was no evident divergence of the results of our third combination from the results of the first and second combinations suggests that our model was not significantly affected by the differences in individual tags. Further studies are encouraged regarding the potential effect of individual tag differences since our conclusion is still limited by sample size.

As more data is added to the learning set, we can expect better performance from the models. Indeed, we showed that the size of the training set can slightly influence the accuracy of the results. Similarly, we can also expect that with more individuals, the constraints and restrictions related to inter-individual differences would also be reduced ([Ladds et al., 2016](#)).

These results on automatic identification of suckling events are very promising for rapid evaluation of larger data sets and will open new opportunities for investigating limited data sets. First, the model may be adjusted to accommodate for incomplete observations (altered/missing video file, night-time recording, *etc.*) using only two sensors (3-axis accelerometer and depth sensor). Secondly, the model may be applied to data from comparable multi-sensor tags that lack visual support (video recordings lacking or too dark, tags without camera such as Acousonde and Dtags, *etc.*).

While these methods will broaden the opportunities in the domain of humpback whale mother-calf behavioral studies (and eventually may be applied to studying other large whales), care must be taken in these early stages. Until the acquisition of large training data occurs (several individuals), researchers should be aware of the limitations of each trained model. For example, possible differences in gaits and behavioral pattern with respect to age ([Noren, Biedenbach & Edwards, 2006](#); [Saloma, 2018](#)) may hinder the generalization ability of the models. For our trained model, we caution that it should be conservatively applied to less than 3-month old non-neonate calves occurring in a shallow water. Nevertheless, a concrete application example of the automatic identification of suckling behavior would be the investigation of the behavioral time budget of mother-calf pairs over 24 h (day and night). The main difficulty in using multi-sensor tags for studying the behaviors of mother-calf pairs concerns the acquisition of sufficiently representative data. Indeed,

tagging whales is a challenge per se and some age classes are more difficult to observe (e.g., neonate calves are rarely observed). Moreover, the tag attachment time on a whale is often limited (few hours on average), thus it is rare to record behaviors of individual whales over long periods (>24 h). Future studies should address the ontogeny aspect of calves' behavior in order to subsequently assess its implication in the field of automatic behavior detections. The development of more durable yet non-invasive tag attachment systems is also highly encouraged as this is the key to acquiring more complete data and thus obtaining more representative learning set for accurate automatic behavior detection.

CONCLUSIONS

Our results provide new knowledge on the suckling behavior of humpback whale calves in their calving ground. Our descriptions, based on videos from the calf's perspective, accelerometer data, and depth data complement previous studies based on surface and sub-surface observations (*Glockner & Venus, 1983; Glockner-Ferrari & Ferrari, 1985; Clapham & Mayo, 1987; Morete et al., 2003; Videsen et al., 2017; Zoidis & Lomac-MacNair, 2017*). We found that suckling is more frequent compared to what has been reported in the feeding area (*Tackaberry et al., 2020*), suggesting a variation of the suckling rate with the calf's age and underlining the importance of the suckling behavior in the calving area. We also confirmed that most suckling events occur at depth, highlighting the importance of using multi-sensor tags equipped with a video camera in order to obtain reliable observations. Finally, we found that suckling behavior is stereotyped, especially characterized by a continuously sustained roll deviating significantly from zero and likely a high FSR and low speed, and can potentially be detected automatically by supervised machine learning. While our results are only based on three tag deployments on humpback whale calves in the breeding ground, they are a proof of method on which future investigations of suckling and nursing behavior in humpback whales can build upon. Our study should be replicated with other baleen whale species for which suckling behavior is still undiscovered.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Author Contributions

- Maevatiana N. Ratsimbazafindranahaka conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Chloé Huetz, Anjara Saloma, Olivier Adam and Isabelle Charrier conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Aristide Andrianarimisa and Joy S. Reidenberg conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

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The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

All methods and approaches were fully approved by the Ministry of Fisheries Resources, Madagascar (National research and collect permits #28/18-MRHP/SG/DGRHP and #36/19-MAEP/SG/DGPA).

The study complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU).

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Data Availability

The following information was supplied regarding data availability:

The raw data are available in the [Supplemental Files](#).

Supplemental Information

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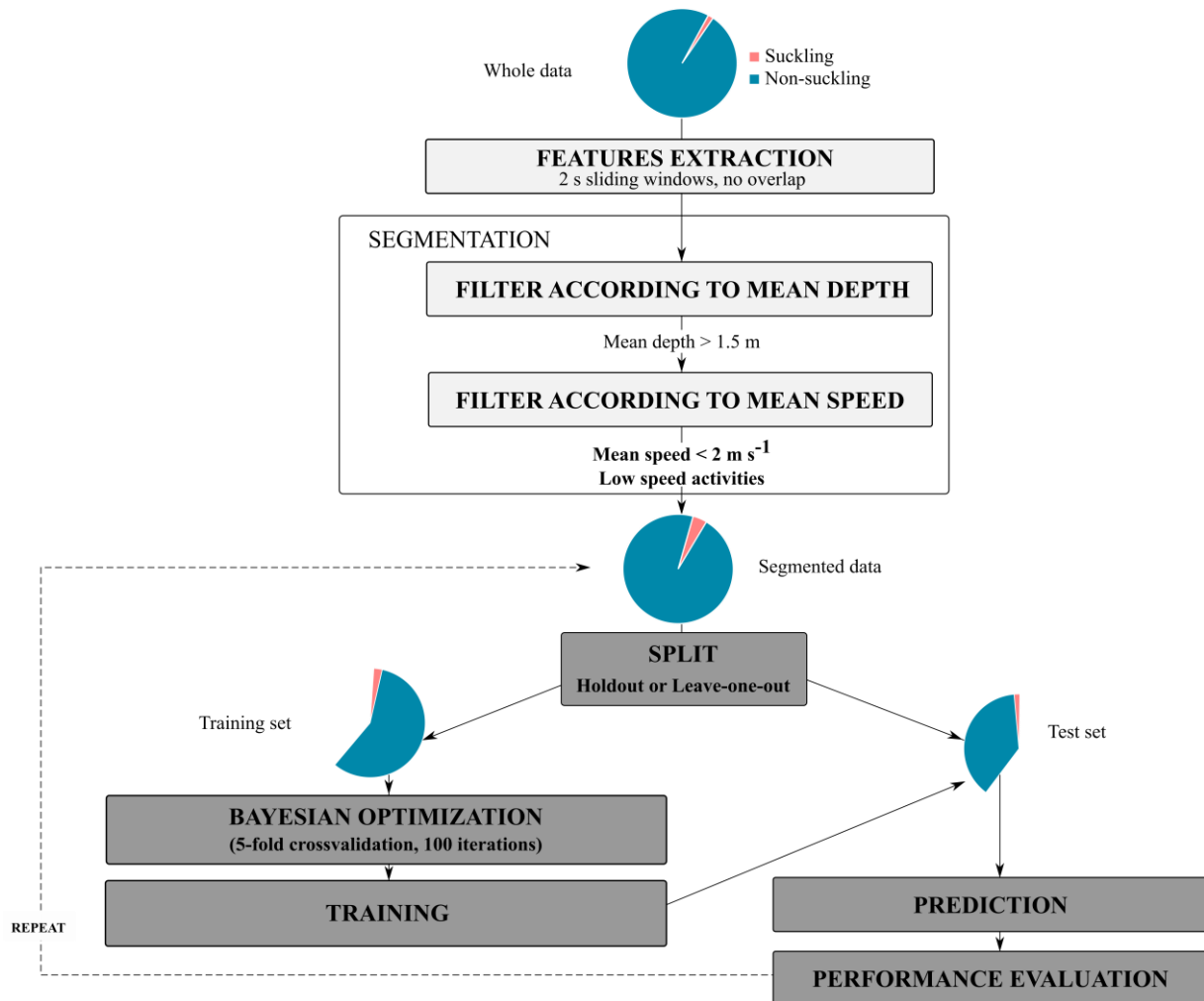


Figure S1. Supervised machine learning workflow for automatically identifying suckling behavior in free-ranging humpback whale calves using CATS cam tag data. The data derived from the 3-axis accelerometer and the depth sensor of the tags, sampled at 10 Hz, were split into 2 s non-overlapping blocks (windows), and each block was labeled either as 'suckling' or 'non-suckling' depending on which behavioral period it fell under (suckling period or any non-suckling period). The data underwent segmentation to remove noise and reduce the class imbalance partially. The thresholds we used (<1.5 m depth and >2 m s^{-1} speed) were based on the known characteristics of the nursing/suckling behavior of humpback whales, and their validity in our dataset was checked to ensure that no suckling events were removed partially or entirely following the segmentation. The pie charts represent the class distribution (suckling versus non-suckling). $N = 18331$ and $N = 7827$ before and after segmentation, respectively



Figure S2. Depth, pitch, roll, speed, FSR, and ODBA during and around suckling events for each calf. Blue, red, and green areas in the depth profile correspond to the dive's descent, bottom, and ascent phases, respectively. Uncolored areas in the depth profile correspond to surface phases. Suckling events are identified in red in the depth profile and by the yellow boxes in the raw pitch(blue)/roll(yellow) profiles. The yellow boxes on top indicate that the calf was observed rolling to the right side on the corresponding

video. The yellow boxes on the bottom indicate that the calf was observed rolling to the left side. Events during which the teat suckled by the calf was clearly identified on the corresponding video are marked with (R) or (L): (R) for the right teat and (L) for the left teat

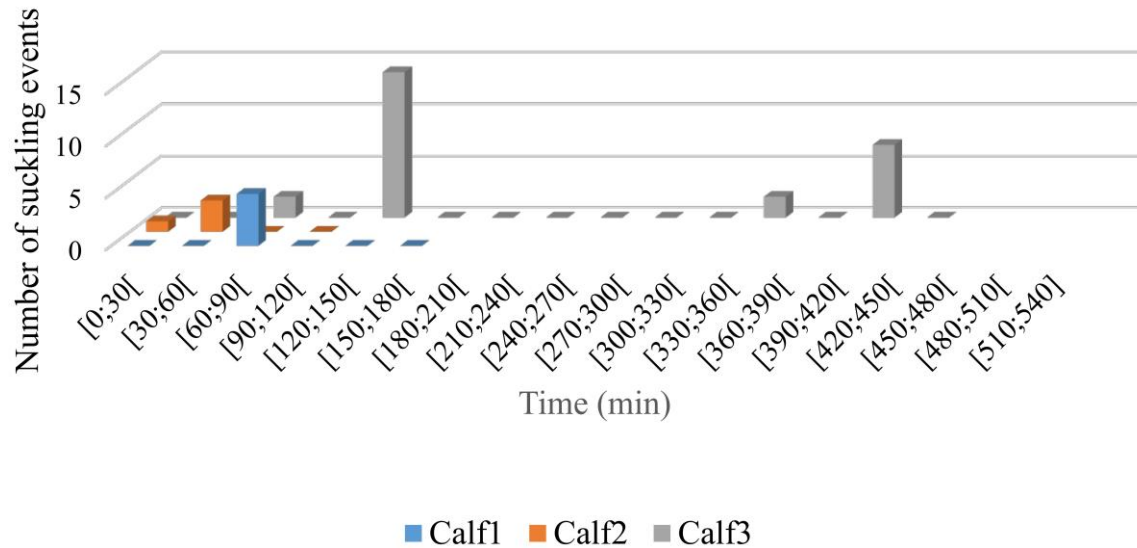


Figure S3. Temporal distribution of suckling events through the deployment duration for three tagged humpback whale calves. Blue, red, and grey bars correspond to Calf1, Calf2, and Calf3, respectively. Tag detached at 164 min for Calf1 and at 98 min for Calf2. For Calf3, the tag detached at 521 min. However, only the first 479 min (92%) of the data was analyzed due to a lack of visibility on the video recording as the evening approached. There was no evidence of trends with suckling frequency increasing later in the deployments. The periods towards the end of the deployments were not necessarily associated with more frequent suckling events

Table S1. Comparison of the number of non-suckling dives during which the calf was observed staying in close proximity beneath the mother for at least five consecutive seconds and the number of suckling dives

Individuals	Number		Suckling dives	Total dives
	Non-suckling dives			
	Calf observed staying in close proximity beneath the mother for at least 5 s during the dive	Calf never observed staying in close proximity beneath the mother for at least 5 s during the dive		
Calf1	17	18	2	37
Calf2	5	2	3	10
Calf3	20	21	9	50

Table S2. Summary table of the mixed-effect models for the characteristics of suckling events. The models included the suckling status and activity phase (descent, bottom, ascent, or surface) as fixed effects and individuals as random effects (reference level = bottom and non-suckling, *i.e.*, bottom non-suckling). The data used in the analysis consisted of individual suckling events (18.8 s average duration) and random assortments of non-suckling segments (20 s duration). Significant P (<0.05 in this study) are marked in bold. CI: Confidence interval. SE: Standard Error of estimate

Response	Fixed effect	Effect estimate (β)	95% CI	SE	t(96)	P
Average depth rate	(Intercept)	0.06	[-0.05, 0.17]	-0.45	1.07	0.285
	Suckling	-0.01	[-0.15, 0.13]	-0.04	-0.19	0.850
	Descent	0.60	[0.48, 0.72]	1.62	9.54	<0.001
	Surface	-0.02	[-0.2, 0.17]	-0.05	-0.19	0.849
	Suckling*Descent	-0.44	[-0.67, -0.22]	-1.20	-3.82	<0.001
	Suckling*Surface	0.03	[-0.27, 0.32]	0.07	0.17	0.863
Average speed	(Intercept)	1.62	[1.28, 1.97]	0.05	9.23	<0.001
	Suckling	-0.10	[-0.3, 0.11]	-0.21	-0.91	0.363
	Descent	0.22	[0.04, 0.4]	0.49	2.42	0.016
	Surface	0.30	[0.02, 0.57]	0.66	2.13	0.033
	Suckling*Descent	-0.21	[-0.54, 0.12]	-0.46	-1.23	0.220
	Suckling*Surface	-0.38	[-0.82, 0.05]	-0.85	-1.74	0.082
Average FSR	(Intercept)	0.09	[0.05, 0.13]	-0.63	4.22	<0.001
	Suckling	0.16	[0.09, 0.22]	1.27	4.95	<0.001
	Descent	0.06	[0, 0.11]	0.46	2.06	0.040
	Surface	0.10	[0.02, 0.18]	0.79	2.41	0.016
	Suckling*Descent	-0.06	[-0.16, 0.04]	-0.47	-1.13	0.258
	Suckling*Surface	-0.12	[-0.25, 0.01]	-0.97	-1.80	0.073
Average ODBA	(Intercept)	0.43	[0.18, 0.67]	-0.04	3.40	0.001
	Suckling	0.05	[-0.11, 0.22]	0.17	0.64	0.522
	Descent	0.16	[0.02, 0.3]	0.49	2.19	0.028
	Surface	0.10	[-0.12, 0.31]	0.30	0.88	0.377
	Suckling*Descent	-0.20	[-0.46, 0.06]	-0.62	-1.51	0.132
	Suckling*Surface	-0.10	[-0.44, 0.24]	-0.32	-0.60	0.551
Average pitch	(Intercept)	0.57	[-8.51, 9.66]	0.25	0.12	0.901
	Suckling	6.36	[0.18, 12.53]	0.42	2.02	0.044
	Descent	-18.26	[-23.58, -12.94]	-1.21	-6.73	<0.001
	Surface	-5.05	[-13.15, 3.06]	-0.34	-1.22	0.222
	Suckling*Descent	12.77	[2.93, 22.61]	0.85	2.54	0.011
	Suckling*Surface	1.41	[-11.45, 14.28]	0.09	0.22	0.829
Average roll	(Intercept)	8.98	[4.22, 13.74]	-0.58	3.70	<0.001
	Suckling	38.46	[31.79, 45.13]	1.83	11.30	<0.001
	Descent	-0.44	[-6.29, 5.41]	-0.02	-0.15	0.882
	Surface	0.64	[-7.98, 9.25]	0.03	0.14	0.885
	Suckling*Descent	-0.25	[-11.06, 10.57]	-0.01	-0.04	0.965
	Suckling*Surface	-11.56	[-25.65, 2.52]	-0.55	-1.61	0.108
Average roll rate	(Intercept)	3.00	[2.06, 3.94]	-0.34	6.25	<0.001
	Suckling	1.17	[-0.05, 2.39]	0.52	1.88	0.060
	Descent	0.32	[-0.75, 1.38]	0.14	0.58	0.559
	Surface	0.28	[-1.3, 1.87]	0.13	0.35	0.726
	Suckling*Descent	0.40	[-1.57, 2.37]	0.18	0.40	0.692
	Suckling*Surface	1.51	[-1.06, 4.08]	0.67	1.15	0.249

Table S3. Comparison of suckling events (18.8 s average duration) and non-suckling segments (20 s duration) with respect to activity phase using Tukey's post-hoc multiple comparison test. Comparisons were computed using the R package *emmeans*. Significant P (<0.05 in this study) are marked in bold. SE: Standard Error of estimate

Responses	Contrast	Estimate (β)	SE	df	t	P
Average depth rate	Descent suckling - Descent non-suckling	-0.46	0.1	98	4.8	<0.001
	Bottom suckling - Bottom non-suckling	-0.01	0.07	98	0.18	1
	Surface suckling - Surface non-suckling	0.01	0.13	96	-0.09	1
Average speed	Descent suckling - Descent non-suckling	-0.30	0.14	96	2.21	0.243
	Bottom suckling - Bottom non-suckling	-0.10	0.11	97	0.91	0.944
	Surface suckling - Surface non-suckling	-0.48	0.19	96	2.48	0.141
Average FSR	Descent suckling - Descent non-suckling	0.10	0.04	98	-2.32	0.197
	Bottom suckling - Bottom non-suckling	0.16	0.03	94	-4.7	<0.001
	Surface suckling - Surface non-suckling	0.04	0.06	96	-0.61	0.99
Average ODBA	Descent suckling - Descent non-suckling	-0.15	0.11	96	1.36	0.752
	Bottom suckling - Bottom non-suckling	0.05	0.08	97	-0.64	0.988
	Surface suckling - Surface non-suckling	-0.05	0.15	96	0.33	0.999
Average pitch	Descent suckling - Descent non-suckling	19.13	4.08	96	-4.68	<0.001
	Bottom suckling - Bottom non-suckling	6.36	3.17	97	-2.01	0.345
	Surface suckling - Surface non-suckling	7.77	5.76	96	-1.35	0.756
Average absolute roll	Descent suckling - Descent non-suckling	38.21	4.54	98	-8.42	<0.001
	Bottom suckling - Bottom non-suckling	38.46	3.56	96	-10.82	<0.001
	Surface suckling - Surface non-suckling	26.89	6.33	96	-4.25	0.001
Average roll rate	Descent suckling - Descent non-suckling	1.57	0.82	98	-1.9	0.406
	Bottom suckling - Bottom non-suckling	1.17	0.64	97	-1.82	0.458
	Surface suckling - Surface non-suckling	2.68	1.15	96	-2.32	0.194

Table S4. Results of the machine learning optimization procedure for automatically identifying suckling in non-labeled data. A Bayesian optimization procedure was run per model type (Ensemble, KNN, Decision tree, SVM) 30 times in order to select the best model (by seeking to minimize classification error). Values are presented following the format mean \pm SD. n represents how often each model was selected by the optimization procedure for each type of classifier over the 30 runs. FPR: False positive rate

Classifier Type	Models	n	Sensitivity	FPR (%)	Precision	Specificity	F-score	Accuracy (%)
Ensemble (30 runs)	AdaBoostM1	17	0.71 \pm 0.04	0.38 \pm 0.09	0.89 \pm 0.02	1	0.79 \pm 0.02	98.48 \pm 0.13
	Bag (Random forest)	4	0.58 \pm 0.05	0.27 \pm 0.1	0.9 \pm 0.04	1	0.71 \pm 0.04	98.08 \pm 0.26
	GentleBoost	9	0.64 \pm 0.14	0.46 \pm 0.27	0.84 \pm 0.12	1	0.72 \pm 0.13	98.11 \pm 0.75
K-Nearest Neighbors (KNN) (30 runs)	Cityblock	15	0.66 \pm 0.05	0.51 \pm 0.24	0.85 \pm 0.05	0.99	0.74 \pm 0.03	98.14 \pm 0.21
	Cosine	1	0.6	0.47	0.84	1	0.7	97.99
	Euclidean	2	0.55 \pm 0.06	0.63 \pm 0.28	0.79 \pm 0.06	0.99	0.65 \pm 0.02	97.6 \pm 0.05
	Minkowski	12	0.69 \pm 0.05	0.44 \pm 0.12	0.87 \pm 0.03	1	0.76 \pm 0.03	98.32 \pm 0.21
Decision tree: (30 runs)	Deviance	19	0.54 \pm 0.11	0.99 \pm 0.51	0.71 \pm 0.08	0.99 \pm 0.01	0.6 \pm 0.06	97.21 \pm 0.29
	Gdi	11	0.54 \pm 0.05	0.84 \pm 0.37	0.74 \pm 0.06	0.99	0.62 \pm 0.03	97.36 \pm 0.22
Support Vector Machine (SVM) (30 runs)	Gaussian	26	0.58 \pm 0.21	0.55 \pm 0.32	0.82 \pm 0.07	0.99	0.64 \pm 0.23	97.78 \pm 0.7
	Linear	2	0.52 \pm 0.01	0.72 \pm 0.16	0.75 \pm 0.04	0.99	0.61 \pm 0.01	97.41 \pm 0.14
	Polynomial	2	0.66 \pm 0.02	1.76 \pm 0.56	0.61 \pm 0.07	0.98 \pm 0.01	0.63 \pm 0.03	96.93 \pm 0.45



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Data S1. Raw data containing characteristics of suckling events (18.8 s average duration) and non-suckling periods (20 s duration) obtained from CATS cam tags deployed on three humpback whale calves in the Sainte Marie channel, Madagascar. Each line corresponds to either a suckling event or a 20-s non-suckling period selected randomly. The corresponding metadata is provided



<https://doi.org/10.7717/peerj.12945>

Data S2. Raw data from CATS cam tags deployed on three humpback whale calves in the Sainte Marie channel, Madagascar, used for testing the automatic identification of suckling behavior using supervised machine learning. Lines correspond to 2 s non-overlapping sliding blocks (windows). The corresponding metadata is provided



<https://doi.org/10.7717/peerj.12945>

Code S1. R scripts for analyzing the behavioral signatures of suckling events and inter-individual differences between suckling blocks

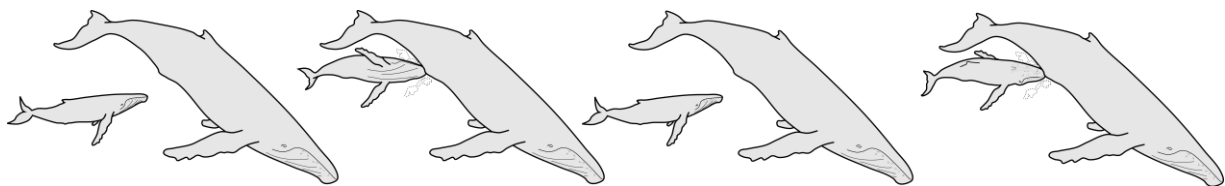


<https://doi.org/10.7717/peerj.12945>

Code S2. MATLAB scripts for tuning and training supervised machine learning algorithms for automatic identification of suckling behavior

Chapter 2. Humpback whale suckling behavior: an insight into the mother-offspring strategy in mysticetes

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Synthesis

How, where, and when is the nursing performed? Further results from a larger sample

Does the nursing pattern change as the calf grows?

Methods

Thirty-seven deployments on calves were used, including 11 CATS cam tag deployments with usable video, one CATS cam tag deployment without usable video, and 25 Acousonde tag deployments. Suckling events in data with video were identified visually. When no usable video was available, the method developed in Chapter 1 was used to automatically identify suckling events using the 11 deployments with video as a training set. When combined with a post-processing step, the detection method achieves a performance of around 80% in sensitivity and 75% in precision. Time spent suckling, laterality, spatial and behavioral context, and suckling rhythm were quantified. Their variation with age was then analyzed, notably using LMMs.

Findings

Suckling events are short (<30 s on average), converging to the results presented in Chapter 1. They represent less than 2% of the calf's time in total. Duration does not change with age. However, the total time spent suckling increases potentially as the calf grows. The calf shows no preference between left and right teats. Similar to what has been found in Chapter 1, it alternates between the two.

As pointed out in Chapter 1, the calf suckles mainly at depth, during the descent or bottom phases of dives. On average, suckling takes place at around 15 ± 4 m for C1, 17 ± 6 m for C2, and 18 ± 8 m for C3 calves. Suckling occurs in sessions that contain bouts of up to six successive events. Sessions occur approximately every two hours, including at night.



Humpback whale suckling behavior: an insight into the mother-offspring strategy in mysticetes

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Abstract

Despite its biological importance, the nursing behavior in baleen whales has been poorly documented mainly because of the challenges in tracking whales in their natural environment. We studied the suckling behavior (nursing from the calf's perspective) in < 3-month-old humpback whale calves off Sainte Marie Island, Madagascar, South Western Indian Ocean (breeding/calving area). We investigated the temporal pattern of the suckling behavior, its spatial and behavioral context, and the ontogeny of these characteristics. We exploited data from both camera-equipped and non-camera-equipped animal-borne multi-sensor tags (Acousonde and CATS cam) collected from 2013 to 2022 (37 calves). Our dataset constitutes the largest sample assembled so far to investigate the suckling behavior in free-ranging whales. We found that the suckling event duration does not vary much with the calves' relative age. The estimated proportion of time spent suckling ranged between 0.8 and 1.6%. The suckling events mainly occurred during the descent and bottom phases of dives and rarely during the ascent phase of dives or surface activities. Strong evidence of humpback whale suckling at night is presented for the first time. We found that suckling events were often performed in bouts of 2–6 events. Suckling bouts mostly occurred less than 10 min apart, and suckling sessions were separated by about 2 h of non-suckling periods. In other words, humpback whale calves suckled several times throughout the day in short sessions similar to terrestrial “followers.” Our results add to the evidence that humpback whales, and potentially most baleen whales, are behaviorally and functionally similar to terrestrial “followers” regarding maternal strategy.

Significance statement

Young mammals rely on the milk provided by their mother to survive during their early life stage. The suckling behavior, i.e., the procurement of milk from the mother, has been widely studied for terrestrial mammals but not for fully aquatic mammals like the baleen whales due to the challenges in tracking them. By placing sensors and cameras on calves, we described the suckling pattern in humpback whales, the most common baleen whale species. We found that the temporal pattern of suckling in humpback whales is similar to those of terrestrial precocial mammals experiencing comparable environments (open habitat with predators): the young suckle frequently but in short sessions. Our results offer a new insight supporting the hypothesis that the rearing strategy used by baleen whales is an aquatic version of the “following” behavior found in these precocial terrestrial species.

Keywords Anti-predation strategy · Cetaceans · Marine habitat · Maternal care · Mother-young interactions

Introduction

Young mammals must obtain care from their mother early in life to survive (Clutton-Brock 1991). The food provided by the mother in the form of maternal milk represents one of the most critical and energetically expensive aspects of this care in mammals (Fisher et al. 2002; Balshine 2012). “Nursing” and “suckling” behaviors (associated with the transfer

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of milk to the offspring, from the mother's perspective and the offspring's perspective, respectively) vary among species (Lent 1974; Rosenblatt et al. 1985; Oftedal et al. 1987; Fisher et al. 2002) and are ultimately influenced by their specific adaptation to the environment and by their life history (e.g., the growth speed and the precociality). For example, among ungulate species, habitat structure and predation pressure are the main drivers of the emergence of two main rearing strategies: the “hiding” strategy for species living in close habitats and the “following” strategy for species in open habitats (Lent 1974; Fisher et al. 2002). The “hiding” strategy corresponds to a scheme where the young remains hidden from the predators in the vegetation while the mother spends most of her time away foraging. During those unsupervised intervals, the young is more vulnerable to predation as the mother cannot guard it. In the hiding strategy, the mother-offspring contact is limited to infrequent but prolonged visits for nursing (Lent 1974; Rosenblatt et al. 1985; Gloneková et al. 2017). The mother must return to where she left her offspring, where it is supposed to be waiting for her. In contrast, the “following” strategy corresponds to a scheme where the mother and the young maintain constant contact. The young follow the mother wherever she goes and is thus nursed frequently and protected by its mother (Lent 1974; Rosenblatt et al. 1985; Fisher et al. 2002; Gloneková et al. 2017). The “following” strategy allows the mother to go where she wants or needs to go, according to her habits or those of her group (and not those of her offspring).

Baleen whales are similar to most ungulates in the fact they give birth to a unique, highly precocial (locomotory, sensorially, and thermoregulatory independent) offspring (Chivers 2009; Gingerich et al. 2009; Skok 2022). Unlike their closest water-loving terrestrial living relatives, the hippopotamuses, whose maternal strategy can be described as neither “following” nor “hider” (Verheyen 1957; Fisher et al. 2002; Pluháček and Bartošová 2011), baleen whales seem to use a maternal strategy consistent with the “following” strategy found in some ungulate species (Taber and Thomas 1982; Thomas and Taber 1984; Szabo and Duffus 2008). It has been proposed that this is due to similarities in the habitat structure (openness of the habitat), the resources distribution (temporally and spatially scattered resources), and the occurrence of predation pressures (e.g., by killer whales, *Orcinus orcas*, Pitman et al. 2015), especially on calves. The studies on mother-calf associations in baleen whales mainly focused on the mother-calf spatial relationship and behavioral synchrony. Whether the nursing behavior in baleen whales falls within the general characteristics of suckling in follower species has yet to be formally investigated.

The challenges in tracking cetaceans (baleen and toothed whales, including dolphins and porpoises) in their natural environment have limited the study of nursing behavior. Boat and aircraft-based observations only allow a partial

description of their behaviors at the sea surface or at most at subsurface (when the water is clear). Even observations by breath-holding or scuba divers are limited since divers cannot keep pace with traveling or diving whales. Furthermore, to the best of our knowledge, there have not yet been any studies based on data collected by autonomous underwater vehicles (AUVs). As a result, most studies have focused only on the nursing behavior of captive species (toothed whales, e.g., Triossi et al. 1998; Clark and Odell 1999a, 1999b). Although valuable for understanding the behavioral adaptations to aquatic life, data from such studies may not represent the natural behavior of cetaceans as the environmental constraints are very different in the wild. Unlike captive animals, free-ranging cetaceans naturally engage in a lot of horizontal (traveling) and vertical (diving) movements in search of food or to move to a more favorable location (predator or boat avoidance, finding a place to rest, etc.).

Several studies have attempted to address the nursing behavior in free-ranging baleen whales from surface and subsurface observations of their behaviors (Glockner and Venus 1983; Thomas and Taber 1984; Glockner-Ferrari and Ferrari 1985; Würsig et al. 1985; Clapham and Mayo 1987; Morete et al. 2003; Hain et al. 2013; Videsen et al. 2017). These studies are significant because they provided the first insights into the nursing modalities, but more in-depth underwater observations could supplement them, especially for a more comprehensive interpretation. Indeed, the surface and subsurface observations are incomplete because behaviors at depth cannot be seen from the surface. Moreover, there needs to be more standardization of how nursing is observed, recorded, and reported, because the mother-calf pairs may display configurations easily mistaken for nursing when observed from above (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022). Finally, the data resolution and the duration of observations are sometimes insufficient for capturing the temporal pattern of suckling. Recent works by Ratsimbazafindranahaka et al. (2022) and Tackaberry et al. (2020) based on camera-equipped animal-borne multi-sensor tags allowed an accurate description of the nursing behavior of humpback whales but were still limited by the sample size since such data acquisition is challenging.

Humpback whales are a good starting point for studying the suckling behaviors in baleen whales. Compared to other baleen whales, they are abundant and present in all oceans, easy to spot as mostly close to the coastlines, and one of the most studied in the world (Clapham 2018), thus facilitating data acquisition and contextualization of the observations. Humpback whales are migratory baleen whales that move between a feeding area close to the poles in summer and a breeding/calving area close to the equator in winter (Braithwaite et al. 2015; Clapham 2018). Prolonged fasting for all individuals except the calves characterizes their stay in the breeding/calving area. The calves feed on maternal

milk during their first six months of life, including during their first migration to the feeding area. After that period, the calves start to feed on prey but also continue to suckle from the mother until weaning at 10 to 12 months old (Clapham 2018). In the present study, we describe the suckling behavior in < 3 months old humpback whale (*Megaptera novaeangliae*) calves. Data were collected using camera-equipped and non-camera-equipped animal-borne multi-sensor tags. We describe the temporal pattern of the suckling behavior, its spatial and behavioral context, and the ontogeny of these characteristics.

Materials and methods

Field site

We conducted our field works off Sainte Marie Island, Madagascar, South Western Indian Ocean (between latitudes 17° 19' and 16° 42' south, and longitudes 49° 48' and 50° 01' east) during the southern winter (July–September) of 2013–2019 and 2021–2022. The area around Sainte Marie Island is an important breeding and calving zone of the South Western Indian Ocean humpback whale population (Trudelle et al. 2018). The calm and shallow waters of the area attract several calving females yearly. A part of the data used in the present study (data in 2018–2019) have been published in a previous study by Ratsimbazafindranahaka et al. (2022).

Tag specifications

We used two models of multi-sensor tags for our study: Acousonde 3B (until 2018) and CATS cam (2018 and afterward). Both models are small and lightweight (not more than 500 g) and are attached to animals via four suction cups (the tags stick for about 4 h on the animals on average but can stick for more than 20 h). They share five main common sensors (3-axis accelerometer, 3-axis magnetometer, pressure/depth sensor, temperature sensor, and light sensor), and both have an integrated hydrophone. In addition, the CATS cam has an HD video camera covering up to 100° field of view. A VHF transmitter attached to the tags allows tracking for tag retrieval.

We used two units of Acousonde and two units of CATS cam. For the Acousonde units, the sampling frequency was set at 10 Hz or 20 Hz for the auxiliary sensors. Their accelerometer sampling rate was set either at 10 Hz (when the auxiliary sensors were set to 10 Hz) or at 400 Hz (when the auxiliary sensors were set to 20 Hz). For the CATS cam units, the sampling frequency of the auxiliary sensors was set to 10 Hz. The accelerometer sampling rate was set at 400 Hz in 2018 and 800 Hz in 2019 and afterward. For the Acousonde units, the hydrophone recorded sounds at a 24.453 kHz sampling rate (16-bit resolution). The CATS cam units'

hydrophone recorded sounds at a 48 kHz sampling rate in 2018 and a 24 kHz sampling rate in 2019 and afterward (also 16-bit resolution). The CATS cam units' camera recorded videos with a 1280 × 720-pixel resolution at 30 frames per second in 2018 and a 1920 × 1072-pixel resolution at 30 frames per second in 2019 and afterward.

Tagging procedures

We deployed the tag(s) on calves (single deployments), or both mother and calf (simultaneous deployments), depending on the opportunity, while humpback whale mother-calf pairs were resting at the surface or moving slowly. The deployments were completed from a 6.40 m rigid motorboat using a 5-m rigid, handheld carbon fiber pole. The approaches are detailed in Huetz et al. (2022) and Saloma et al. (2022). Tags were placed on the back (CATS cam), in the dorsal fin area, or slightly on the flank of the animals (Acousonde).

We estimated each calf's relative age using coloration, skinfolds, and the angle of unfurling of its dorsal fin (Cartwright and Sullivan 2009; Faria et al. 2013; Huetz et al. 2022; Saloma et al. 2022): C1 (neonate)—calf presenting some folds, scars (assumed to be caused at birth by the barnacles located on the genital slit of the mother), and skin color that tends to be light grey dorsally and white ventrally and with less than ~45° dorsal fin furl; C2—very young but non-neonate calves having more than ~45° but less than about 70° dorsal fin furl; and C3—older calves (but < 3 months old) that have unfurled dorsal fin (approximately > 70°).

Tagged animals were not followed after the tagging to prevent exacerbating any disturbance of their behavior. After tag deployment or an aborted attempt, we slowly moved away in the opposite direction of the mother-calf pair. We retrieved the tags a few hours or a day after the tagging after they detached from the animals (usually due to the tagged animal rubbing against another individual, surface active behavior, etc.). It was not possible to record data blind because our study involved focal animals in the field.

Sensor data processing

Data from all sensors were downloaded as MT files for the Acousonde units and as CSV files for the CATS cam units, imported into MATLAB (Mathworks), and calibrated using dedicated scripts (CATS Matlab toolkit, <https://github.com/wgough/CATS-Methods-Materials>, Cade et al. 2021). We performed a preliminary inspection for each deployment to check if all sensors recorded data correctly and if the tag recorded at least one dive (essential for data calibration). Deployments not meeting these criteria were considered unsuccessful and irrelevant to the present study, and were thus discarded. For successful deployments, all data

were downsampled to obtain a common sampling rate of 10 Hz across all sensors, and depth data (in meters) were smoothed with a 0.5 s running median filter. The output sampling frequency was set to 10 Hz in all computations described hereafter. Sensor readings were rotated to match the animal's orientation frame using established methods (Johnson and Tyack 2003; Cade et al. 2021) and then used to document the whale's orientation (pitch, roll, and heading, in degree) (Johnson and Tyack 2003; Cade et al. 2021). We low-pass filtered the pitch and roll data to obtain body posture without fluke stroke signal (0.2 Hz low-pass filter, Simon et al. 2012). As a proxy for the whale's forward speed for all deployments, we used the flow noise extracted from the sound recorded by the tags' hydrophone (66–94 Hz frequency band, Cade et al. 2017). Indeed, flow noise is known to be related to speed (Finger et al. 1979; Izadi et al. 2018). We applied a z-score scaling for each whale to obtain a speed relative to the mean (relative speed hereafter). We did not use the "tag jiggle" recorded in the original high-frequency accelerometer data, as Cade et al. (2017) proposed, because high-frequency data were unavailable for some of our deployments (the accelerometer sampled at only 10 Hz in some deployments). We also did not attempt to calculate the absolute speed from the flow noise (Cade et al. 2017) because the available data in the deployments were not always sufficient for a good absolute speed estimation (insufficient data points for a robust regression of the orientation corrected depth rate against flow noise). Additionally, we calculated the overall dynamic body acceleration (ODBA, in G-force) as per Wilson et al. (2006), the roll rate (in degree /second), and the depth rate (in meter/second) using scripts from the Animal Tag toolbox (<http://www.animaltags.org>). ODBA values for each whale were divided by the whale's median ODBA to normalize the deployment effects on ODBA (Isojunno et al. 2016), such as those due to variable tag position and tag model. We will refer to these values as the nODBA (normalized ODBA).

Depth data were used to determine various diving phases and to identify surface activity. We defined "diving" as any submergence to a depth of > 10 m (Stimpert et al. 2012; Huetz et al. 2022; Ratsimbazafindranahaka et al. 2022). Dives were divided into three phases: "descent," "bottom," and "ascent." The bottom phase was defined as the segment at > 85% of the maximal dive depth for a dive (Stimpert et al. 2012). The descent phase was defined as the segment starting at the surface immediately preceding the bottom phase. Inversely, the ascent phase was defined as the segment directly following the bottom phase and ending at the surface.

CATS cam data labelling

Suckling events in the CATS cam data from calves were identified in the recorded video footages following

Ratsimbazafindranahaka et al. (2022) and Tackaberry et al. (2020). A suckling "event" was defined as a period during which the tip of the calf's snout continuously touched (> 2 s) one mammary teat of the mother, and a milk cloud, even in low density, was observed in the water during the event or upon release of contact. For each suckling event (referred to as visually confirmed suckling events), we computed its corresponding activity phase (descent, bottom, ascent, or surface), along with the average depth, depth rate, relative speed, nODBA, pitch, roll, and roll rate (summarized in Fig. S2, supporting information).

Machine learning model for automatically detecting suckling "blocks"

Model training

Ratsimbazafindranahaka et al. (2022) have shown that the suckling behavior in humpback whales has very distinctive kinematic signatures. When data are divided into non-overlapping 2 s "blocks," blocks corresponding to suckling events can be automatically detected with high precision and low false positive rate (FPR) based on the depth-derived and accelerometer-derived data alone using supervised machine learning (AdaBoostM1 model). We thus considered such an approach as a basis to detect suckling events in our calf data lacking of exploitable videos (i.e., CATS cam data corresponding to camera not working, not directed forward, nighttime—and Acousonde data, all referred to as data "without video" hereafter) using calf data with exploitable videos (i.e., CATS cam data corresponding to camera directed forward and with enough visibility, referred to as data "with video" hereafter).

For the model training, the data processing chain was as follows: first, the learning set was defined as the labelled calves' CATS cam data with video subdivided into non-overlapping blocks of 2-s duration (labeled as suckling vs. non-suckling); second, a set of features (see below) was computed for each block; third, a machine learning model (AdaBoostM1) was trained on the learning set using a 15-run Bayesian Optimization approach with 5-fold cross-validation (see details regarding the machine learning workflow in the study by Ratsimbazafindranahaka et al. 2022). The initial set of features chosen for the machine learning process were the summary statistics of various kinematic data (the mean, minimum, maximum, kurtosis, skewness, variance of depth, depth rate, relative speed, nODBA, pitch, roll, and roll rate). However, after analyzing the inter-individual differences in the features using a random forest (RF) analysis following Ratsimbazafindranahaka et al. (2022), we chose to exclude the maximum, mean, and minimum values for both depth

and relative speed. These six features were identified as contributing the most to the inter-individual difference in suckling (Fig. S1, supporting information). Excluding them can help improve the general ability of the machine learning model to detect suckling blocks. The number of runs we used for the optimization of the machine learning model was chosen to optimize processing speed while still having relatively stable results.

As per the “data segmentation” described by Ratsimbazafindranahaka et al. (2022), blocks that were *a priori* considered as unlikely to correspond to suckling events were directly excluded from all of our machine learning process (from learning to validation and application described below). These blocks were those too close to the surface (depth < 1.5 m, as periods corresponding to suckling events were never seen at less than 1.5 m depth), or of high-speed activities (relative speed < 1.5, as suckling behavior was never seen being performed at high speed, Fig. S2). Such blocks were therefore attributed by default to non-suckling.

Validation of the suckling block detection

To estimate the ability of our machine learning procedure to correctly detect suckling blocks, we used a leave-one-out design (LOO). The procedure described above was replicated but using the data with videos from $N - 1$ calves as learning set. The machine learning model trained with this learning set was then tested on the remaining calf (test deployment). In other words, the trained model was used to detect the suckling blocks in the test deployment. Three main evaluation metrics were calculated by comparing the predicted labels with the true labels: the sensitivity, the precision, and the FPR. The analysis was repeated N times, leaving out a different calf each time (i.e., using a different test deployment each time, $N = 11$ calves). The LOO is a good approach to determine the performance of the machine learning procedure as it simulates the present situation where a set of labelled data is used to label new, unlabeled data usually coming from a new individual. Our method is expected to reach similar performance regardless of the tag’s model (Acousonde or CATS cam) since both tag models contain similar sensors.

Suckling events detection in data without videos

Extension of the suckling block detection to event detection

The detection of suckling events when no visual cues were available (i.e., for data without video) was performed in two steps. In step 1, the trained machine learning model was applied on the data without video to detect suckling blocks. Similar to the learning set, the data without video

were subdivided into non-overlapping 2 s blocks and segmented beforehand. In step 2, the block detection results were combined with the known characteristics of suckling events in order to go from suckling blocks to suckling events. Each suckling event has been shown by Ratsimbazafindranahaka et al. (2022) to correspond to a positive or negative deviation of the roll from zero as the calf rolls to the right or left to reach one mammary teat. The transition from detected suckling blocks to suckling events was thus performed automatically in the step 2 by locating the roll deviation corresponding to each block or each block group and then by applying some exclusion rules to retain the most probable suckling events. We considered that a deviation period starts when the absolute roll exceeds 20° and ends when it reaches back 20° . This threshold was determined based on the typical characteristics of the suckling events confirmed by video (see Fig. S2). For a deviation period to be considered as a suckling event, (1) the number of blocks falling in it must exceed one (a criterion that was based on the probability of detecting a suckling block, see “Results”), (2) it must not contain parts corresponding to blocks too close to the surface (depth < 1.5 m) or with high speed (relative speed > 1.5, i.e., same thresholds as in the segmentation process), (3) its duration must be less than 100 s (about twice the maximum duration of the visually confirmed suckling events, see “Results”).

Validation of the suckling events detection

To validate the ability of our method for detecting suckling events, as a first evaluation, we extended the LOO presented previously to the event detection level described above. The suckling events in each test deployment were identified based on the detected blocks (i.e., the blocks detected by the model that learned from the data with good videos of $N - 1$ calves). The sensitivity and the precision of the event detection for each test were then calculated by confronting the predicted suckling events with the true suckling events. Additionally, the false event rate (FER, count h^{-1}) was calculated for each test deployment by dividing the number of false suckling events (false positives) with the data duration (in hours). Finally, we compared the start and end times of the correct predicted suckling events to the corresponding actual start and end times to obtain the start time errors and the end time errors. We then tested the statistical significance of the difference between the start and the end time errors using a Wilcoxon signed rank test. Furthermore, we checked if the start and the end time errors were related to the duration of the predicted events using linear models (LM). The duration of the predicted events was log-transformed in the models

because initial data inspection suggested a logarithmic relation.

As a second evaluation, we checked if the characteristics of the suckling events detected in the data without videos were similar to those of the visually confirmed suckling events. We compared the duration, the average depth, relative speed, normalized ODBA, pitch, roll, and roll rate using linear mixed-effects models (LMMs). The LMMs were estimated in R software (R core team, <https://www.r-project.org/>) using REML (Restricted Maximum Likelihood, *lme4* package, Bates et al. 2015). We included event type as a fixed effect (automatically detected vs. visually confirmed events) and individuals as random effects. In addition to the performance evaluations above, we checked the detection results on simultaneous deployments (mother and calf tagged simultaneously). We calculated the vertical distance between the mother and the calf (strictly speaking, the vertical distance between the tags) and checked if it complied with plausible nursing configuration during the detected suckling events (Fig. S3). We expected the vertical distances during nursing to range between (1) the minimum distance case where the mother is almost vertical, and the calf is almost horizontal in the water column (calf's tag level about 1–2 m above the mother's tag level), and (2) the maximum distance case where the mother is almost horizontal, and the calf is almost vertical (calf's tag level about 5–6 m below the mother's tag level). The average is expected to correspond to the calf's tag level being 2–3 m below the mother's tag level. These expectations are based on the known nursing configuration reported in the literature (Glockner-Ferrari and Ferrari 1985; Zoidis and Lomac-MacNair 2017; Ratsimbazafindranahaka et al. 2022), the tag placements, and the reported average dimensions and body proportions of mothers and calves found in the area (Ratsimbazafindranahaka et al. 2021).

Data analysis

To compare the suckling events' duration between age classes, we used a LMM that included the calf's age class as a fixed effect and individuals as a random effect. To compare time spent suckling per age class, we separately calculated the percentage of time spent suckling for each age class. Only deployments with more than two successive hours of data were included in the calculation of the percentage of time spent suckling. This two-hour cut-off was chosen to ensure that long non-suckling periods between suckling sessions, which can last about two hours (see "Results"), are also approximately captured and thus reducing overestimation of the percentage of time spent suckling.

The roll deviation during a suckling event is known to be associated with the suckled teat (Ratsimbazafindranahaka

et al. 2022). When the calf suckles on the right teat, it rolls to the right, and a positive average roll is recorded. Inversely, when the calf suckles on the left teat, it rolls to the left, and a negative average roll is recorded. To check whether the calves show a side preference when suckling, we counted the events with a positive average roll and those with a negative roll. Where applicable, the suckling side was also visually checked on the video. We compared the occurrence of suckling on the right and the left using a chi-squared test. We also counted the number of times the calf changed sides between two successive suckling events. In addition, we compared the duration of the suckling events on the right and the left using a LMM that included the side as a fixed effect and individuals as a random effect.

Regarding the activity context, the number of suckling events corresponding to each activity phase per age class was counted. These data provide an overview of the distribution of suckling events among the different activity phases. To compare suckling depth between the different age classes, we used a LMM that included the calf's age class as a fixed effect and individuals as a random effect.

To get an insight into the suckling rhythm, we examined the frequency distribution of the inter-suckling intervals using 1-min and 10-min bins. Additionally, we checked whether the suckling events are isolated or in bouts following Ratsimbazafindranahaka et al. (2022). To investigate whether suckling happened during the night, we calculated the total number of suckling events between sunset and sunrise. Between July and September, the sunset and sunrise in Sainte Marie, Madagascar, are around 1730 and 0530 local time, respectively. We thus used 1800 and 0500 local time as conservative values for defining the beginning and end of the night.

When applicable, standard deviations (SDs) are presented along with the mean in the format mean \pm SD. Statistical model assumptions were checked graphically (homoscedasticity, independence, and normality of the residuals). The LMMs were followed by Tukey's post hoc multiple comparisons tests using the R package *emmeans* (Lenth et al. 2018) when more than two groups were compared and a statistical difference was detected. The statistical significance level was set to $\alpha = 0.05$. The important terms and parameters used throughout this study are summarized in Table 1.

Results

Over the nine fieldwork seasons, we obtained 18 successful single Acousonde calf deployments, 12 successful single CATS cam calf deployments, and seven successful simultaneous Acousonde deployments from 37 mother-calf pairs. One CATS cam deployment had the camera directed downward the whole time and

Table 1 Glossary of important terms and parameters used in this paper

Term/parameter	Definition
Ascent phase	Dive segment directly occurring after the bottom phase and ending at the end of a dive (Stimpert et al. 2012)
Automatically detected suckling event	Suckling event detected using an automatic detection method that was trained using labelled data with video
Block	One element among all non-overlapping 2-s blocks that constitute a deployment data stream
Bottom phase	Dive segment at > 85% of the maximal dive depth of a dive (Stimpert et al. 2012)
Data with video	Deployment data or data segments with exploitable videos (CATS cam data corresponding to the camera directed forward and with enough visibility)
Data without video	Deployment data or data segments lacking exploitable videos, such as Acousonde data or CATS cam tag data segment corresponding to the camera not working, not directed forward, or corresponding to the nighttime
Depth	Depth (in m, sampled at 10 Hz) obtained from the pressure sensor
Depth rate	Vertical velocity (in m s^{-1} , sampled at 10 Hz) obtained from the depth data. A positive value indicates a downward movement, and a negative value indicates an upward movement
Descent phase	Dive segment starting at the beginning of a dive and ending at the start of the bottom phase (Stimpert et al. 2012)
Dive	Submergence to a depth of > 10 m (Stimpert et al. 2012; Huetz et al. 2022; Ratsimbazafindranahaka et al. 2022)
Inter-bout interval	Time interval between successive suckling bouts
Inter-session interval	Time interval between successive suckling sessions
Inter-suckling interval	Time interval between successive suckling events
normalized ODBA	Overall Dynamic Body Acceleration (Wilson et al. 2006) divided by the median (Isojunno et al. 2016) (sampled at 10 Hz)
Nursing	Behavior of a lactating adult mammal associated to the transfer of milk to the young (Hall et al. 1988)
Nursing/suckling bout	One series of successive nursing/suckling events. For the humpback whale, it can be considered as a series of events occurring less than a minute apart (Ratsimbazafindranahaka et al. 2022).
Nursing/suckling event	One continuous 'on-teat' period
Nursing/suckling session	One series of successive nursing/suckling bouts. For some species, the nursing session may be continuous (i.e., composed of one long bout). In such case, bouts and sessions represent the same thing.
Pitch	Angle of rotation (in $^{\circ}$, sampled at 10 Hz) of the body around the transversal axis. A positive value indicates nose up, and a negative value indicates tail up.
Relative speed	Forward speed proxy (sampled at 10 Hz) obtained by quantifying the flow noise recorded by the tag's hydrophone.
Roll	Angle of rotation (in $^{\circ}$, sampled at 10 Hz) of the body around the longitudinal axis. A positive value indicates a rolling to the right, and a negative value indicates a rolling to the left.
Roll rate	Angular speed (in $^{\circ} \text{s}^{-1}$, sampled at 10 Hz) around the longitudinal axis
Suckling	Behavior of the young to obtain milk from the mammary gland (breast) through the nipple or teat (Hall et al. 1988)
Surface activity	Period between two successive dives
Visually confirmed suckling event	Suckling event identified visually using the video from the CATS cam tags. A visually confirmed suckling event corresponds to a period during which the tip of the calf's snout was seen continuously touching (> 2 s) one mammary teat of the mother, and a milk cloud was observed in the water during the event or upon release of contact (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022).

this was considered as a deployment without video. For the simultaneous deployments, one did not have overlapping data for the two individuals (i.e., the tag detached from the first individual before the second was tagged). Thus, the calf deployment was considered like a single deployment, and the deployment on the mother was discarded. Our dataset consisted of 112.21 h of Acousonde data, including 29.53 h of data from the mothers of six studied calves (simultaneous

deployments) and 46.8 h of CATS cam data, including 39.14 h of data with exploitable videos in total (Table S1). The data from three of the 12 calves CATS deployments included in the present study correspond to the data from three individuals published in the study by Ratsimbazafindranahaka et al. (2022).

From the 11 CATS deployments with videos, we labeled 79 visually confirmed suckling events. The average visually confirmed suckling events duration was 18.5 ± 8.3 s (range

= 4.8–51.2 s). The general characteristics of these events are shown in Fig. S2 along with the characteristics of 20 s non-suckling segments selected randomly for comparison ($N = 214$). Our suckling event detection method found 165 suckling events in the CATS dataset without video and Acousonde data. The average duration of the automatically detected suckling events was 31.4 ± 17 s (range = 8.9–91.7 s).

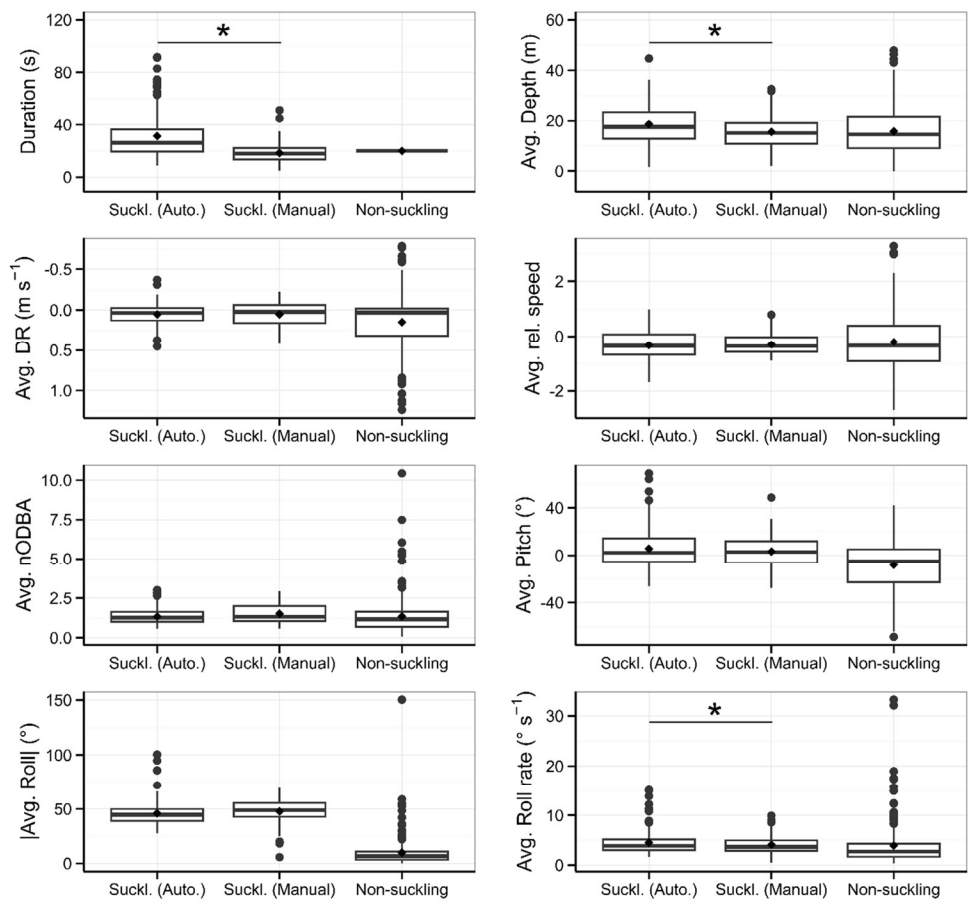
Ability of the machine learning method to detect suckling blocks

With the 11 CATS cam deployments, there were 11 splitting combinations for the LOO tests to assess the block detection performance. Two deployments did not have any suckling events. For these deployments, the only performance metric we calculated was the false positive rate (FPR). With the supervised machine learning, the mean sensitivity in detecting suckling blocks was 0.43 (range = 0.15–0.84, $N = 9$). On average, the precision was 0.79 (range = 0.63–0.93, $N = 9$). The average FPR was 0.34% (range = 0.06–0.88%, $N = 11$).

Validity of the suckling events detection

Using the detected suckling blocks to identify suckling events in the tests, the average precision was 0.82 (range = 0.5–1, $N = 9$), and the average sensitivity was 0.75 (range = 0.2–1, $N = 9$). The false event rate (FER) was 0.36 event per hour on average (range = 0–0.94 event per hour, $N = 11$), i.e., the equivalent of about one false suckling event per 3 hours of data on average. The automatically detected start times were on average located at 3.1 ± 4.3 s before the actual start (range = -20.1–15.6 s) and the automatically detected end times at 1.1 ± 2.6 s after the actual end (range = -4.5–13.6 s). The difference between these errors was statistically significant (Wilcoxon signed rank test, $V = 1547.5$, $P < 0.001$). There was a weak but statistically significant logarithmic relationship between the automatically detected durations and the start time errors (LM with log-transformed automatically detected duration, $R^2 = 0.09$, $P = 0.022$). Regarding the relationship between the automatically detected durations and the end time errors, no statistically significant trend was found (LM with log-transformed automatically detected duration, $R^2 = 0.01$, $P = 0.588$).

Fig. 1 Characteristics of the automatically detected and visually confirmed suckling events. Suckl. (Auto.): Automatically detected suckling events, Suckl. (Manual): visually confirmed suckling events, Avg.: average, DR: depth rate, rel.: relative, nODBA: normalized overall dynamic body acceleration. Suckling data are plotted alongside randomly selected non-suckling data (20 s segments) for reference ($N = 214$). The mean and median are indicated by diamond marks and bold horizontal lines, respectively. The first and the third quartiles correspond to the lower and upper hinges, respectively. The whiskers extend to the most extreme data points within $1.5 \times$ the interquartile range outside the box. Data beyond the end of the whiskers are plotted individually as points. (*) indicates a statistically significant difference between the automatically detected and visually confirmed suckling events ($P < 0.05$, linear mixed-effects model)



The mean duration of the automatically detected suckling events was higher than the mean duration of visually confirmed suckling events (Figs. 1 and S2). The difference, although moderate, was statistically significant (LMM, $\beta = -8.73$, $P = 0.002$). The mean average depth and mean average roll rate of the automatically detected suckling events were also higher compared to visually confirmed suckling events (Figs. 1 and S2). These differences were statistically significant but yet relatively small (LMM, average depth: $\beta = -3.6$, $P = 0.045$; average roll rate: $\beta = -0.87$, $P = 0.034$). The remaining characteristics were relatively close and not statistically different for both visually confirmed suckling events and automatically detected suckling events (LMMs, average depth rate: $\beta = 0.01$, $P = 0.685$; average relative speed: $\beta = 0.13$, $P = 0.303$; average normalized ODBA: $\beta = 0$, $P = 0.971$; average pitch: $\beta = -6.31$, $P = 0.061$; average absolute roll: $\beta = 2.02$, $P = 0.363$; Fig. 1).

Thirty-two suckling events were detected in five simultaneous Acousonde deployments (no suckling events in one simultaneous deployment). We found that the average depth difference between the calf and the mother was 2.5 ± 2.1 m. The minimum depth difference was -1.2 m and the maximum was 6.5 m (i.e., the calf's tag was at 1.2 above and 6.5 m below the mother's tag, respectively).

Time spent suckling and laterality

Due to the difference between the visually confirmed suckling events and the automatically detected suckling events regarding the duration, we separated the two in all analyses involving the suckling duration. Regarding the time spent suckling, we also separated the analyses for deployments in which all suckling events were identified automatically (thus Acousonde deployments and CATS cam deployment without video during the whole deployment) and for

deployments with visually confirmed suckling events (for which part without video were not considered).

The duration of the suckling events was similar for C1, C2, and C3 calves (Table 2). In our LMMs, for the visually confirmed suckling events, the effect of C3 class on the duration of suckling events was positive but statistically non-significant (C3: $\beta = 1.93$, $P = 0.542$, Reference: C2, no C1 data available). For the automatically detected suckling events, both the effect of C2 and C3 classes on the duration of suckling events were positive but statistically non-significant (C2: $\beta = 0.04$, $P = 0.995$, C3: $\beta = -1.39$, $P = 0.845$, Reference: C1). In addition, the difference in duration of suckling events for C2 and C3 calves was small and statistically non-significant (Tukey's post hoc test, C2 vs. C3, $\beta = 1.44$, $P = 0.954$).

Eight deployments included more than two hours of consecutive video data. In these data, the percentage of time spent suckling was higher in C3 calves than in C2 calves (Table 2). Additionally, 15 deployments in which suckling events were all automatically detected had data longer than 2 h (14 Acousonde deployments and one CATS cam deployment without video). The percentage of time spent suckling in these data was similar for the C2 and C3 calves, although it was slightly higher in C3 (Table 2). No sufficiently long deployment was available for C1 for calculating the proportion of time spent suckling.

We did not find any side bias in the context of suckling behavior. The calves suckled to the right teat almost as often as to the left teat ($\chi^2 = 0.803$, $df = 1$, $P = 0.37$, Table S2). The calves tended to alternate between the right and left teats between successive suckling events. A change in the suckling side was observed in 68% of successive suckling events. In addition, the duration of suckling to the right (mean = 29.3 ± 16.2 s, range = 8.9 – 91.7 s, $N = 86$) and to the left (mean = 33.7 ± 17.7 s, range = 12.6 – 74.6 s, $N = 79$) did not

Table 2 Duration of suckling events and proportion of time spent suckling according to the relative age in young humpback whale calves (< 3 months old). The analyzes were separated in such a way so that the duration-related parameters were comparable

Calf's relative age	C1	C2	C3
Suckling event durations (s): visually confirmed, mean \pm SD (range, N)	No data	17.5 \pm 8.6 (5.9–51.2; N = 31)	19.1 \pm 8.1 (4.8–44.9; N = 48)
Suckling event durations (s): automatically detected, mean \pm SD (range, N)	29.7 \pm 10.7 (12.5–45.8; N = 10)	30.3 \pm 11 (14.3–65.2, N = 39)	31.9 \pm 19.1 (8.9–91.7, N = 116)
% of time spent suckling	No data	0.85 ^a 1.5 ^c	1.34 ^b 1.58 ^d

^aProportion calculated using five deployments with video in which all suckling events were visually confirmed (considering part with > 2 h consecutive video only).

^bProportion calculated using three deployments with video in which all suckling events were visually confirmed (considering part with > 2 h consecutive video only)

^cProportion calculated using four deployments without video in which all suckling events were automatically detected (> 2-h duration each)

^dProportion calculated using 11 deployments without video in which all suckling events were automatically detected (> 2-h duration each)

show statistically significant differences (LMMs, right vs. left: $\beta = -3.79$, $P = 0.121$). When we considered the suckling events as clustered in bouts (see “[Suckling rhythm and occurrence at night](#)”) and looked at the first suckling side (the suckling side of the sole event in the case of isolated suckling event), we also did not find any striking side bias except for one individual (Table S3).

Activity and spatial context of suckling

The suckling events mainly occurred during descent and bottom phases of dives for all age classes. Suckling events at the surface and during ascent phases were not common (Table 3). Suckling events occurred at a mean average depth of 14.5 ± 3.7 m (10.2–19.6 m, $N = 10$) in C1 calves, at 16.7 ± 5.5 m (5–34.1 m, $N = 70$) in C2 calves, and at 18.2 ± 8.1 m (1.6–44.7 m, $N = 164$) in C3 calves. The effect of age class on the average suckling depth was positive but weak

Table 3 Number of suckling events found in each activity phase for C1, C2, and C3 humpback whale calves (< 3 months old). The data included both visually confirmed and automatically detected suckling events. The total number suckling events recorded per age class is shown alongside each count

Age classes	Phases			
	Surface	Descent	Bottom	Ascent
C1	0/10	3/10	6/10	1/10
C2	4/70	14/70	50/70	2/70
C3	17/164	27/164	111/164	9/164

and statistically non-significant (LMM, C2: $\beta = 3.04$, $P = 0.521$; C3: $\beta = 4.56$, $P = 0.310$; Reference: C1). In addition, the difference in average suckling depth in C2 and C3 calves was small and statistically non-significant (Tukey’s post hoc test, C2 vs. C3, $\beta = -1.52$, $P = 0.819$).

Suckling rhythm and occurrence at night

Inter-suckling intervals appeared globally to be bimodal (Fig. 2). The major mode was between 0 and 10 min, and the minor mode was around 120 and 130 min. In other words, suckling events are highly grouped (often occurring less than 10 min apart), and groups of suckling events are separated by about 2 h. Such a pattern is particularly evident in long deployments (Fig. 3). On a smaller timescale, the suckling events appeared to be either isolated (102/244 events) or in series of 2–6 successive events occurring less than a minute apart (142/244 events grouped in 52 series). The data suggest thus an organization of the suckling events in bouts (series of events occurring less than a minute apart), which are in turn organized in sessions (series of bouts occurring mostly less than 10 min apart).

Only six deployments recorded data during the night and thus provided nighttime data. The deployments covered nighttime between 1800 and 0500 local time (about 15% of the whole calf dataset, Fig. 3). All deployments with long nighttime data (> 1 h) were on C3 calves. Twenty-nine suckling events at night were found in these data (12% of the whole suckling events found).

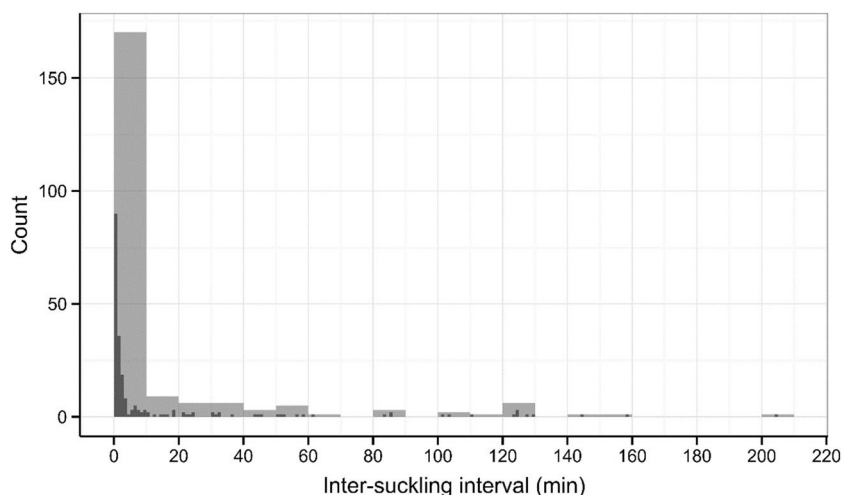


Fig. 2 Frequency distribution of the inter-suckling intervals observed in 29 young humpback whale calves (< 3 months old). The distribution is presented at two scales: at a more global timescale in light gray (bin width of 10 min), and at a smaller timescale in dark gray (bin width of 1 min). We can observe (1) a peak at 0–10 min, which

can be broken down into inter-suckling intervals of < 1 min corresponding to the intervals between successive suckling events of the same bouts, and (2) a peak at 120–130 min, corresponding to the typical inter-session interval

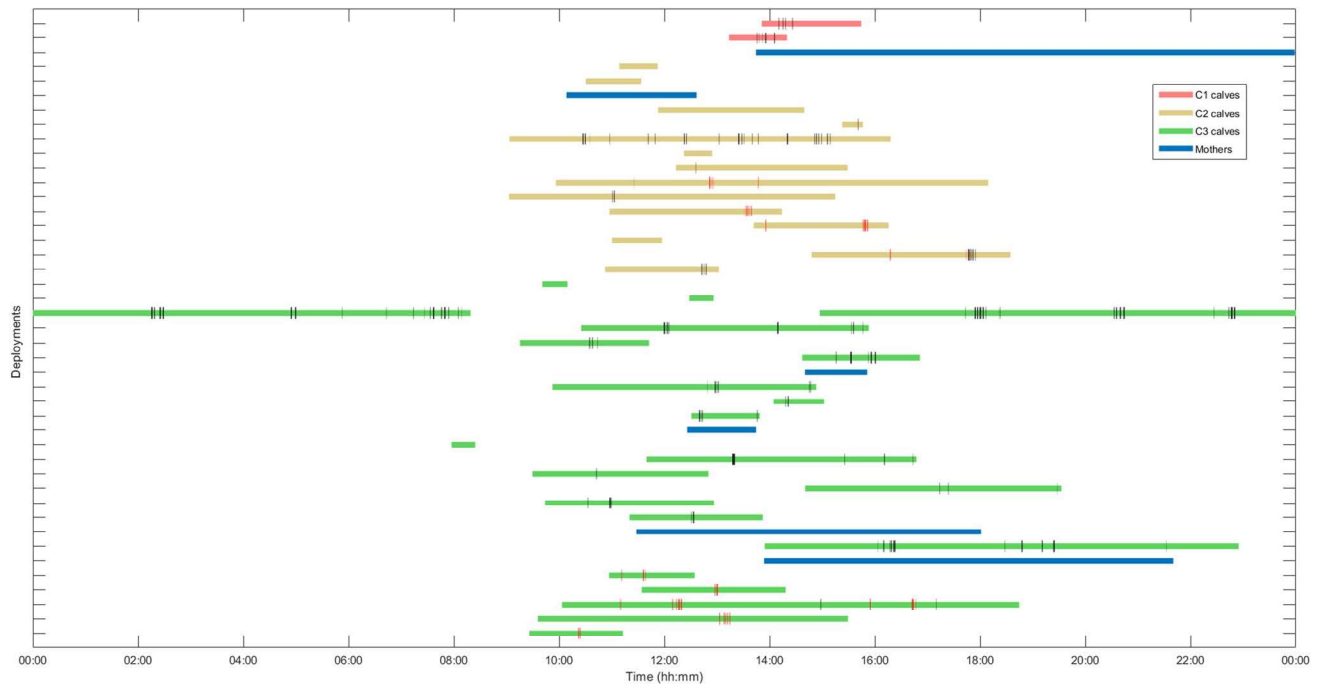


Fig. 3 Summary of the deployments used for studying the suckling behavior and the occurrence of suckling events in each calf deployment. Each deployment (each tick in the vertical axis) corresponds to one distinct individual. Each horizontal line represents the time period when the tag was on the target animal. When available, suc-

cessful deployments on mothers are shown below their respective calves. Suckling events are represented with red vertical dashes for visually confirmed suckling events (by video) and black vertical dashes for automatically identified suckling events

Discussion

Our study investigated the suckling/nursing behavior of humpback whales, by exploiting data from camera-equipped and non-camera-equipped animal-borne multi-sensor tags (Acousonde and CATS cam). We described the temporal pattern of the suckling behavior, its spatial and behavioral context, and the ontogeny of these characteristics. We based our study on combining kinematic data with visual cues (CATS cam data with video) and kinematic data lacking visual cues (Acousonde data, nighttime CATS cam data, and CATS cam data without exploitable video). We found that suckling events were short, stereotyped, and can be detected automatically. The proportion of time spent suckling was relatively low and we failed to find clear age-related change in time spent suckling. Furthermore, we did not find any evidence regarding the existence of suckling side preference. However, we found clear alternating pattern between suckling on the right teat and on the left teat (or vice-versa). Suckling events occurred mostly at depth, so during dives and rarely during surface activities. Our nighttime data strongly supports that suckling events occur also at night. The analyses regarding the inter-suckling intervals suggested that suckling events are highly clustered in time in

humpback whales, and the sessions are separated by around two hours of non-suckling periods.

In addition to the data from three calves published by Ratsimbazafindranahaka et al. (2022), our base dataset (CATS cam data) for detecting suckling events in the absence of video included data with visually confirmed labels from eight new calves. With the new data, the average duration of the visually confirmed suckling events matched the result of the study by Ratsimbazafindranahaka et al. (2022) (mean = 19 ± 9 s, $N = 32$) and was similar to the result of the study by Tackaberry et al. (2020) for older calves in the feeding grounds (> 6 months old calves, 23 ± 7 s, $N = 11$). The kinematic characteristics of the suckling events (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022) were also confirmed by the additional data. Specifically, the suckling events were primarily characterized by a sharp increase in average absolute roll, an increase in swimming effort, and sometimes a decrease in swimming speed. We found no behavior similar to suckling but without a visible milk cloud within our data with videos. Our data thus suggest that some milk was always available for the calf every time the calf suckled or, in other words, that most suckling events in young calves are nutritive. Such observation suggests a behavioral and biological adaptations that maximize

nutritive suckling. In terrestrial mammals, the young do not likely need to spend more energy related to locomotory effort to keep the suckling configuration. They thus can afford to use the suckling behavior as mother-calf relationship reinforcement and for comfort in addition to the nutritive function (Wolff 1968; Lent 1974; Hall and Williams 1983). For whales, since the calf generally needs to put effort into sustaining grips on the mammary gland (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022), suckling without any nutritive value may be disadvantageous due to energetic cost.

Our method for detecting suckling events in data lacking visual cues using visually labeled data had high robustness. Indeed, our tests showed that the method allowed the detection of most suckling events in a deployment (high sensitivity) with high confidence (high precision) and with a very low amount of false positives. Furthermore, the tests on simultaneous Acousonde data (simultaneous Acousonde deployment on the mother and the calf) showed that the automatically detected suckling events (i.e., in calves) followed the known nursing configuration (of the mother-calf pair) presented in the literature (Glockner-Ferrari and Ferrari 1985; Zoidis and Lomac-MacNair 2017; Ratsimbazafindranahaka et al. 2022). Indeed, the depth recorded by the calf's tag was at most 1.2 m higher or 6.5 m lower than the depth recorded by its mother's tag and on average the calf's tag was at 2.4 m below the mother's tag.

Our automatic detection method overestimated the duration of individual suckling events, which was expected. Indeed, when a video is available, we can exactly see when the calf starts touching the mother's teat. Whereas, in data lacking video, the detection of the start and end of a suckling event is only based on the roll deviation and thus the method cannot find the exact moment the calf touched the mother's teat. As a result, few seconds before and after the actual suckling event may be included in the event. Our analyses on the start and end time errors suggested that the added time in the detected suckling events is mostly pre-suckling. It may correspond to the calf still positioning itself to suckle and agree with the sequences we observed in the video data: the calf usually initiates its rolling behavior in advance when targeting the teat and thus already begin to display behavior similar to when it is already locked on the nipple up to several seconds before the actual suckling event. The high variability in the start and end time errors and their quasi-independence from the predicted duration suggests a source of error that is challenging to control. It limits the possibility of including an adjustment factor for the suckling duration. With that being said, the difference induced by the duration over-prediction is unlikely to affect the conclusions of the present study as it should still allow capturing any existing trend related to the suckling behavior. To facilitate interpretations, the analyses of the visually and automatically

identified/detected suckling events in the present study were separated to take into account these differences. To take into account that there is an over-prediction of the duration, it may be appropriate to regard the automatically detected suckling event as a continuous period encompassing both the on-teat and the pre-on-teat periods corresponding to the positioning phase during which the calf started to match its rolling side with the targeted teat. The other characteristics of the automatically detected suckling events were similar to the characteristics of the visually confirmed events. Thus, the method appears to detect suckling events effectively.

In this study, the proportion of time spent suckling, which can be associated to the suckling effort, was several times superior to the proportion reported in the feeding ground (0.3%, Tackaberry et al. 2020). The developmental stage of the calves can partly explain this difference. Calves on breeding grounds are very young calves (< 3 months old) still relying entirely on maternal milk. In comparison, calves on feeding grounds are older (> 6 months old) and already feeding on prey (Clapham 2018), thus potentially having decreased benefits and interest in getting maternal milk. The higher proportion of time spent suckling in the breeding ground compared to the feeding grounds may also be related to a reduction of the nursing opportunity given by the mother to the calf in the feeding grounds due to an increased mother-offspring conflict as the calf grows (Trivers 1974).

With respect to the relation between age and the time spent suckling, both data with and without video indicated an increasing trend of the time spent suckling (time spent suckling tend to be higher for C3 compared to C2 age classes). However, the trend observed in data without video was less obvious. As only C2 and C3 age classes were well represented, we could not tell if the time spent suckling in C1 calves, i.e., freshly born/very young calves, differed from the older classes. In several mammals, including ungulates, the suckling rate decreases slowly during the mid-stage period of dependence on the mother, and differences primarily exist during the very early stage (very high suckling rate), especially as the young attempt to get colostrum (the first form of milk produced by the mammary glands, containing nutrients and immunoglobulins crucial for building their initial immunity) as quickly and frequently as possible while it is still available, and towards the weaning time (Ofstedal et al. 1987; Triossi et al. 1998; Clark and Odell 1999a, 1999b; Skok 2022). An increasing trend may exist for species with offspring constrained to rapidly grow, as in phocids (Ofstedal et al. 1987), to optimize the growth speed as the young's nutritional needs increase. This may explain the increasing trend we observed in young humpback whales. In migrating baleen whales, it is believed that the rapid growth of the calf is crucial, especially in preparation for the long migration to the feeding ground (Lockyer 1984; Corkeron and Connor 1999; Braithwaite et al. 2015). Further studies regarding

the temporal dynamics of the milk content and, notably, the transition from colostrum to mature milk are encouraged to better understand the ontogeny of suckling in humpback whales. The available data in this regard are indeed still very limited (e.g., Oftedal 1993).

Although population-level lateralized behavior has been found in humpback whales (Clapham et al. 1995; Canning et al. 2011), it does not appear to be the case regarding suckling. The results regarding the suckling side preference did not support the previous research conducted on a smaller sample (Zoidis and Lomac-MacNair 2017). In monotocous mammals (i.e., mammals having only one offspring at a time), while there should not be a preference since the teats are equally available for the sole young, there may be a suckling preference associated with asymmetry in brain processing ability (Skok 2022). Several studies suggested the existence of lateral preferences in mother-infant pairs in cetaceans due to brain lateralization (Karenina and Giljov 2018). However, as Karenina and Giljov (2018) pointed, such preference may not manifest in the final positioning of suckling. Indeed, the confirmation of the identity of the mother for suckling by the calf, the only step that may require the use of the dominant hemisphere for social processing in the context of suckling (Karenina and Giljov 2018), is only needed before initiating the suckling. The absence of side preference, even in terms of duration, also likely excludes milk availability asymmetry between teats (Karenina and Giljov 2018). As in Ratsimbazafindranahaka et al. (2022), we found a typical pattern of alternation between successive suckling events from one side to the other. It has been suggested that it may be related to whales' milk production/storage/ejection system (Ratsimbazafindranahaka et al. 2022). Alternating the suckled teat would allow one breast to refill in preparation for the subsequent ejection. It is also important to note that studies on lateral preferences in mother-calf pairs in cetaceans were mostly conducted on toothed whales (Karenina and Giljov 2018). Toothed whales' head are anatomically asymmetrical, unlike baleen whales' head (Coombs et al. 2020). This anatomical difference between the two groups may induce differences in the level of behavioral laterality found in each of them.

The results regarding the activity and spatial context match those mentioned in earlier studies (Videsen et al. 2017; Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022). Suckling at depth may be associated with calf's buoyancy control and diving performance (Videsen et al. 2017; Ratsimbazafindranahaka et al. 2022). Videsen et al. (2017) also suggested that it may be a strategy for coping with the noise associated with the surface. More noises are near the surface due to the waves and wind, and the sound does not propagate well. The mother may prefer to be at depth to have better acoustic vigilance during potential vulnerability periods, such as while nursing.

Our results present the first strong evidence of baleen whale suckling at night. Nighttime suckling in humpback whales may even be almost as frequent as during the day (12% of the suckling events we found corresponded to the nighttime data representing 15% of the total data). In terrestrial precocial mammals, suckling is less frequent during the night (e.g., ewes, Gordon and Siegmann 1991; giraffes, Saito et al. 2020), but it probably relates to the general activity pattern (predominant inactivity periods during the night). Saito et al. (2020) advanced that because the mother is often in a recumbent posture as she rests, the access to the nipples is more difficult for the young during the night (Saito et al. 2020). This situation, however, does not apply to whales as they do not have any known resting posture that would limit access to the nipples. Moreover, humpback whales likely do not specifically use the nighttime for resting. Indeed, males are, for example, known to show more intense singing activity at night (Au et al. 2000; Kobayashi et al. 2021). In addition, a study on their feeding ground showed that they can be very active at night and that resting occurs throughout the day and night (Friedlaender et al. 2013). The occurrence of suckling during the night demonstrates baleen whales' remarkable ability to navigate and locate a specific target (here the teat) in very low light conditions. While baleen whales probably have vision adapted to low light levels, it has been suggested that their vision is not as efficient during the night (Goldbogen et al. 2011; Izadi et al. 2018). As in the prey detection context (Goldbogen et al. 2011; Izadi et al. 2018), suckling calves likely use a combination of different sensory modalities (chemoreception, touch, vision, and hearing) to locate and grasp mammary teats during the night successfully.

The cyclic suckling sessions throughout the day we found may be an inevitable mother-young strategy that mitigates the need for the mother to feed the calf for rapid growth intensely and to engage in other crucial activities in the breeding season and during migration (e.g., traveling). The mothers need to travel a lot (up to 100 km per day) to move to calm resting areas with their calves (Trudelle et al. 2016, 2018; Dulau et al. 2017) or to reach the feeding area (Szabo and Duffus 2008; Tyson et al. 2012; Clapham 2018). The observed temporal pattern of suckling would give the mother time to move with her calf to a zone with less disturbance and less predation risk while they stay in the breeding/calving area. Ultimately, these time windows would also give the mother-calf pair the time to travel to reach the feeding area during the peak season. Indeed, even if suckling may be performed while moving as suggested by our current data and by previous studies (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022), it still requires the pair to slow down to facilitate the calf's attachment to the nipple (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022). The 2-h intervals between suckling sessions may also correspond

to the optimal time needed for the calf to digest the milk before the subsequent sessions. Similar inter-session intervals have been reported in American bison, a terrestrial mammal that uses the “following” strategy (Green 1986). In contrast to what we found in humpback whales, however, the suckling sessions found in American bison were mainly composed of just one continuous suckling bout with suckling events spaced by less than 10 s pauses (i.e., suckling bout is basically synonym of suckling session). The difference may be related to whale calves holding their breath while suckling, which limits the time for long continuous suckling bout. Young humpback whale calves go up to the surface to breathe after about 2 min under water on average (Huetz et al. 2022). Sessions must thus be divided into a few bouts to allow the calf to breathe, similar to when young hippos are suckling under water (Pluháček and Bartošová 2011). Despite the particularity associated to the adaptation to aquatic life, the suckling pattern in humpback whales falls into the common characteristics of species using the following strategies where the young are nursed several times a day in short sessions, unlike in species that use the hiding strategies (Lent 1974; Rosenblatt et al. 1985; Fisher et al. 2002; Gloneková et al. 2017). In terrestrial followers, the following strategy has been described as a way to reduce predation on young in open habitats while allowing the mother not to interrupt various vital activities for a prolonged time to nurse (Lent 1974; Rosenblatt et al. 1985; Fisher et al. 2002; Gloneková et al. 2017). This hypothesis is consistent with the ecology of baleen whales. Indeed, whales live in habitats that can be qualified as open, which do not provide cover to the young against predators (killer whales, Pitman et al. 2015) and they exploit temporally and spatially scattered resources.

We were constrained regarding comparing our results with other studies on other species. Due to variability and sometimes ambiguity regarding how suckling duration and inter-suckling intervals are defined in the available literature, direct comparison between studies of suckling regarding the duration and temporal pattern is challenging (Lent 1974; Oftedal et al. 1987). Most of the time, the reported durations correspond to both on-teat periods (i.e., suckling events) and off-teat intervals between successive on-teat periods. An arbitrarily chosen off-teat time limit was usually set to group successive suckling events into bouts and/or sessions of suckling on which duration is calculated. The demarcation usually has no biological foundation (Blank and Yang 2015). Different values regarding the duration and inter-suckling intervals may be obtained depending on the chosen limit. A more appropriate approach to describe and compare the duration and temporal pattern of suckling would be to systematically report suckling event durations along with the frequency distribution of inter-suckling intervals. This approach would allow seeing whether the young grab the teat (suckle) for a prolonged period or not, whether the suckling events are

regularly dispersed (unimodal distribution) or clustered in time (multimodal distribution), and whether among species the clustering or periodicity is different or not. That being said, our results globally agree with the general suckling characteristics attributed to the following strategy found in ungulates experiencing predation in an open environment. Our study thus reinforces the status of the humpback whale, and potentially most baleen whales, as being both behaviorally and functionally similar to terrestrial “followers” in terms of mother-young strategy (Szabo and Duffus 2008; Tyson et al. 2012).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03369-9>.

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Author contributions MNR, CH, IC, OA, and AS conceived the ideas and designed methodology; MNR, CH, IC, OA, and AS collected the data; MNR led the writing of the manuscript. All authors interpreted the data, contributed critically to the drafts, and gave final approval for publication.

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Data availability The dataset generated and analyzed during the current study are available in the Supplemental Data S1.

Declarations

Ethics approval All methods and approaches were reviewed and approved by the Ministry of Fisheries Resources, Madagascar, under the Malagasy national research permits #44/13-MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #46/15-MRHP/SG/DGRHP, #28/16-MRHP/SG/DGRHP, #26/17-MRHP/SG/DGRHP and #28/18-MRHP/SG/DGRHP, #36/19-MAEP/SG/DGPA, #30/21-MAEP/SG/DGPA, and #54/22-MPEB/SG/DGPA and complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU). We took great care to minimize animal disturbances by respecting a strict protocol: slow speed approach, brief deployment time, and interruption of the tagging procedure when avoidance behaviors have been detected. In addition, tagging were only done by experienced operators. Tagged animals were not followed after the tagging to prevent exacerbating any disturbance of their behavior.

Conflict of interest The authors declare no competing interests.

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Supplementary information

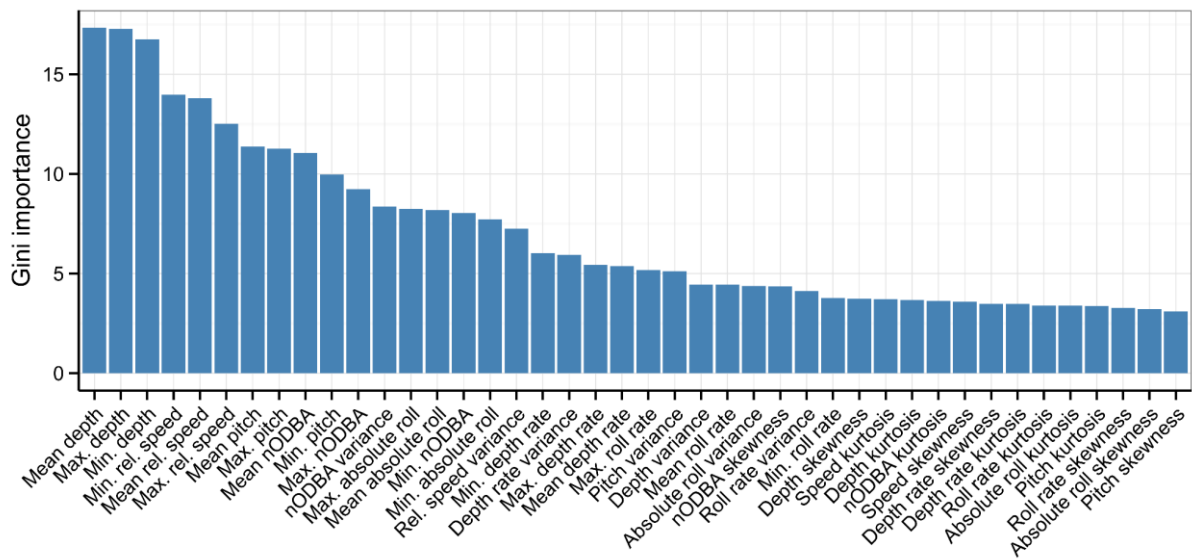


Figure S1. Gini importance of different features in classifying suckling blocks by individuals using a Random Forest algorithm. Max.: maximum. Min.: Minimum. rel.: relative. nODBA: normalized Overall Dynamic Body Acceleration. The out-of-the-bag error rate was 23.99%

We (1) performed a Random Forest (RF) classification of the suckling blocks by individuals to check the existence of inter-individual differences regarding the characteristics of the suckling blocks (features), (2) analyzed the features' contribution to the differentiation, and (3) identified a set of features to be excluded (those with the highest contribution in the individual differentiation) in order to reduce the difference because inter-individual variations may reduce the generalization ability of a machine learning model in an automatic detection framework. The RF analysis indicated that there was a slight inter-individual difference. Indeed, the classification error rate, indicated by the out-of-the-bag error rate, was low (out-of-the-bag error rate = 23.99%). The importance (Gini importance) of each feature in the classification is shown in Figure S1 above. For the exclusion of features, we set a simple cut-off that is a compromise between excluding a sufficient number of high Gini importance features to considerably reduce the inter-individual differences and keeping as many informative features as possible for identifying suckling blocks. We thus chose to exclude the first six features: the maximum, mean, and minimum values for both depth and relative speed. When these features were not included in a second RF analysis, the out-of-the-bag error rate when classifying individuals increased to 36.54%, showing that the inter-individual difference dropped significantly without these features.

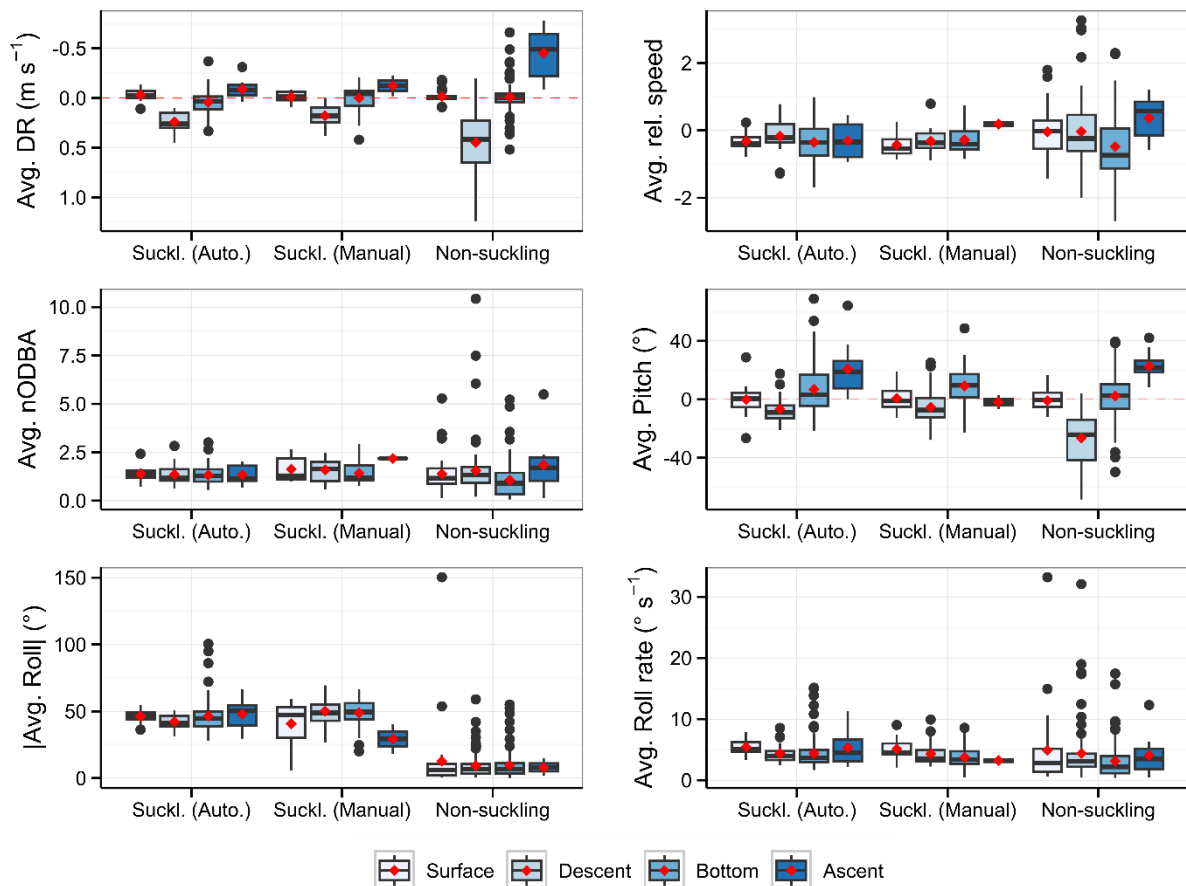


Figure S2. Characteristics of the automatically detected suckling events (31.4 s average duration) and visually confirmed suckling events (18.5 s average duration) found in Acousonde and CATS cam deployments on calves. The data are broken down by activity phase. Suckl. (Auto.): automatically detected suckling events, Suckl. (Manual): visually confirmed suckling events, Avg.: average, DR: depth rate, rel.: relative, nODBA: normalized Overall Dynamic Body Acceleration. Suckling data are plotted alongside randomly selected non-suckling data (20 s segments) for comparison (N = 214). The mean and median are indicated by red diamond marks and bold black horizontal lines, respectively

Compared to non-suckling segments, the visually confirmed suckling events had a mean average depth rate closer to zero. They also had a mean average pitch closer to the horizontal (0°) even during the descent and ascent phases. In some cases, the average pitch during suckling took an extremely positive value (i.e., calf directed upward at almost 50° relative to the horizontal). However, it never took an extremely negative value (all recorded negative average pitch were > -30°, i.e., calf only slightly directed downward at most when suckling). Compared to non-suckling segments, the mean average relative speed during suckling was slightly lower during the surfacing and descent phases and slightly higher during the bottom and ascent phases. Unlike non-suckling, the average relative speed was always between -1 and 1 when the calf was suckling. The mean average normalized ODBA (nODBA), and the mean average roll

rate during suckling were slightly higher than when not suckling. The average nODBA and roll rate for suckling events rarely took very high value compared to non-suckling. Finally, the mean absolute average roll was exceptionally high during suckling events compared to non-suckling segments. The absolute average roll during suckling reached more than 45° . The automatically detected suckling events followed the same trend observed in the visually suckling confirmed events regarding the characteristics.

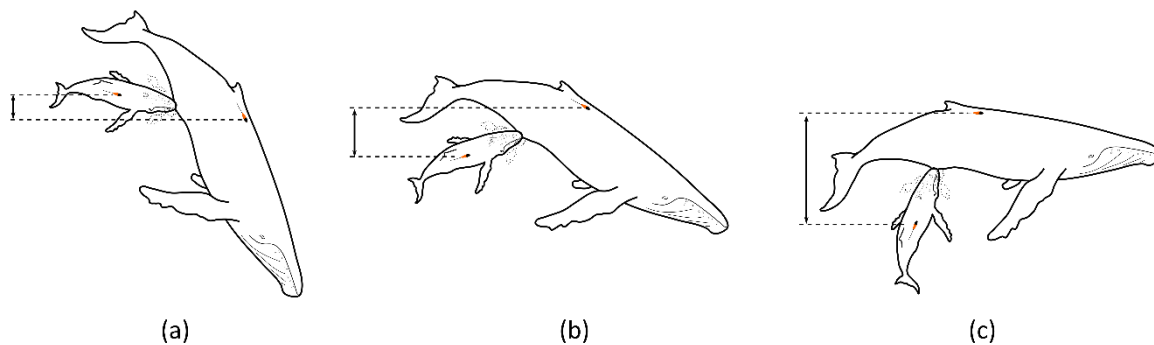


Figure S3. Schematic representation of the expected vertical distance between the humpback whale mother and calf considering various possible nursing configurations. The animal-borne tags used to record the behaviors are illustrated in orange. The calf is represented suckling on the right teat (thus rolling to the right). The vertical distances between the mother and the calf (strictly speaking, the vertical distance between the two tags) are represented by double arrows. (a) The extreme case where the mother is almost vertical, and the calf is almost horizontal in the water column. (b) The expected typical configuration. (c) The extreme case where the mother is almost horizontal, and the calf is almost vertical. The configurations are based on the known nursing configuration reported in the literature. Considering the average dimensions and body proportions of mothers and calves in the studied population (Appendix II), the vertical distance is expected to be about 1-2 m, 2-3 m, and 5-6 m in (a), (b) and (c) respectively

Table S1. Summary of the deployments used for studying the suckling behavior in humpback whale

Deployment ID	Pair ID	Category	Age ^a	Tag on date (local) dd-mmm-yyyy hh:mm	Tag off date (local) dd-mmm-yyyy hh:mm	Duration (h): all data	Duration (h): data with 'good' video	Tag model ^b
dep8_10sept2014_Calf	G013	Calf	C1	10-Sep-2014 13:51	10-Sep-2014 15:44	1.89	0.	Acousonde
dep8_18aout2016_Calf	G023	Calf	C1	18-Aug-2016 13:13	18-Aug-2016 14:19	1.10	0	Acousonde
dep8_18aout2016_Mother	G023	Mother	A	18-Aug-2016 13:44	18-Aug-2016 23:58	10.24	0	Acousonde
dep1_20aout2014_Calf	G006	Calf	C2	20-Aug-2014 11:08	20-Aug-2014 11:52	0.73	0	Acousonde
dep15-03.09.2017_Calf	G038	Calf	C2	03-Sep-2017 10:30	03-Sep-2017 11:33	0.48	0	Acousonde
dep15-03.09.2017_Mother	G038	Mother	A	03-Sep-2017 10:08	03-Sep-2017 12:36	2.47	0	Acousonde
dep6-13.08.2017_Calf	G028	Calf	C2	13-Aug-2017 11:52	13-Aug-2017 14:39	2.78	0	Acousonde
dep7-15.08.2017_Calf	G029	Calf	C2	15-Aug-2017 15:22	15-Aug-2017 15:46	0.39	0	Acousonde
dep8-16.08.2017_Calf	G030	Calf	C2	16-Aug-2017 09:03	16-Aug-2017 16:18	7.25	0	Acousonde
dep9_11sept2014_Calf	G014	Calf	C2	11-Sep-2014 12:22	11-Sep-2014 12:54	0.54	0	Acousonde
dep9-21.08.2017_Calf	G031	Calf	C2	21-Aug-2017 12:13	21-Aug-2017 15:28	3.26	0	Acousonde
Orange_01Sept2022_Calf*	G039	Calf	C2	01-Sep-2022 09:56	01-Sep-2022 18:09	8.21	6.70	CATS cam
Orange_05Sept2022_Calf	G040	Calf	C2	05-Sep-2022 09:02	05-Sep-2022 15:14	6.19	5.62	CATS cam
Orange_07Aout2022_Calf	G041	Calf	C2	07-Aug-2022 10:57	07-Aug-2022 14:14	3.27	2.88	CATS cam
Orange_13Sept2022_Calf	G042	Calf	C2	13-Sep-2022 13:42	13-Sep-2022 16:15	2.56	2.56	CATS cam
Orange_15Aout2022_Calf	G043	Calf	C2	15-Aug-2022 11:00	15-Aug-2022 11:57	0.95	0.95	CATS cam
Orange_30Aout2022_Calf*	G046	Calf	C2	30-Aug-2022 14:48	30-Aug-2022 18:34	3.77	2.97	CATS cam
Orange_31July2022_Calf	G047	Calf	C2	31-Jul-2022 10:52	31-Jul-2022 13:02	2.15	0	CATS cam
dep1_01aout2016_Calf	G016	Calf	C3	01-Aug-2016 09:40	01-Aug-2016 10:09	0.48	0	Acousonde
dep11_17sept2014_Calf	G015	Calf	C3	17-Sep-2014 12:28	17-Sep-2014 12:56	0.46	0	Acousonde
dep12-26.08.2017_Calf*	G033	Calf	C3	26-Aug-2017 14:57	27-Aug-2017 08:19	17.36	0	Acousonde
dep13-28.08.2017_Calf	G034	Calf	C3	28-Aug-2017 10:25	28-Aug-2017 15:53	5.46	0	Acousonde
dep14-01.09.2017_Calf	G036	Calf	C3	01-Sep-2017 09:15	01-Sep-2017 11:42	2.45	0	Acousonde
dep2_02aout2016_Calf	G017	Calf	C3	02-Aug-2016 14:37	02-Aug-2016 16:51	2.24	0	Acousonde
dep2_02aout2016_Mother	G017	Mother	A	02-Aug-2016 14:40	02-Aug-2016 15:51	1.18	0	Acousonde
dep2_22aout2014_Calf	G007	Calf	C3	22-Aug-2014 09:52	22-Aug-2014 14:53	5.01	0	Acousonde
dep2-04.08.2017_Calf	G025	Calf	C3	04-Aug-2017 14:04	04-Aug-2017 15:02	0.96	0	Acousonde
dep4-10.08.2017_Calf	G026	Calf	C3	10-Aug-2017 12:30	10-Aug-2017 13:48	1.30	0	Acousonde
dep4-10.08.2017_Mother	G026	Mother	A	10-Aug-2017 12:26	10-Aug-2017 13:44	1.31	0	Acousonde
dep5_29aout2014_Calf	G010	Calf	C3	29-Aug-2014 07:57	29-Aug-2014 08:24	0.45	0	Acousonde
dep5-11.08.2017_Calf	G027	Calf	C3	11-Aug-2017 11:39	11-Aug-2017 16:47	5.13	0	Acousonde
dep6_08sept2014_Calf	G011	Calf	C3	08-Sep-2014 09:29	08-Sep-2014 12:50	3.34	0	Acousonde
dep7_09sept2014_Calf*	G012	Calf	C3	09-Sep-2014 14:40	09-Sep-2014 19:32	4.87	0	Acousonde
dep7_12sept2013_Calf	G005	Calf	C3	12-Sep-2013 09:44	12-Sep-2013 12:56	3.21	0	Acousonde
dep7_17aout2016_Calf	G022	Calf	C3	17-Aug-2016 11:20	17-Aug-2016 13:52	2.53	0	Acousonde
dep7_17aout2016_Mother	G022	Mother	A	17-Aug-2016 11:28	17-Aug-2016 18:01	6.55	0	Acousonde

dep9_05sept2016_Calf*	G024	Calf	C3	05-Sep-2016 13:54	05-Sep-2016 22:54	9.01	0	Acousonde
dep9_05sept2016_Mother	G024	Mother	A	05-Sep-2016 13:53	05-Sep-2016 21:40	7.78	0	Acousonde
Jaune_06aout2019_Calf	G048	Calf	C3	06-Aug-2019 10:56	06-Aug-2019 12:34	1.61	1.61	CATS cam
Jaune_14sept2018_Calf	G049	Calf	C3	14-Sep-2018 11:34	14-Sep-2018 14:18	2.48	2.48	CATS cam
Orange_09aout2019_Calf*	G050	Calf	C3	09-Aug-2019 10:03	09-Aug-2019 18:44	7.95	6.42	CATS cam
Orange_19Aout2022_Calf	G044	Calf	C3	19-Aug-2022 09:35	19-Aug-2022 15:29	5.88	5.88	CATS cam
Orange_26Aout2022_Calf	G045	Calf	C3	26-Aug-2022 09:26	26-Aug-2022 11:12	1.78	1.07	CATS cam

^a relative age. For the calves, the relative age was estimated based on the coloration, skinfolds, and angle of furling of the dorsal fin. C1: neonate, C2: very young but non-neonate, C3: older calves (but <3 months old), A: adult.

^b Acousonde: animal-borne multi-sensor tag not equipped with a camera. CATS cam: animal-borne multi-sensor tag equipped with a camera.

*Calf deployment with available nighttime data (i.e., with data between 1800 and 0500 d+1 local time)

Table S2. Suckling side preferences in humpback whale calves tagged with Acousonde or CATS cam tags. The counts include visually confirmed suckling events and automatically detected suckling events. Deployments in which no suckling events have been detected are not shown

Deployment/Calf ID	Suckling event counts	
	Left (Negative roll)	Right (Positive roll)
dep12-26.08.2017_Calf	20	16
dep13-28.08.2017_Calf	6	6
dep14-01.09.2017_Calf	2	3
dep2-04.08.2017_Calf	1	2
dep2_02aout2016_Calf	3	4
dep2_22aout2014_Calf	4	3
dep4-10.08.2017_Calf	3	3
dep5-11.08.2017_Calf	4	5
dep6_08sept2014_Calf	0	1
dep7-15.08.2017_Calf	0	1
dep7_09sept2014_Calf	2	1
dep7_12sept2013_Calf	4	3
dep7_17aout2016_Calf	0	3
dep8-16.08.2017_Calf	10	13
dep8_10sept2014_Calf	1	4
dep8_18aout2016_Calf	4	1
dep9-21.08.2017_Calf	0	1
dep9_05sept2016_Calf	6	9
Jaune_06aout2019_Calf	1	3
Jaune_14sept2018_Calf	2	3
Orange_01Sept2022_Calf	3	2
Orange_05Sept2022_Calf	1	2
Orange_07Aout2022_Calf	5	6
Orange_09aout2019_Calf	14	13
Orange_13Sept2022_Calf	5	7
Orange_19Aout2022_Calf	5	5
Orange_26Aout2022_Calf	2	2
Orange_30Aout2022_Calf	6	5
Orange_31July2022_Calf	1	2
Total	115	129

Table S3. Starting side preferences when performing bouts of suckling events (events spaced less than a minute apart) in humpback whale calves tagged with Acousonde or CATS cam tags. The counts include visually confirmed suckling events and automatically detected suckling events. Deployments in which no suckling events have been detected are not shown. Note that isolated suckling events (i.e., events that are individually more than a minute apart from any other suckling events) are also included in the counts

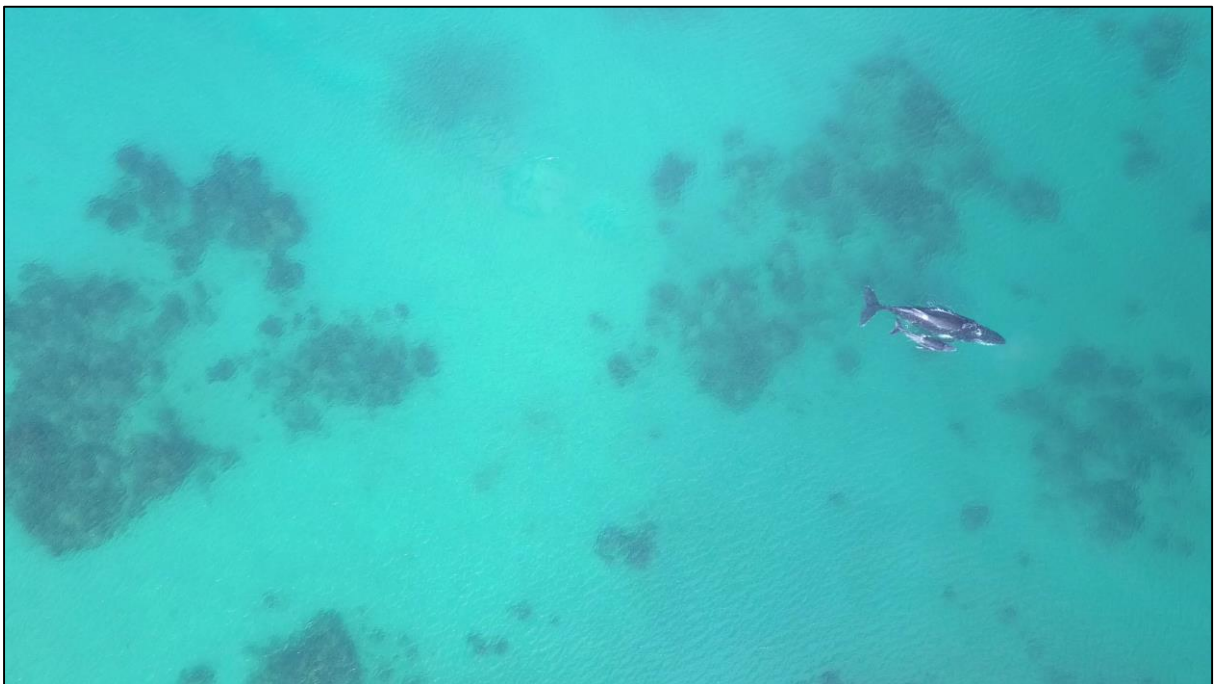
Deployment/Calf ID	Suckling series counts	
	Left (Negative roll)	Right (Positive roll)
dep12-26.08.2017_Calf	16	16
dep13-28.08.2017_Calf	4	3
dep14-01.09.2017_Calf	2	1
dep2-04.08.2017_Calf	1	1
dep2_02aout2016_Calf	2	4
dep2_22aout2014_Calf	2	2
dep4-10.08.2017_Calf	2	1
dep5-11.08.2017_Calf	1	3
dep6_08sept2014_Calf	0	1
dep7-15.08.2017_Calf	0	1
dep7_09sept2014_Calf	2	1
dep7_12sept2013_Calf	1	1
dep7_17aout2016_Calf	0	2
dep8-16.08.2017_Calf	9	12
dep8_10sept2014_Calf	1	3
dep8_18aout2016_Calf	3	1
dep9-21.08.2017_Calf	0	1
dep9_05sept2016_Calf	4	5
Jaune_06aout2019_Calf	1	2
Jaune_14sept2018_Calf	1	1
Orange_01Sept2022_Calf	3	2
Orange_05Sept2022_Calf	1	2
Orange_07Aout2022_Calf	2	2
Orange_09aout2019_Calf	9	2
Orange_13Sept2022_Calf	1	2
Orange_19Aout2022_Calf	3	1
Orange_26Aout2022_Calf	0	1
Orange_30Aout2022_Calf	4	2
Orange_31July2022_Calf	1	2
Total	76	78



<https://doi.org/10.1007/s00265-023-03369-9>

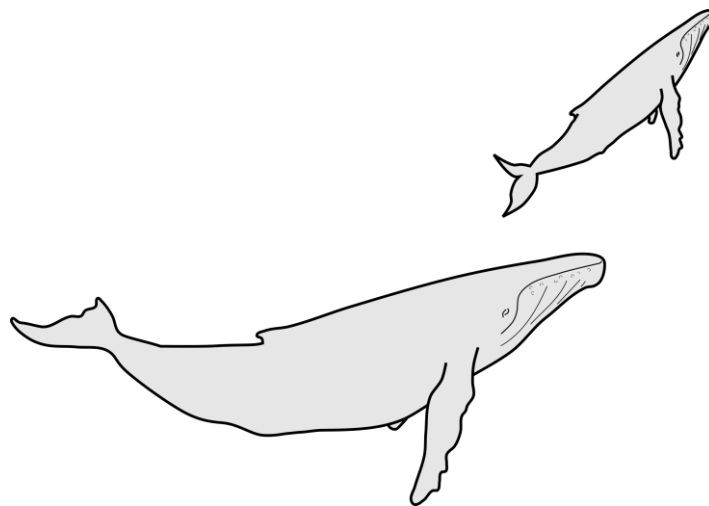
Data S1. Dataset generated and analyzed during the study

Part II: Keeping up with mom: the swimming behavior of humpback whale mother-calf pairs



Chapter 3. Time budget and behavioral synchrony of humpback whale mother-calf pairs

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Synthesis

How are the swimming and resting activities of mother-calf pairs organized in time?

Methods

Tag dataset from 47 mother-calf pairs was used: data from 31 single deployments on calves, 10 single deployments on mothers, and six simultaneous deployments (thus, 53 individuals). A HMM was used to model the time organization of the activities of the mothers and the calves based on their swimming speed. The variation of this time organization with age was then investigated using LMM. With the simultaneous deployments, the behavioral synchrony was analyzed by calculating the proportion of synchronized behavior, the behavioral independence score, and Hinde's association index.

Findings

Calves switch between resting, milling, moderate swimming, and fast swimming more often than mothers. The proportion of resting time is similar from C1-C2 to Adults (mothers). The proportion of time milling, however, decreases. The time spent resting is potentially lower in mothers accompanied by younger calves. The mother and the calf are often found in synchrony up to 50% of the time with respect to their behavior. Generally speaking, the mother and the calf can both be responsible for the behavioral synchrony, but one is more likely to take responsibility than the other, depending on the context. For instance, resting and fast swimming are scheduled by the mother.

Abstract

In capital breeders, like most mysticetes whales, the mothers rely on a limited energy reserve to care for their young while sustaining themselves. Understanding the activities and time budget can inform how the energy is allocated in mother-young pairs and its relation to the development of the young. In the present study, we compared the time budgets of the mothers and the calves in humpback whales, investigated the changes in time budgets as the calves age, and assessed the mother-calf behavioral synchrony using suction cup tag data collected in Sainte Marie, Madagascar. We found that mothers and calves allocated much of their time to resting. We also found that young calves tended to engage more in milling than older calves. The calves displayed some degree of independence in their behaviors but were also frequently observed synchronizing their activities with their mothers (50% of the time on average). Depending on the nature of the activity, the initiation of an activity by the pair could be driven by either the calf or the mother. Our study provided additional knowledge for understanding the behavioral dynamics and interactions within mother-calf pairs in aquatic capital breeders.

Keywords: breeding area, cetacean, multi-sensor tags, ontogeny, parent-offspring interactions

Introduction

Mammals, like birds in general, are known for their highly elaborate forms of parental care. Most often provided mainly by the mother in mammals, parental care takes various forms, such as providing the nutrients required for embryo development, protection, feeding, learning, etc. (Balshine, 2012; Clutton-Brock, 1991). The purpose of parental care is to improve the fitness of the offspring, and it is a costly investment that can reduce the survival chances of the parents themselves or limit their future reproduction (Balshine, 2012; Clutton-Brock, 1991). For female mammals, food provisioning in the form of maternal milk represents one of the most critical and costly aspects of this care (Braithwaite et al., 2015; Gittleman & Thompson, 1988; Oftedal, 2000).

In species producing young that are locomotory, sensorially, and thermoregulatory independent relatively early after birth, the maternal care strategy generally falls into either the 'hider' or 'follower' category (Fisher et al., 2002; Lent, 1974). In the case of 'hiding' species, the mother and young are not permanently together. The young remain in a 'hiding place' while the mother is foraging. The pair only reunites from time to time, mainly for nursing. In the 'follower' species, the young follow its mother wherever she goes, and the two individuals show a fairly marked synchronization in their behavior (Green, 1993; Lent, 1974). These two strategies are known to be linked to predation pressure, habitat structure, and life history (Fisher et al., 2002).

The mother and the offspring's behavior changes with the evolving offspring's independence and energetic needs (Trivers, 1974). Early after birth, the mother usually displays more behaviors directed at establishing and strengthening the mother-offspring bond than when the offspring is older (Lent, 1974; Nowak et al., 2000). Such behaviors involve intense contact and interactions (tactile, visual, acoustic, etc.) and highly defensive responses of the mother against approaching conspecifics (Lent, 1974). In addition, the mother is more vigilant because the risk of predation on a very young individual is high (Blank et al., 2015). Moreover, she can adjust her behavior to match what the young can or cannot do (Huetz et al., 2022; Szabo & Duffus, 2008). Indeed, even when an offspring can rapidly move around on its own, regulate its temperature, and has already functional senses, its physical performance remains limited at first (Herrel & Gibb, 2006; Huetz et al., 2022; Noren et al., 2006), and it still has to learn and develop various skills and traits crucial for its survival (Bekoff, 1972).

Among marine mammals, mysticetes fall into the category known as capital breeders. They build up a reserve of energy in the feeding area and use it to reproduce later in the breeding area (Bannister, 2018; Lockyer, 1984). In this sense, mothers have a limited energy reserve to care for their calf during at least the first few months of its life. They must minimize their energy consumption and save energy for the upcoming migration while producing milk for their unique calf (Bejder et al., 2019; Braithwaite et al., 2015; Clapham, 2018). As for the calf, it must optimize the energy allocated to its growth and to various activities essential for its cognitive and social development (Braithwaite et al., 2015). The maternal strategy of mysticetes has been described as equivalent to the 'follower' strategy observed in terrestrial ungulates (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2023; Szabo & Duffus, 2008; Tyson et al., 2012).

Humpback whales (*Megaptera novaeangliae*), one of the most common and well-studied baleen whale species, undertake extensive migrations between the feeding and breeding areas (Clapham, 2018). Humpback whale calves are born in the winter in the breeding area and stay with their mother for about one year (Clapham, 2018). Their first three months of life are spent in the breeding area, a period during which they build up a blubber layer and rapidly grow in preparation for the migration towards the feeding ground (Corkeron & Connor, 1999). They only start to feed on prey when they reach about seven months old (Clapham, 2018). The time budget of each individual of the mother-young pair can inform on the energy allocation, on the development of the calves, as well as on the level of dependence of the calves on their mother during the critical phase of the calf's development in the breeding ground. Thus, in the present study, we investigated the time budget of mother-calf pairs and evaluated the synchrony of their activities. More specifically, we assessed whether the time budget changes with the calves' age and whether those of the mothers and the calves are similar. We also quantified the level of synchronization of their activities and identified which individual of the dyad leads the activities.

Materials and methods

Dataset

We used an animal-borne multi-sensor tag dataset from 47 mother-calf pairs off Sainte Marie Island, Madagascar, South Western Indian Ocean, during the winter (July-September) of 2013-2019 and 2021-2022 tagged either with Acousonde 3B or CATS cam (only for calves). The dataset consisted of data from 31 single tag deployments on calves, 10 single deployments on mothers, and six simultaneous deployments (i.e., the mother and the calves were both tagged, and their data overlapped in time). They included pressure data sampled at 10 Hz (sampled initially at 20 Hz for some individuals but then downsampled for consistency) and sound data sampled at 12 kHz (sampled initially at 24kHz, 24.453 kHz, or 48 kHz but then downsampled for consistency). Other data were available but irrelevant to the present study (3D acceleration, compass data, etc.). Detailed tagging procedures and specifications have been presented elsewhere (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022, 2023; Saloma et al., 2022).

For each individual, we computed the depth (in meters) and the whale's relative forward speed (relative speed hereafter) with a sampling frequency of 10 Hz. The depth was obtained from the pressure data. It was smoothed with a 0.5 s running median filter. The relative speed was calculated as the z-scored flow noise (per individual) extracted from the sound data (66-94 Hz frequency band, Cade et al., 2017). We associated each deployment (each individual) to an age class (C1, C2, or C3 for the calves – see below, or A – Adult – for the mothers). Mothers were further categorized into A-C1, A-C2, or A-C3, depending on the age of their dependent calf.

The relative age of the calves was estimated based on skin coloration, skinfolds, and the angle of unfurling of their dorsal fin (Cartwright & Sullivan, 2009; Faria et al., 2013; Huetz et al., 2022; Ratsimbazafindranahaka et al., 2023; Saloma et al., 2022): C1 (neonate) for calves presenting some folds, scars, and skin color that tends to be light grey dorsally and white ventrally and with less than $\sim 45^\circ$ dorsal fin furl; C2 for very young but non-neonate calves having more than $\sim 45^\circ$ but less than about 70° dorsal fin furl; and C3 for older calves (but < 3 months old) that have unfurled dorsal fin (approximately $> 70^\circ$).

Behavioral states modeling

We used the hidden Markov model (HMM) to model the time organization of the activities of the mothers and the calves. For this purpose, we computed the average relative speed of each whale on a non-overlapping 20 s sliding windows basis as the input time series data (i.e., the sampling unit for the modeling corresponded to one 20 s windows). HMMs are commonly used for modeling and analyzing behavioral time series in cetaceans (DeRuiter et al., 2017; Tennessen et al., 2019). We modeled the activities as a first-order four-state Markov chain that gives rise to the observed

swimming speed. In the model, we assumed that all state transitions were possible. We constructed the HMM using the `depmixS4` package (Visser & Speekenbrink, 2010) in R (R Core Team, <https://www.r-project.org/>). We included the relative speed (assumed to have a Gaussian distribution) as the response. The model was fitted by maximum likelihood estimation using the expectation-maximization (EM) algorithm in the `depmixS4` package following the framework described by Tennessen et al. (2019). Finally, the Viterbi algorithm was applied to find the most likely state sequence that best translates to the observed behavior (the relative speed).

The model choice was motivated by the observation in the field and from animal-borne camera tags (Ratsimbazafindranahaka MN, unpublished data) of four distinct behavioral states associated with a typical swimming speed each for both the mother and the calf: resting, milling, directed moderate swimming, and directed fast swimming. The resting state corresponds to the whale being static or quasi-static (speed less than one knot). The milling state is when the whale wanders/is lolling around (e.g., a calf circling its mother) at a speed likely corresponding to their global average speed, thus less than their average traveling speed (around 2.8-3.5 knots, Chittleborough, 1953). In contrast to resting and milling, the states qualified as directed swimming refers to activities corresponding to a swimming speed higher than the average: the first to the usual travel speed (directed moderate swimming), and the second to a more hasted traveling (directed fast swimming, e.g., flight behavior). Although we refer to them as directed here, they do not necessarily imply a straight movement. The term instead refers to an apparent motivation of the whale to intentionally move from one point to another. We chose to use a model in its simplest possible form as the goal was only to capture the general activity pattern of the individuals in mother-calf pairs.

Data analysis

Time budget and ontogeny

With the state sequences from the HMM, we established the time budget for each individual. In other words, we calculated the proportion (in %) of time spent in each behavioral state for each whale. Then we tested whether the proportion of time spent in a given state varies with age class using linear models in R, followed by Tukey's post-hoc multiple comparisons test with adjusted *P*-values using the *emmeans* package (Lenth et al., 2018) when a statistically significant effect was detected. We also tested whether the proportions vary depending on the category of the mothers. For the analysis, we transformed each proportion of interest into a log-ratio of proportion using one of the states as a reference, i.e.:

$$\text{log-ratio}_{\text{state of interest}} = \log \left(\frac{\text{proportion}_{\text{state of interest}}}{\text{proportion}_{\text{reference}}} \right)$$

Such transformation is required in compositional data analysis for the standard statistical approaches to be valid (Aitchison, 1986). The choice of the reference for the

transformation is arbitrary because of the permutation invariability property of the log-ratio approach (Aitchison, 1986). In our analyses, we used the proportion of time spent in directed swimming (i.e., directed moderate swimming + directed fast swimming) as a reference. The grouping of directed moderate swimming and directed fast swimming into one broad class was because the directed fast swimming state contained zero proportion, preventing us from calculating a log-ratio with the directed swimming state either as a reference or as a state of interest. All proportions of time spent in each state per whale were assumed to be independent of the deployment length. Exploratory analyses supported this assumption.

Behavioral synchrony

We analyzed the behavioral synchrony between the mother and the calf using the data from simultaneous deployments ($N = 6$). We time-aligned the calf's predicted state sequence with the mother's predicted state sequence (only overlapping periods were considered). As the internal clock of the tag units sometimes had several seconds of delay (time drift), simultaneous mother-calf data had to be manually aligned. For the process, we used sound cues detected in both units to align the mothers' and calves' data (crew voices recorded between the tagging time and the moment the tags were turned on, impact noises recorded prior to tagging, or even distant male songs) (Huetz et al., 2022).

We calculated the proportion of synchronized behavior for each aligned pair, the behavioral independence scores (calculated for each state), and Hinde's association index (Hinde & Atkinson, 1970). The proportion of synchronized behavior was calculated as the time corresponding to the mother and calf being in the same state relative to the total simultaneous data length. The behavioral independence score for each state was calculated as the ratio of the total time spent in the state to the time spent in that state at the same time as the other individual of the pair. The Hinde's index was obtained with the following formula that takes as argument the number of times the mother and the calf initiated or terminated a bout of synchronized state (respectively, M_I and M_T for the mother and C_I and C_T for the calf):

$$\text{Hinde's index} = (M_I / (M_I + C_I)) - (M_T / (M_T + C_T))$$

The Hinde's index varies between -1 and $+1$, corresponding to the calf or the mother being exclusively responsible for the synchrony. For the calculation, an individual was considered as having initiated a bout of synchronized state when it changed its behavioral state to synchronize with the other individual. Conversely, it was considered as having terminated the synchronized bout when it changed its behavior state and broke the synchrony (Fellner et al., 2013). It is worth noting that in our framework, synchrony does not necessarily assume spatial proximity and spatial synchrony.

Results

A total of 202.63 h of data were analyzed from all 53 individual deployments (41 single deployments + 6 simultaneous deployments). The analyzed time per deployment was 3.82 h on average (range = 0.39 – 17.36 h). For the behavioral synchrony study, 13.65 h of simultaneous mother-calf data from the six simultaneous deployments were used. The analyzed time per simultaneous deployment was 2.28 h on average (range = 0.48–7.77 h). Among the 37 calves, two were C1 calves, 14 were C2 calves, and 21 were C3 calves. Due to the low number of C1 calves, we pooled them with the C2 calves for the statistical tests (C1-C2 calves). Among the 16 mothers, one was with C1 calf (A-C1), three were with C2 calf (A-C2), and 12 were with C3 calf (A-C2). As we only had one A-C1, we pooled her with the A-C2 for the statistical tests (A-C1/C2).

Our HMM model successfully captured the general activity pattern of the whales. The corresponding transition probabilities are presented in Figure S1. The HMM captured (i) a state with a mean average speed of about one standard deviation below the global average swimming speed (resting: mean average relative speed = -1.1 ± 0.5 , range = -3.8 – 0.3 ; $N = 8594$), (ii) a state with a mean average speed coinciding with the global average swimming speed (milling: mean average relative speed = -0.1 ± 0.3 , range = -1.1 – 1.3 , $N = 13254$), (iii) a state with a mean average speed of about half a standard deviation above the global average swimming speed (directed moderate swimming: mean average relative speed = 0.6 ± 0.3 , range = -0.3 – 1.5 , $N = 10747$), and (iv) a state with a mean average speed of more than one standard deviation above the global average swimming speed (directed fast swimming: mean average relative speed = 1.3 ± 0.4 , range = -0.2 – 3.6 , $N = 3733$). On average, the C1-C2, the C3, and the mothers (A) switched from one state to another 22 ± 9 , 20 ± 7 and 17 ± 8 times per hour, respectively (range, C1-C2: 9–41 switches per hour, C3: 7–36 switches per hour, A: 9–38 switches per hour).

The two C1 calves spent 24% and 30% of time resting, respectively, 40% and 47% of time milling, 11% and 20% in directed moderate swimming, and 10% and 20% in directed fast swimming. The C2 calves spent on average 22% of time resting (range = 9–31%), 43% of time milling (range = 23–77%), 27% of the time in directed moderate swimming (range = 12–51%), and 10% of the time in directed fast swimming (range: 0–16%). The C3 calves spent on average 22% of time resting (range = 13–38%), 39% of time milling (range = 14–62%), 31% of the time in directed moderate swimming (range = 12–51%), and 9% of the time in directional fast swimming (range: 3–16%). The mothers spent on average 26% of the time resting (range = 15–41%), 31% of time milling (range = 14–57%), 29% of the time in directed moderate swimming (range = 10–43%), and 14% of the time in directed fast swimming (range: 3–25%) (Figure 1). We found no statistically significant effect of age on the proportion of time resting (linear model with log-ratio transformed response: $F_{2, 50} = 1.29$, $P = 0.283$). However, we detected a statistically significant effect of age on the proportion of time milling (linear

model with a log-ratio transformed response: $F_{2, 50} = 3.76, P = 0.03$). The linear model revealed a gradual decrease in the proportion of time milling from C1-C2 to A (mothers). The proportion of milling for mothers was statistically different compared to C1-C2 calves (Tukey's post-hoc test, A vs. C1-C2, $\beta = -0.58, P = 0.023$) but not statistically different compared to C3 calves (Tukey's post-hoc test, A vs. C3, $\beta = -0.332, P = 0.227$). In addition, the difference between C1-C2 and the C3 calves was not statistically significant (Tukey's post-hoc test, A vs. C3, $\beta = 0.246, P = 0.435$).

The A-C1/C2 mothers spent on average 20% of time resting (range = 16–26%), 40% of time milling (range = 37–43%), 27% of the time in directed moderate swimming (range = 17–33%), and 13% of the time in directed fast swimming (range: 8–20%). With respect to the A-C3 mothers, on average, the time spent resting was 28% (range = 15–41%), the time spent milling was 28% (range = 14–57%), the time in directed moderate swimming was 30% of (range = 10–43%), and the time in directed fast swimming was 14% of (range: 3–25%) (Figure 1). Although the time spent resting was lower in A-C1/C2 mothers and the time spent milling was higher, we failed to find a statistically significant difference with calf's age class (linear model with log-ratio transformed response, A-C1/C2 vs. A-C3, resting: $F_{1, 14} = 2, P = 0.179$; Milling: $F_{1, 14} = 2.07, P = 0.172$).

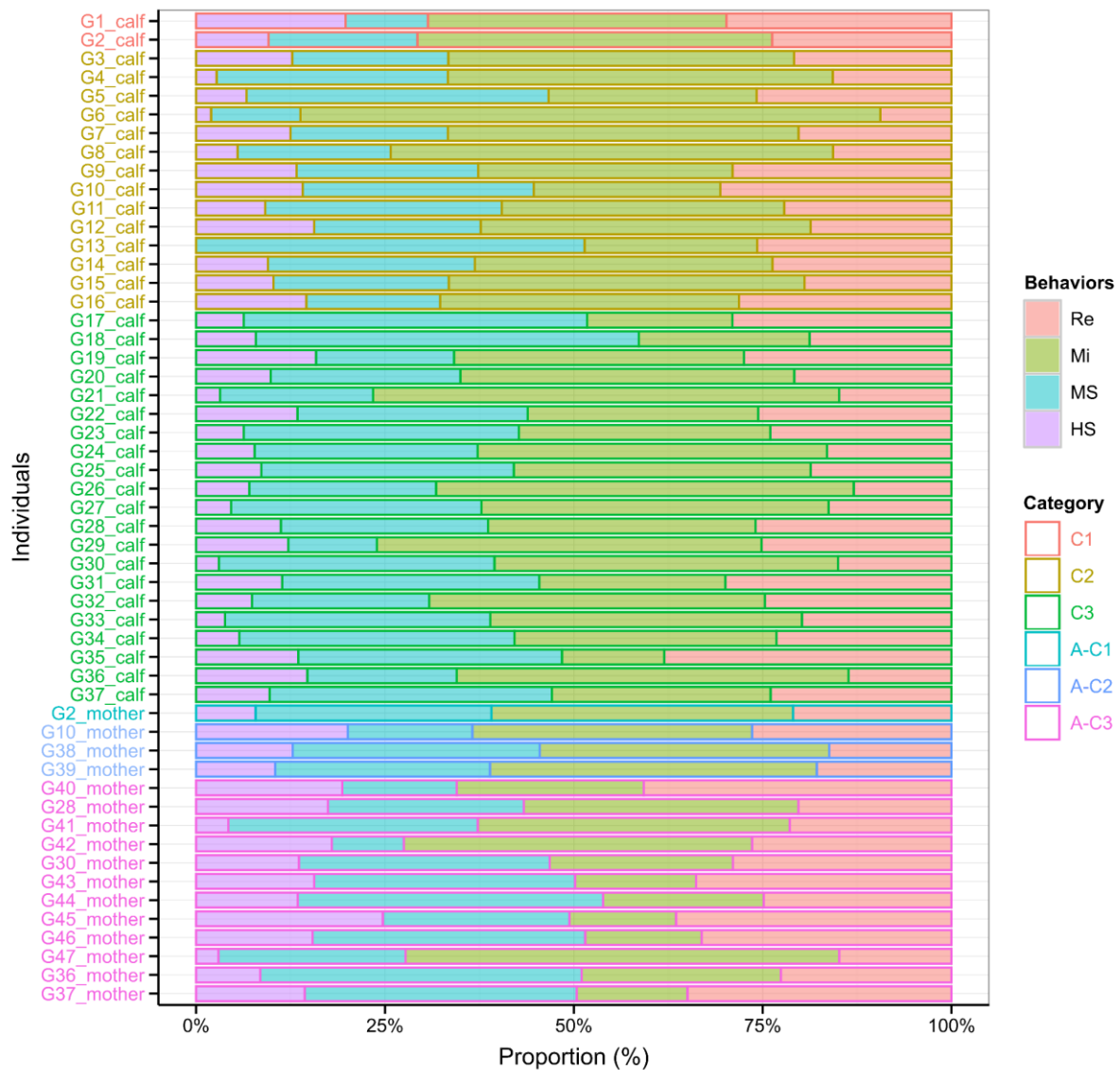


Figure 1. Behavioral time budget of 47 calves and 16 mothers in a breeding area off Sainte Marie, Madagascar. The behaviors were modeled using a hidden Markov model (HMM) based on the relative swimming speed. Re: resting, Mi: milling, MS: directional moderate swimming, and HS: directional fast swimming. C1, C2, and C3 represent the relative age of the calves estimated based on skin coloration, skinfolds, and the angle of unfurling of their dorsal fin. A corresponds to Adults (mothers), further categorized according to the age of their dependent calf. Age (C1-C2 vs. C3 vs. A) had no statistically significant effect on the proportion of time resting (linear model with log-ratio transformed response: $F_{2, 50} = 1.29$, $P = 0.283$). However, it had a statistically significant effect on the proportion of time milling (linear model with a log-ratio transformed response: $F_{2, 50} = 3.76$, $P = 0.03$)

Complete results on the behavioral synchrony in six mother-calf pairs are presented in Table 1. An example of paired mother-calf data (pair G28) showing the behavioral synchrony between the mother and the calf is presented in Figure 2. The proportion of synchronized behavior per pair, relative to the total simultaneous data, ranged from 34

to 79% (median = 50%). The behavioral independence ranged from 1.04 to 6.6 in calves (median = 1.11) and from 1.11 to 2.16 in mothers (median = 1.55) for the resting state, from 1.33 to 5.32 in calves (median = 3.39) and from 1.03 to 4.05 in mothers (median = 1.66) for the milling state, from 1.29 to 2.08 in calves (median = 1.53) and from 1 to 5.12 in mothers (median = 1.9) for the directed moderate swimming state, and from 1.01 to 1.68 in calves (median = 1.01) and from 1.01 to 7.45 in mothers (median = 1.78) for the directed fast swimming. The Hinde's index of association ranged from -0.3 to 0.7 (median = 0.12).

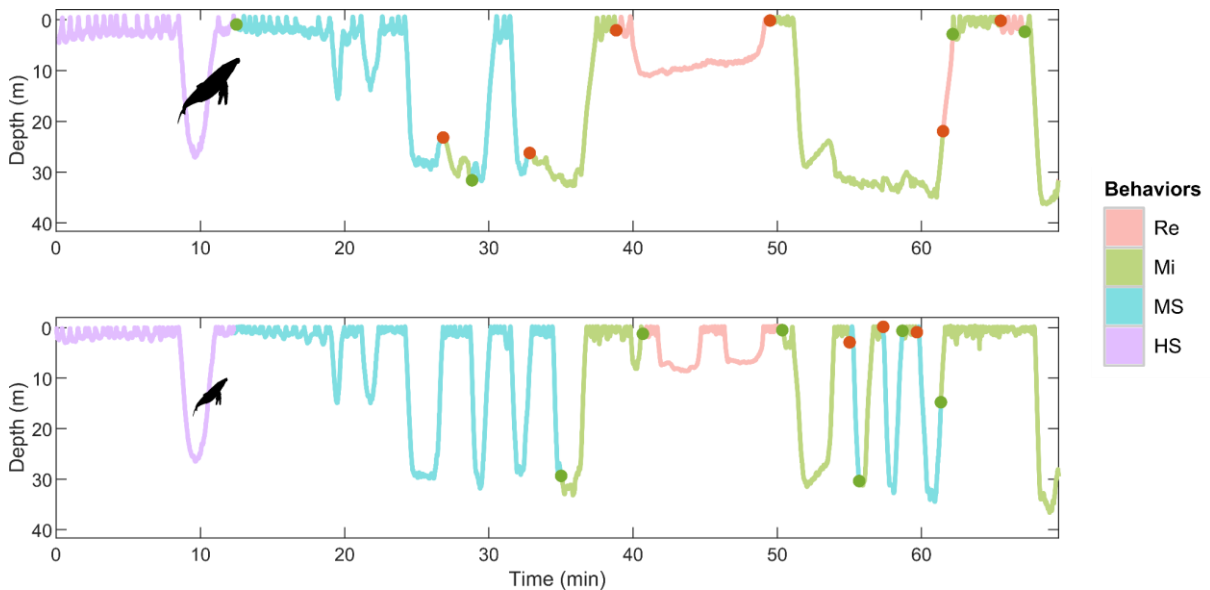


Figure 2. Dive profile of a simultaneously tagged mother (top) and calf (bottom) showing the behavioral synchrony between the two. Re: resting, Mi: milling, MS: directional moderate swimming, and HS: directional fast swimming. Seventy-nine percent of the total simultaneous data presented a synchronized behavioral state (i.e., the calf and the mother were in the same state). Green and red dots represent each time the individual initiated and terminated a bout of synchronized state, respectively. The number of times the mother and the calf initiated and terminated a bout of synchronized state gave a Hinde's index of -0.3. The index suggested that while the calf tends to match its behavior to its mother's behavior more often compared to its mother (negative value), the mother and the calf were almost equally responsible for maintaining the two's behavioral synchrony (value close to zero)

Table 1. Synchronized behaviors of six mother-calf pairs off Sainte Marie, Madagascar. HS: directional fast swimming, MS: directional moderate swimming, Mi: milling, and Re: resting. Async.: no period of synchrony has been observed

Pair ID	Calf's age	Total synchronized state (%)	State	Behavioral independence scores		Initiation		Termination		Hinde's index
				Calf	Mother	Calf	Mother	Calf	Mother	
G2	C1	34	HS	async.	async.	7	6	6	6	0
			MS	1.62	5.12					
			Mi	4.96	2.81					
			Re	2.3	2.01					
G10	C2	46	HS	1.01	1.55	1	6	6	1	0.71
			MS	1.31	2.36					
			Mi	5.32	4.05					
			Re	6.6	1.11					
G28	C3	79	HS	1.01	1.01	6	4	3	6	-0.3
			MS	1.44	1					
			Mi	1.33	1.51					
			Re	1.1	1.63					
G30	C3	46	HS	1.68	7.45	11	19	18	12	0.25
			MS	2.08	1.02					
			Mi	3.39	1.64					
			Re	1.06	2.16					
G36	C3	54	HS	1.01	2.08	11	16	12	15	0.04
			MS	2.03	3.86					
			Mi	2.73	1.03					
			Re	1.04	1.39					
G37	C3	66	HS	1.37	1.78	41	53	60	35	0.2
			MS	1.29	1.44					
			Mi	3.39	1.67					
			Re	1.12	1.47					

Discussion

Our objective was to assess the time allocation patterns of humpback whale mother-calf pairs and estimate the level of synchrony in their activities. We aimed to compare the time budgets of the mothers and calves, investigate any changes in the quantified time budget as the calves age, quantify the degree of synchronization between their activities, and determine which individual within the pair is the leader. Although we based our study on the use of suction cup tags, which only partially inform on the daily life of mothers and their calves, our study allowed us to gain additional knowledge on the behavioral dynamics and interactions within humpback whale mother-calf pairs. We observed that mothers and calves allocated a substantial portion of their time to resting (up to 41% of the time in mothers). Additionally, we found that the time spent milling, a behavior associated with slow wandering movement, was highest in young calves and tended to decrease as they aged. Although the calves displayed some degree of independence in their behaviors, they also frequently engaged in activities similar to their mothers (50% of the time on average). Interestingly, our result suggested that the initiation of specific activities within the pair could be driven by either the calf or the mother, depending on the nature of the activity.

Our result on the time spent resting is in accordance with previous results suggesting that mothers and calves rest frequently to minimize their energy consumption (Bejder et al., 2019). For the mothers, energy saving is crucial as they do not feed for a prolonged period while having to produce milk for their calf (Braithwaite et al., 2015; Clapham, 2018). Optimizing the time spent resting minimizes the decline in body condition and thus ensures sufficient milk production to nurse their calf and secure enough energy reserve left to migrate back to the feeding ground. For the calves, a low activity level helps maximize energy allocation into growth (Braithwaite et al., 2015). Our data suggested that the mothers with younger calves tend to spend less time resting and more time milling compared to mothers with older calves, although further data are needed as our test with a small sample failed to detect a statistically significant difference. Depending on the age of the calf, a mother may have to adjust her activity budget because of the specific needs of her calf at various development stages. The need for maternal vigilance can be, for example, at its highest shortly after the calf's birth (Blank et al., 2015). As the calf grows, its awareness of dangers improves, it becomes increasingly mobile, and it has improved locomotory autonomy. Thus, the level of vigilance of the mother can gradually decrease. Similarly, the need for maternal stimulations for the imprinting and to strengthen the mother-young bond, especially for species that use the following strategy, is maximal during the early post-partum phase (Lent, 1974). As such, the humpback whale mothers may be constrained to rest less often at first. Furthermore, as the calf grows, its milk consumption typically increases, resulting in higher energy demands for the mother (Trivers, 1974). Consequently, the mother with an older calf may require more rest to save energy and meet the needs of her growing offspring and for the upcoming migration. Further

investigations on the potential difference in the time budget of the mothers in relation to their maternal experience should be undertaken as we may expect a more optimized time budget in experienced females (primiparous vs multiparous females). However, it is important to acknowledge the inherent challenges associated with such research, particularly the challenge of re-sighting the same whale over multiple years.

Regarding the time spent milling in calves, past studies suggested that young cetaceans tend to swim continuously to train swimming and develop locomotor muscles (Cartwright & Sullivan, 2009; Thomas & Taber, 1984). Calves spending much time milling may also be just a display of a more playful nature of young individuals, which is also crucial for cognitive and social development (Bekoff, 1972; Burghardt, 2005).

Calves often engaged in the same activity as their mother, as expected for species adopting a 'following' anti-predator strategy. For instance, in American bison, experienced mothers and their calves engage in the same activity type 52% of the time on average. For novice mothers, the level of synchrony is about 35% (Green, 1993). Mother-young behavioral synchrony may serve as a way to strengthen bonds, establish social relationships, and mediate social interactions (Ham et al., 2023). The behavioral synchrony described here must be distinguished from dive and spatial synchrony, which are expected to be even higher, as suggested by previous studies on humpback whales (Huetz et al., 2022; Tyson et al., 2012). It is likely that the calf, even when engaging in a different activity than its mother, stays mainly close to her.

The Hinde's index of association we found displayed high variability. It was close to zero for most of the pairs. Taken globally, the mother and the calf appear thus almost equally responsible for maintaining the two's behavioral synchrony. However, depending on the context, the individual who takes the lead in engaging in a given activity can be, in fact, the calf or the mother. The mothers were more likely to engage in resting and directed fast swimming alone than the calves, which suggests that the resting activities and the directed fast swimming are scheduled/imposed by the mothers. In contrast, the calves are responsible for synchrony (i.e., they rest mostly when their mother rests or swim fast when their mother does so). The mother chooses when or where to rest and when to change pace because she is more aware of the surrounding dangers. This may explain why Huetz et al. (2022) found that the mothers tend to take the lead in the context of dive initiation. Both the mother and the calf could engage in milling independently of the other individual's milling activity. However, we found that the calves were way more likely to engage in milling alone. Such results show the importance of milling for the development of calves. To some extent, both the mother and the calf could also engage in directed moderate swimming independently of the other individual's directed moderate swimming. In addition to side-by-side traveling during which the pair would engage in directed moderate swimming with a common goal (to travel), directed moderate swimming can also be

associated with various individual contexts/goals. For instance, the two individuals have different breathing constraints, meaning they may come up at the surface for air (thus potentially engage in directed moderate swimming to reach the surface) at different times. In addition, in case of separation, one individual may swim at a moderate speed to reunite with the other.

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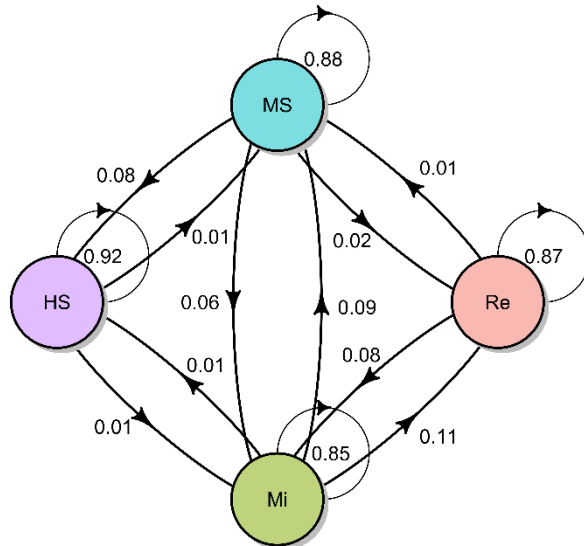
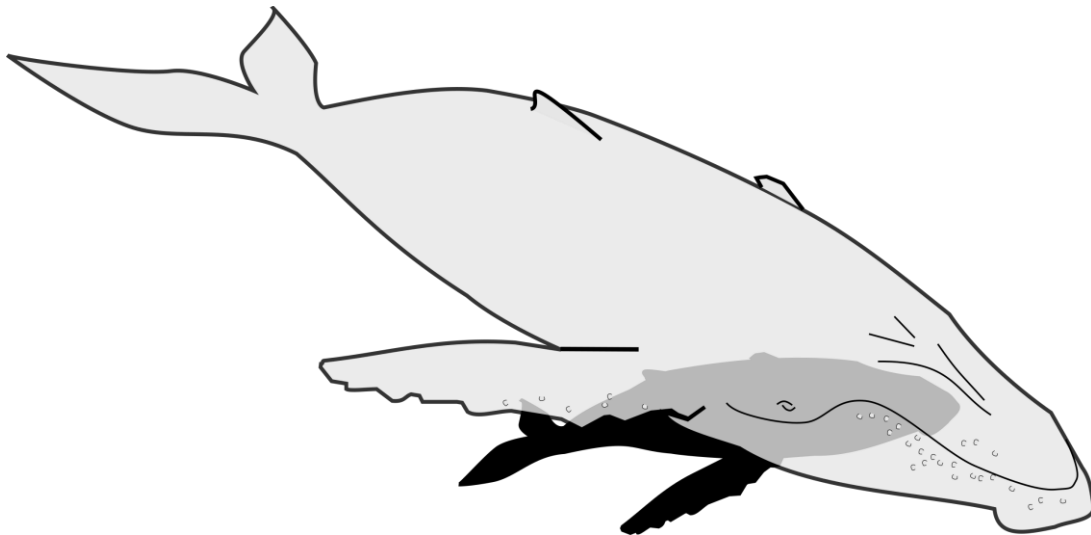
Supplementary information

Figure S1. Transition probabilities between four behavioral states in the hidden Markov model capturing the activity patterns of mothers and calves in humpback whale pairs. Re: resting, Mi: milling, MS: directional moderate swimming, and HS: directional fast swimming. The arrow indicates the transition from one state to the next state. The probability is indicated adjacent to the corresponding line

Chapter 4. Adaptive buoyancy control during shallow dives in humpback whales

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Upcoming submission

Synthesis

Are there swimming skills that the adult has but the calf does not? If any, how do mother-calf pairs cope with it?

Methods

Tag dataset from 47 mother-calf pairs was used (Acousonde and CATS cam tag data, as in Chapter 3). The relation between the swimming vertical direction, the swimming effort (ratio of fluke stroke rate to absolute speed), the depth, and the age were investigated using LMM. The depths of occurrence of stationary periods were also compared by age, and the spatial configuration of the mother-calf pair was checked for data from CATS cam tags.

Findings

The calves are unable to control their buoyancy, but the adults do. Unlike adults (mothers), the calves put more effort to swim downward than upward when close to the surface and more effort to swim upward than downward when at greater depth. In other words, the calf's swimming effort when vertically moving depends on the depth, relating to the ambient pressure change affecting buoyancy. The calves can remain stationary only at a specific depth (around 18 m for C3 calves). Otherwise, they must be helped by their mother by staying below her, pressed against her ventral part if above this specific depth (i.e., at shallow depths and thus with positive buoyancy), or resting on the seafloor if below this specific depth (i.e., when with a negative buoyancy).

Summary

Marine mammals have been proposed to have a passively changing buoyancy depending on the depth due to the collapse/expansion of their lungs as the ambient pressure changes. Consequently, their vertical movements are characterized by either active swimming or gliding, depending on the depth. Mysticetes have been described to have the same passive mechanism for buoyancy change without considering that their unique respiratory system, including two major air-containing spaces, can potentially provide the ability to change their buoyancy to enhance their vertical movements actively. Here, we present evidence supporting the hypothesis that mysticetes actively change buoyancy during shallow dives through analysis of diving data from multi-sensor tags placed on humpback whale mother-calf pairs. We show that adult female humpback whales displayed low effort to swim downward and upward regardless of the depth. In addition, they were able to stay stationary at varying depths. Calves displayed depth-dependent swimming effort and could only remain stationary with external help or at a specific depth.

Keywords: Baleen whales, swimming behavior, buoyancy, depth, ascent, descent, biologging, mother-young, aquatic habitat, respiratory system

Introduction

Aquatic animals evolved various adaptations to move vertically within the water column (Alexander, 1982; Pelster, 2009). For example, many shark and squid species rely on the angle of attack of their fins to go up or down and continuously swim to maintain a given depth or to ascend because their bodies are denser than the water. Most teleost fish regulate body density relative to water density by changing the volume of gas in their swim bladder. This facilitates nearly effortless vertical movements or enables maintaining neutral buoyancy. Marine mammals are thought to use the passive collapse/expansion of their lungs (due to changes in ambient pressure with depth) to aid descent/ascent (Miller et al., 2004; Skrovan et al., 1999; Williams et al., 2000). Archimedes' principle states that the upward buoyant force is equal to the weight of the displaced fluid. This force pushes the body up to the sea surface in shallow depths, but below a specific depth, D_{neutral} , this force decreases and allows the body to sink. Marine mammals modulate the energetics of swimming to accommodate these forces at various depths. At a depth above D_{neutral} , they actively swim to descend but effortlessly glide on ascent. The effort to descend decreases as their gas-filled organs (mainly the lungs) collapse, making their bodies less buoyant and denser. In contrast, at a depth below D_{neutral} , they effortlessly glide on the descent but must actively swim to ascend. The effort to ascend decreases as their gas-filled organs expand, making them more buoyant and less dense. This relationship between changes in hydrostatic pressure, buoyancy, and swimming kinematics has been initially demonstrated in pinnipeds (mainly seals and sea lions) and odontocetes (mainly small

toothed whales such as dolphins) (Miller et al., 2004; Skrovan et al., 1999; Williams et al., 2000), but it has been less studied in mysticetes (baleen whales).

Mysticetes are often compared to odontocetes with respect to their buoyancy and are expected to share the same swimming pattern during dives (Goldbogen et al., 2006; Nowacek et al., 2001; Williams et al., 2000). However, past studies do not take into account the unique anatomy of the respiratory system of mysticetes that may provide some control over their buoyancy (i.e., serving as an active ballast) (Adam et al., 2013; Gandilhon et al., 2015; Reidenberg, 2018, 2022). The respiratory system of mysticetes consists of paired nasal passageways, pharynx, larynx, trachea, paired lungs, and laryngeal sac – an organ not found in any other marine mammal species (Reidenberg, 2018, 2022; Reidenberg & Laitman, 2007). In this system, the air can go between the lungs and laryngeal sac, linked together at the rostral end of the trachea through the paired arytenoid cartilages that support the U-fold (vocal folds homolog) of the larynx (Reidenberg, 2018, 2022; Reidenberg & Laitman, 2007). It has been proposed that baleen whales can circulate air between the lungs and the laryngeal sac to increase the duration of apnea, produce sounds, and adjust buoyancy (Adam et al., 2013; Gandilhon et al., 2015; Reidenberg, 2018, 2022).

In the present paper, we tested the hypothesis that mysticetes can change their buoyancy to facilitate positioning and movements at different depths, using the humpback whale mother-calf pairs in their breeding ground as a model. Humpback whales are migratory, spending the summer in mid or high-latitudes (peri-polar) to feed and the winter in low-latitudes (peri-equatorial) to breed and give birth without feeding (Clapham, 2018). In this context, lactating females rely entirely on their energetic reserve to produce milk while sustaining themselves, making it even more important to optimize the energy allocated to other activities (Bejder et al., 2019; Braithwaite et al., 2015). By using diving data from animal-borne multi-sensor tags placed on mothers and calves, we analyzed the changes in swimming efforts at various depths during upward (ascent) and downward (descent) swimming movements and determined the depth at which the whales were able to stay stationary (neutral buoyancy).

Methods

Dataset

We used data from animal-borne multi-sensor tags deployed on 47 mother-calf pairs off Sainte Marie Island, Madagascar, South Western Indian Ocean, either on the back of the calf (31 mother-calf pairs), the mother (10 mother-calf pairs), or simultaneously on both (6 pairs) collected during the winter of 2013-2019 and 2021-2022. The multi-sensor tag used on most whales was the Acousonde 3B, except for 12 calves tagged with CATS cam. The Acousonde tags include a pressure sensor, a temperature sensor, a hydrophone, a 3D accelerometer, and a 3D magnetometer. The CATS cam includes

the same sensors plus a video camera. Detailed tagging procedures and tag specifications have been published previously (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022, 2023; Saloma et al., 2022). Each deployment (individual) was initially associated with an age class (Ratsimbazafindranahaka et al., 2023): C1 ($N = 2$) – neonate, C2 ($N = 14$) – very young but non-neonate, C3 ($N = 21$) – older calves but < 3 months old (calves of the year), or Adult ($N = 16$) – the mothers. Due to the limited sample, C1 calves were grouped with C2 calves into one category, C1-C2.

For each deployment, we extracted the depth (in meters), the depth rate (in meters/second), the vertical acceleration (in meters/second²), the body posture (body pitch and roll, in degree), and the fluke stroke signals (in degree) (Ratsimbazafindranahaka et al., 2022; Simon et al., 2012) at a sampling rate of 10 Hz. Stroking was identified when the fluke stroke signals exceeded a threshold set for each individual (mean = $1.5 \pm 0.8^\circ$, range = $0.5\text{--}5^\circ$) by visual inspection as there are evident differences in stroking and non-stroking periods (López et al., 2015). From the identified fluke strokes, we calculated the Fluke Stroke Rate (FSR, in Hz) on the basis of half-strokes (López et al., 2015; Ratsimbazafindranahaka et al., 2022). Finally, we computed two proxies of the forward speed: (1) the relative speed based on the flow noise recorded by the tag's hydrophone (66-94 Hz frequency band) (Cade et al., 2017) and (2) the absolute speed as the orientation-corrected depth rate, $\Delta\text{depth}/\sin(\text{pitch})$ (Cade et al., 2021; Miller et al., 2004). The flow noise was rescaled to represent a relative speed ranging from 0 to 1, corresponding to the minimum and the maximum detected speed, respectively. The absolute speed was only calculated when $|\text{pitch}|$ exceeded 30° (Narazaki et al., 2018).

Data analysis

Comparison of the swimming effort during downward and upward swimming

We subdivided all continuous periods with available absolute speed into 5-second duration segments, which were then used as the units of analysis. We categorized each segment as either downward (pitch < -30°) or upward (pitch > 30°) swimming and calculated the ratio of FSR to absolute speed as a proxy for the swimming effort (Noren et al., 2006). In addition, we calculated the average depth. We then modeled the relationships between the swimming effort (log-transformed response), depth, age, and swimming vertical direction (fixed effects) using a linear mixed-effects model (LMM), estimated in R (R core team, <https://www.r-project.org/>) with the *lme4* package (Bates et al., 2015), followed by a Type II ANOVA test. We included the interaction between the fixed effects and added individuals as random effects. Compliance with the model assumptions was checked graphically. The LMM was followed by Tukey's post-hoc tests (R package *emmeans*) (Lenth et al., 2018) to compare the swimming effort between swimming directions at 5, 15, 30, and 45 m depth for each age class.

Segments with an absolute speed of 0.5 m s^{-1} or less were excluded from the analysis as considered stationary or quasi-stationary.

Description of the stationary behaviour

For each deployment, we located all periods during which the individual was stationary and calculated the corresponding average depth. A stationary period was defined as a $>10 \text{ s}$ continuous period during which the relative speed was <0.2 (i.e., speed less than 20% of the maximum speed recorded for each individual), the depth rate was $<0.05 \text{ m s}^{-1}$, and the vertical acceleration was $<0.05 \text{ m s}^{-2}$. For each calf tagged with a CATS cam (thus with video data available), we audited the video corresponding to each stationary period using BORIS v.7.9.22 (Friard & Gamba, 2016) to note the calf's position relative to its mother at that time.

Results

Adult female humpback whales exert similar effort to swim downward and upward at any given depth, but calves do not

A total of 2072 downward (428 from C1-C2 calves, 1388 from C3 calves, and 256 from adults) and 1549 upward (308 from C1-C2 calves, 1107 from C3 calves, and 134 from adults) segments were extracted for the analysis of the swimming effort. We found a statistically significant interaction effect of depth, age, and swimming vertical direction on the swimming effort (Type II ANOVA, $\chi^2 = 18.88$, $df = 2$, $P < 0.001$). For both C1-C2 and C3 calves, the swimming effort during upward swimming was lower compared to downward swimming when at shallow depth. This discrepancy narrowed with increasing depth until reaching a depth at which the relationship reversed (around 35 m for the C1-C2 calves and 18 m for C3 calves, yellow stars in Figure 1), and the effort during upward swimming became higher than downward swimming with widening discrepancy with increasing depth (Figure 1). For the adult females, the swimming effort during upward and downward swimming was similar regardless of the depth (Figure 1). There was a statistically significant difference in effort between downward and upward swimming for the C1-C2 calves at 5 and 15 m and a statistically non-significant difference at 25, 35, and 45 m (Table 1). For the C3 calves, the post-hoc tests indicated a statistically significant difference at all tested depths (Table 1). For the mother, no statistical difference was found at any of the tested depths (Table 1).

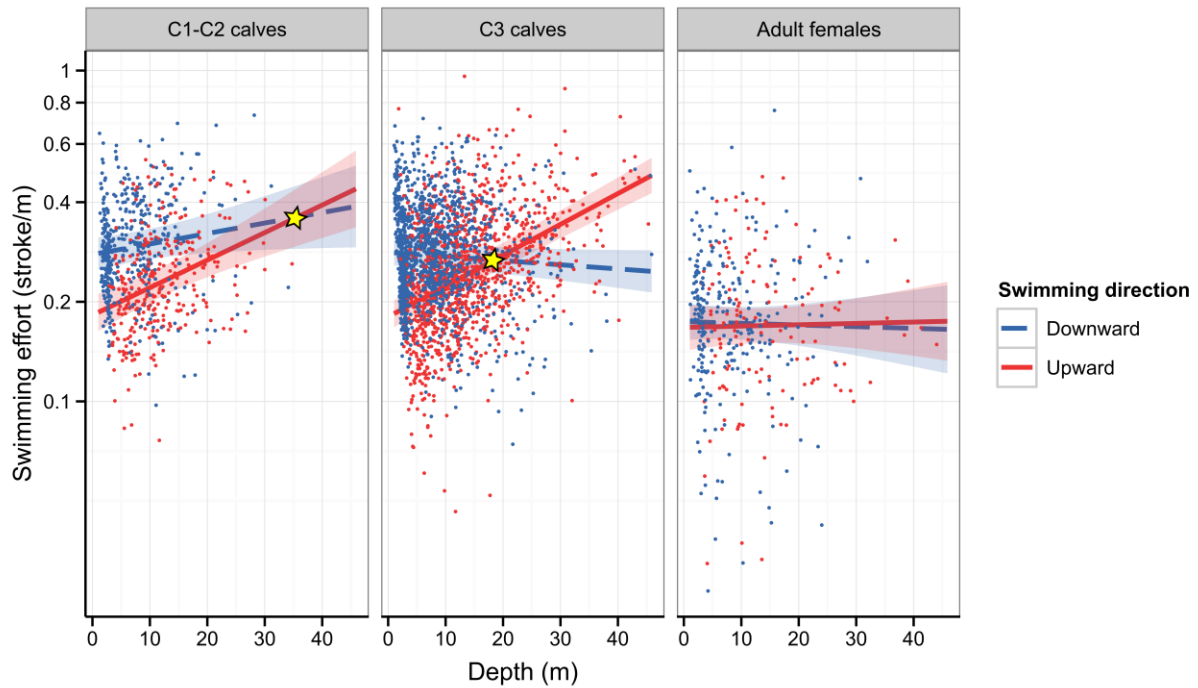


Figure 1. Relation between the swimming effort, depth, and direction for C1-C2 calves, C3 calves, and Adult females. Each point on the graph represents a 5 s swimming segment, either upward (red dots) with a pitch greater than 30° or downward (blue dots) with a pitch less than -30° . The lines represent the regression from a linear mixed-effects model (LMM): solid red lines for upward swimming and dashed blue lines for downward swimming. For C1-C2 and C3 calves, the effort exerted during upward swimming was lower compared to downward swimming when swimming at shallow depths. However, as the depth increased, the swimming effort during upward and downward swimming became more similar until reaching a certain depth where a transition occurred (intersections between the solid red line and the dashed red line, indicated by yellow stars). Beyond this depth, the effort exerted during upward swimming became higher. On the other hand, for the adult females, the swimming effort during upward and downward swimming remained similar regardless of the depth, as indicated by the quasi-superposition of the solid red line and the dashed blue line

Table 1. Comparison of the swimming effort between downward (Down) and upward (Up) swimming at 5, 15, 25, 35, and 45 m using Tukey's post-hoc multiple comparisons tests following a linear mixed-effects model (LMM) for three age classes C1-C2 calves, C3 calves, and Adult females. Bold *P*-values indicate statistically significant differences

Depth (m)	C1-C2		C3		Adult	
	Down/Up	<i>P</i>	Down/Up	<i>P</i>	Down/Up	<i>P</i>
5	1.438	<0.001	1.387	<0.001	1.031	0.995
15	1.277	<0.001	1.087	<0.001	1.009	1
25	1.134	0.649	0.853	<0.001	0.988	1
35	1.007	1	0.668	<0.001	1.967	>0.999
45	0.894	0.989	0.524	<0.001	1.947	>0.999

Humpback whales are able to stay stationary at varying depths

Most adult females and a significant proportion of the C3 calves could be found stationary at varying depths (Figure 2A): the range was at least 5 m in 1/7 C1-C2 calves, 7/13 C3 calves, and 10/16 mothers. By inspecting the video data when available, we found that the C1-C2 calves were always below their mother, pressed against her when stationary (circle symbols in Figure 2A, Figure 2B, 36 stationary periods from four calves). On average, the stationary periods occurred at 5.7 ± 6 m depth (range = 1.2–17.4 m). The C3 calves were observed stationary and mostly close to their mother, but without touching her (diamond symbols in Figure 2A, Figure 2C, 22/23 stationary periods from three calves) at 18 ± 1.5 m depth (range = 16.1–23 m). During the stationary period at 23 m (the observed maximum depth at which a calf was observed stationary), the calf rested on the seafloor (Figure 2D, Video S1, supplemental information). We observed a C3 calf staying stationary below the mother, pressed against her only on one out of 23 occasions, at 2.1 m depth.

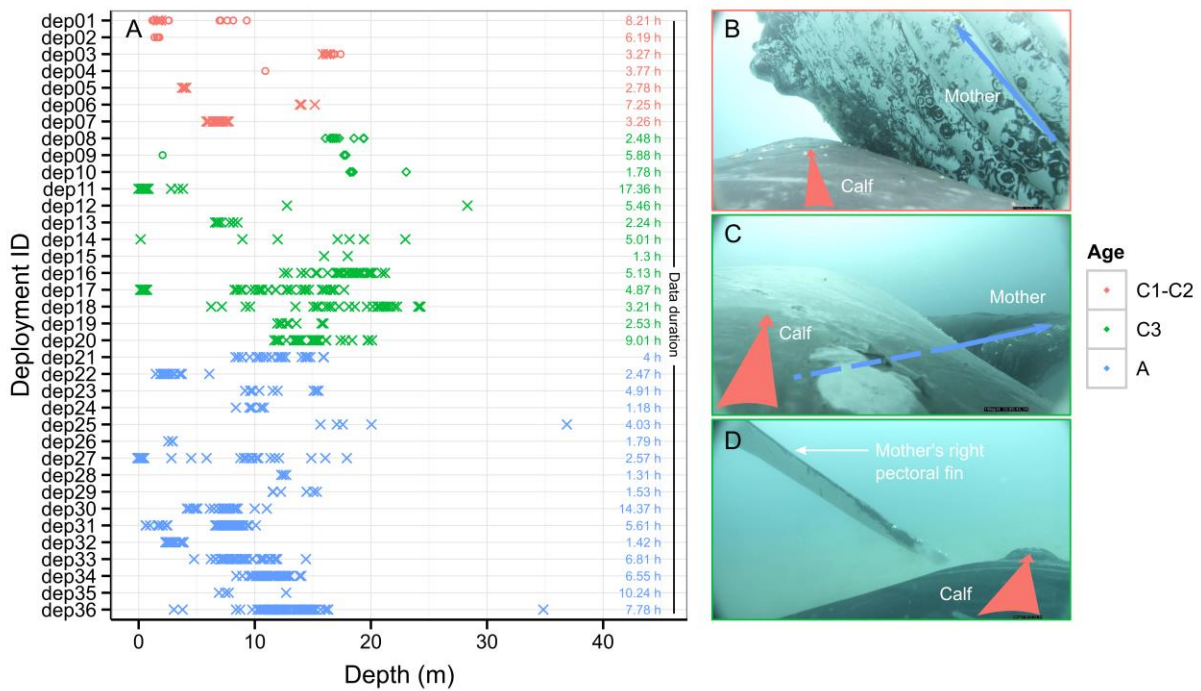


Figure 2. Stationary behaviour of humpback whale calves and adult females. (A) Depths at which a stationary period > 10 s occurred for seven C1-C2 calves (red), 13 C3 calves (green), and 16 adult females (blue). Several individuals, and in particular the adult females, stayed stationary at varying depths. Cross symbols indicate data without video (either data from Acousonde tags or data during misdirected camera from CATS cam tags). Circle symbols indicate periods during which the calf was visually confirmed (from video data, thus only for CATS cam data) to be below its mother and pressed against her and concerned only C1-C2 calves, except one period in one C3 calf (dep09). These periods corresponded to depths above the depth at which the calves displayed similar effort to go up and down (around 35 m for the C1-C2 calves and 18 m for C3 calves; see also Figure 1). Diamond symbols indicate periods during which the calf was visually confirmed (from video data, thus only for CATS cam data) to be close to its mother but not touching her and concerned only C3 calves. These periods corresponded mostly to depths at which the C3 calves displayed similar effort to go up and down (18 m). (B) A C1-C2 calf observed staying below its mother and pressed against her at 7.1 m depth. (C) A C3 calf staying stationary at 17.3 m depth next to its mother without touching her. (D) A C3 calf observed staying stationary at 23 m depth, resting on the seafloor. See also Video S1, Supplemental information. (B–D) Red and blue arrows indicate the longitudinal axis of each individual in the images and point toward the snout

Discussion

The generally described vertical swimming patterns of marine mammals (Miller et al., 2004; Skrovan et al., 1999; Williams et al., 2000) were not observed in our results on adult female humpback whales. Instead, we found that adult female humpback whales

exerted similar effort to swim downward and upward at any depth. However, the described patterns align well with our results on humpback whale calves. The calves exerted more effort to swim downward than upward in shallow depths and more effort to swim upward than downward at greater depths. This observation suggests that a calf's swimming effort depends on the depth, which is related to the ambient pressure change. However, our results on adult female humpback whales suggest a different mechanism. Adult female humpback whales have some control over their buoyancy that allows them to optimize their swimming efficiency regardless of the depth and swimming direction by reducing buoyancy to descend or increasing it to ascend. This control appears absent in calves < 3 months old because it is still developing. This precise control likely needs a learning process, probably obtained during breaching activities, which are also frequently observed in calves in the breeding area (calves born in the season). Our statements are also corroborated by the observed stationary behaviour. We found that both the adult females and the calves can stay stationary with no movements at various depths. However, for calves, unless at a depth where they are neutrally buoyant due to the ambient pressure (estimated to be around 18 m for C3 calves and 35 m for C1-C2 calves, see Figure 1), external help (mainly from their mother) appears to be needed. Within the range where they would require more effort to go downward than upward (thus positive buoyancy), they were always found positioned below their mother, pressed against her, likely to prevent accidental surfacing. Conversely, within the range where they would require more effort to go upward than downward (thus negative buoyancy), they may rest on the seafloor.

We argue that the ability to control the buoyancy is a unique feature of mysticetes among mammals, as one of the potential underlying mechanisms lies in the particular characteristics and specific structure of their respiratory system (Adam et al., 2013; Gandilhon et al., 2015; Reidenberg, 2018, 2022; Reidenberg & Laitman, 2007). The tension of the surrounding tissues and several anatomical elements of the mysticete respiratory tract can potentially isolate the system from the effects of ambient pressure. Most importantly, mysticetes may be able to control the volume of the inhaled air, especially by changing the volume of the laryngeal sac, and thus modulate their buoyancy depending on the situation (Adam et al., 2013; Gandilhon et al., 2015; Reidenberg, 2018, 2022; Reidenberg & Laitman, 2007). There are several valves that may isolate portions of the respiratory tract, including a) the blowholes that are tightly closed at rest, b) the epiglottis that isolates the nasal cavities from the larynx, c) the arytenoid cartilages that, when opposed with a large thick cushion on the cricoid cartilage, fully isolates the laryngeal sac from the trachea and the lungs. In addition, the surrounding bones, cartilage, and strong muscles help stabilize the volumes of these chambers. Regarding this last point, the nasal cavities are positioned between the bones of the skull and mesorostral and alar cartilages; the trachea is reinforced by complete circular cartilaginous rings on all its length; and the laryngeal sac is surrounded by a thick layer of skeletal muscles (Reidenberg & Laitman, 2007).

Williams et al. (2000) found that adult blue whales become negatively buoyant at around 18 m, a conflicting result compared to our findings. However, the sample they used (three dives from one individual) likely failed to capture the general swimming pattern associated with the buoyancy control. Interestingly, only the dive profile of the blue whale showed a significant depth overlap between the descent's terminal glide and the ascent's terminal glide among the presented dive profiles from different species (Figure 1 in Williams et al., 2000). It may be because the whale gained momentum from the active swimming phase, but it may also indicate the absence of a fixed depth at which the buoyancy switches from positive to negative in mysticetes due to the active control of their respiratory system. Alternatively, the buoyancy control may only have evolved in humpback whales, thus explaining the differential swimming behaviour reported in other mysticete species between descent and ascent (e.g., blue whale, Williams et al., 2000; right whale, Nowacek et al., 2001). Dive depth should also be considered. While mysticetes may be able to control their buoyancy, it may only apply to shallow dives (e.g., dives within the range we observed at least – 0–60 m depth) as the pressure may be too strong at significantly greater depth. Future work should focus on the analysis of data recorded during deep dives (up to 616 m for humpback whales, Derville et al., 2020). In those cases, the whale may suffer respiratory system collapse and decreased buoyancy, enabling long descent glides as in Nowacek et al. (2001). Nevertheless, the potential ability to control buoyancy should be investigated further. Even if buoyancy control only occurs at relatively shallow depths, it may have implications for energetic costs in mysticetes, particularly adult females who may be conserving energy while swimming with or nursing calves near the surface. In a recent study where the same model was used for baleen and toothed whales for calculating the energetic cost of breaches, a particularly high expense was returned (Segre et al., 2020). Since mysticetes generally live on their energetic reserve during the breeding season, engaging in such an energy-expensive activity in the long term, especially for lactating females, is counter-intuitive. The hypothesis of a buoyancy control may solve this issue, as a voluntary change to positive buoyancy at depth may significantly reduce the required effort to accelerate toward the surface and breach.

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<https://doi.org/10.5281/zenodo.8362299>

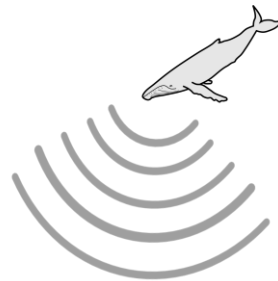
Video S1. Videotape corresponding to the C3 calf observed staying stationary at 23 m depth, resting on the seafloor. The video starts with the calf below the mother, still non-stationary (relative speed ≥ 0.2 , depth rate $\geq 0.05 \text{ m s}^{-1}$, and vertical acceleration $\geq 0.05 \text{ m s}^{-2}$), and the seafloor not visible yet. The calf then slowly went down, and the seafloor started to be visible. From 00:34, the calf appeared to touch the seafloor, and the stationary criteria were met (relative speed < 0.2 , depth rate $< 0.05 \text{ m s}^{-1}$, and vertical acceleration $< 0.05 \text{ m s}^{-2}$ for at least 10 s duration) for about 11 s. The recorded depth was 23 m. Subsequently, the calf remained at the bottom, but the very conservative stationary criteria were not met anymore. At 01:20, the calf ascended to the surface to breathe. In the immediately following dive, the calf returned to the bottom and rolled against the seafloor (02:08). The tag recorded a depth of 24 m at that time, which corresponds to the local seafloor level and thus likely to the seafloor level when the calf was stationary in the previous dive, as no traveling behaviour suggesting a significant location change was observed in-between. The 1 m difference between the depth recorded during the stationary period (level of the calf's back) and the seafloor level supports the observation that the calf rested on the seafloor during the stationary period. Note that the video speed is $\times 10$ from 01:25 to 01:58

Part III: Mother-calf vocalizations: from who, what, when, why?



Chapter 5. Who's talking? Vocal communication in humpback whale mother-calf pairs

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*Revision submitted to **Animal Behaviour***

Synthesis

In which context do the mother and the calf use vocalizations, and what functions do the vocalizations potentially have? On the spatial context and the difference in vocal behavior and attributes

Methods

Depth and sound data from six mother-calf simultaneous Acousonde deployments were used. The two tracks (mother and calf sound data) were audited simultaneously as a stereo recording to label social calls depending on whether it was heard on both channels (unknown emitter) or only on one of them (thus very likely to be from the mother or the calf if only on the mother or the calf channel, respectively) and according to their type based on previously established catalog. An RF analysis was then used to compare the acoustic characteristics of the calls likely from the mother and the calls likely from the calf and to automatically identify the caller identity for the calls with an unknown emitter. The vertical distance at which the calls were emitted relative to the other individual was compared for the calls from the mother and the calf. The occurrence of vocal exchange (one individual replying vocally to another) was also analyzed.

Findings

Humpback whale mother-calf pairs produce social calls at a rate of about 11 calls/hour, and they mainly use low-frequency calls. A higher fundamental frequency characterizes the calves' calls compared to those of the mothers, and the RF model can predict the emitter identity. The calf is responsible for the acoustic contact during periods of vertical separation, and the mother rarely vocally responds to the calf's calls. A particularly relevant finding is that most calls recorded by a tag placed on an individual in mother-calf pairs are likely from the tagged individual.

Abstract

In the context of the mother-calf relationship in mammals, offspring must communicate their needs to their mother to influence her behaviour and ensure they benefit from maternal care, for example, using vocalizations. In humpback whales, *Megaptera novaeangliae*, unlike the songs of adult males, the vocalizations of mother-calf pairs (social calls) have been poorly studied, namely because of technical limitations. Our study used simultaneous acoustic tag deployments on the mother and the calf and a machine learning approach to identify the caller and study the dynamics of vocal communication as well as the potential biological function of calls in mother-calf pairs. We estimated a mother-calf combined vocal output of about 11 calls/hour and identified a repertoire mainly composed of low-frequency (LF) calls for both the mother and the calf. We identified significant differences in acoustic characteristics of the LF calls, particularly fundamental frequency (F0), between mothers and calves, hinting at a mechanism for differentiating signals from young with signals from adults by females. Furthermore, we found that calves are primarily responsible for acoustic contact during periods of vertical separation, and in general, mothers do not respond vocally to the calls from their calves. Our results represent a new step toward understanding the mother-young pair's acoustic interactions in humpback whales and the underlying mechanism of mother-young acoustic communication in fully aquatic large mammals.

Keywords: baleen whale, breeding ground, maternal care, parent-offspring interaction, social call, sound production

Introduction

The survival of young mammals and, thus implicitly, the reproductive success of females depends on successful maternal care (Clutton-Brock, 1991). In this context, the young must communicate their need to their mother to influence their mother's behaviour and ensure they benefit from maternal care (Gubernick & Klopfer, 1981; Lent, 1974; Nowak et al., 2000). Conversely, mothers must communicate with their offspring, for example, to stimulate them and to encourage them to follow (Lent, 1974) and to express their needs in maternal care (food, warmth, protection against predators) (Gubernick & Klopfer, 1981). Successful maternal care usually includes targeted investment to avoid spending effort on non-filial offspring and maximize the chance of perpetuating the mother's genetic material (Clutton-Brock, 1991). In species with precocial offspring (locomotory, sensorially, and thermoregulatory independent young very soon after birth) or those living in large groups or colonies (e.g., ungulates, otariids, etc.), this involves, for instance, the ability of the mother and the offspring to mutually recognize each other through chemical, acoustic, or visual communication (Charrier et al., 2022; Lent, 1974; Martin et al., 2022).

In an aquatic environment, acoustic signalling is the best communication strategy as acoustic signals are efficient at short and long ranges and easy to detect, identify, and localize, given an appropriately adapted auditory system. In contrast, visual and chemical cues do not provide such advantages. Cetaceans (baleen and toothed whales) are very well known to use acoustic signals in all crucial biological functions: navigation, foraging, breeding, predator avoidance, social contact, and care of the young (for review see Clark & Gagnon, 2022; Tyack, 2019).

The humpback whale, *Megaptera novaeangliae*, is one of the most studied baleen whale species as it occurs in all oceans and is easily observable along coastlines during its annual migration (Clapham, 2018). Previous studies on the acoustic communication of humpback whales have primarily focused on males' song behaviour. The use and function of non-song vocalizations are yet to be investigated in depth.

Non-song vocalizations are variable through time, interrupted by silent periods, apparently unpredictable, and do not show the rhythmic, consistent, and continuous repetitive temporal pattern of songs by males (Silber, 1986; Tyack, 1981) and are commonly considered as social 'calls.' Only recent studies have shown that humpback whale mother-calf pairs use acoustic signalling, particularly social calls (Cusano et al., 2022; Indeck, Girola, et al., 2021; Indeck et al., 2022; Saloma et al., 2022; Videsen et al., 2017; Zoidis et al., 2008). However, most of these calls' behavioural context and biological function still need to be better understood. Social calls are expected to play a significant role in the mother-calf pair's synchronization and social bond since vocal communication can convey various information such as individual identity (Martin et al., 2022) and physical attributes (Briefer & McElligott, 2011; Reby & McComb, 2003). As in other species, some social calls in mother-offspring groups may correspond to contact, distress, and begging calls (Carlson et al., 2020). Humpback whale calves' social calls appeared to elicit the mother's approach and were assumed to be potentially isolation or "alarm" calls by the calf to alert and(or) call the mother (Zoidis et al., 2008). Furthermore, certain calls linked to active dives of the calf were attributed to a cohesive function aimed at maintaining contact (Videsen et al., 2017). On another note, Indeck et al. (2022) found that during resting, when mothers and calves are more likely to not be in close contact, mother-calf pairs exhibited increased vocal activity, suggesting the role of the social calls as contact calls. An even relatively undocumented aspect of mother-calf communication in humpback whales and in baleen whale species in general concerns the existence of vocal exchanges, i.e., whether one individual responds vocally to the other's vocalisations. Vocal exchanges can be particularly useful in the context of mother-calf communication as they may serve for mutual recognition, contact maintenance, and reassurance (Pika et al., 2018).

Animal-borne acoustic multi-sensor tags (referred to as tags hereafter) enable the remote, fine-scale description of the behaviour of whales along with their acoustic activities (Johnson & Tyack, 2003), and as such, they became a powerful tool for

studying acoustic communication in humpback whale mother-calf pairs (Cusano et al., 2022; Indeck et al., 2022; Indeck, Girola, et al., 2021; Indeck, Noad, et al., 2021; Saloma et al., 2022; Videsen et al., 2017). One remaining big challenge in using such tags concerns, however, the identification of the sound emitter. Even if tags enable more comprehensive insights thanks to their integrated hydrophone, assigning the recorded vocalizations to an individual remains debatable (Goldbogen et al., 2014; Saddler et al., 2017). Indeed, the tags may record all surrounding sounds, including both the vocalizations from the tagged individual and nearby conspecifics. For groups with individuals spatially close to each other, like mother-calf pairs, it is considered that most vocalizations from the two individuals can be recorded by one tag placed either on the mother or on the calf. In other words, it is considered that the calls recorded by one tag represent the combined vocal outputs of the two individuals. Matching between accelerometer and sound signals has been suggested for assigning a call to a tagged whale (Goldbogen et al., 2014). However, this has only been applied to very low-frequency sounds from solitary species such as blue whales. A later study showed that in the case of non-solitary animals, vocalizations from nearby individuals could also be recorded in the accelerometer signals of the tagged animal (Saddler et al., 2017). Indeck et al. (2021) proposed the use of an unsupervised machine learning algorithm to globally cluster social calls from tags placed on mothers into two groups (one assigned to the mothers and the other to the calves). While interesting, such an approach is limited because an unsupervised machine learning algorithm only splits the data into a defined number of clusters so that the intra-cluster variation is small and the inter-cluster variation is large. Since social calls can also be classified into well-marked types (regardless of who produced it, for instance, barks, snorts, basses, etc.), the algorithm may report clusters based solely on the acoustic characteristics of the call types and not based on individual vocal differences of the emitters. As a result of such challenges, it remained difficult to clearly investigate various aspects of mother-calf acoustic communication by direct comparisons. Are calls emitted by adults and calves in humpback whales acoustically different and potentially encoding physical attributes (e.g., young vs. adult or small individual vs. large individual)? How can such calls reach the intended receiver in mother-calf pairs? What is the context in which each individual emits these calls, and is there evidence of an acoustic dialogue between the mother and the calf? In addition to these unanswered questions, the estimated overall call rate of mother-calf pairs remains uncertain, primarily because most call rate estimations were based on single deployments, typically on the mother (e.g., Cusano et al., 2022; Indeck et al., 2022). Such estimations overlook that it is improbable for the vocalizations of two animals, even closely associated, to be equally likely recorded by a tag placed on one of them.

In the present study, we investigated whether social calls potentially encode physical attributes and examined the vocal behaviours in adult female humpback whales and their young. More specifically, we tested whether there is an acoustic signature attributed to calves and mothers (young vs. adults), whether the vocal activities of the

mothers and the calves differ depending on the spatial context (separation vs. reunion), and whether a pattern in vocal exchanges occurs. In addition, we quantified the vocal activity level of mother-calf pairs (i.e., call rate). In order to achieve our goals, we proposed an alternative method for identifying the sound emitter identity using tags deployed simultaneously on mothers and their calves.

Materials and Methods

Field site

We collected the data off Sainte Marie island, Madagascar, South Western Indian Ocean (between latitudes 17° 19' and 16° 42' South, and longitudes 49° 48' and 50° 01' East) during the southern winter (July-September) of 2016 and 2017. The area around Sainte Marie island is among the most important breeding and calving areas for humpback whales in the South Western Indian Ocean (Trudelle et al., 2018). The present study is part of an ongoing study on humpback whale mother-calf interactions conducted since 2013 in the area.

Tag specifications

We used two units of Acousonde 3B for our study. Acousonde tags are small, lightweight tags (<400 g) attached to whales via four suction cups. They include a hydrophone and five primary auxiliary sensors (3-axis accelerometer, 3-axis magnetometer, pressure/depth sensor, temperature sensor, and light sensor). Each Acousonde unit was coupled with a VHF transmitter used for tag retrieval. For both units, the hydrophone recorded sounds at a 24.453 kHz sampling rate (16-bit resolution). The hydrophone's sensitivity/clip level was -187 dB re 1 V/ μ Pa. The sampling frequency for one of the Acousonde units was set at 10 Hz for all auxiliary sensors. For the other one, the sampling frequency of the auxiliary sensors was set at 20 Hz, except for the accelerometer, which was set at 400 Hz. Although the two units recorded auxiliary data at different sampling frequencies, all data were downsampled to 10 Hz for consistency in subsequent analyses.

Tagging procedures

We deployed the tags on the mother and the calf in mother-calf pairs from a 6.40 m rigid motorboat using a 5 m rigid handheld carbon fiber pole. The tagging order for the two individuals depended on the opportunity. The approaches we used are detailed in Huetz et al. (2022) and Saloma et al. (2022). Tags were placed on the top lateral side of the animals (Supplemental Figure S1). Laterally positioned tags minimize periods during which the tag is out of the water and thus allow optimized sound recordings. The pairs were not followed after tagging to avoid disturbance, and the tags were retrieved after a few hours or the next day when they detached from the animals (usually due to rubbing against the other individual, surface active behaviour, etc.). As

we did not follow the tagged animals, we did not have information on the extent to which the tags may have changed location on the animals throughout the deployments. We assumed that similar to the CATS cam tag (another model of suction-cup tags but with a camera), location changes are, if any, usually relatively small. For instance, within a deployment of about 8 hours, the tag displacement is approximately less than half a meter toward the animal's tail before the tag detachment (personal observation). As in previous studies (Indeck et al., 2022; Indeck, Girola, et al., 2021; Videsen et al., 2017), we conducted all the analyses described hereafter without considering the potential impact of varying tag locations, which is expected to be small.

Data processing

The sounds from the hydrophone and the data from the auxiliary sensors were downloaded as MT files and imported into MATLAB (Mathworks). The sound files were then downsampled to 12 kHz. The auxiliary data were calibrated using dedicated scripts adapted from the CATS Matlab toolkit (<https://github.com/wgough/CATS-Methods-Materials>, Cade et al., 2021). Deployments with data that could not be calibrated following the routine were discarded. This included for example, deployments with a high axial imbalance in the accelerometry and magnetometer data. As mentioned above, for consistency, all auxiliary data were downsampled to obtain a common sampling rate of 10 Hz across all sensors. The depth data (in meters) were then smoothed with a 0.5 s running median filter.

The internal clocks of the two units deployed on mother-calf pairs simultaneously were not always well synchronized (there may be several seconds of delay). Thus, we used sound cues detected in both units to align and synchronize the mothers' and calves' data (i.e., crew voices on the boat board after the tag setups, impact noises recorded prior to tagging, or even distant male songs). Only overlapping mother-calf data (sound and auxiliary data) were included in the study (i.e., data from the tagging time of the second individual to the moment one of the tags detached).

Acoustic analysis

We analysed simultaneously the sounds recorded by the calf's tag and those recorded by the mother's tag as a stereo recording (the calf as the first channel – calf channel, and the mother as the second – mother channel) using Avisoft SASLab Pro version 5.3.01 (Avisoft Bioacoustics, Nordbahn, Germany). We produced spectrograms of the stereo acoustic recordings using a 1024-point Fast Fourier Transform, 75% overlap, and Hamming window.

We inspected the audio files aurally and visually to isolate clearly distinguishable presumed vocally produced social 'calls' (i.e., not including social sounds such as surface percussive sounds – breaches, slaps –, apparent bubble sounds, rubbing sounds, etc.). We distinguished social calls from the surrounding male songs based on

temporal patterns and overlaps (Saloma et al., 2022). Social calls do not show rhythmic, consistent, and continuous temporal repetitive patterns like songs (Silber, 1986; Tyack, 1981).

For each clearly audible and distinguishable social call, we labelled it as 'Calf' if it was audible and visually distinguishable in the calf channel only, as 'Mother' if audible and distinguishable in the mother channel only, and 'Both' if audible and visually distinguishable in both the calf and the mother channels (in all cases, the time of occurrence and the fundamental frequency matched). If a call was audible and visually distinguishable on the calf channel, but there was a loud noise recorded on the mother channel at the corresponding time (e.g., surfacing noise), the call was labelled as 'Calf - Unsure.' Similarly, if a call was audible and visually distinguishable on the mother channel, but there was a loud noise recorded on the calf channel at the corresponding time, the call was labelled as 'Mother - Unsure.' We assumed that social calls detected only on the calf channels, thus labelled 'Calf,' are likely to be social calls produced by calves; calls detected only on the mother channels, thus labelled as 'Mother,' are likely to be produced by mothers; and calls detected on both calf and mother channels, thus 'Both' are either produced by the calves or by the mothers. Such assumptions relied on a general premise in tag-based studies that the vocalisations by an individual would be at least recorded by the tag directly placed on it.

We also categorized the call based on the peak frequency observed on the spectrogram as either a low-frequency call (LF, peak frequency ≤ 160 Hz), mid-frequency harmonic call (MF, $160 < \text{peak frequency} \leq 700$ Hz), high-frequency harmonic call (HF, peak frequency > 700 Hz), amplitude modulated call (AM, a combination of long harmonic and amplitude modulated components with peak frequency ranging from 20 to 300 Hz), or pulsed call (PS, low-frequency sounds repeated rhythmically) (Saloma et al., 2022). Furthermore, a type (name) was attributed by aurally and visually comparing the social call with spectrograms, descriptions, and examples from previous descriptions of social call types found in the same area (see the catalogue in Saloma et al., 2022). The robustness of such aural-visual classification (77% agreement when tested with an automatic classifier), as demonstrated by Saloma et al. (2022), provided enough accuracy for the scope of our study. Sounds that might be recorded during brief and rare periods where the tag was out of the water were not included in the present study. Out-of-the-water periods were identified as periods at the surface corresponding to a sudden change in ambient noise and directly preceding and following a splashing sound associated with the transition from water to air (usually when the whale emerges to breathe).

For each labelled call, we used the data from the pressure sensor to calculate the corresponding vertical distance between the mother and her calf (depth difference between the two individuals, in meters). In addition, we measured nine acoustic features for calls with SNR > 6 dB (on the clearest signal and with SNR > 6 dB of the two

channels if the call was detected on both channels): the duration (Dur, in s), the peak frequency (Fmax, in Hz), the first, second and third energy quartile frequency (Q25, Q50, Q75 respectively, in Hz), the energy below 100 Hz for LF and PS calls, below 300 Hz for MF and AM calls, and below 900 Hz for HF calls (ebelow, in %), the frequency bandwidth within which the total energy fell within 12 dB of Fmax (Bdw, in Hz), and the fundamental frequency (F0, in Hz). The spectral characteristics were measured on the averaged spectrum (frequency ranges: 30-1000 Hz for LF and PS calls, 100-6000 Hz for MF and AM calls, and 500-6000 Hz for HF calls). All spectral characteristics' measurements were performed automatically except for the F0, which was measured manually using the harmonic cursor available in Avisoft SASLab Pro for finding harmonic structures. Frequencies were measured on a linear scale as we were equally interested in all frequencies within the already restricted bandwidth of analysis (0-6 kHz), from the F0 (usually of very low frequency) to the highest harmonics. The signal-to-noise ratio (SNR, in dB) was calculated as the ratio between the measured call received level (RL) and ambient noise level. The RL (in dB SPL re 1 μ Pa Root Mean Square) was measured using a 0.125 s window covering the loudest section of the call (Videsen et al., 2017). The ambient noise level (in dB SPL re 1 μ Pa Root Mean Square) was taken as the lowest of the noise power measurements among 0.5 s intervals throughout the 10 s period prior to each call (Parks et al., 2011).

The RL and SNR were only used for assessing the quality of the recorded signals for further acoustic measurements and not for assigning an emitter to each call (see below). Indeed, the comparison of RL and SNR between the mother and calf channels to assign an emitter to each call is very limited as these values are highly dependent on the noises recorded by the tag at a given time, which can be completely different for the two individuals due to difference in activities (difference in swimming speed, location – surface vs. at depth, etc.), physical attributes, and tag placement.

Data analysis

To assess the occurrence of acoustic signatures attributed to calves or mothers, we first examined the frequency distribution of each call type (determined qualitatively) per labels ('Calf,' 'Mother,' 'Both,' and 'Unsure'). Then we compared the temporal and spectral characteristics of calls labelled as 'Calf' and those labelled as 'Mother' in a multivariate analysis, using a Random Forest (RF) algorithm for classification. Specifically, we trained a balanced RF model in R (R core team, <https://www.r-project.org/>) with the package *randomForest* (Liaw & Wiener, 2002) to classify the calls into either 'Calf' or 'Mother' based on the measured temporal and spectral characteristics (Dur, Fmax, Q25, Q50, Q75, ebelow, Bdw, and F0). The balanced RF design maintained equal sample sizes for each class ('Calf' vs. 'Mother') in the classification and thus prevented over-representation of the most represented class (Chen et al., 2004). Only calls for which all acoustic parameters have been measured were included. The number of variables randomly selected at each split was set to 2.

The number of trees grown was set to 500. The misclassification rate was calculated as the out-of-bag (OOB) error rate (Liaw & Wiener, 2002). The accuracy of the classification (calculated as $1 - \text{OOB error rate}$) was compared to a prediction by chance (0.5 or 50% since there are two balanced classes) to evaluate how much the prediction by RF is better than a random allocation of class. In addition, multidimensional scaling (MDS) was applied to visualize the dissimilarities in the calls across the two classes using the proximity matrix from the RF algorithm (Hennelly et al., 2017). The Gini index, which gives the importance of the variables used for the classification, was used to identify the most informative acoustic characteristic(s), allowing the discrimination of the calls labelled as 'Calf' and those labelled as 'Mother.' As the separation between the main call categories (LF, MF, HF, etc.) in humpback whales is relatively pronounced (Dunlop et al., 2008; Saloma et al., 2022), we deemed it reasonable to consider them separately (i.e., different RF models). However, only LF calls were well-represented (see Results). Thus, we only conducted an RF analysis for LF calls, these ones being the most common calls in humpback whale mother-calf pairs (Saloma et al., 2022).

After checking for the occurrence of acoustic signatures attributed to calves and mothers, we used the trained RF model to assign an emitter to calls recorded simultaneously on both channels or uncertain (i.e., those labelled as 'Both' or 'Unsure') and thus obtain a presumed emitter for all of these calls. Then, to assess whether there was a difference in the distance at which each protagonist (calf or mother) emitted calls relative to the other one, we compared the vertical distance between the pair at the time of call production for the two presumed emitters using a Mann-Whitney U test in R. Furthermore, to get an insight into the vocal exchanges between the calf and its mother, we analysed the calves' and mothers' call temporal patterns. All calls (the LF calls previously used in the RF analysis and the remaining calls) were included to consider the pairs' global vocal activities. The emitter identity of the MF and HF calls recorded simultaneously on both channels was kept as 'undefined' since the trained RF model was only for LF calls. The emitter identity of all LF calls for which some acoustic parameters could not be measured was also kept as 'undefined.' We grouped the calls into sequences with breaks based on the calf's diving/surfacing behaviour. For instance, we considered all calls within the same dive (any submergence to a depth of > 10 m, Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022; Stimpert et al., 2012) or surface activity period (the period between two successive dives) as part of one sequence. For each sequence, we characterized the succession pattern of the mother-calf calls. Using a pairwise exact multinomial test with FDR-adjusted P , we compared the occurrence of sequences with exchanges between the calf and the mother, the occurrence of sequences composed only of calls from the calf, and the occurrence of sequences composed only of calls from the mother. Furthermore, we characterized the context of the sequences. The context included whether the calf's activity was synchronized with the mother's activity (the calf and mother diving or being at the surface together) or whether the individuals of the pair were vertically separated. If the behaviour corresponding to the sequence was a dive, we determined whether the descent was

synchronized (both the calf and the mother initiated a dive, and the mother was still at a ≤ 10 m depth when the calf left the surface), corresponded to reunion dive (the mother was already at > 10 m depth when the calf left the surface), or was a lone dive (the mother was still at the surface depth when the calf reached 10 m depth). In addition, we determined whether the ascent was synchronized (both the calf and the mother went back to the surface, and the mother was at a ≤ 10 m depth when the calf reached the surface) or separated (the calf went back to the surface, but the mother was still at > 10 m depth when the calf reached the surface, either because the calf went up rapidly compared to the mother or because the mother stayed at depth). When the behaviour corresponding to the sequence is a surface activity, we determined whether the activity was synchronized (calf's surface activity between successive synchronized ascent and synchronized descent), partially synchronized (partial overlap of the calf's surface activity with its mother's surface activity, because the previous ascent from dive and/or the subsequent descent was/were not synchronized), or corresponding to the calf being alone at the surface (the mother stayed at depth).

Where applicable, Standard Deviations (SDs) are presented along with the mean in the format mean \pm SD. Non-parametric statistical tests were used in our analyses because of the small sample size and the non-normality of the data. The statistical significance level was set to $\alpha = 0.05$.

Results

Over the two fieldwork seasons, we performed 13 simultaneous mother-calf deployments (i.e., 13 mother-calf pairs). However, only six were considered in the present study as the others showed insufficient overlapping time (less than half an hour) or were not possible to calibrate following the chosen calibration routine. The analysed simultaneous deployments data lasted 2.3 ± 2.8 hours on average (range = 0.5–7.8 hours, total = 13.7 hours) and corresponded mainly to daytime. All the pairs included in the study were not accompanied by any escort at the time of the tagging except one (dep04).

A total of 113 distinguishable social calls were detected. LF calls were the most represented (98/113 calls), followed by MF calls (14/113 calls), and finally by HF calls (1/113 calls). About 11 calls per hour were produced on average by a mother-calf pair (range = 5–15 calls/hour/pair, $N = 6$). Although no PS calls were reported, we must note that we found some low-frequency sounds rhythmically repeated that may be considered pulsed sounds. However, these sounds were very mechanical and percussive. While we do not exclude the possibility of mysticetes being able to produce such sounds vocally, we chose not to consider these sounds as vocalizations due to uncertainty.

A total of 28 calls were detected only in the mother channels (i.e., labelled as 'Mother'), and 47 were detected only in the calf channels (i.e., labelled as 'Calf'). A total of 33 calls

were simultaneously detected in both calf and mother channels (i.e., labelled as 'Both'). The five remaining calls were labelled as 'Calf - Unsure' as they were seen on calf channels but unconfirmed on the corresponding mother channel due to the presence of loud noise (mostly surfacing time). The distribution of the detected calls per type per category is shown in Figure 1, and a representative spectrogram of each of them is presented in Supplemental Figure S2. The most common calls could be attributed to 'bark,' 'bass,' 'snort' (LF calls), and 'groan' (MF calls). 'Barks' were either detected only on the calf channels (although some were labelled as 'Calf - Unsure') or simultaneously on both mother and calf channels. No 'barks' were detected in the mother channels alone. 'Basses' were detected mostly on the calf channels alone. 'Snorts' and 'groans' were detected in calf or mother channels alone or both channels. The other calls such as 'burp,' 'gru,' 'thwop,' and 'wop,' 'heek,' 'whoop,' 'wiper,' and 'HF groan' were less common and were never detected at the same time in both channels, except for 'thwop' (one case). The 'HF groan' is a new name we attributed to a type of call that did not fall within the social calls previously described in the same area. The name relates to its similarities with the groans but with higher frequencies (>700 Hz).

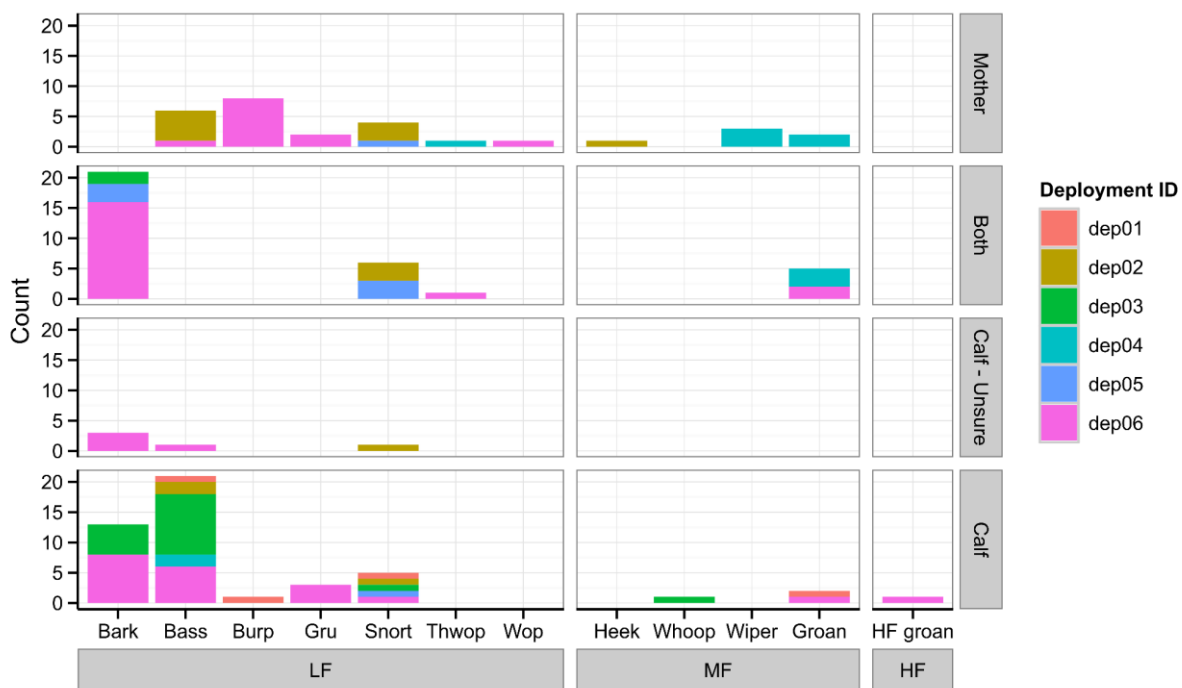


Figure 1. Distribution of the social calls per category and per type recorded in mother-calf simultaneous deployments. LF: Low-frequency calls. MF: Mid-frequency calls. HF: High-frequency calls. 'Calf': calls detected in the calf channels only. 'Mother': calls detected in the mother channels only. 'Both': calls detected in both calf and mother channels at the same time. 'Calf - Unsure': calls detected on the calf channels but with uncertain categorization as 'Calf' or 'Both' due to a loud noise recorded on the mother channel at the corresponding time (e.g., surfacing noise). 'Mother - Unsure' (not shown as no call fell within this label): similar to 'Calf - Unsure' but concerning the calls detected on the mother channels

The calls labelled as 'Mother' and those labelled as 'Calf - Unsure' were produced mainly when the calf and the mother were vertically close to each other, i.e., when approximately at the same depth (calf-mother vertical distance, 'Mother': mean = 1 ± 0.9 m, range = 0 – 4.3 m, $N = 28$; 'Calf - Unsure': mean = 1.5 ± 1.2 m, range = 0.2 – 2.9 m, $N = 5$). Calls labelled as 'Calf' and those labelled as 'Both' were, however, produced at more variable vertical distances, from short to relatively long (vertical) distances (calf-mother vertical distance, 'Calf': mean = 4.7 ± 6 m, range = 0 – 25.8 m, $N = 47$; 'Both': mean = 6 ± 5.6 m, range = 0.1 – 23.9 m, $N = 33$). An example of dive profiles of one mother-calf pair plotted along with the occurrence of calls is shown in Figure 2.

The eight acoustic features (Dur, Fmax, Q25, Q50, Q75, ebelow 100 Hz, Bdw, and F0) measured for 62 LF calls (28 'Calf,' 5 'Calf - Unsure,' 17 'Mother,' 12 'Both') are shown in Figure 3 and in Supplemental Table S1. For the classification of the calls labelled as 'Calf' and 'Mother' based on their acoustic features, the trained random forest showed a global accuracy of prediction of 80% (OOB error rate = 20%, Figure 4). This accuracy was greater than the accuracy expected by chance in a balanced dataset (50%). Although there was some overlapping in the multidimensional scaling (MDS) plot, most of the LF calls originally labelled as 'Calf' and those originally labelled as 'Mother' appeared to occupy distinct regions (Figure 4). The acoustic variable showing the highest importance for the classification was F0 (Gini index: 4.11) and was followed by Q25, ebelow 100Hz, Fmax, Q75, Q50, Bdw, and then Duration (Gini index: 2.15, 2.06, 1.96, 1.85, 1.82, 1.53, 1.51, respectively).

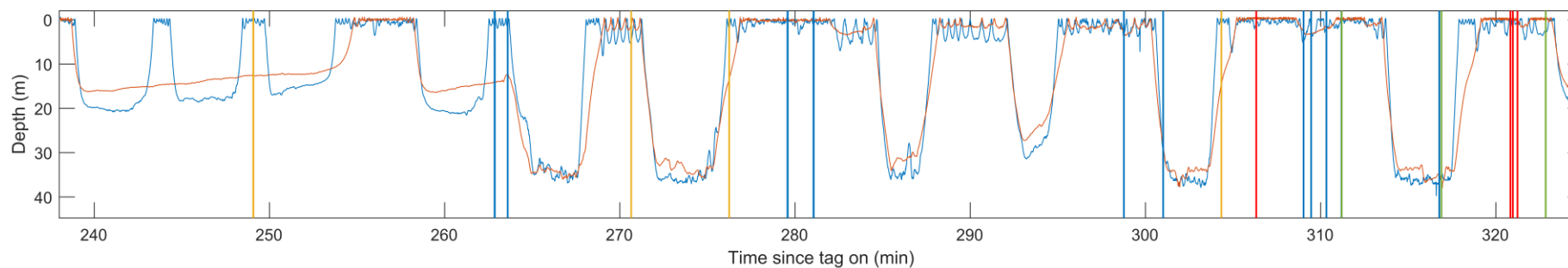


Figure 2. Dive profiles of a female humpback whale and her calf tagged simultaneously with Acousonde tags. Red and blue curves correspond to the mother and the calf's dive profile, respectively. The vertical lines correspond to the occurrence of social calls detected simultaneously in the mother and calf channels (yellow, labelled as 'Both'), detected only in the mother channel (red, labelled as 'Mother'), heard only in the calf channel (blue, labelled as 'Calf'), and heard in the calf channel but unconfirmed on the corresponding mother channel due to the presence of loud noise (green, labelled as 'Calf - Unsure')

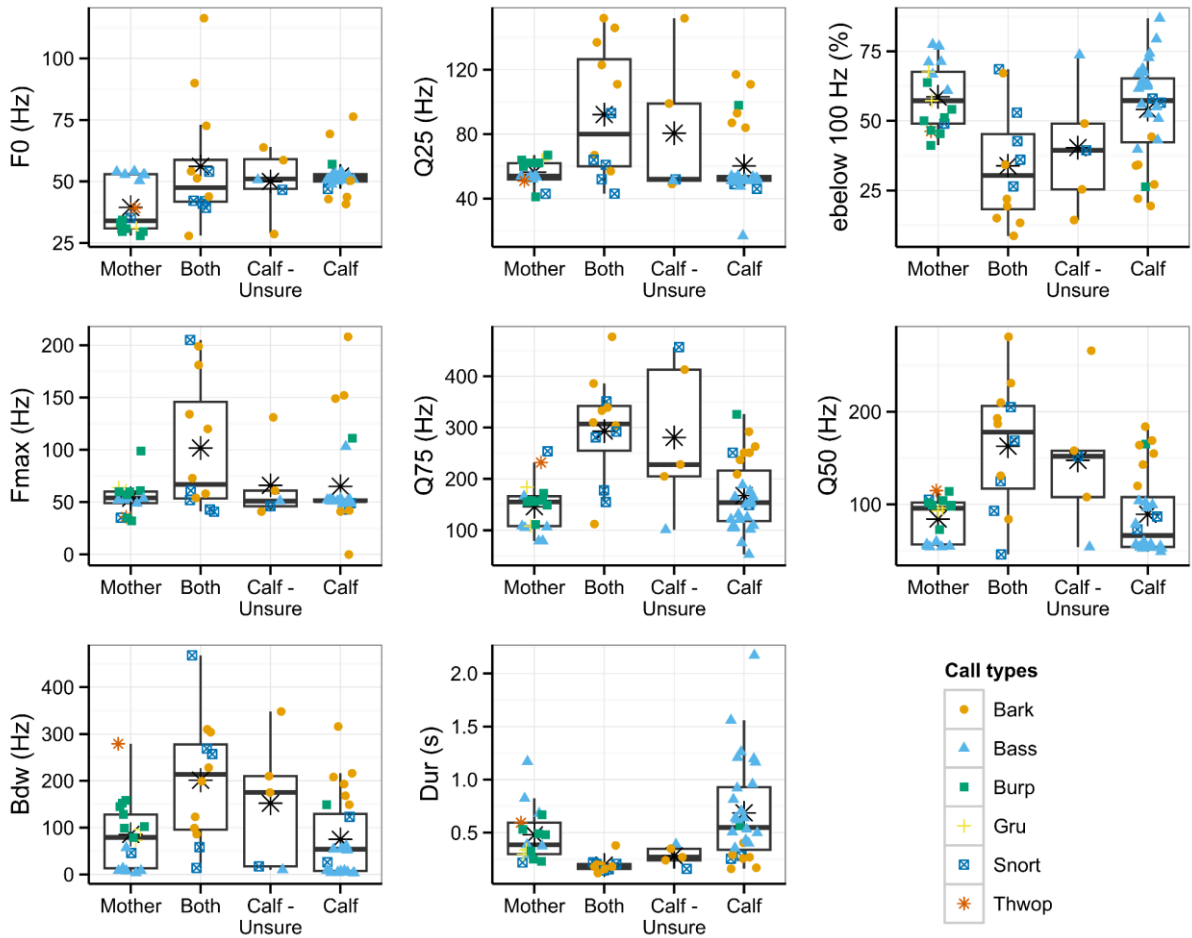


Figure 3. Temporal and spectral characteristics of 62 Low-frequency (LF) calls detected in six mother-calf simultaneous deployments. 'Mother': calls detected in the mother channel only. 'Both': calls detected in both the calf channel and mother channel at the same time. 'Calf - Unsure': calls detected in the calf channel and with loud noise recorded on the mother channel at the corresponding time. 'Calf': calls detected in the calf channel only. F0: fundamental frequency. Fmax: peak frequency. ebelow 100 Hz: energy below 100 Hz. Q25, Q50, Q75: first, second, and third energy quartile frequency, respectively. Bdw: frequency bandwidth within which the total energy fell within 12 dB of Fmax. Dur: duration. Coloured symbols represent different call types: filled orange circles correspond to 'barks,' filled light blue triangles to 'basses,' filled green squares to 'burps,' yellow plus symbols to 'grus,' dark blue squares with a cross to 'snorts,' and red star symbols to 'thwops'

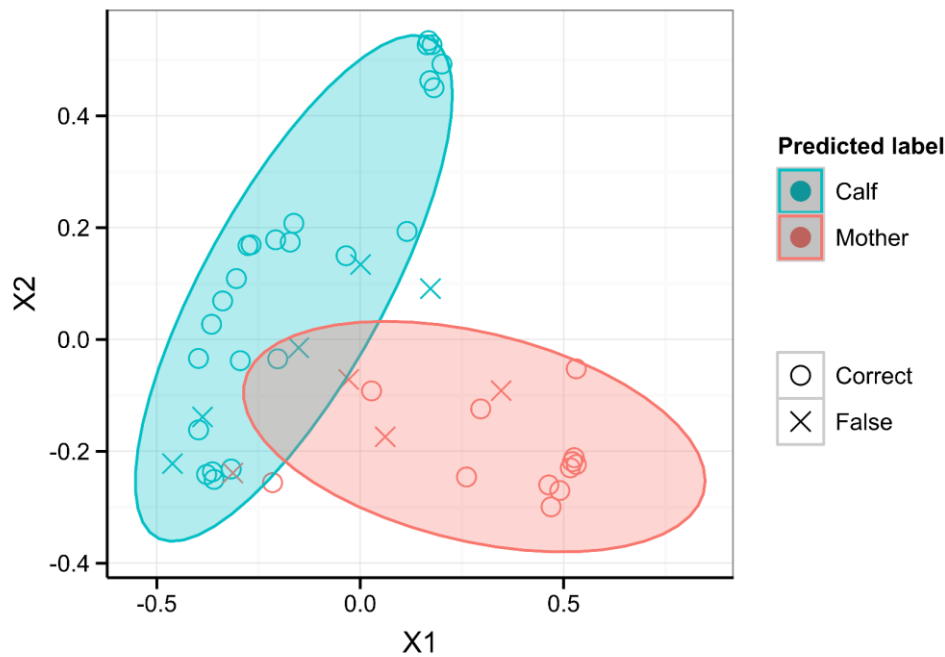


Figure 4. Multidimensional scaling (MDS) plot from the Random Forest (RF) algorithm using eight acoustic parameters across the Low-frequency (LF) calls labelled as 'Calf' and 'Mother.' Ellipses (80%) are drawn to emphasize closeness between the calls with the same original label

Ten LF calls detected simultaneously in both mother and calf channels ('Both') were attributed to calves by the trained RF model. The two remaining calls were attributed to the mothers. For the LF calls detected on the calf channels but with a loud noise recorded on the mother channels at the corresponding time ('Calf - Unsure'), four were attributed to calves. The remaining one was attributed to a mother. In total, 42 LF calls were thus attributed to calves and 20 to mothers.

The examination of the distribution of the vocalizations with respect to the vertical distance between the calf and mother indicated that the LF calls from the mothers were mainly produced when the pair was vertically close to each other. In contrast, the LF calls presumably from calves were produced when the calves were either close or far from their mother (from around 10 m below the mother to 25 m above the mother, Figure 5). The absolute vertical distance between the pair at the time of call production was 4 ± 4.7 m on average (range = 0.1–23.9 m; $N = 42$) for calls presumably from calves and 1.2 ± 1.1 m (0–4.2 m; $N = 20$) for calls presumably from mothers. The difference in absolute vertical distance at the time of call production for the mother as the emitter versus the calf as the emitter was statistically significant (Mann-Whitney U test, $W = 581$, $P = 0.015$). All calls labelled as 'Both' from calves were produced when the calf was above the mother or approximately at the same level as the mother in the water column (Figure 5).

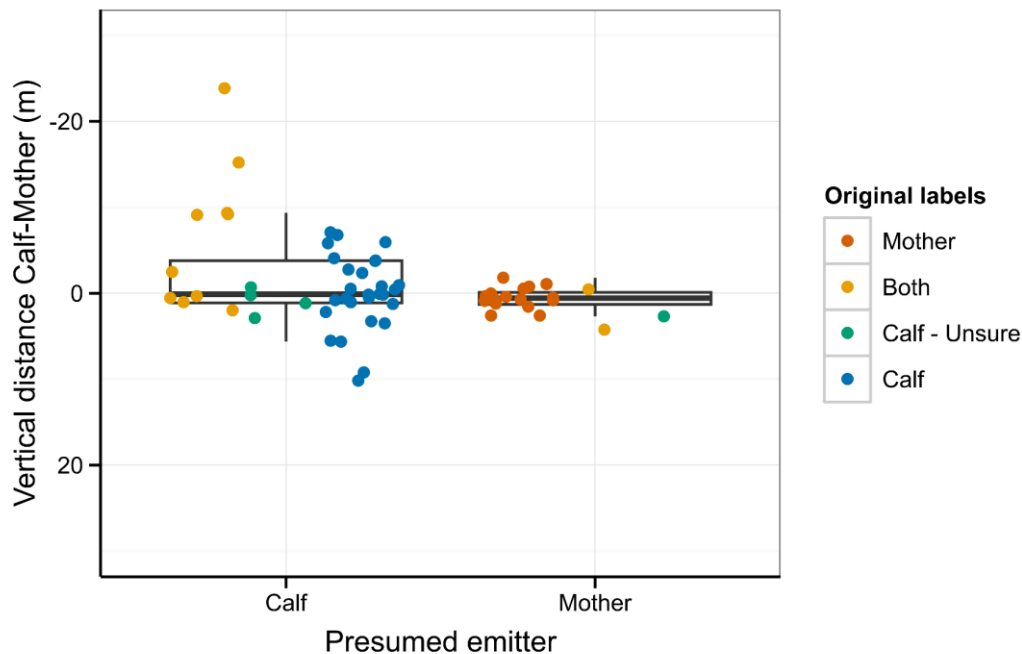


Figure 5. Calf-mother vertical distances at the production time of Low-frequency (LF) calls by the two presumed emitters: mothers and calves. A negative value indicates that the calf was above the level of the mother, and inversely, a positive value indicates that the calf was below the level of the mother. LF calls originally labelled as 'Mother' (red), i.e., only detected in the mother channels, were assumed to be calls from mothers, and conversely, LF calls originally labelled as 'Calf' (blue), i.e., only detected in the calf channels, were assumed to be calls from calves. A Random Forest (RF) model was used to predict the emitter when the LF calls were detected simultaneously in the two channels ('Both,' yellow) or when the LF calls were detected on the calf channels and there was a loud noise recorded on the mother channels at the corresponding time ('Calf - Unsure,' green)

With all 113 distinguishable calls considered, we identified 41 mother-calf call sequences (Table S2, Supplemental information). Although we called it sequence in the present study, sometimes a 'sequence' was composed of one isolated call (15/41 sequences). Ten sequences contained one or several calls with undefined emitter identity and thus were not considered as they did not allow meaningful conclusions. Sequences consisting only of calls from the calf (21 sequences) were statistically more frequent than sequences consisting of an exchange between the mother and the calf (five sequences, exact multinomial test, $P = 0.004$) and sequences consisting only of calls from the mother (also five sequences, exact multinomial test, $P = 0.004$). The sequences consisting of an exchange between the mother and the calf were encountered as often as the sequences consisting only of calls from the mother (exact multinomial test, $P = 1$). In all of the five sequences with vocal exchange between the mother and calf, the mother was the one to initiate the dialogue. The vocal exchanges between the mother and the calf appeared to occur mostly when the

mother and calf were both at the surface (Table S2, Supplemental information). The vocal sequences consisting only of calls from the calf occurred in various contexts, from synchronous activities to cases of vertical separation. The sequences consisting only of calls from the mother were mostly when both were at the surface.

Discussion

Our study investigated the vocal behaviour of adult female humpback whales and their young calves. We present a new estimation of the global vocal activities of mother-calf pairs. Furthermore, we identified the potential differences in vocal attributes between the mothers and their calves, which is critical to future studies dealing with mother-calf vocal communication and interactions and allowed us to draw the conclusion that social calls in mother-calf pairs potentially encode physical attributes. More importantly, our findings allowed us to show how mother-calf pairs use low-frequency calls (LF) in the context of vertical spatial separation and to understand which individual initiates vocal exchanges. The method we used for identifying the emitter was based on the use of mother-calf simultaneous tag deployments paired with a machine learning technique (Random Forest or RF).

The call rate in mother-calf pairs (i.e., combined vocal activities of mother and calf) was estimated to be about 11 calls/hour on average. This new estimation from simultaneous mother-calf tag deployments likely better captures the combined vocal activities of humpback whale mother and calf compared to estimation from single deployments. Indeed, our results show that calls emitted by one individual are not necessarily recorded on the other individual's tag in mother-calf pairs. Most calls detected on the calf channel (i.e., calls only detected on the calf channel as well as calls detected simultaneously on the calf and mother channels), at least for LF calls, are likely from the calf only. Similarly, most vocalizations detected and marked as 'Mother' on the mother channel are likely from the mother only, although at a lower proportion compared to calves, as a great proportion of the calls recorded on both the mother and the calf channels were categorized as calls emitted by calves. As we may expect then, our estimated call rate was higher than those reported in the literature from single deployments on mothers (Cusano et al., 2022; Indeck et al., 2022). Cusano et al. (2022) reported an average of 5 calls/hour, and Indeck et al. (2022) reported an average call rate likely way less than 10 calls/hour if the calls supposedly from calves and supposedly from mothers are combined. The call rate we reported remains, however, lower than those reported for mother-calf pairs accompanied by an escort and other social groups without calves (Cusano et al., 2022; Rekdahl et al., 2015). Our result thus still supports the idea of mother-calf pairs maintaining a low level of acoustic activity to reduce the probability of predators' and males' detection that may impact them (Cusano et al., 2022; Indeck et al., 2022; Videsen et al., 2017).

Although a high diversity of calls has been found, a few specific call types were more common and frequent than others, such as LF calls. These common and frequent LF calls included call types such as 'barks' and 'snorts' also found in mother-calf pairs from other study areas (Cusano et al., 2022; Dunlop et al., 2008; Indeck, Girola, et al., 2021). Such call types may be associated with the main activities of the mother-calf pairs (nursing, when the calf wanders around its resting mother, etc.). The less common ones may be associated with less common and highly specific situations (e.g., distress). Our results suggested that several call types were shared by the mothers and the calves and indicated that the mothers and calves may have, to some extent, a common call repertoire. Yet, our Random Forest (RF) highlighted a significant difference in acoustic characteristics between the calls from the mothers and from the calves. The most discriminative parameter was the fundamental frequency (F0). These results thus support that the LF calls used by mothers and calves, regardless of the type, potentially encode physical attributes of the individuals (relatively small individuals, the calves, and relatively larger individuals, the mothers). In several terrestrial mammal species, it has been observed that smaller or younger individuals produce vocalizations with higher fundamental frequency compared to older ones (Ey et al., 2007; Martin et al., 2021; Taylor & Reby, 2010). This trend is thought to be related to changes in the anatomy of the vocal tract as individuals age/grow, which generate honest information for receivers (Ey et al., 2007; Fitch & Hauser, 2003; Taylor & Reby, 2010). Although the vocal apparatus of baleen whales differs from all other mammal species (Adam et al., 2013; Reidenberg, 2022), we can also expect that there are growth-related anatomical changes in the components of the vocal production system (volume of the laryngeal sac, diameter of resonant tract, etc.). Such honest acoustic signals (i.e., signals conveying information that is a true indicator of some characteristics of the sender) may facilitate the rapid identification of signals from young individuals by the mothers, which then triggers maternal responses. The occurrence of differences between mothers' and calves' call characteristics is very encouraging as it may be exploited to discriminate the two in acoustic recordings from single animal-borne tags using supervised machine learning methods (e.g., RF). Of course, the possibility of calls from surrounding individuals outside the mother-calf pairs (e.g., escort non-song vocalisations) being recorded by the tag and thus mistakenly considered as calls from the mothers or the calves cannot be completely ruled out. However, such cases are expected to be rare, considering that the surrounding individuals are unlikely closer to the tagged individual than the other individual of a pair, as it has been suggested by video data from camera-equipped animal-borne tag (CATS cam) placed on calves in the same area (MN Ratsimbazafindranahaka, unpublished data). These surrounding individuals should have their calls even less likely to be recorded by the tag than the other individual of the pair. It should be noted that our study did not take into account the potential impact of varying tag locations on the animals (between different individuals and throughout a given deployment). We assumed that such impact was minor, but as noted by Clayton et al. (2023), the variation of the recorded acoustic

parameters as a result of such tag slips is yet to be investigated.

Results from our dataset composed of LF calls suggested that the mother's calls are mostly produced when vertically close to her calf. On the other hand, only the calf emitted calls at a long vertical distance from its mother. Given such context, these calls probably serve as contact calls, i.e., calls used by the calf to communicate its identity and position to the mother and/or to call the mother. As already shown above, these calls are signals that may transmit honest signals, at least regarding whether the sender is a young individual who needs care. Since the mother essentially stays approximatively at the same place or moves very slowly most of the time (resting) (Bejder et al., 2019), she does not necessarily have to indicate her position to her calf. Conversely, the calf being, in general, more mobile, wandering around (milling) (Bejder et al., 2019) while the mother is resting, it needs to communicate its position and maintain acoustic contact with its mother to prevent separation. Further studies are needed to confirm whether, in addition to transmitting information on the age/size, the calls from calves also encode precise individual signatures (Martin et al., 2022). Such a pattern is expected for species with some risk of misdirected maternal care (Lent, 1974; Martin et al., 2022; Nowak et al., 2000). Regarding the vocal exchanges between the mother and the calf, we found that vocal sequences heard in mother-calf pairs were predominantly composed of calls from the calf, which is in line with the hypothesis of the calf being the driver of the acoustic contact, although, most were unsuccessful in eliciting a vocal response from their mothers. The vocal exchanges we detected occurred mostly when the dyad was close to each other (vertically speaking) and may correspond to instances of vocal interactions to reinforce the social bond. As suggested by Chereskin et al. (2022) and Pika et al. (2018), vocal exchanges can indeed function as a mechanism for social bonding. As our dataset only allowed spatial analysis on the vertical plane, we cannot rule out that the mother and calf were further away from each other in the horizontal plane during these vocal exchanges. It is, however, known in other baleen whale species observed from above that, horizontally speaking, the calves are mostly very close to their mother 90% of the time (within 1/4 of the mother's body length) (Taber & Thomas, 1982). It is possible that the main instances of separation are vertical, which are more related to the calf's breathing capacity (Huetz et al., 2022; Tyson et al., 2012). Datasets from tags equipped with a camera with a large field of view may help in addressing such aspects in future studies. Due to a limited sample, we could not specifically target the other main call categories (mid-frequency, high-frequency, and pulsed calls), and thus, further investigations and simultaneous deployments are needed to better understand the context and source of these other vocalizations.

As already stated above, the method we used in the present study was based on mother-calf simultaneous tag deployments. The combined and time-aligned acoustic data from the calves' tags and mothers' tags allowed us to highlight that in a pair, the calf's tag does not record several calls from the mother, and conversely, the mother's

tag does not record several calls from the calf. The fact that one individual's tag does not record several calls from the other individual does not imply that several vocal signals emitted by the calf do not reach the mother and vice versa in the mother-calf pairs. Such circumstances would not benefit the pairs in the context of mother-calf interactions where the calf needs to communicate to its mother to influence her behaviour and vice-versa (Gubernick & Klopfer, 1981; Lent, 1974; Nowak et al., 2000) and where the pair needs to minimize vocal activities to avoid eavesdropping predators or males that may try to mate with the mother (Cusano et al., 2022; Indeck et al., 2022; Videsen et al., 2017). Several possible explanations exist for the calls from one whale not always being recorded by a tag placed on a nearby individual, and all of them imply constraints and challenges in the context of mother-calf acoustic interactions. One explanation is that one whale (let us call it the receiver) creates a body mass acoustic screen that attenuates the call when the other vocalizing individual (let us call it the emitter) is on the opposite side of its tag (i.e., generally below the receiver since the tags tended to be dorsally placed). The screening effect of the body has been, for example, evidenced in king penguins (Aubin & Jouventin, 1998). For whales, further investigations are needed to evaluate the extent to which their body can attenuate the sound transmission in an underwater setup. Although constituted of water in a significant proportion, the large body of whales comprises tissues of different densities and non-negligible volumes (bones, fat, air-filled organs, etc.). The degradation of sounds during propagation in the natural environment should not be neglected. The body mass screening hypothesis can explain why the calls, presumably from calves, are recorded on both tags, mostly when calves are above the level of their mother and not below and reciprocally for the mothers. The receiver's body mass screening effect may also be coupled with specific spatial radiation of sounds produced by the emitter. Indeed, we may expect a larger ventral radiation of vocalizations in baleen whales, given the ventral position of their vocal apparatus (Adam et al., 2013; Reidenberg, 2022). The effect of the distance between individuals of the pair can be excluded, as there was no apparent correlation between the decreasing vertical distance between mother-calf and the detection of calls on both tags. Another explanation for the calls only sometimes being detected in both channels is the difference in the mother's and calf's activity at a given time. Higher swimming speed for one individual or a change in tag position may, for example, induce more flow noise in its tag, thus reducing the detectability of the calls. These explanations on how the signals may propagate to reach the intended receiver have important implications for the communication and behaviour of the mother-calf pairs. First, the presence of individuals (e.g., escorts) between the mother and the calf may thus disturb the mother-calf acoustic interactions and may increase the risk of separations. Second, the ventral radiation implies a more efficient acoustic transmission of information from the calf during vertical separation where the calf is above the mother (the most common configuration as the mother usually stays at the bottom while the calf goes to the surface more often, Huetz et al., 2022), but less efficient from the mother unless she changes her posture.

Conclusion

Our study explored the vocal behaviour of adult female humpback whales and their calves, with a primary focus on potential differences in vocal attributes and vocal interactions. Using simultaneous tagging of both the mother and her calf in six pairs and a machine learning approach, we were able to better capture the vocal activities of mother-calf pairs and examine which individual vocalizes in the pair. We estimated a higher vocal activity in mother-calf pairs than previously reported, although the results still aligned with the hypothesis that mother-calf pairs maintain a low level of acoustic activity to avoid being detected by predators or males. Furthermore, we showed that the calf is the main responsible for acoustic contact during periods of vertical separation, and usually, the calls from the calf do not elicit vocal responses from the mother. LF calls were the main calls used by mother-calf pairs, which gave an insight into the calls potentially associated with routine situations (e.g., contact calls), and our study suggested that differences in acoustic characteristics, especially fundamental frequency (F0), between adults and calves, exists and such differences may aid in rapid identification of the signals from the young by the mother, which could play a role in encouraging maternal responses. Our research contributes to the understanding of the underlying mechanism of mother-offspring interactions in fully aquatic large mammals and emphasizes the vital role of calves' social calls in maintaining contact with the mother.

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Supplementary information

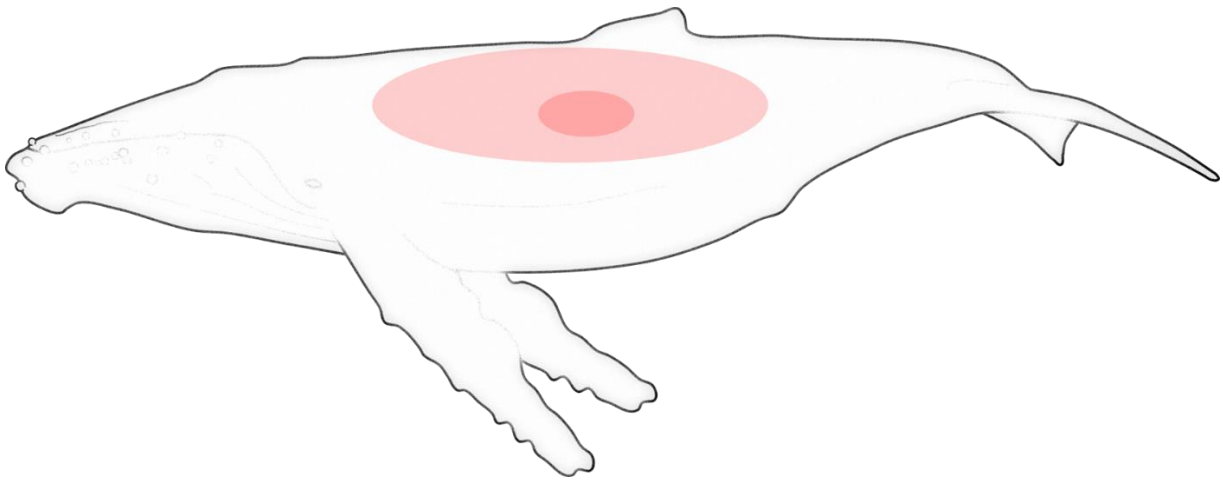


Figure S1. Schematic representation of the area where the Acousonde tags were placed for studying the vocal communication in mother-calf pairs off Sainte Marie, Madagascar. Note that the tag can be placed either on the right side or on the left side. The small red area corresponds to the targeted spot, and the light red area (including the small red area) corresponds to the area within which the tags were typically successfully placed

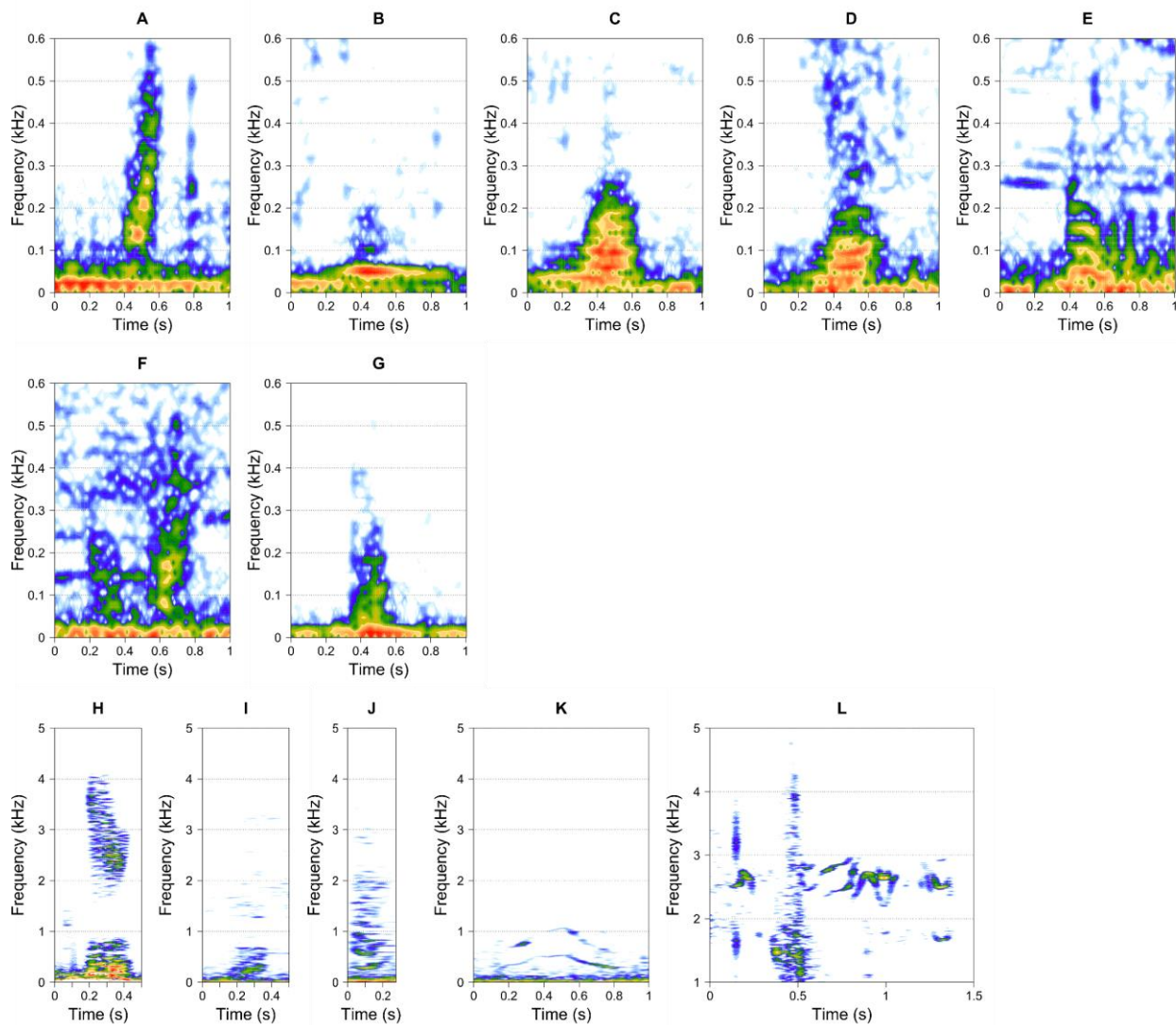


Figure S2. Representative spectrograms of the 12 social call types recorded in six simultaneous mother-calf Acousonde tag deployments off Sainte Marie, Madagascar. Low-frequency (LF) calls: (A) bark, (B) bass, (C) burp, (D) gru, (E) snort, (F) thwop, (G) wop. Mid-frequency (MF) calls: (H) heek, (I) whoop, (J) Wiper, (K) Groan. High-frequency (HF) call: (L) HF groan. These call types have already been described in detail in a previous study of the mother-calf pairs' vocal repertoire of the same population by Saloma et al. (2022), except for the HF groan. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using the *Seewave* package in R

Table S1. Temporal and spectral characteristics of 62 Low-frequency (LF) calls detected in six mother-calf simultaneous deployments. Values are presented in the format mean \pm SD (min – max). 'Mother': calls detected in the mother channel only. 'Both': calls detected in both the calf and mother channels at the same time. 'Calf - Unsure': calls detected in the calf channel and with loud noise recorded on the mother channel at the corresponding time. 'Calf': calls detected in the calf channel only. F0: fundamental frequency. Fmax: peak frequency. ebelow 100 Hz: energy below 100 Hz. Q25, Q50, Q75: first, second, and third energy quartile frequency, respectively. Bdw: frequency bandwidth within which the total energy fell within 12 dB of Fmax. Dur: duration. Parameters are presented in order of importance as suggested by our Random Forest (RF) analysis for differentiating calls from mothers and from calves

	Mother	Both	Calf - Unsure	Calf
<i>N</i>	17	12	5	28
F0 (Hz)	39.5 \pm 10.5 (28.0 – 54.0)	56.2 \pm 25.1 (28.0 – 116.0)	50.0 \pm 13.5 (29.0 – 64.0)	52.2 \pm 6.7 (41.0 – 76.0)
Q25 (Hz)	56.4 \pm 7.5 (41.0 – 67.0)	92.2 \pm 39.8 (43.0 – 152.0)	80.6 \pm 45.1 (49.0 – 152.0)	60.2 \pm 22.1 (16.8 – 117.0)
ebelow 100 Hz (%)	58.6 \pm 11.7 (41.2 – 77.4)	33.9 \pm 20.4 (8.7 – 68.5)	40.4 \pm 22.8 (14.3 – 73.7)	54.1 \pm 17.7 (19.4 – 86.9)
Fmax (Hz)	53.8 \pm 15.5 (32.0 – 99.0)	101.8 \pm 63.3 (41.0 – 205.0)	66.0 \pm 37.1 (41.0 – 131.0)	65.1 \pm 42.2 (0.0 – 208.0)
Q75 (Hz)	145.9 \pm 49.0 (79.0 – 254.0)	293.2 \pm 102.3 (112.0 – 477.0)	280.8 \pm 149.5 (101.0 – 457.0)	167.5 \pm 68.7 (52.7 – 326.0)
Q50 (Hz)	84.3 \pm 23.4 (54.1 – 115.0)	162.9 \pm 68.3 (46.0 – 281.0)	147.6 \pm 78.2 (54.0 – 266.0)	89.4 \pm 44.2 (49.0 – 184.0)
Bdw (Hz)	85.5 \pm 73.2 (3.6 – 279.0)	201.2 \pm 130.5 (14.0 – 468.0)	152.0 \pm 142.0 (10.0 – 348.0)	74.9 \pm 83.0 (2.9 – 316.0)
Dur (s)	0.5 \pm 0.2 (0.2 – 1.2)	0.2 \pm 0.1 (0.1 – 0.4)	0.3 \pm 0.1 (0.2 – 0.4)	0.7 \pm 0.5 (0.2 – 2.2)

Table S2. Mother-calf call succession patterns and their behavioral context. The total number of calls is provided next to the deployment ID for each deployment (mother-calf pair). The separation of the calls into sequences was based on the calf's diving/surfacing behaviours

Deployment ID	Sequence (count)	Context	
Dep01 (total = 4)	C-C (2)	Reunion dive (the mother was already at depth) and synchronous ascent	
	C (1)	Synchronous surface activity	
	C (1)	Synchronous descent and separated ascent (the mother stayed at depth) The call occurred before the vertical separation	
Dep02 (total = 16)	M-M-M-M (4)	Tagging of the mother, Synchronous surface activity	
	C-C (2)	Synchronous surface activity	
	M-M-M-C-C (5)	Synchronous surface activity	
	M-C-M-C-M (5)	Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred after the reunion	
Dep03 (total = 19)	C-C-C-C (4)	Tagging of the calf, Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred before the reunion The mother was already joining the surface before the call sequence	
	C-C-C-C (4)	Partially synchronous surface activity (the calf was at the surface before the mother) The mother started to go to the surface after the second call The call sequence occurred before the reunion	
	C (1)	Calf at the surface (The mother stayed at depth)	
	C (1)	Synchronous descent and separated ascent (the mother stayed at depth) The call occurred before the vertical separation	
	C (1)	Reunion dive (the mother was already at depth) and synchronous ascent The call occurred upon reunion at depth	
	C-C (2)	Lone dive (the calf was joined by the mother right after) and separated ascent (the calf arrived at the surface first)	
	C-C (2)	Synchronous descent and separated ascent (the mother stayed at depth) The calls occurred before the vertical separation	
	C-C-C -C (4)	Synchronous descent and separated ascent (the calf arrived at the surface first) The calls occurred before the vertical separation	
	Dep04 (total = 11)	M-M-M-M-?-?-?-M-M (9)	Tagging of the mother, Synchronous surface activity The call sequence occurred immediately after the tagging
		C (1)	Synchronous surface activity
C (1)		Synchronous descent and ascent The call occurred before the ascent	
Dep05 (total = 8)	M-C (2)	Synchronous surface activity	
	?-? (2)	Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred before the reunion The mother already started to go to the surface before the call sequence	
	C-C-?-? (4)	Partially synchronous surface activity (The calf was at the surface before the mother) The call sequence occurred after the reunion	
Dep06 (total = 55)	C (1)	Tagging of the calf, Synchronous surface activity The call occurred immediately after the tagging	
	M-M (2)	Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred after the reunion	
	M-M (2)	Synchronous surface activity	
	?-? (2)	Partially synchronous surface activity (the mother dove before the calf) The call sequence occurred before the separation	

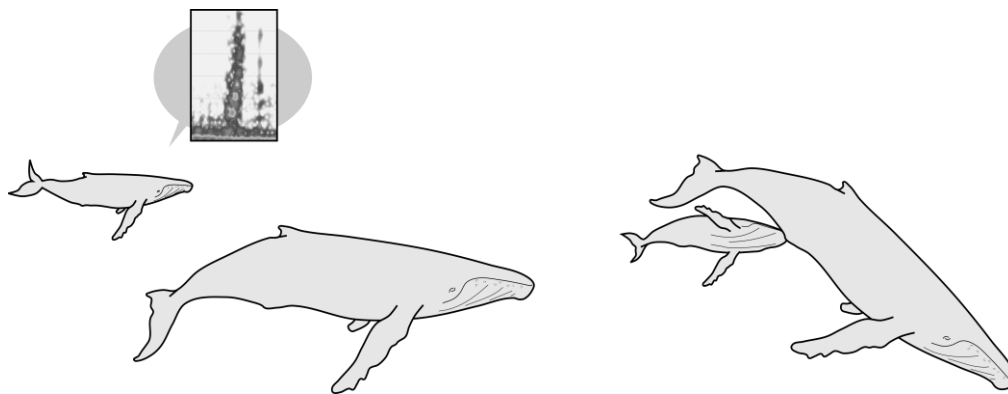
Chapter 5

?-? (2)	Calf at the surface (the mother stayed at the bottom)
C-C-C -C (4)	Calf at the surface (the mother stayed at the bottom)
? (1)	Partially synchronous surface activity (the calf was at the surface before the mother) The call occurred after the reunion
?-C-C-C -C (5)	Partially synchronous surface activity (The calf was at the surface before the mother) The first call occurred before the reunion The remaining calls occurred after the reunion
C (1)	Partially synchronous surface activity (the calf was at the surface before the mother, and the mother dove before the calf)
C (1)	Reunion dive (mother at depth) and separated ascent (the calf arrived at the surface before the mother)
?-M-C-C-C-C-C (7)	Partially synchronous surface activity (The calf was at the surface before the mother, and the mother dove before the calf) The first call occurred before the reunion The remaining calls occurred after the reunion, before the separation
C-C (2)	Reunion dive (mother at depth) and separated ascent (calf arrived at the surface first) The calls occurred before the vertical separation
M-M-M-C (4)	Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred after the reunion
M (1)	Synchronous descent and separated ascent (the calf was at the surface before the mother)
M-C-M-M-M-C (6)	Partially synchronous surface activity (the calf was at the surface before the mother) The call sequence occurred after the reunion
M (1)	Partially synchronous surface activity (The calf was at the surface before the mother) The call occurred after the reunion
C (1)	Calf at the surface (The mother stayed at the bottom)
C-?-C-? (4)	Calf at the surface (The mother stayed at the bottom)
?-C-?-C-?-? (7)	Calf at the surface (The mother stayed at the bottom)
C (1)	Partially synchronous surface activity (the calf was at the surface before the mother) The call occurred before the reunion

(C) call from the calf. (M) Call from the mother. (?) Call with undefined emitter

Chapter 6. Behavioral context of call production in humpback whale calves

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Upcoming submission

Synthesis

In which context do the mother and the calf use vocalizations, and what functions do the vocalizations potentially have? On the behavioral context of vocal productions in calves

Methods

Data from eight calf CATS cam deployments were used. The acoustic characteristics of the recorded social calls were measured and used in an HCPC to objectively identify relatively homogeneous groups of calls that were then referred to as call types. Given the result in Chapter 5, the calls were assumed to be from the calf. Each deployment was broken down into sequences consisting of suckling sessions, surface play sessions, traveling (in synchrony with the mother), milling, response to tagging, and resting using the results of Chapter 2 and Chapter 3. For each continuous period corresponding to each behavioral state, the call rate and the presence/absence of each identified call type were noted. I then tested with an RF analysis whether the recorded vocalizations and the behavioral state were related.

Findings

Milling, resting, and traveling are mainly associated with silence. Surface play sessions, response to tagging, and suckling sessions are associated with call rates of about 0.1, 0.1, and 0.5 calls/min, respectively. According to the RF analysis, the suckling sessions are mainly associated with two sets of low-frequency calls that are quite similar: one with an average fundamental frequency of 40 Hz and an average duration of 0.7 s and another with a fundamental frequency of 45 Hz and an average duration of 0.3 s. Surface play sessions are more associated with sets of mid-frequency calls with whoop-like sounds. However, these sessions are also usually associated with other call types without a consistent association pattern.

Abstract

Humpback whale calves have been previously shown to vocalize, but the behavioral context of their calls and especially the role of their calls in the context of mother-calf interactions is still poorly documented due to the challenges in studying them at sea. In the present study, we investigated the behavioral context of call production using data from camera-equipped animal-borne multi-sensor tags. Behavioral states, including suckling sessions, were identified using previously developed methods that combine data from accelerometer, depth sensor, and camera. Call types were attributed using a clustering technique. The relation between calls and behavioral states was investigated by testing if the presence/absence and call rate predict the occurrence of a given state. We found that milling, resting, and traveling (in synchrony with the mother) are mainly associated with silence. Surface play sessions, response to tagging, and suckling sessions were associated with high call rates. The suckling sessions appeared to be mainly associated with two sets of low-frequency calls corresponding, for instance, to the burping, barking, and snorting sounds that were previously described in mother-calf pairs. Surface play sessions were more associated with sets of mid-frequency calls with whoop-like sounds and several other call types (without a consistent association pattern). This study offers a preliminary insight into humpback whale mother-calf communication, including the identification of potential begging calls for the first time.

Keywords: mother-offspring, begging, baleen whales, classification

Introduction

Mammals mainly rely on their mother during their early life stage to survive. Their mother provides critical care such as food provisioning, protection from predators, warmth, teaching, etc. (Balshine, 2012; Clutton-Brock, 1991). For such care to be optimal, the mother and offspring must communicate with each other. For instance, the offspring must communicate its needs to its mother (Gubernick & Klopfer, 1981; Lent, 1974; Nowak et al., 2000). In the case of mammals that use the 'following' anti-predation strategy, the mother needs to encourage following when necessary to ensure that the offspring stays in proximity so she can protect it (Lent, 1974). More generally, both the mother and the offspring need to communicate their identity to each other so that the mother avoids spending resources on non-filial young (targeted investment) and the offspring avoid going towards potentially aggressive conspecifics (Lent, 1974; Nowak et al., 2000; Okabe et al., 2012). Various modalities are used, such as olfactory, visual, tactile, and acoustic communication (Lent, 1974; Nowak et al., 2000; Okabe et al., 2012).

In an aquatic environment, the use of acoustic signaling is one of the best strategies to communicate as acoustic signals are efficient at both short and long-range and easy to detect and localize, whereas visual and chemical cues do not provide such

advantages. As such, the cetaceans or whales, a group of fully aquatic mammals, evolved a communication system that is mainly based on sounds that are vocally produced or not (Dudzinski et al., 2009). Non-vocal sounds produced by baleen whales include percussive sounds from surface activities such as tail slaps, pectoral slaps, breaching, etc. The vocally produced sounds encompass songs (Dudzinski et al., 2009; Edds-Walton, 1997; Payne & McVay, 1971; Tyack, 1998, 1999) and social calls (Dudzinski et al., 2009; Payne, 1978; Silber, 1986; Tyack, 1998). They are produced by circulating air from the lungs to the laryngeal sac or vice versa to vibrate the U-fold (Adam et al., 2013; Gandilhon et al., 2015). Songs are vocalizations organized in a repeated manner and in long bouts, while social calls are variable through time, interrupted by silent periods, apparently unpredictable, and not showing a stereotyped rhythmic, consistent, and continuous temporal pattern of the same level as songs (Silber, 1986; Tyack, 1981).

Humpback whales produce social calls in various contexts. Unlike songs that are produced primarily by males and mainly associated to reproduction (Dudzinski et al., 2009; Edds-Walton, 1997; Payne & McVay, 1971; Tyack, 1998, 1999), social calls are used by all categories of individuals (female, male, calf), whether they are in small groups or in large groups, in the breeding ground, in the feeding ground or during the migration (Cerchio & Dahlheim, 2001; D'Vincent et al., 1985; Dunlop et al., 2007, 2008; Dunlop, 2016, 2017; Epp, Fournet, & Davoren, 2021; Epp, Fournet, Silber, et al., 2021; Fournet et al., 2015; Indeck et al., 2021; Rekdahl et al., 2017; Rekdahl et al., 2013; Saloma et al., 2022; Silber, 1986; Stimpert, 2010; Stimpert et al., 2011; Zoidis et al., 2008). As highly vocal animals with relatively large vocal repertoire, it is expected that social calls are used for various purposes in humpback whale mother-calf pairs, such as to maintain contact, to send alarms, and to initiate critical behaviors such as nursing, etc.

Only a few studies attempted to understand whether humpback whale calves use social calls to communicate with their mothers and whether social calls are associated with a particular context. Zoidis et al. (2008) observed that some social calls appear to elicit the mother's approach and are isolation or "alarm" calls by the calf to alert and/or call the mother. Videsen et al. (2017) suggested that suckling initiation is not based on acoustic cues but rather tactile ones, which was unexpected. Additionally, some calls associated with active dives were attributed to a cohesive function to maintain contact (Videsen et al., 2017). Interestingly, Indeck et al. (2022) found that during resting, an activity associated with more frequent separation, the vocal activity in mother-calf pairs was more intense, supporting the hypothesis that some calls function as contact calls. Ratsimbazafindranahaka et al. (2023b) suggested that the calf is the main responsible for acoustic contact during periods of separation. One of the main limitations of the various studies on the function of social calls in calves was the fact that the context was mostly associated with the vocal activities (call rates) and not specific call types.

Several challenges make it difficult to study the behavioral context of social call production in whale calves. First, the existence of graded calls, in addition to discrete calls, makes it challenging to objectively separate social calls into distinct call types (Epp, Fournet, & Davoren, 2021; Saloma et al., 2022). The gradation of calls makes it difficult to establish sufficiently reproducible call labels (call types) that can be specifically associated with behaviors. Nevertheless, unsupervised classification (Fournet et al., 2015) can be an alternative, or a starting point, to group calls into relatively homogeneous clusters and identify if a set of closely related calls is specifically used in a given context. Another challenge concerns the data acquisition itself. Animal-borne multi-sensor tags are now routinely used to study the behaviors and the vocalizations of whales (e.g., Indeck et al., 2021, 2022; Ratsimbazafindranahaka et al., 2023b; Videsen et al., 2017) as they allow to track and accurately describe the underwater activities of whales and focus on an individual. Unfortunately, when the studied individual is a mother or a calf, the identification of the caller is problematic as it has been suggested that the calls recorded by a tag placed on a mother would also record calls from the calf and vice-versa. Studies attempting to associate vocalizations to behaviors in mother-calf groups thus did not make a distinction between the calls from the mother and from the calf and assumed that the studied calls represent the total vocal output of the mother-calf pair. Recent results based on data from simultaneous deployments on mother and calf, however, suggested that most calls recorded by a tag placed on a calf are likely from the calf, at least for low-frequency calls (which represent the majority of calls produced in mother-calf pairs) (Ratsimbazafindranahaka et al., 2023b).

In the present study, we investigated the behavioral context of social calls recorded by tags equipped with a camera placed on calves off Sainte Marie Island, Madagascar, South Western Indian Ocean, with the assumption that a tag placed on a calf mainly records the calls from the calf. Our objective was to gain insights into the relationship between activities and calf vocalizations and understand the potential roles of the various call types they use.

Methods

Dataset

We used data from the CATS cam tag, a set of sensors including a depth sensor, a 3-axis accelerometer, a hydrophone, and a video camera, placed on the back of eight humpback whale calves, for which the sound recorded by the hydrophone was not saturated (usually due to very high flow noise, which is related to tag placement and orientation). The average data duration per calf was 4.1 ± 2.5 hours (range = 1-8.2 hours), and the total was 32.6 hours. The data were collected off Sainte Marie Island, Madagascar, South Western Indian Ocean, during the winter of 2022 and are part of the data presented in Ratsimbazafindranahaka et al. (2023a, 2023c). Detailed

tagging procedures and tag specifications have been presented elsewhere (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022, 2023a; Saloma et al., 2022).

Call analysis

We analyzed the vocalizations recorded by the tags using Avisoft SASLab Pro version 5.3.01 (Avisoft Bioacoustics, Nordbahn, Germany). We produced spectrograms of the acoustic recordings using a 1024-point Fast Fourier Transform, 75% overlap, and Hamming window. We inspected the audio files aurally and visually to isolate clearly distinguishable social 'calls,' i.e., sounds vocally produced and excluding non-vocally produced social sounds such as surface percussive sounds – breaches, slaps –, apparent bubble sounds, rubbing sounds, etc. We distinguished the social calls from the male songs in the background based on the temporal pattern and overlaps (Saloma et al., 2022). For each distinguishable social call, we measured seven acoustic features: the duration (Dur, in s), the peak frequency (Fmax, in Hz), the first, second and third energy quartile frequency (Q25, Q50, Q75 respectively, in Hz), the frequency bandwidth within which the total energy fell within 12 dB of Fmax (Bdw, in Hz), and the fundamental frequency (F0, in Hz). The spectral characteristics were measured on the averaged spectrum (frequency ranges: 30-1000 Hz for low-frequency calls with peak frequency <160 Hz, and 100-6000 Hz for mid- and high-frequency calls with peak frequency from 160 to 700 Hz and >700, respectively). All spectral characteristics' measurements were performed automatically except for the F0, which was measured manually using the harmonic cursor available in Avisoft SASLab Pro for finding harmonic structures on the averaged spectrum.

Behavioral state definition

The data from each calf were broken down into sequences constituted by six possible behavioral states: suckling session (*Su*), surface play session (*Pl*), traveling (*T*), milling (*Mi*), response to tag deployment (*Tg*), and resting (*Re*). These states were defined by a classification algorithm using a combination of depth, 3D accelerometer, sound, and video data. First, the data were globally broken down into four base states – two directly corresponding to *Re* and *Mi* and two corresponding to two general trends, moderate directed swimming and fast directed swimming – based on the calf's relative speed (obtained by z-scoring the flow noise recorded by the hydrophone within the 66-94 Hz frequency band, Cade et al., 2017), using a first-order Hidden Markov Model trained on multi-sensor tag data collected since 2013 (see Ratsimbazafindranahaka et al., 2023c). Concurrently, suckling events were visually identified on the video data (Ratsimbazafindranahaka et al., 2023a), except during periods of uncertainty due to tag movement (camera not directed forward). During those exceptions (12.2% of the data), the suckling events were identified automatically based on the 3D accelerometry data and depth data using the supervised automatic detection method described in Ratsimbazafindranahaka et al. (2023a). Subsequently, (1) any state during which a

suckling event occurred was considered as a suckling session (*Su*), and any state directly before it was included as part of the session, (2) any directed swimming state during which the calf is observed displaying surface active behaviors (breaches, head slaps, pectoral slaps, etc.) was considered as surface active playing session (*Pl*), (3) any directed swimming state (moderate or fast), except those occurring immediately after the tagging, were considered as traveling (*T*) if the mother was swimming alongside the calf at approximately the same pace, (4) any directed swimming state (moderate or fast) during which the mother was resting or was not swimming alongside the calf was considered as also milling (*Mi*), and (5) any state immediately after the tagging was considered as response to tagging (*Tg*).

Statistical analyses

Cluster analysis of the social calls

We used a cluster analysis to objectively identify relatively homogeneous groups of calls, referred to as call types. The relevant number of clusters was determined using the *NbClust* package (Charrad et al., 2014) in R (R core team, <https://www.r-project.org/>). The Calinsky and Harabasz (CH) index was used as it has been shown to be among the indexes with the best performance in determining the number of clusters (Milligan & Cooper, 1985). We set the minimum cluster number to 6 to avoid capturing just the main categories of calls (Low-frequency, Mid-frequency, High-frequency, Pulsed, and Amplitude-modulated; Dunlop et al., 2007; Epp, Fournet, & Davoren, 2021; Fournet et al., 2018; Saloma et al., 2022; Zoidis et al., 2008). Once the relevant number of clusters was determined, we used a Hierarchical Clustering on Principal Components (HCPC) to group the social calls using the *FactoMineR* R package (Lê et al., 2008). The principal components (i.e., PC scores) were computed using the seven measured acoustic features as input variables in a principal component analysis (PCA).

Analysis of the behavioral context of call production

For each continuous period corresponding to a state, we calculated the call rate (count/minute) and noted the presence/absence of each identified call type. To investigate how the produced calls and behavioral states relate to each other, we tested whether the information on the rate of production of calls and the type of calls produced allowed the prediction of the behavioral states using a balanced random forest classification. We used the R package *rfPermute* (Archer, 2018), which allows the estimation of the statistical significance of the variable importance metrics (here, the importance of the call rate and the presence/absence of each call type) in the prediction by permuting the response variable (here the behavioral states). In our model, the number of variables to be randomly selected at each split was set to 3, and the number of trees grown was set at 1000.

Results

A total of 508 social calls were detected and labelled in the data from eight deployments on calves. Each deployment has been subdivided into 88 ± 66 segments on average (range: 18–212 segments, total: 700 segments) based on automatic classification of the behavioral states. The average duration of the segments was 2.8 ± 3.9 min (range = 0.3–36 min). Most of the segments corresponded to milling (*Mi*, 63%), followed by resting (*Re*, 27%), traveling (*T*, 7%), surface playing (*Pl*, 2%), suckling session (*Su*, 2%), and finally tagging response (*Tg*, 1%).

Main call types recorded

The Calinsky and Harabasz (CH) index suggested the occurrence of 13 main call types that were then successfully identified using a Hierarchical Clustering on Principal Components (HCPC) (call type #1 to #13, Figure 1). Examples of calls from each type are presented in Audio S1 (Supplemental information). The first two principal components (Dim1–Dim2) explained 76% of the sample variance (Figure S1, Supplemental information). Dim1 was primarily positively correlated to the spectral characteristics, whereas Dim2 was positively correlated to the call duration (Dur). The type #1–3 calls were constituted by low-frequency sounds. Type #1 calls were long – about 2 ± 0.6 s on average, and type #3 were relatively short – about 0.3 ± 0.1 s on average, and type #2 calls were in between these two (Figure 1, Table S1, Supplemental information). Type #4 and #5 calls showed similar spectral characteristics and time duration (overlap on the Dim1 and Dim2) but were of higher frequencies compared to type #1–3 calls (Figure 1, Table S1, Supplemental information). They mainly differed in their bandwidth (Bdw) and fundamental frequency (F0) (The average F0 of type #4 calls was more than twice the average F0 of the type #5 calls, while the average Bdw of type #4 was less than 1/3 of the average Bdw of type #5 calls) (Table S1, Supplemental information). Type #6–9 calls overlapped along Dim1 but spread more on Dim2. Among these four call types, type #7 appeared to have the narrowest bandwidth, the highest F0 (434 ± 41 Hz on average), and the longest duration (1 ± 0.6 s on average, Figure 1, Table S1, Supplemental information). Type #8 had the lowest F0 (65 ± 53 Hz on average, Table S1, Supplemental information). Type #6 and #9 had similar F0, but type #9 had a clearly broader band (about four times the Bdw of type #6) and had, in fact, the broadest band among type #6–9 (Figure 1, Table S1, Supplemental information). The remaining types, type #10 and #13, had more energy in high frequencies (average Fmax > 1300 Hz) compared to all other main call types. Type #10 and #11 calls had broader bands and were shorter compared to type #12 and #13 (average Bdw almost five times or more than type #12's and #13's average Bdw and average Dur not more than two-thirds of type #12's and #13's Dur), but type #10 had higher Fmax (about four times) and with a narrower band (about the half) than type #11 (Figure 1, Table S1, Supplemental information). Type #12 and #13 were represented by only a single call each and were high frequency calls with narrow

bandwidth. The type #12 call had a much higher F0 (eight times) compared to type #13 (Figure 1). Type #3 was the most abundant main type (59%) and was common to all calves, followed by type #2, that were also relatively abundant (16%) and found in all calves except one. Each remaining call type only constituted <1% to 9% of all calls detected and were at most common to only half of the studied calves (Figure S2, Supplemental information).

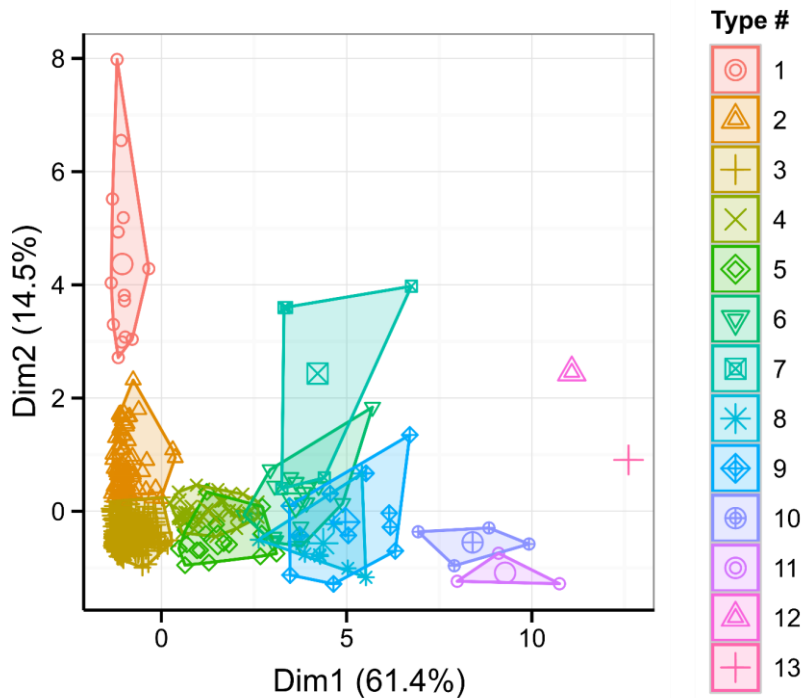


Figure 1. Hierarchical Clustering on Principal Components (HCPC) showing the identified main call types (delimited by polygons) and calls within each of them (small symbols). Cluster centers are indicated by bigger symbols. Thirteen call types were identified. The calls are dispersed along Dim1 axis, which is positively correlated to spectral characteristics (F0, Fmax, Q25, Q50, and Q75 and Bdw), and dispersed along Dim2, which is highly correlated to duration (Dur)

Behavioral states and call production

Milling (*Mi*), Resting (*Re*), and Travelling (*T*) states were mostly associated with silence (median call rate = 0 calls min⁻¹), although on rare occasions, they have been associated with a high level of vocal production (call rate >1 calls min⁻¹ in 21/423 *Mi*, in 3/192 *Re*, and in 2/50 *T*; range, *Mi*: 0–11 calls min⁻¹; *Re*: 0–2 calls min⁻¹; *T*: 0–3 calls min⁻¹, Figure 2A). In contrast, Surface play session (*Pl*), reaction to tagging (*Tg*), and Suckling session (*Su*) states tended to be associated with a call production at an average rate (median) of 0.1 calls min⁻¹ (range = 0–8 calls min⁻¹), 0.1 calls min⁻¹ (range = 0–2 calls min⁻¹), and 0.5 calls min⁻¹ (range = suckling, 0–2 calls min⁻¹), respectively.

The random forest analysis correctly predicted 29% of the behavioral states based solely on the presence/absence of each of the 13 main call types and the call rate (Table 1). This percentage of correct prediction was statistically significantly greater than the result expected by chance, which is about 17% ($P < 0.001$). The random forest analysis was able to correctly predict the states corresponding to *Re* and *Su* at rates that were statistically significantly greater than the values expected by chance (Table 1). However, it failed to correctly predict the states corresponding to *Pl* and *Tg* at rates statistically significantly greater than the values expected by chance but close to the significant level for *Pl* (Table 1). The correct prediction rate was zero for *Mi* and *T*. *Mi* was primarily confused with *Re* but sometimes with *Tg*, *Pl*, and *Su*. *T* was also primarily confused with *Re* and, on some occasions, with *Tg* and *Pl*, but never with *Su*.

The variables contributing the most (statistically significant contribution) to the prediction of *Su* were, by decreasing order of importance, the presence of type #3 and #2 calls, the high call rate, and, to a lesser extent, the presence of type #8, #5, and #6 calls (Figure 2). For *Pl*, the variables contributing the most to its prediction were the presence of type #4 and #6 calls (Figure 2). Regarding *Re*, the information on the presence/absence of several call types and the call rate were important in its prediction as it was mainly associated with silence (thus the absence of most calls in general, Figure 2).

Table 1. Result of a random forest analysis (confusion matrix) in predicting the behavioral states based on the presence/absence of the 13 main call types identified and the call rate. *Mi*: milling, *Pl*: surface active playing session, *Tg*: response to tagging, *Re*: resting, *Su*: suckling session, *T*: traveling. Bold *P* indicates a statistically significant difference between the correct prediction rate and the rate expected by chance

	Predicted class						% correct	% chance	<i>P</i>	
	<i>Mi</i>	<i>Pl</i>	<i>Tg</i>	<i>Re</i>	<i>Su</i>	<i>T</i>				
<i>Mi</i>	0	8	21	371	23	0	0	17	1	
<i>Pl</i>	0	4	2	7	2	0	27	17	0.09	
True class	<i>Tg</i>	0	0	2	4	2	0	25	17	0.135
	<i>Re</i>	0	1	2	187	2	0	97	17	0
	<i>Su</i>	0	0	4	3	5	0	42	17	0.008
	<i>T</i>	0	1	3	42	4	0	0	17	1
	Overall							28	17	0

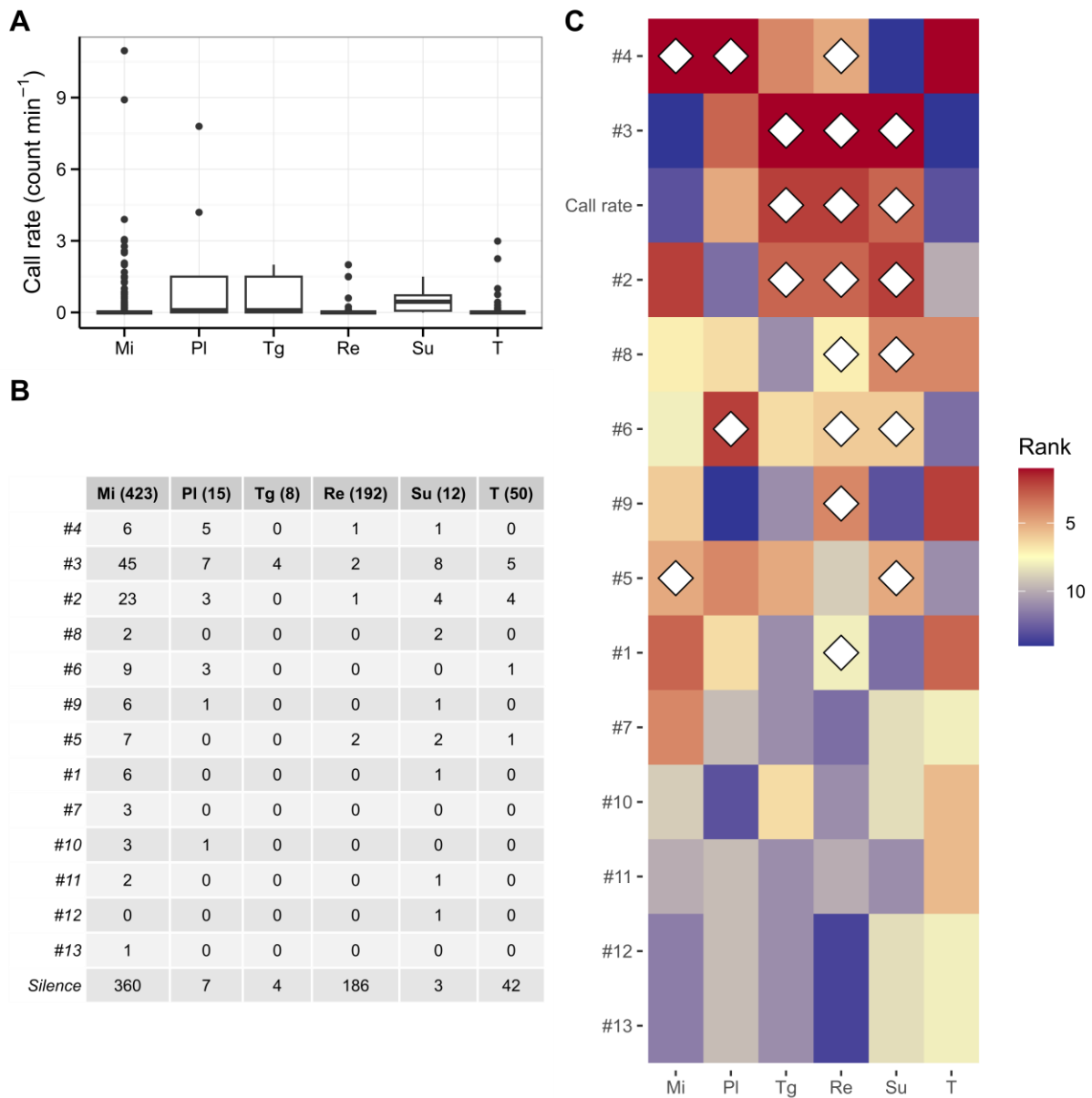


Figure 2. Relation between the behavioral states *Mi*, *PI*, *Tg*, *Re*, *Su*, and *T*, and the produced calls. *Mi*: milling, *PI*: surface active playing session, *Tg*: response to tagging, *Re*: resting, *Su*: suckling session, *T*: traveling. (A) Call rates by behavioral state. *Su*, *PI*, and *Tg* were associated with higher call rates compared to *Mi*, *Re*, and *T*, which were mainly associated with silence. (B) Relation between the call type produced, numbered from #1 to #13, and the behavioral states. Each count represents the number of segments per behavioral state during which the specified call type was detected. The number of segment per behavioral state during which no call was detected are presented in the bottom row (silence). (C) Ranked importance of the presence/absence of each call type and the call rate in predicting the behavioral state in a random forest analysis. The heat map presents importance scores scaled by ranked importance. The diamonds indicate statistically significant scores. The predictors are sorted by Mean Decrease Accuracy. The most significant variables contributing to the prediction of *Su*, by descending order of importance, were the presence/absence of type #3 and #2 calls,

the call rate, and the presence/absence of type #8, #5, and #6 calls. In the case of *Pl*, the variables with the greatest contribution to its prediction were the presence/absence of type #4 and #6 calls. As for *Tg*, the variables that played a crucial role in its prediction were the presence/absence of type #3 calls, the call rate, and the presence/absence of type #2 calls. In predicting *Re*, the presence/absence of several call types, along with the call rate, were important since *Re* is predominantly associated with the absence of most calls in general

Discussion

Our initial objective was to identify the context of call production by the calves using data from animal-borne tags. We assumed that the calls recorded by the tags (placed on calves) were from the calves, based on the results in Ratsimbazafindranahaka et al. (2023) on low-frequency calls that most calls recorded by a tag placed on the calf are mainly from the calf (about 90% of the calls). Due to the potential existence of graded calls in humpback whales and especially in calves (Epp, Fournet, & Davoren, 2021; Saloma et al., 2022), we used an unsupervised approach to group social calls with similar acoustic characteristics. Our result suggested that the call rate and the production (or non-production) of one or several specific call types may be related to the behavior of the calf. Indeed, we found that these parameters can be sufficient to predict the occurrence of a specific behavioral state in a given data segment. It is especially true for two main behaviors: the suckling behavior and the resting behavior, and likely the play behavior.

Suckling sessions were associated with a higher call rate than any other behavioral states on average and were mainly associated with type #3 and type #2 calls. Qualitatively speaking, these calls corresponded mainly to low frequency calls such as burps, barks, wops, thwops, snorts, basses, and grunts presented in the literature (Dunlop et al., 2007, 2008; Epp, Fournet, & Davoren, 2021; Fournet et al., 2015; Indeck et al., 2021; Rekdahl et al., 2013; Saloma et al., 2022; Stimpert et al., 2011; Zoidis et al., 2008). Most of these calls have been identified as very common in humpback whale repertoire and were suggested to be calls with important social functions (Saloma et al., 2022). Here, our results suggest that one such function is related to the neonate feeding behavior. They may serve as begging calls in mother-calf pairs to initiate nursing.

Both surface active playing sessions and tagging responses were also associated with a high call rate but could also be associated with silence. For the playing state, various call types could be associated with it, but only the presence of type #4 and #6 calls had statistically significant importance in its prediction. These calls qualitatively corresponded mainly to the whoops presented in the literature (Saloma et al., 2022) and may be associated with a positive emotion expressed during a playful state. In addition, the production of diverse call types during play may be associated with the

calf playing with its own voice and practicing its vocal repertoire randomly, or it can also be a byproduct of high physical activity. In rats, the production of some call types is, for example, potentially closely tied to breathing (Winkler & Bryant, 2021). In mysticete whales, as the surface active play involves rapid vertical swimming and breaching, the air circulation within the respiratory system (from the lungs to the laryngeal sac or vice versa) in response to the changing ambient pressure and the calf's attempt to play with its buoyancy (Adam et al., 2013; Gandilhon et al., 2015) may result in similar phenomena where sounds are produced involuntarily. On a side note, in some cases, the low-frequency calls produced by the calf during surface playing sessions were associated with the production of bubbles (Ratsimbazafindranahaka MN, personal observation), corroborating the hypothesis of some calls being tied to breathing while playing at the surface. Resting was mostly associated with silence, which is expected since resting corresponds to periods of low activity during which both the mother and calf are usually in the same behavioral state (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2023c; Tyson et al., 2012). The absence of a clear pattern in the calls associated with traveling suggests that the calf does not need to vocalize to synchronize movements with its mother. The side-by-side swimming configuration may be sustained based mainly on vision, and the mother may adjust her pace automatically without the need for the calf to signal her. In terrestrial ungulate species using the 'following' strategy, such maternal behavior has been referred to as 'pacing,' a behavior that has been proposed to induce a maximal following response by the offspring (Lent, 1974). In these species, it is known that the young instinctively follow a moving object of an appropriate size (Lent, 1974).

Our study provides a first assessment of the context of call production in humpback whale calves and suggests the potential function of some of the call types, ultimately shedding light on their communication patterns and behavior. For the first time, the potential begging calls of humpback whale calves have been identified. Such results help us understand the underlying mechanism of mother-young acoustic communication in exclusively aquatic mammals. Further investigations are needed on a larger sample to assess the biological functions of other call types, and playback experiments could be carried out to investigate the function of some calls identified in the present study in a controlled setup.

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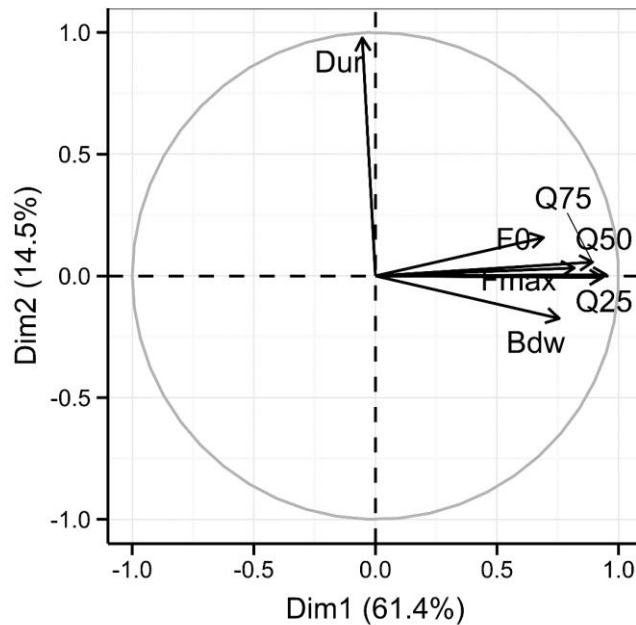
Supplementary information

Figure S1. Correlation circle of a Principal Component Analysis synthesizing the acoustic features of the calls detected in CATS cam tag deployments on eight calves. Percent on each dimension axis (Principal Component) gives the explained variance. The first two components (Dim1 and Dim2) explain 76% of the variance. Dim1 was primarily positively correlated with the frequency characteristics (F0 and Fmax), the power distribution (Q25, Q50, and Q75), and the Bdw. Dim2 was correlated with Dur (temporal feature)

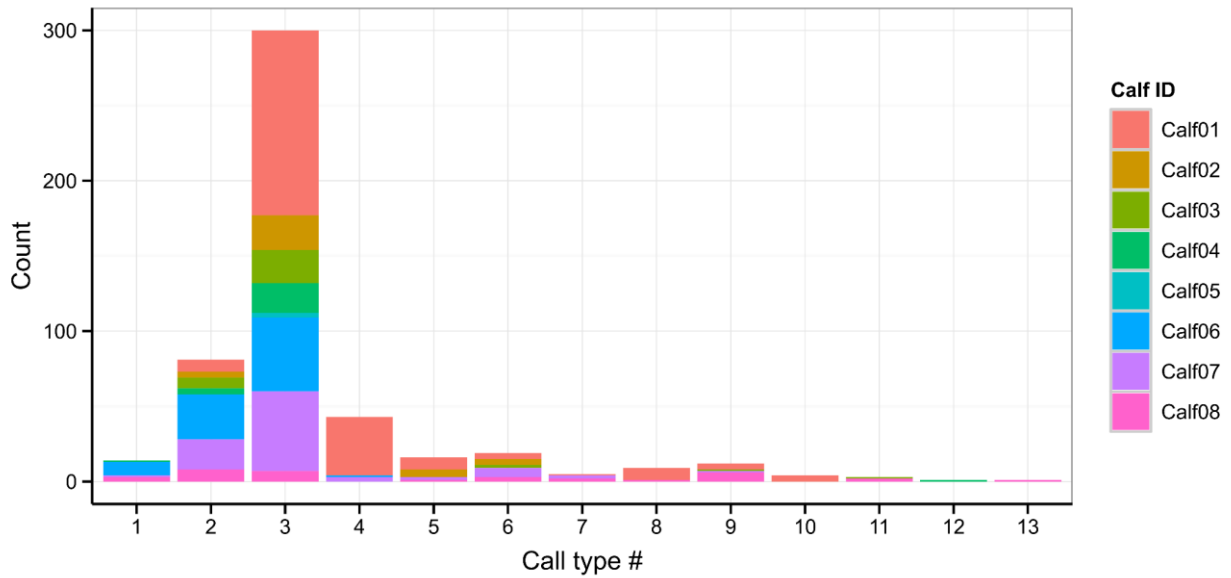


Figure S2. Frequency of the calls from CATS tag deployments on calves by type identified using a Hierarchical Clustering on Principal Components (HCPC) and by individuals. Type #3 calls, which accounted for 59% of the main types, were the most abundant and present in all calves. Type #2 calls, on the other hand, were relatively abundant (16%) and found in all calves except one. The remaining call types comprised less than 1 to 9% of all detected calls and were only common to a maximum of half of the total calves examined

Table S1. Characteristics of the 13 call types (#1–13) from eight calves tagged with a CATS cam tag identified using a Hierarchical Clustering on Principal Components (HCPC). The values are presented in the form mean±SD (min–max)

Type #	N	Dur (s)	F0 (Hz)	Fmax (Hz)	Q25 (Hz)	Q50 (Hz)	Q75 (Hz)	Bdw (Hz)
1	14	2±0.6 (1.4–3.3)	40±15 (24–82)	46±20 (30–86)	61±21 (37–112)	128±57 (67–278)	297±156 (115–627)	87±51 (8–158)
2	81	0.7±0.2 (0.5–1.2)	40±17 (16–141)	56±34 (28–187)	68±36 (33–297)	126±72 (39–523)	261±137 (95–768)	88±59 (4–304)
3	300	0.3±0.1 (0.1–0.5)	45±22 (22–137)	57±38 (0–290)	68±28 (33–150)	122±56 (36–348)	241±113 (42–741)	128±110 (5–659)
4	43	0.3±0.1 (0.1–0.5)	204±49 (120–334)	217±63 (106–416)	215±48 (143–316)	363±134 (190–782)	1153±549 (275–2431)	189±135 (14–550)
5	16	0.3±0.1 (0.1–0.6)	79±56 (26–186)	190±68 (64–370)	285±133 (131–647)	539±208 (246–896)	1039±502 (375–2405)	686±147 (483–943)
6	19	0.3±0.1 (0.2–0.8)	186±83 (30–292)	216±80 (134–445)	366±133 (175–644)	1099±423 (603–2498)	2909±581 (1916–4341)	371±284 (29–833)
7	5	1±0.6 (0.3–1.5)	434±41 (396–497)	588±338 (405–1190)	487±212 (345–863)	657±308 (444–1190)	1811±499 (931–2144)	172±212 (11–436)
8	9	0.2±0.1 (0.1–0.5)	65±53 (38–205)	717±74 (667–910)	644±162 (287–800)	889±131 (708–1126)	1721±950 (981–3826)	901±331 (505–1470)
9	12	0.4±0.2 (0.1–0.9)	186±91 (55–313)	263±141 (142–670)	634±137 (436–968)	1145±278 (755–1494)	2013±408 (1347–2458)	1510±291 (1136–2018)
10	4	0.2±0.1 (0.1–0.3)	210±79 (105–296)	1388±165 (1154–1532)	852±217 (626–1083)	1401±211 (1136–1640)	2217±488 (1722–2824)	1656±420 (1042–1939)
11	3	0.3±0.1 (0.3–0.4)	161±80 (69–210)	324±105 (210–416)	943±545 (407–1497)	2216±209 (2053–2452)	3451±353 (3055–3735)	3009±1074 (2000–4138)
12	1	0.6	993	988	963	1675	4111	363
13	1	0.5	123	2099	2024	2280	3398	301



<https://doi.org/10.5281/zenodo.8362299>

Audio S1. Example of calls from each identified cluster

General discussion



1. Summary of the work performed and findings

Throughout this thesis, I presented novel perspectives on three aspects of mother-calf interactions in humpback whales – the suckling/nursing behavior, the swimming behavior, and the acoustic communication – during the first three months of life of the calf using animal-borne multi-sensor acoustic tag data collected since 2013 off Sainte Marie Island, Madagascar. In Part I, Chapters 1 and 2, for the first time, thanks to an automatic behavioral identification method I developed during the thesis, robust details on how, where, and when the suckling/nursing occurs in humpback whales have been obtained, answering my first research question. From these results, I reached the conclusion that the humpback whales' suckling/nursing behavior is very stereotyped. The calf leans to one side to better reach one of the two mammary teats of its mother and access the milk, and with a rhythmic movement of its tongue, it stimulates the milk ejection or limits milk loss into the water. As for the mother, she leans slightly downwards, i.e., nose down, as if to present her breasts to the calf. The mother-calf pair usually keeps moving while nursing, but the speed is reduced, and in general, the calf exhibits a relatively high swimming effort to maintain the suckling posture. The results also led me to conclude that humpback whale mothers nurse mainly at depth, with a tendency to get deeper as the calf grows. The on-teat periods, or suckling events, are relatively short, lasting less than 30 s, but are performed repeatedly, alternating between the right and left teats (or vice versa), organized in bouts occurring less than 10 minutes apart and grouped into sessions occurring every two hours or so, including at night. Furthermore, the time spent suckling by the calves represents less than 2% of their time, and there is potentially an increase in the suckling frequency with age.

In Part II, Chapter 3, a close examination was conducted on the activities of mother-calf pairs to understand their activities on a fine scale and to address the question of how the swimming behaviors of mother-calf pairs are organized. In Part II, Chapter 4, one specific aspect of the difference in swimming abilities between adults and calves, the ability to control buoyancy, was explored. The findings suggested that resting takes a considerable amount of time in the time budget for both the mother and the calf. However, calves, particularly the very young ones, often go into a milling state, moving slowly, probably wandering around the mother. Additionally, mothers with very young calves tend to rest less than those with older ones. The results also pointed out that the mother and the calf are often synchronous in their activities and suggested that there is a behavioral adjustment by both the mother and the calf with respect to the other's behavior. Depending on the context, either the calf or the mother can take the lead in initiating a given activity. The data supported that the mother is the one who imposes resting periods and fast swimming. On the other hand, each individual can be milling independently, but the calf more often initiates it than the mother. Similarly, routine swimming can be initiated solo by either the mother or the calf. Regarding buoyancy, the behavioral data has shown for the first time that the humpback whale can change its buoyancy at will to optimize its swimming efficiency and that such ability

is absent in calves. Calves thus need to acquire this ability, probably through learning and organ maturation, but until then, they have to rely on their mother to assist them in managing their buoyancy at different depths. Down to a certain depth, they have to wedge themselves under their mother to remain stationary, and they have to put more swimming effort when descending.

In the final part, Part III, the question on the context of vocalizations (social calls) in mother-calf pairs was addressed in two steps. First, in Chapter 5, simultaneous mother-calf tag deployments were used to understand which individual usually vocalizes and to comprehend the relationship between vertical separation and vocal production. The results supported that social calls are produced more frequently than previously reported for mother-calf pairs, and the social calls are predominantly emitted by the calf, especially in the event of vertical separation. Moreover, a slightly higher pitch characterizes the social calls from the calf. Surprisingly, the mother appeared to rarely vocally respond to the calf. The mother mainly vocalizes when she is at the same depth as her calf, and it is also mainly during these moments that vocal exchanges take place. Through Chapter 5, I concluded that a tag placed on the calf can be sufficient for studying the calf's vocalizations because, in the end, vocalizations from the mother are rarely recorded by the calf's tag. This conclusion led to Chapter 6, where the results of Part I and II for the camera-equipped tag data from calves were combined and analyzed along with the sound data to take a closer look at the behavioral context of calf social calls. With the analyses conducted in Chapter 6, I found that nursing sessions are associated with an increased call rate. The associated calls are not just any call types but a somewhat defined set of social calls corresponding to low-frequency calls of short duration. I also showed that periods of surface playing activity are associated with high vocal activity (high call rate), but the produced social calls varied. Surprisingly, I found no social calls associated with traveling. It seems that traveling, as well as resting, are mainly associated with silence. It thus suggests that calves use a specific set of social calls to initiate nursing, produce several call types when playing, and don't vocalize much with the mother when travelling or resting.

While the nursing, swimming, and vocal behavior have already been addressed to some extent in humpback whales and other related marine species, my results represent new and critical elements for a better understanding of the dynamics of maternal care, the development of skills crucial to the survival of young whales, and the importance of acoustic signals for maintaining mother-calf contact, optimizing maternal care, and maintaining social bonds in a marine environment. Some studies have for example already investigated the nursing behavior in dolphins (Clark & Odell, 1999a, 1999b; Triossi et al., 1998), beluga whales (J. M. Russell et al., 1997), sperm whales (Sarano et al., 2023), and humpback whales (Tackaberry et al., 2020; Videsen et al., 2017; Zoidis & Lomac-MacNair, 2017). Also, several studies have investigated the mother-calf swimming behavior and energy management in baleen whales (e.g., Bejder et al., 2019; Huetz et al., 2022; Ratsimbazafindranahaka, 2019; Smultea et al., 2017; Taber & Thomas,

1982; Thomas & Taber, 1984) and in toothed whales (e.g., Fellner et al., 2013; Noren, 2008; Noren et al., 2006, 2008; Noren & Edwards, 2011). Similarly, the acoustic communication between the mother and the calf was of particular interest both in baleen (e.g., Indeck et al., 2021, 2022; Nielsen et al., 2019; Parks et al., 2019; Videsen et al., 2017) and toothed whales (e.g., Ames et al., 2021; S. L. King et al., 2016; Sayigh et al., 2023). Most of these studies were, however, either limited to captive animals, based on limited observations (surface or subsurface observation, small sample, etc.), or constrained by unsolved technical limitations (e.g., challenges in identifying the emitter of sounds when animal-borne acoustic tag sound data are used).

The end goal of maternal care is to maximize the young's chance of survival and thus contribute to the mother's reproductive success and the perpetuation of her genes (Balshine, 2012; Clutton-Brock, 1991). Globally speaking, maternal care touches on various aspects such as food supply, protection against environmental hazards, locomotor assistance, and learning facilitation (Balshine, 2012; Clutton-Brock, 1991). In order to provide care to their young, the humpback whale mothers, being aquatic, face unique challenges linked to the characteristics of their environment compared to terrestrial mammals. In this regard, my work, as discussed below, highlights that the humpback whale displays a complex and multi-faceted form of maternal care that has adapted to cope with its various environmental constraints.

2. Taking care of a young in an exclusively aquatic environment

First of all, in terms of nursing behavior, humpback whales have developed (or kept) behavior that is comparable to what has been observed in terrestrial mammals living in open environments with predators, the following strategy (Fisher et al., 2002; Lent, 1974). However, the nursing behavior of humpback whales must take into account the fact that the calf has to go to the surface to breathe (Cartwright & Sullivan, 2009; Huetz et al., 2022; Szabo & Duffus, 2008). Thus, it is expected that the calf is nursed frequently, but the sessions are fragmented. My results matched this expectation as I found that nursing sessions are divided into several bouts between which the calf can go to the surface to breathe. The calf is also nursed at depth, potentially to avoid surface noises associated with waves and wind and thus enabling the mother to be more alert to predators (Videsen et al., 2017), to avoid boats, or to facilitate calf's attachment to nipples and ease suckling configuration by exploiting depths where the calf is neutrally buoyant (Videsen et al., 2017). Nursing is increasingly intense as the calf grows during its early life stage (<3 months old), likely to optimize its growth speed (Oftedal et al., 1987) in preparation for the upcoming long migration to the feeding ground and to enhance its chances of avoiding predation. Nursing in humpback whales likely diminishes in intensity only when the calf finally begins to feed on prey (at around seven months old; Clapham, 2018). While nursing in other species is not only for feeding purposes but also to comfort the young (Hall & Williams, 1983; Lent, 1974; Wolff, 1968), in humpback whales, it might be that nursing is only to feed the calf or

maximized to be always nutritive, due to the constraints related to aquatic life. Indeed, suckling in an aquatic environment requires a certain level of locomotor activity to maintain a good functional posture for successful milk transfer (Chapters 1 & 2; Tackaberry et al., 2020). Performing it without any energetic gain (nutritive value), given its potential energetic cost, may be disadvantageous.

One particular aspect that I have highlighted is the buoyancy control. Buoyancy control is essential for species living in an aquatic environment and exploiting various depths (Alexander, 1982; Pelster, 2009). In humpback whales, as the neonate is not yet able to control its buoyancy, the physical contact between the mother and the young has taken on a function that does not exist at all in land mammals and that has never been documented in other groups of marine mammals: the mother acts as a physical support for the calf to prevent it from popping up involuntarily to the surface. This is a remarkable adaptation illustrating the emergence of a new form of maternal care in response to a specific context imposed by the environment. In other species, this type of configuration may only be used as a form of tactile communication, to hide the young from predators, or to promote heat exchange.

3. Acquiring new skills beside mother

One of the advantages for young mammals of growing up alongside their mother is that they have the time and opportunities to develop complex behaviors that are useful later for survival and that can be plastic, either through self or social learning, but under the mother's supervision (Alonso-Alvarez & Velando, 2012; Caro, 1980; Hoppitt et al., 2008; B. J. King, 1991). In the case of the humpback whale, several aspects of the calf's behavioral development are made possible by the unique interactions with its mother. First, the mother adapts her behavior to the age of the calf. The mother is more vigilant, more active, and probably interacts more often with the calf at birth and during its first weeks of life. This likely corresponds to an early stimulation by the mother for the cognitive and locomotor development of the calf (Davis et al., 2017; Liu et al., 2000). Since the mother is at her maximum vigilance when the calf is still very young, the calf can start 'experimenting' with its environment and aptitudes. As has been shown for right whales and dolphins, young calves swim continuously to develop their muscles and quickly grasp how to move around in their environment (Cartwright & Sullivan, 2009; Thomas & Taber, 1984). As mentioned above, suckling occurs at greater depths as the calf grows, so it is conceivable that the mother gradually imposes diving constraints on the calf to swim at greater depths to enable it to develop its diving and buoyancy control skills. Similar schemes concerning the dive duration have been suggested (Huetz et al., 2022; Szabo & Duffus, 2008). The mother gradually lengthens her dives so that the calf improves its apnea. As pointed out previously, mother humpback whales appear to impose behaviors such as resting or fast swimming. These instances are also likely important for the development of the calf. Through them, the calf can learn to identify resting areas, dangers, and how to avoid them.

Globally speaking, humpback whale mother-calf pairs, based on their time budget, employ a strategy that appears to be a compromise between minimizing energy expenditure and engaging in activities related to the calf's locomotor development, as previously suggested in past studies (Bejder et al., 2019; Ejr n s & Sprogis, 2021). For the mothers, such a strategy ensures a sufficient reserve for maternal care (in particular milk production) and for migration. For the calves, it ensures optimal growth, securing, as already stated above, the ability to undertake the upcoming migration and enhancing the chances of avoiding predation.

4. Communicating with mother

My work on acoustic communication highlighted the importance of the use of sound by mother-calf pairs to communicate as expected, given that it is one of the most effective means of communication in the aquatic environment (Au & Hastings, 2008; Ladich & Winkler, 2017). In the water and in the context of mother-calf interactions, the main modality of communication should not rely on vision, should propagate over a reasonable distance, and must be fast. It should not rely on vision because the visibility underwater can be affected by water turbidity, depth, etc. It should also propagate over a reasonable distance because, although the mother and the calf are in close proximity most of the time, there are frequent vertical separations as the mother often remains at depth while the calf swims to the surface to breathe. Finally, it must be fast because rapid response by the other individual is usually crucial. Acoustic communication meets these requirements and, as such, is used by mother-calf pairs to ensure permanent contact and prevent premature separation, potentially to maintain strong social bonds, and to quickly send messages to coordinate vital activities such as nursing.

The richness of the vocal repertoire of mother-calf pairs has the potential to convey an extensive range of messages. One might expect acoustic communication to be used in many aspects of the life of mother-calf pairs and thus features patterns where certain types of calls are associated with specific behaviors or social interactions. However, from what I have found, this is not totally the case. For example, social calls are used sparingly during traveling. In these cases, other potentially non-acoustic signals, such as visual and tactile, are probably used. The use of visual and tactile signals for activities associated with close spatial relationships would not be surprising because both can work for short-range communication underwater. Among the extant terrestrial relatives of whales that also use the 'following' strategy, the coordination of movements, for example, tends to be based on 'pacing,' where the mother adjusts her speed to allow the calf to follow her and keep her in sight, and the calf would just tend to follow the movement of the individual it sees moving beside it (which should be the mother) (Lent, 1974). Humpback whale mother-calf pairs can probably do the same as long as there is sufficient visibility for the calf to distinguish the mother's silhouette.

5. Limitations, future directions, and concluding remarks

The present work provides, for the first time, a detailed description of a little-known aspect of baleen whale suckling/nursing behavior and explores in greater depth points concerning the activities of mother-calf pairs and their acoustic communication. The results undoubtedly contribute to a better understanding of the close bond between mother and calf and its implication in the survival and development of the calf. However, the work is limited to a portion of a population of humpback whales in the breeding area, thus also restricted to dependent calves less than three months old. In addition, it is restricted to a geographical area corresponding to a relatively shallow sea of about 35 m depth on average (Trudelle et al., 2016). Yet, humpback whale calves stay with their mother until they are one year old (Chittleborough, 1958; Clapham, 2018). During their dependent period, they also pass through the migratory route, then the feeding area (Baraff & Weinrich, 1993; Chittleborough, 1958; Clapham, 2018; Steiger & Calambokidis, 2000). The calves and their mothers, even during the breeding and calving periods, may occupy areas with water much deeper than 35 m depth. For example, humpback whale mother-calf pairs off West Maui, Hawaii, occupy waters up to about 120 m deep (Pack et al., 2022). It would thus be interesting to extend the studies presented in my thesis to other whale populations in other geographic areas and contexts (migration and feeding) to generalize the results better and capture the calf's development until weaning and the evolution of its relationship with its mother. For instance, such an extension would help pinpoint the stage at which conflicts between the mother and the calf emerge as the cost of caring for the calf becomes detrimental to the mother's future reproduction (Trivers, 1974).

Another limitation is the data being primarily restricted to daytime data. How mother-calf interactions occur at night remains mostly unclear. Nonetheless, the data I exploited have already given a first glimpse of this interaction. For instance, I showed that nursing also occurs at night. Deploying tags later in the day could help better fill in the gaps. Developing new tag attachment systems so that the tags stay on the whales longer would also be beneficial. Darts-based attachment systems have existed for a long time and can provide longer deployment duration (Szesciorka et al., 2016). However, they may not be of interest at present, as one of the main objectives is to be as non-invasive as possible during data collection, both for animal welfare reasons and to ensure good quality data.

On another note, the challenges specific to my studies in terms of data collection may have implications for my interpretations of the results. My entire thesis is based on placing tags on whales. However, the tagging process is a complicated and potentially hazardous challenge for the data collection operators as it requires a very close approach to the whales. As such, although the sampling is assumed to be random, the field team and I have often been driven to focus on resting individuals. Moreover, some of the whales we chose to approach may have been easier to approach than others

depending on their arousal state, their personality, their age or maternal experience (primiparous vs multiparous females), and even their previous experience with humans. How this could have induced a bias in the database remains undefined. For example, did the way we sampled the whales induce a pseudo-selection to the extent that my results only represent the behaviors of individuals with a particular personality (Biro, 2013; Biro & Dingemanse, 2009)? Studies on the personality of whales and tests to compare tagging approach success according to personality profiles could answer such questions.

Although the data I present constitute one of the most extensive datasets from multi-sensor tags for studying mother-calf pairs (57 deployments from 2013 to 2022), we could have done more with more funding and more time in the field. Our main limitation was mostly for the simultaneous mother-calf tag data. As placing a tag on one individual usually puts the mother-calf pair in a more alert state in the coming minutes, it is challenging to sequentially place a tag on the mother and then on the calf or vice versa. In the current context, the only way to collect more tag data would be to multiply sampling efforts to maximize the chances of tagging success. It has to be said, however, that there has been a significant improvement in our approach technique since the very first tag was placed back in 2013. Thanks to such improvements, I expect future data collection successes to be multiplied.

As the whale searches and pre-tagging observations were carried out from a boat, there was a significant gap in the data concerning each studied individual, limiting the analyses I was able to conduct. There was a lack of precision when estimating the age of the calves, and I had no reliable data on the sex of the individuals. The estimation of the age in my studies was based solely on the angle of inclination of the calf's dorsal fin (Cartwright & Sullivan, 2009; Faria et al., 2013; Huetz et al., 2022), a non-invasive approach already used routinely, and which, in all cases, enabled me to address to some extent the questions I was interested into. Unfortunately, this approach only gives a relative age, whereas a more accurate estimate would be beneficial. An alternative method I have planned to estimate age was to use a photogrammetry technique I developed (Ratsimbazafindranahaka et al., 2021; Appendix II) to estimate size and relate it to age since the two are closely linked. However, the management of the drone launches and the drone batteries in parallel with the approaches for the tagging was very challenging, and on several occasions, we did not have drones available in the field. Moreover, the photogrammetric approach would still only give a rough age estimation. With respect to the sex, from the boat, it was difficult to get visual access to the calf's genitals. An approach based on genetic analysis, using biopsy samples, would provide the sex of the individuals (Bérubé & Palsbøll, 1996). A common technique to biopsy whales involves crossbows with purpose-designed arrows (Gauthier & Sears, 1999). Although such equipment was available in the field, we preferred not to use it on the individuals we were interested in because shooting before tagging reduces the chances of successful tagging approaches, and trying to biopsy

after tagging could corrupt the quality of the data recorded by the tags because the biopsy approaches induce more disturbance. Finding solutions to collect both data on age and sex would be beneficial as it would give more temporal precision on the behavioral development of the calf and help understand whether there is an ontogenic divergence between males and females. For instance, a particularly relevant question concerns whether there is a link between baleen whale dimorphism (females being larger than males) and suckling intensity. Additionally, it would be interesting to compare acoustic communication between male and female calves to shed light on the ontogeny of songs. Data on the mother's age would also be beneficial, as it can be used to show how maternal care and potential breeding success vary with maternal experience. Developing tagging poles that allow both the collection of tissue samples and tagging could be the way forward for studies on these topics.

The communication components of my thesis were exclusively focused on the acoustic channel and social calls. Aspects concerning non-vocal and non-acoustic signals, such as tactile or visual signals, were not explored. Vocal communication is an essential point in the current context where there is more and more marine noise pollution (Chahouri et al., 2022) and because vocalizations are predominant in cetaceans. However, a more comprehensive analysis could explore other communication modalities. In my studies, for example, I found that although humpback whales potentially use social calls to initiate nursing, there are cases where nursing occurs without the calf vocalizing. A closer look at the behavioral sequences of the mother and calf prior to nursing, using data from simultaneous mother-calf tag deployments, could shed light on other modes of communication in humpback whales. These analyses were planned but still need to be completed. I aim to finish them in a future project.

An important point to consider that I did not address and would require quantification in the future is the impact of tagging on the observed behaviors of humpback whale mother-calf pairs. In my thesis, this impact was considered minimal on the scale of all the data I analyzed. The impact of tagging on humpback whale mother-calf pairs is considered to occur approximately mainly in the first 10 minutes of the deployment (Bejder et al., 2019; Stimpert et al., 2012). In my data, I noted that mother-calf pairs usually stop any hasted swimming in response to tagging within less than 10 minutes, which corresponds to what has been reported by Bejder et al. (2019) and Stimpert et al. (2012). I, however, acknowledge that these observations are not sufficient for quantifying the real extent of the tagging impact because of the lack of a baseline for what is really a 'normal' behavior. Pre- and post-tagging tracking and observations would provide a basis for comparison and would allow us to quantify the impact of the tagging more precisely.

Despite various logistic and technical challenges, my studies have provided new answers concerning multiple facets of mother-calf relationships in humpback whales. I particularly highlighted the aspects of nursing behavior, swimming behavior, and acoustic communication. This thesis is the first to precisely describe an entirely aquatic species' suckling/nursing pattern in its natural environment. It also offers new insights into the control of buoyancy and its ontogeny. Finally, it offers a new perspective on the context of vocalizations in humpback whale mother-calf pairs and thus provides a better understanding of the various roles of social calls. Generally speaking, this thesis provides valuable insights into how the mother-calf behaviors adapted to the unique challenges of the marine environment and how the close relationship between the mother and the calf contributes to the development and survival of the calf. It also proposes several new approaches that can be entirely or partially applied to studying cetaceans in general in their natural environment. Additionally, it highlights several technical challenges that need to be overcome, pointing to several research directions. Beyond what has been mentioned above, it would be really interesting to extend the present work to other species of entirely aquatic mammals and other marine mammals. Comparative studies on various species of marine mammals would indeed provide insights into the universality or uniqueness of the behaviors I described here. *Over and above its usefulness as a collection of knowledge that could guide conservation measures and future studies, I hope the present work will awaken fascination and curiosity, raising awareness and motivating species protection and conservation.*

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Appendix



Appendix I. Related scientific paper produced in parallel to the main research (1/2)

Social calls in humpback whale mother-calf groups off Sainte Marie breeding ground (Madagascar, Indian Ocean)

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ABSTRACT

Humpback whales (*Megaptera novaeangliae*) use vocalizations during diverse social interactions or activities such as foraging or mating. Unlike songs produced only by males, social calls are produced by all types of individuals (adult males and females, juveniles and calves). Several studies have described social calls in the humpback whale's breeding and the feeding grounds and from different geographic areas.

We aimed to investigate for the first time the vocal repertoire of humpback whale mother-calf groups during the breeding season off Sainte Marie island, Madagascar, South Western Indian Ocean using data collected in 2013, 2014, 2016, and 2017.

We recorded social calls using Acousonde tags deployed on the mother or the calf in mother-calf groups. A total of 21 deployments were analyzed. We visually and aurally identified 30 social call types and classified them into five categories: low, medium, high-frequency sounds, amplitude-modulated sounds, and pulsed sounds.

The aural-visual classifications have been validated using random forest (RF) analyses. Low-frequency sounds constituted 46% of all social calls, mid-frequency 35%, and high frequency 10%. Amplitude-modulated sounds constituted 8% of all vocalizations, and pulsed sounds constituted 1%. While some social call types seemed specific to our study area, others presented similarities with social calls described in other geographic areas, on breeding and foraging grounds, and during migrating routes. Among the call types described in this study, nine call types were also found in humpback whale songs recorded in the same region. The 30 call types highlight the diversity of the social calls recorded in mother-calf groups and thus the importance of acoustic interactions in the relationships between the mother and her calf and between the mother-calf pair and escorts.

Subjects Animal Behavior, Marine Biology, Zoology

Keywords Acoustic communication, Baleen whale, Vocal repertoire, Mother-offspring relationship

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INTRODUCTION

Baleen whales, like other cetaceans (toothed whales), use acoustic communication in many social contexts such as predator alert, foraging cooperation, mating, individual identification, and parental care (Edds-Walton, 1997; Tyack, 1999; Dudzinski, Thomas & Gregg, 2009). Sounds used by baleen whales include vocalizations and sounds generated by active surface behaviors (breaching, tail or pectoral fins slapping, *etc.*). Some baleen whales' vocalizations, attributed to males, are organized in a repeated manner and in long bouts to constitute what is called a 'song' (Edds-Walton, 1997; Tyack, 1999; Dudzinski, Thomas & Gregg, 2009). Baleen whales also produce non-song vocalizations called 'social calls' (Payne, 1978; Tyack, 1981; Silber, 1986). Unlike songs, social calls have been described as variable through time, interrupted by silent periods, apparently unpredictable, and not showing the rhythmic, consistent and continuous temporal pattern of songs (Tyack, 1981; Silber, 1986). While all social groups in all species of baleen whales potentially produces social calls, social calls produced by mother-calf pairs have been proposed to have the particularity of being produced at a low rate and/or at a low amplitude to minimize the risk of alerting predators (Videse et al., 2017; Nielsen et al., 2019; Parks et al., 2019).

Humpback whales are baleen whales known for their complex, highly structured, and organized songs produced by males in breeding areas (Payne & McVay, 1971) but they also generate social calls. Humpback whales' social calls have been the subject of several studies, both in feeding or breeding grounds, as well as on migration routes (D'Vincent, Nilson & Hanna, 1985; Silber, 1986; Cerchio & Dahlheim, 2001; Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Stimpert, 2010; Stimpert et al., 2011; Rekdahl et al., 2013; Fournet, Szabo & Mellinger, 2015; Rekdahl et al., 2017; Epp et al., 2021; Epp, Fournet & Davoren, 2021; Indeck et al., 2021). Distinct acoustic units of vocalization or "call types" were generally defined either using an automatic clustering method based of several acoustic parameters (Stimpert, 2010; Stimpert et al., 2011; Fournet, Szabo & Mellinger, 2015) or an aural-visual classification (Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Rekdahl et al., 2013, 2017; Fournet, Szabo & Mellinger, 2015; Fournet et al., 2018; Epp et al., 2021; Epp, Fournet & Davoren, 2021; Indeck et al., 2021) validated using a supervised automatic classification (*e.g.*, discriminant function analysis–DFA, Classification and Regression Tree–CART, or random forest–RF) or not. The recordings were obtained using moored or towed hydrophones (Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Stimpert, 2010; Rekdahl et al., 2013, 2017; Fournet, Szabo & Mellinger, 2015; Fournet et al., 2018; Epp et al., 2021; Epp, Fournet & Davoren, 2021), using hydrophone carried by divers (Zoidis et al., 2008), or using animal borne tags (Stimpert, 2010; Stimpert et al., 2011; Indeck et al., 2021).

Humpback whales' social calls vary from low to high-frequency calls and differ in their general structure (Silber, 1986; Dunlop et al., 2007; Rekdahl et al., 2013). Social calls can be categorized into a broad class or category according to their general characteristics (*e.g.*, Dunlop et al., 2007; Zoidis et al., 2008; Fournet et al., 2018; Epp, Fournet & Davoren, 2021). Humpback whale vocal repertoire has been described as a mix of discrete call types (call types acoustically distinct from one another and with little variation) and graded call types

(call types with varying characteristics that form a continuum and represented by some common cases and by intermediate forms) (Epp, Fournet & Davoren, 2021). The variation of call types in humpback whale is likely related to factors such as age, sex, or body mass (Cerchio & Dahlheim, 2001; Epp, Fournet & Davoren, 2021).

Social calls are produced by the same sound generator as for songs, located inside the respiratory system, composed of the lungs (air source), the laryngeal sac (air source and acoustic resonator), and the nasal cavities (another resonator) (Adam et al., 2013). Individuals in all group compositions produce social calls: lone individuals, multiple animals, pairs, and mother-calf pairs accompanied or not by escorts (Dunlop, Cato & Noad, 2008).

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 were reported to be produced when whales are predominantly in groups of three or more adults, in surface-active groups including both females and males (Silber, 1986). Although up to now only few direct quantitative comparisons were conducted and most comparisons were based on aural and visual characteristics, several studies suggested that some calls types are shared between humpback whales from different regions (Dunlop et al., 2007; Stimpert et al., 2011; Fournet, Szabo & Mellinger, 2015; Rekdahl et al., 2017; Epp, Fournet & Davoren, 2021).

The first confirmed recording of humpback whale calves' social calls was performed by Zoidis et al. (2008) using a technique involving a two-element hydrophone array. It has been suggested that calves' vocal repertoire is limited and vocalizations are simple in structure, short, predominantly composed of low frequencies, and have a relatively narrow frequency bandwidth (Zoidis et al., 2008). Humpback whales are known to be vocal learners (Tyack, 1998; Janik, 2014). Although mostly described for male songs, the vocal learning likely also apply to social calls. Calf might have to learn and master their calls, or aspects of them (Tyack, 1998; Epp, Fournet & Davoren, 2021).

Up to now, the biological functions of social calls remain unclear. Visual observations from surface activity suggested that social calls could serve either as a sign of aggression among males competing for the 'principal escort' status (Tyack, 1983; Baker & Herman, 1984; Silber, 1986) or, in some specific breeding competitive contexts, depending on sex and group composition, among adults as a deterrent to dissuade approach from other whales of same or opposite sex (Tyack, 1983).

Mother-calf pairs constitute the only stable social association on breeding grounds in humpback whales. Calves are born in a rich acoustic environment filled with songs and social calls. Recent acoustic studies on the social calls of humpback whales investigated vocal production from mother-calf pairs (Dunlop et al., 2007; Fournet, Szabo & Mellinger, 2015; Recalde-Salas et al., 2020; Indeck et al., 2021) with an attempt to assign social calls to females or calves. Identifying the sound source remains a real challenge (Saddler et al., 2017; Indeck et al., 2021), and thus further investigations are needed to accurately assign social call types to mothers or calves.

The social calls of humpback whales in the South Western Indian Ocean remained poorly documented. This present study aimed to investigate the repertoire of social calls

recorded by suction-cup acoustic tags (Acousonde 3B) attached to female humpback whales or their calf off Sainte Marie island, Madagascar, South Western Indian Ocean, during four breeding seasons. Our goal was to complement the knowledge of acoustic communication in poorly documented yet critical social groups such as mother-calf groups and to contribute to the global catalogue of humpback whale social calls. The social calls described in breeding and foraging grounds are likely to be different, as they are produced in different behavioral contexts. Such knowledge is thus crucial to better understand the biological function of social calls, but also to investigate dialects and thus vocal learning of social calls. In addition, the description of the repertoire of social calls in mother-calf groups is a crucial material for investigating the role of acoustic communication in humpback whale mother-calf interactions in the future.

MATERIALS AND METHODS

Study area

We collected acoustic data during winters 2013, 2014, 2016, and 2017 in the coastal waters off Sainte Marie island, Madagascar, South Western Indian Ocean (between latitudes 17° 19' and 16° 42' South, and longitudes 49° 48' and 50° 01' East), where mother-calf pairs come in these relatively calm and shallow waters (*Trudelle et al., 2016*).

Data collection and tagging procedure

We used Acousonde 3B (www.acousonde.com) attached to females or calves *via* four suction cups, a non-invasive attachment system, to record sounds. We deployed tags from a 6.40 m rigid motorboat using a 5 m handheld carbon-fiber pole. The boarding team consisted of staff experienced in successfully approaching mother-calf pairs: one operator (boat pilot), photographer, note-taker, and tagger. While the boarding team may change between outings, the team composition was always respected and each team member held one role within a whole outing. The tags were placed on the back, near the dorsal fin of the animal. Calves were tagged using one of the two approaches described in *Stimpert et al. (2012)* and in *Huetz et al. (2022)* in order to minimize disturbance to the mother-calf pair. Tagging efforts were terminated if the pair displayed avoidance behavior or if the calf was not successfully tagged within 30 min. Immediate behavioral response of the animals to tagging was recorded as in *Stimpert et al. (2012)*. All mother-calf pairs were photo-identified to avoid double-sampling within the calving season. Tagged animals were not followed after tag deployment to avoid any further disturbance of their behavior. After tag deployment or an aborted attempt, the boat slowly moved away in the opposite direction of the mother-calf pair. The tag was retrieved after few hours or the following day, when it detached itself from the animal (usually as a consequence of rubbing against the mother, surface active behavior, *etc.*). The Fisheries Resources Ministry, Madagascar, fully approved all experimental protocols (Research and Collect permits #44/13-MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #28/16-MRHP/SG/DGRHP, and #26/17-MRHP/SG/DGRHP). This present study complies with the European Union Directive on the protection of animals used for scientific purposes (EU Directive 2010/63/EU).

For each spotted group with mother-calf pair, approaches similar to touristic boats, complying with Madagascar's Code of Conduct for whale watching activities (Inter-ministerial decree March 8th, 2000), were adopted: the boat's speed was reduced gradually at 800 m distance from the spotted group. The observation area for mother-calf groups was set at a 200 m radius around them. We used this distance to observe the groups before tag deployment. We noted the group composition: lone mother-calf pair (MC) or mother-calf pair accompanied by one or several escorts (MCE). Behavioral observations and photo-identification were obtained concurrently for each group, and the calf's relative age was estimated using the angle of furling of its dorsal fin ([Cartwright & Sullivan, 2009](#); [Huetz et al., 2022](#)): C1 (neonate)-calf presenting some folds, scars, and skin color that tends to be light grey dorsally and white ventrally and with less than 44° dorsal fin furl ([Faria et al., 2013](#)), C2: very young but non-neonate calves having more than 45° but less than 72° dorsal fin furl, and C3: older calves that have unfurled dorsal fins (>72°). Depending on the opportunity and on how the group behaved, we tagged the calf or the mother using either a passive or active approach, as described in [Stimpert et al. \(2012\)](#) and [Huetz et al. \(2022\)](#).

We did not follow the animals after tag deployment to avoid further disturbance of their behavior. This means that change in group composition during the data recording is unknown. MC could be joined by other escort(s) or escort(s) in MCE might have left. Our tagging processes lasted 21 min on average and never exceeded 30 min (*i.e.*, our maximum duration to tag a whale). Beside the mother-calf recordings, we also punctually recorded several male songs using a towed Aquarian H2a hydrophone deployed from the boat (engine off).

Vocal repertoire and acoustic analysis

We downloaded the audio files from the tags as *.MT files, converted them to *.WAV format using GoldWave software (GoldWave Inc., St. John's, Canada), and analyzed them using Avisoft SASLab Pro version 5.207 (Avisoft Bioacoustics, Nordbahn, Germany). We produced spectrograms of the acoustic recordings using 1,024-point Fast Fourier Transform, 75% overlap, and Hamming window.

Social calls that were clearly audible and distinguishable were aurally and visually identified, classified, and then compared with social call catalogues available in the literature ([Dunlop et al., 2007](#); [Dunlop, Cato & Noad, 2008](#); [Zoidis et al., 2008](#); [Stimpert et al., 2011](#); [Rekdahl et al., 2013, 2017](#); [Fournet, Szabo & Mellinger, 2015](#); [Epp, Fournet & Davoren, 2021](#); [Indeck et al., 2021](#)). Call types qualitatively similar to call types described in these catalogues (reference catalogue hereafter) were given the same name. New names were assigned for the remaining call types onomatopoeically, as the behavioral context or biological function of these new call types is still unknown and the main acoustic structure can be common to several call types (*e.g.*, several call types can be low-frequency upsweep calls). Distant song units could not be confused with social calls in our dataset as songs can be easily recognized by their well-organized temporal pattern. Additionally, we used 16 of the recorded male songs to determine if some social calls were similar to males' song units.

Table 1 Measured temporal and spectral characteristics for each identified social call.

Measurements	Abbreviation	Description
Manual measurements		
Duration (s)	Dur	Total duration of the social call (a)
Fundamental frequency (Hz)	F0	Fundamental frequency (b)
Frequency excursion (Hz)	Fexc	Difference between the higher and lower frequencies (c) Measured only when applicable For harmonic-structured calls, Fexc was measured on the first visible frequency band
Automatic measurements		
Peak frequency (Hz)	Fmax	Frequency at which the maximum amplitude level occurs (b)
1 st energy quartile frequency (Hz)	Q25	Frequency below which 25% of the total energy occurs (b)
2 nd energy quartile frequency (Hz)	Q50	Frequency below which 50% of the total energy occurs (b)
3 rd energy quartile frequency (Hz)	Q75	Frequency below which 75% of the total energy occurs (b)
Frequency bandwidth (Hz)	Bdw	Frequency bandwidth within which the total energy fell within 12 dB of Fmax (b)
Pulse rate (Hz)	PR	Number of pulse per second as measured using the pulse train analysis function in Avisoft SASLab Pro PR was considered to be zero for calls without a pulsed structure

Note:

(a) Measured on the oscillogram. (b) Measured on the averaged spectrum. (c) Measured on the spectrogram.

For each identified social call, we measured nine temporal and spectral characteristics (Table 1). Similar to *Dunlop et al. (2007)*, we categorized social calls as either low-frequency sounds (LF), mid-frequency harmonic sounds (MF), high-frequency harmonic sounds (HF), amplitude modulated sounds (AM), noisy and complex sound (NC), or pulsed sounds (PS). LF corresponds to calls with peak frequency below 160 Hz. MF corresponds to calls with a peak frequency ranging from 170 to 550 Hz. HF corresponds to calls with a peak frequency above 700 Hz. AM corresponds to sounds consisting of a combination of long harmonic and amplitude modulated components with peak frequency ranging from 20 to 300 Hz. NC corresponds to broadband calls or harmonic calls with additional noise-like features. PS corresponded to low-frequency sounds repeated rhythmically. Representative spectrograms (Hamming window, FFT window size: 1,024 pts, 90% overlap) for the identified social calls were generated using the *Seewave* package (*Sueur, Aubin & Simonis, 2008*) in R software (*R Core Team, 2021*).

To obtain an overview of the intensity of sounds recorded in mother-calf groups, we measured the received level (in dB re 1 μ Pa RMS) of the most common and aurally and visually easily identifiable call types using the Root Mean Square (RMS) function in Avisoft SASLab Pro. We considered only 10 good quality calls with a signal-to-noise ratio above 10 dB and without overlap for each selected call type. Using such criteria, calls selected for such measurements are likely produced by individuals constituting the focal mother-calf group (*i.e.*, the mother, the calf, and possibly the escort if present). Mother-calf pair don't gather with other pairs, so the only calls detected from our recordings can only come from individuals of the focal groups. Songs are highly different, so no confusion could be made. A similar procedure was used previously on humpback whale mother-calf pairs in Western Australia (*Videsen et al., 2017*).

Statistical analysis

To validate our aural-visual classification of calls by categories and by types, we performed random forest (RF) analyses ([Thiebault et al., 2019](#); [Indeck et al., 2021](#)) using the *randomForest* ([Liaw & Wiener, 2002](#)) package in R. We calculated the global accuracy of the RF classification of calls by categories and by types (defined as accuracy = 1 – OOB, where OOB stands for out-of-bag error, the misclassification error rate) and computed the Gini index, which gives the importance of the variables used for the classification. We only included acoustic variables that were primarily measurable for most of the calls: Dur, Fmax, Q25, Q50, Q75, and PR. We included only call types for which we had at least six exemplars. The number of variables to be randomly selected at each split was set at 2 (as we had only six variables), and the number of trees grown was set at 500. We used a balanced RF design to maintain equal sample sizes of each category or type in the classification and avoid the over-representation of the most represented classes ([Chen, Liaw & Breiman, 2004](#)). In this design, each tree of the RF is built with the same number of calls per category or per type (*i.e.*, the smallest number of calls for a given category or type).

RESULTS

Tag deployments

We performed 62 successful tag deployments (35 on calves and 27 on mothers) during the four years of data collection. Acoustic data were usable for 21 deployments (21 different mother-calf groups): seven deployments on mothers and 14 deployments on calves ([Table 2](#)). The other deployments were not analyzed due to the high background noise level or their short durations (less than 30 min). Background noise was mainly present 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. Of the 21 studied groups, we identified 12 as MC and nine as MCE. Three groups had a C1 calf, three had a C2 calf, and 15 had a C3 calf. We detected social calls in all of the studied groups.

Social call classification

A total of 2,033 social calls were clearly distinguishable. Aural-visual characteristics allowed the classification of these calls into 30 call types representing five of the six main categories suggested by [Dunlop et al. \(2007\)](#) ([Table S1](#)): low-frequency sounds (LF), mid-frequency harmonic sounds (MF), high-frequency harmonic sounds (HF), amplitude modulated sounds (AM), and pulsed sounds (PS). We did not find any call corresponding to the noisy and complex sound (NC) category. Eleven call types were named after qualitatively similar calls in the reference catalogue we used and 17 were given new name as they appeared qualitatively different ([Table S1](#)). Audio examples of call types are provided ([Audio S1](#)).

Low-frequency sounds (LF)

LF was the most represented category (46%, $N = 925/2,033$). Eleven call types were within the LF category: “100 Hz sound”, “bass”, “boom”, “gru”, “snort”, “burp”, “guttural”, “thowp”, “wop”, “bark”, and “drum” ([Fig. 1](#)). “Bass” and “wop” ([Figs. 1B and 1I](#)

Table 2 Details of the tagging sampling effort. MC: lone mother-calf pair. MCE: mother-calf pair accompanied by one or several escorts.

Date	Tagged individual	Group type	Calf's relative age	Analyzed recording duration (hh:mm)
07/08/2013	Mother	MCE	C3	04:05
16/08/2013	Mother	MCE	C1	01:22
05/09/2013	Mother	MC	C3	01:26
09/09/2013	Mother	MCE	C3	00:39
12/09/2013	Calf	MC	C3	03:14
15/09/2013	Calf	MCE	C3	01:06
05/08/2013	Mother	MC	C3	05:15
24/08/2014	Mother	MC	C3	02:00
26/08/2014	Mother	MCE	C2	14:23
29/08/2014	Calf	MC	C3	00:27
08/09/2014	Calf	MCE	C3	03:27
09/09/2014	Calf	MC	C3	05:00
10/09/2014	Calf	MC	C1	02:15
11/09/2014	Calf	MCE	C2	00:35
17/09/2014	Calf	MC	C3	00:28
11/08/2016	Calf	MCE	C2	05:38
17/08/2016	Calf	MCE	C3	07:14
18/08/2016	Calf	MC	C1	10:14
05/09/2016	Calf	MC	C3	07:46
28/08/2017	Calf	MC	C3	05:32
01/09/2017	Calf	MC	C3	02:30

Note:

C1 (neonate): calf presenting some folds, scars, and skin color that tends to be light grey dorsally and white ventrally and with less than 44° dorsal fin furl. C2: very young but non-neonate calves having more than 45° but less than 72° dorsal fin furl. C3: older calves that have unfurled dorsal fins (>72°).

respectively) were the most common LF calls (heard in eight groups each), followed by “100 Hz” and “thowp” (Figs. 1A and 1H) (seven groups), “gru” and “snort” (Figs. 1D and 1E) (six groups), and by “boom” (Fig. 1C) (four groups). The remaining LF calls were rare (heard in two groups for “drum”, Fig. 1K, and only one group for “guttural”, “burp”, and “bark”, Figs. 1G, 1F and 1J respectively). “Burp”, “bark”, and “drum” were only heard in MC groups. The remaining LF calls were heard in both MC and MCE groups. “Bass” (Fig. 1B) was a harmonic sound with a fundamental frequency below 40 Hz on average, and can sometimes be masked by background noise. “Wop” (Fig. 1I) and “thowp” (Fig. 1H) were brief harmonic upsweep sounds similar in frequency but different in duration. The “100 Hz” call (Fig. 1A) was a long, relatively flat call. “Gru” (Fig. 1D) was a short harmonic sound like “snort” but with more spaced harmonics. “Snort” (Fig. 1E) can be produced in sequences. “Boom” (Fig. 1C) was a harmonic sound produced either in sequence or alone. “Boom” was frequently produced in series with “100 Hz” following a well-defined order (100 Hz–boom–boom–100 Hz). “Guttural” (Fig. 1G) appeared to be a “composite call” consisting of non-overlapping “gru” and “heek” (MF) not separated with

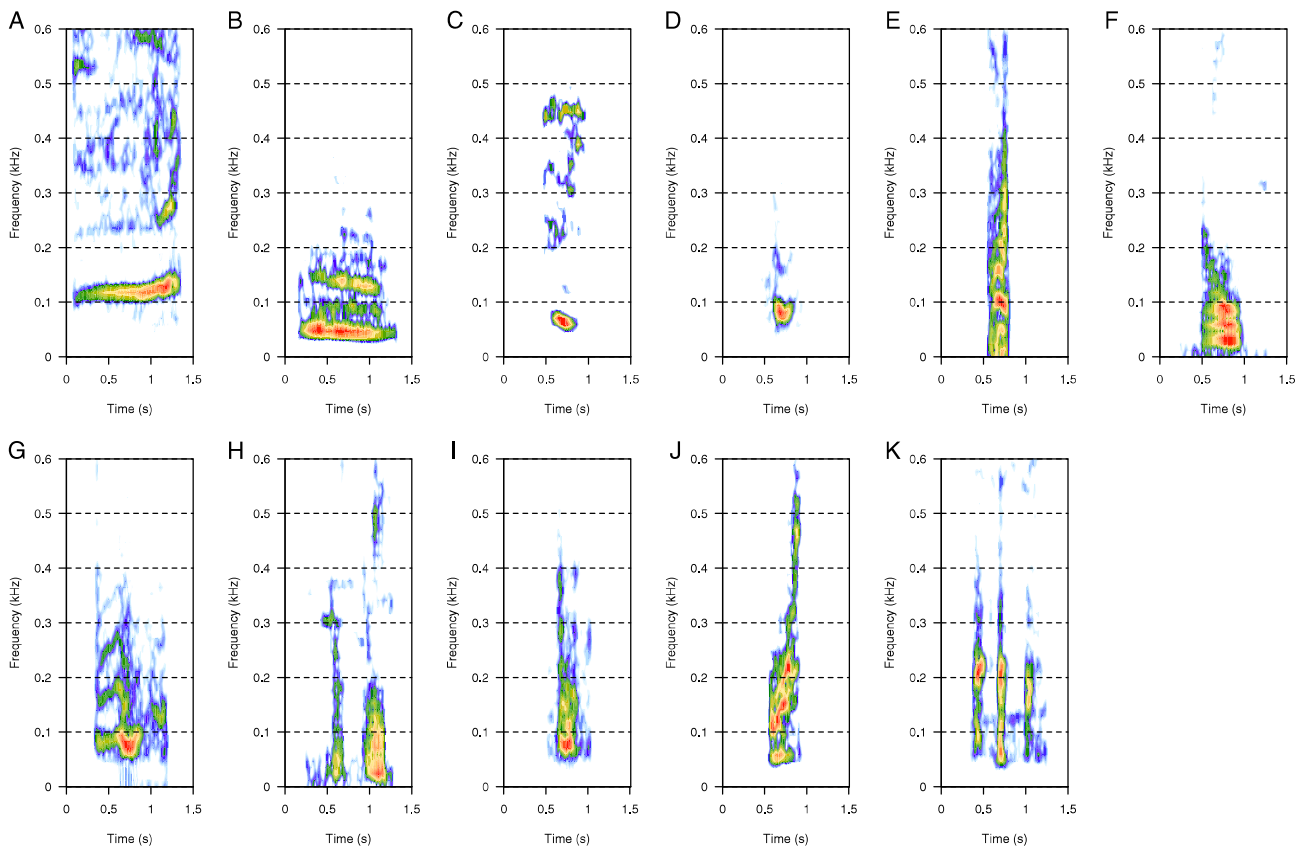


Figure 1 Spectrograms of low-frequency sounds (LF). (A) 100 Hz, (B) bass, (C) boom, (D) gru, (E) snort, (F) burp, (G) guttural sound, (H) thwop, (I) wop, (J) bark, (K) drum. Most of the LF sounds were harmonic-structure sounds, produced alone, except for boom and snort that can be produced in sequences. Drum sounds were always produced in series. Spectrogram parameters: Hamming window, FFT window size: 1,024 pts, 90% overlap. Generated using the *Seewave* package in R. [Full-size !\[\]\(1663bb69f307a960345edb0e712f8c02_img.jpg\) DOI: 10.7717/peerj.13785/fig-1](https://doi.org/10.7717/peerj.13785/fig-1)

a silence. “Drum” (Fig. 1K) was a very short call always produced in series, and “burp” (Fig. 1F) was a short harmonic sound with several close harmonics. “Bark” (Fig. 1J) was a short harmonic sound with ascending frequency modulation.

Mid-frequency harmonic sounds (MF)

MF was the second most represented category (35%, $N = 718/2,033$). Eight call types were within the MF category: “groan”, “downsweep”, “woohoo”, “trumpet”, “heek”, “whoop”, “wiper”, and “creak” (Fig. 2). “Heek” was the most common MF call (heard in nine groups), followed by “whoop” (seven groups), “downsweep” and “woohoo” (five groups), and by “trumpet” (three groups). “Groan”, “wiper”, and “creak” were uncommon (heard in one group only) and were only heard in MC groups. The remaining MF calls were heard in both MC and MCE groups. “Heek” (Fig. 2E) was a short MF call with a variable frequency modulation pattern (ascending, descending, or modulated). In some instances, heek was produced with “gru” (LF), with a short silence separating the two vocalizations to constitute a “combined call”. “Whoop” (Fig. 2F) was a long upsweep call starting with a flat

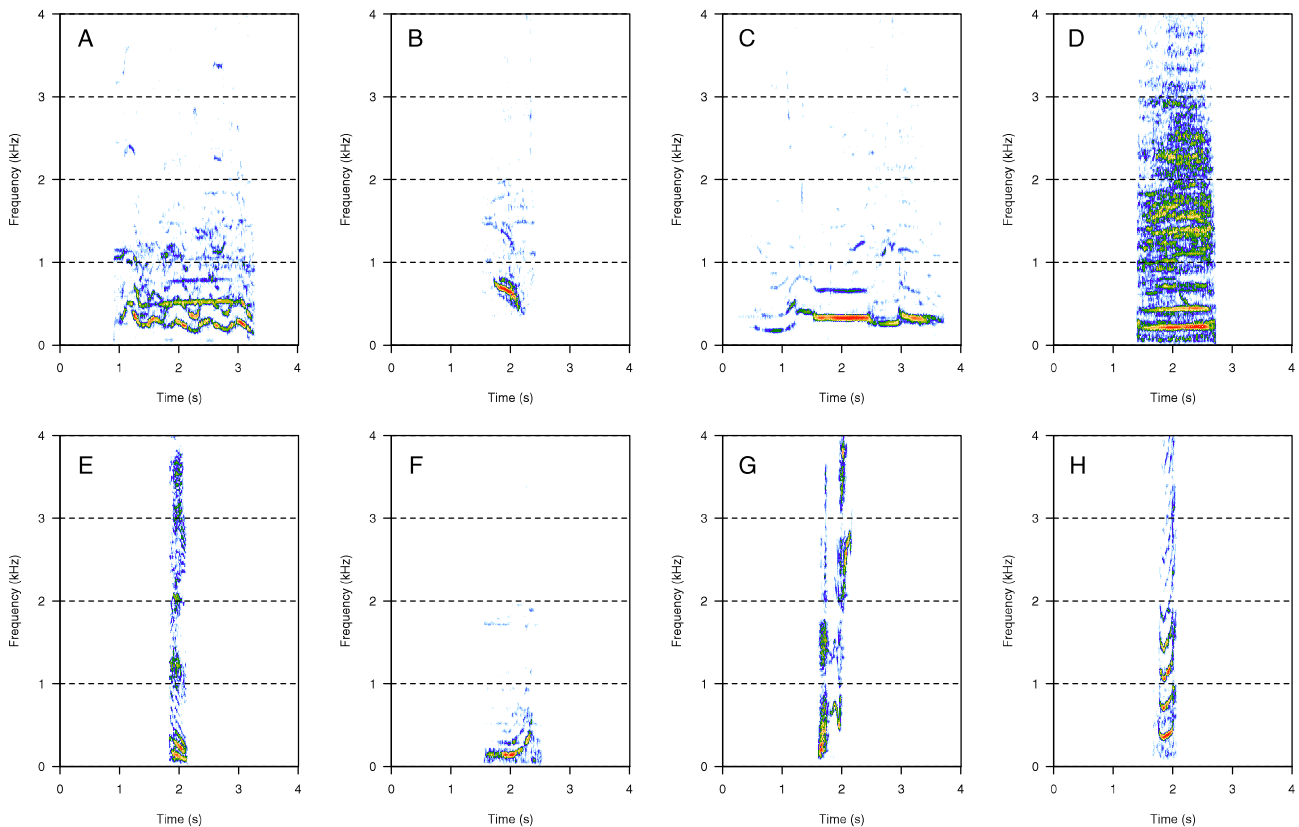


Figure 2 Spectrograms of mid-frequency harmonic sounds (MF). (A) Groan, (B) downsweep, (C) woohoo, (D) trumpet, (E) heek, (F) whoop, (G) wiper, (H) creak. Downsweep, woohoo and trumpet calls were also found in humpback whale songs recorded around the study site. Heeks were produced in association with Grus (LF) in some instances. Spectrogram parameters: Hamming window, FFT window size: 1,024 pts, 90% overlap. Generated using the *Seewave* package in R. [Full-size !\[\]\(fcc3264021d438d9732560e78099f674_img.jpg\) DOI: 10.7717/peerj.13785/fig-2](https://doi.org/10.7717/peerj.13785/fig-2)

part and fast ascending frequency. “Downsweep” (Fig. 2B) was a long call showing a descending frequency slope with well-spaced harmonics. “Woohoo” (Fig. 2C) was a long-duration call (*i.e.*, several seconds) showing a variable frequency-modulated pattern. “Trumpet” (Fig. 2D) was a call produced alone or associated with “gru” or “slight snort”. “Downsweep”, “woohoo”, and “trumpet” were found in humpback whale songs recorded around the study site. “Groan” (Fig. 2A) was a long harmonic call. “Wiper” (Fig. 2G) was a short harmonic sound with a U-shape frequency modulation pattern, always produced in series (four to five repetitions) but with a random temporal pattern. “Creak” (Fig. 2H) was a composite call constituted by two different non-overlapping successive sounds without silence, and it showed the widest frequency bandwidth.

High-frequency harmonic sounds (HF)

HF was the third most represented category (10%, $N = 202/2,033$). Two social calls were within this category: “squeak” and “ascending shriek” (Fig. 3). Both were quite common: squeak (Fig. 3A) was heard in seven groups, and “ascending shriek” (Fig. 3B) was heard in

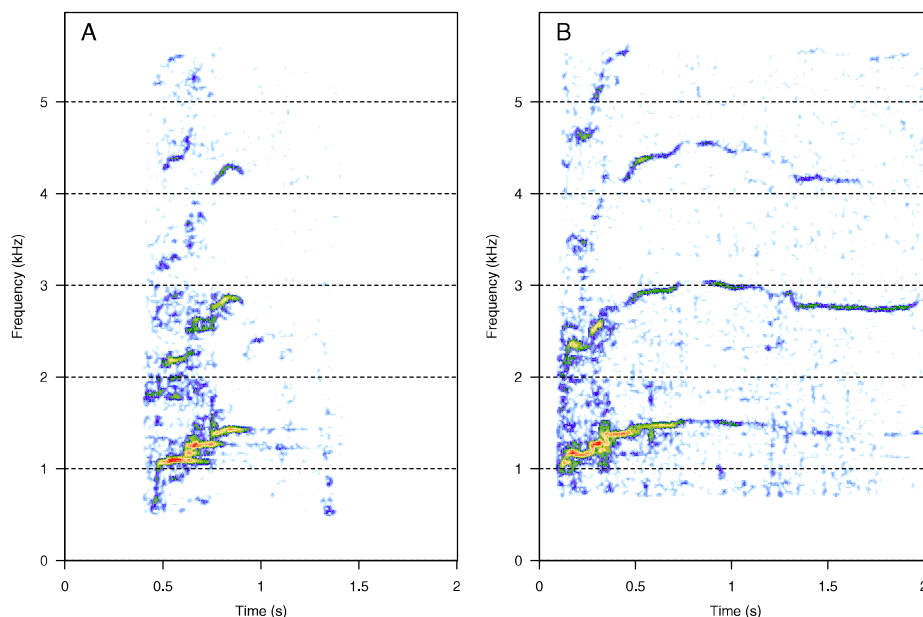


Figure 3 Spectrograms of high-frequency sounds (HF). (A) Squeak, (B) ascending shriek. Squeaks were very short calls with frequencies above 1 kHz and ascending shrieks were among the longest social call types with the highest frequencies among all call types. Spectrogram parameters: Hamming window, FFT window size: 1,024 pts, 90% overlap. Generated using the *Seewave* package in R.

Full-size [DOI: 10.7717/peerj.13785/fig-3](https://doi.org/10.7717/peerj.13785/fig-3)

four groups. “Squeak” and “ascending shriek” were heard in both MC and MCE groups. “Squeak” was a very short call with frequencies above 1 kHz, and “ascending shriek” was one of the longest social calls with the highest frequencies amongst all. Both call types were also found in humpback whale songs recorded around the study site.

Amplitude modulated sounds (AM)

AM was the fourth most represented category (8%, $N = 167/2,033$). Five social calls were within the AM category: “door”, “whine”, “trill”, “bug sound”, and “AM grunt” (Fig. 4). “AM grunt” (Fig. 4E) and trill (Fig. 4C) were the most common MF calls (heard in six and five groups, respectively). The remaining calls were relatively uncommon since they were heard only in one group each. “Door” (Fig. 4A) was heard in an MC group. “Whine” (Fig. 4B) and bug (Fig. 4D) were found in MCE groups only. “Trill” and “AM grunt” were heard in both MC and MCE groups. “Trill”, “door”, “whine”, and “bug” are long calls ranging from 1 to 5 s duration with a peak frequency ranging from 100 to 400 Hz. They were produced in bouts of random durations. “AM grunt” was short and, while commonly produced alone, it was sometimes associated with LF calls such as “gru” or “snort”. “Whine”, “trill”, and “bug” were also found in humpback whale songs recorded around the study site.

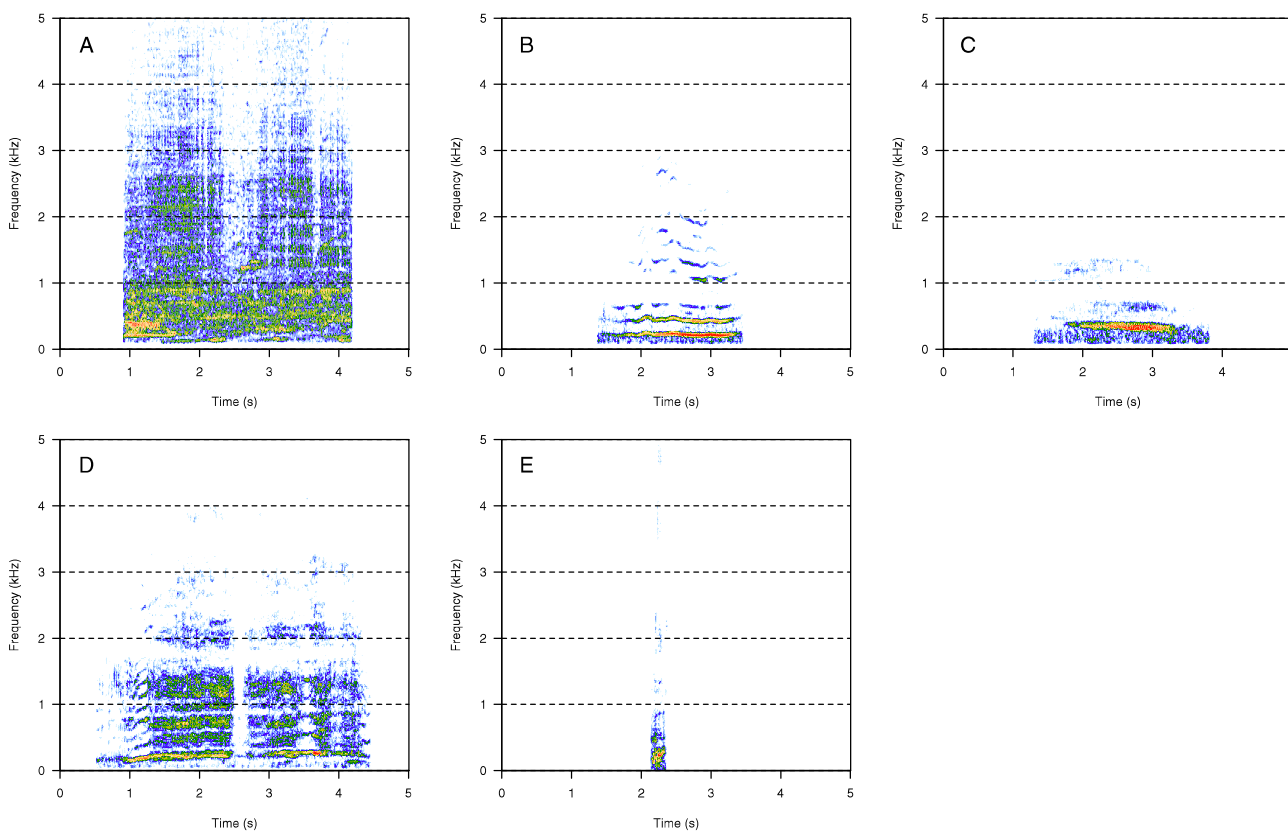


Figure 4 Spectrograms of amplitude-modulated sounds (AM). (A) Door, (B) whine, (C) trill, (D) bug sound, (E) AM grunt. Except for AM grunts, AM sounds are long calls ranging from 1 to 5 s with a peak frequency between 100 and 400 Hz, produced in bouts of random durations. Whine, trill, and bug sounds were also found in humpback whale songs recorded around the study site. Spectrogram parameters: Hamming window, FFT window size: 1,024 pts, 90% overlap. Generated using the *Seewave* package in R. [Full-size !\[\]\(ba1b80118482ccef74a5d718ca4d7242_img.jpg\) DOI: 10.7717/peerj.13785/fig-4](https://doi.org/10.7717/peerj.13785/fig-4)

Pulsed sounds (PS)

PS was the least represented category (1%, $N = 21/2,033$). Four social calls were classified in this category: “fry”, “bubble sound”, “moped”, and “gloop” (Fig. 5). These calls consisted of a repetition of very short, low-frequency sounds, and they were pretty uncommon. “Fry” (Fig. 5A) was heard in two groups and the remaining PS calls were heard in only one group each. “Fry” was heard in both MC and MCE groups. “Bubble sound” (Fig. 5B) was heard in a MC group. “Moped” (Fig. 5C) and “gloop” (Fig. 5D) were only found in MCE groups.

Aural-visual classification validity

For the validation of our classification RFs, 757 social calls representing 17 call types were used for the analyses (social calls for which Dur, Fmax, Q25, Q50, Q75, and PR were all measured). These analyzed social calls exclude call types for which we had less than six exemplars. The analyzed call types were: 100 Hz, bass, boom, gru, snort, burp, thowp, wop, downsweep, woohoo, trumpet, heek, whoop, squeak, ascending shriek, trill, and fry.

The RF showed a global accuracy of prediction of 93% for classifying the calls into the five

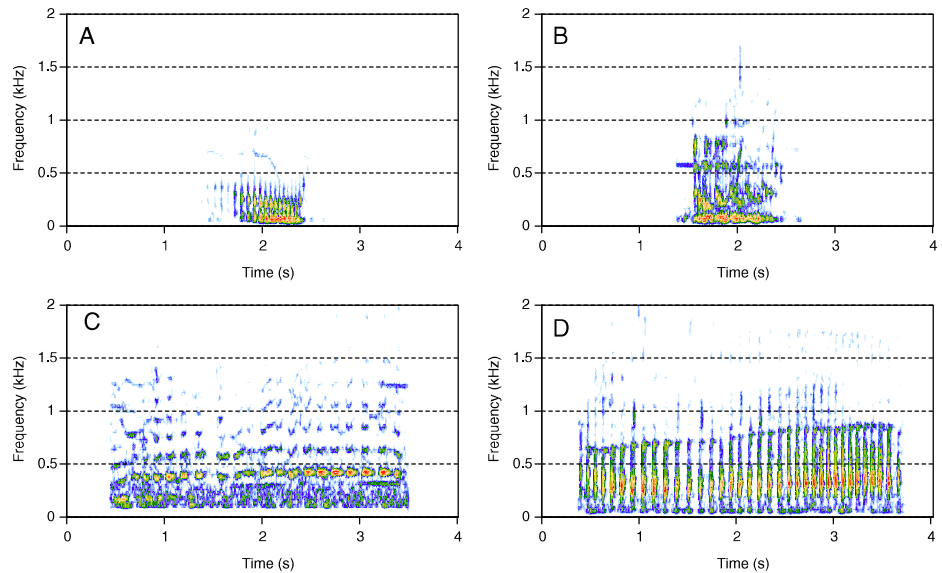


Figure 5 Spectrograms of pulsed sounds (PS). (A) Fry, (B) bubble sound, (C) moped, (D) gloop. PS are repetitive short and low frequency sounds. Spectrogram parameters: Hamming window, FFT window size: 1,024 pts, 90% overlap. Generated using the *Seewave* package in R.

Full-size  DOI: [10.7717/peerj.13785/fig-5](https://doi.org/10.7717/peerj.13785/fig-5)

Table 3 Random forest classification matrix for mother-calf groups' social call categories.

		Predicted class					Error
		AM	HF	LF	MF	PS	
True class	AM	21	0	0	2	0	0.09
	HF	0	94	0	0	0	0
	LF	0	0	438	16	0	0.04
	MF	17	7	8	143	0	0.18
	PS	0	0	0	0	11	0
Variables		Q25	Fmax	PR	Dur	Q50	Q75
Gini index		10.24	10.18	6.93	6.85	5.1	4.68

Note:

The overall error rate (out-of-bag error rate, OOB) was 7%. The last column indicates the classification error for each main call category. The bottom lines show the used acoustic variables along with the Gini index reflecting their relative importance in the classification.

defined main categories (OOB error rate = 7%, [Table 3](#)). The acoustic variables showing the highest importance for the classification were Q25, Fmax, and PR (Gini index: 10.24, 10.18, and 6.93 respectively, [Table 3](#)). Most call categories showed low individual classification error rates. For classifying the calls by types, the RF showed a global accuracy of prediction of 77% (OOB error rate = 23%, [Table 4](#)). The acoustic variables showing the highest importance for classification were Fmax, Q25, and Dur (Gini index: 32.10, 31.78, and 26.94 respectively, [Table 4](#)). Of the 17 calls included in the RF analysis, only four call types showed exceptionally high error rates ($\geq 50\%$): gru, snort, throwp, and wop. These call

Table 4 Random forest classification matrix for mother-calf groups' social call types.

		Predicted class																Error	
		100 Hz	Bass	Boom	Gru	Snort	Burp	Thowp	Wop	Downsweep	Woohoo	Trumpet	Heek	Whoop	Squeak	Ascending shriek	Trill		Fry
True class	100 Hz	132	0	7	0	4	0	0	0	0	0	0	8	0	0	0	0	0	0.13
	Bass	0	49	0	4	1	2	0	1	0	0	0	0	0	0	0	0	0	0.14
	Boom	18	0	121	0	3	0	0	1	0	0	0	13	0	0	0	0	0	0.22
	Gru	0	1	1	6	0	1	3	0	0	0	0	0	0	0	0	0	0	0.5
	Snort	4	0	0	2	21	0	8	4	1	0	0	3	0	0	0	0	0	0.51
	Burp	0	0	0	1	0	12	0	1	0	0	0	0	0	0	0	0	0	0.14
	Thowp	1	0	1	1	5	0	0	1	0	0	0	0	0	0	0	0	0	1
	Wop	0	1	0	0	2	1	2	5	0	1	0	0	0	0	0	0	0	0.58
	Downsweep	0	0	0	0	0	0	0	0	27	8	0	0	5	0	1	1	0	0.36
	Woohoo	0	0	0	0	0	0	0	0	6	18	0	0	0	0	0	4	0	0.36
	Trumpet	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	3	0	0.23
	Heek	2	0	0	0	0	0	0	0	0	0	0	11	0	1	2	0	0	0.31
	Whoop	0	0	0	0	0	0	0	0	6	4	2	3	61	0	0	0	0	0.2
	Squeak	0	0	0	0	0	0	0	0	0	0	0	1	0	68	7	0	0	0.11
	Ascending shriek	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	0	0	0.11
	Trill	0	0	0	0	0	0	0	0	2	2	1	0	0	0	0	18	0	0.22
	Fry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0
Variables	Fmax	Q25		Dur		Q50		Q75		PR									
Gini index	32.10	31.78		26.94		24.78		20.74		7.52									

Note:

The overall error rate (out-of-bag error rate, OOB) was 23%. The last column indicates the classification error for each main call type. The bottom lines show the used acoustic variables along with the Gini index reflecting their relative importance in the classification.

Table 5 Received level measured for the most common aurally and visually easily identifiable call types.

Calls types	Mean \pm SD amplitude received level (in dB re 1 μ Pa RMS)	N	Tagged individual
100 Hz	141 \pm 4	10	Mother
Bass	154 \pm 6	10	Mother
Boom	135 \pm 3	10	Mother
Trill	132 \pm 2	10	Mother
Heek	145 \pm 6	10	Calf

types may share features with other call types (short, harmonic, and low-to-medium frequency calls).

Received level

Five call types were selected for the calculation of the received level: three LF ("100 Hz", "bass", and "boom"), one AM ("trill"), and one MF sound ("heek"). The received level ranged from 132 to 154 dB re 1 μ Pa RMS with an average of 141 dB re 1 μ Pa RMS ($N = 50$, 10 per call type; Table 5).

DISCUSSION

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 grounds as well as on migratory routes (*Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Stimpert, 2010; Rekdahl et al., 2013; Fournet, Szabo & Mellinger, 2015; Recalde-Salas et al., 2020; Epp et al., 2021; Epp, Fournet & Davoren, 2021; Indeck et al., 2021*). The aural-visual analysis allowed us to identify 30 social calls distributed into five main call categories (LF, MF, HF, AM, PS) for mother-calf groups off Sainte Marie island. Our RF analyses showed a globally high agreement rate that demonstrates our aural-visual classification's robustness. However, some call types had low agreement rate in the RF compared to others (e.g., "gru", "snort", "thowp", and "wop"). This may be due to the fact that the repertoire is composed of discrete call types and graded call types (*Epp, Fournet & Davoren, 2021*). Call types with low agreement in the RF may correspond to graded calls. The existence of graded calls in mother-calf groups is not surprising since a high variation is expected. These groups are composed of individuals with different attributes (young and small individual in the process of maturing its calls, adult female, and potentially an adult male) that are likely related to call characteristics (*Cerchio & Dahlheim, 2001; Epp, Fournet & Davoren, 2021*).

We could not establish if sounds were produced either by the mother or the calf or by any nearby conspecifics (i.e., escort) in our acoustic recordings. The accelerometer data of the tag (*Goldbogen et al., 2014*) could not be used to assign caller identity as the sampling rate used was 10 Hz, and even if our sampling rate was higher than 10 Hz, the close spatial proximity between a mother and her calf makes such methodology unreliable (*Saddler et al., 2017*). On the other hand, received levels alone are insufficient for assigning caller identity as most calls may show low amplitude levels, and several animals may be present around the tagged animal (*Stimpert et al., 2020*). The calls described in the present study are thus considered as the acoustic output of mother-calf groups (including possible escort). Further investigations are still needed to assign each recorded social call to an individual. We are currently planning to explore the possibility of using simultaneous deployment of Acousonde tags on the mother and the calf to determine the caller's identity. Combining the received level of the same call on two different tags and the vertical distance between the mother and her calf (obtained from the diving profile) may allow the attribution social call to the corresponding individual.

Nine call of types out of 30 we aurally and visually identified were similar to song units recorded off the Sainte Marie island between 2013 and 2017 and were detected even in groups identified as MC, except for whine and bug sound. Assuming that mother-calf group composition did not change through the recordings' duration, the detection of sounds similar to song units in groups composed only of a female and a calf (MC groups) suggests that female humpback whales (or even calves) are able produce sounds with similar acoustic features as males' song units.

Some social calls recorded in mother-calf groups off Sainte Marie island presented qualitative similarities to those described in other geographic areas during the breeding,

feeding seasons, or migrating routes and were assumed to be the same call type. Those calls included snort, thowp, wop (also known as whup), bark, groan, trumpet, squeak, ascending shriek, trill, and AM grunt (*Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Stimpert et al., 2011; Rekdahl et al., 2013, 2017; Fournet, Szabo & Mellinger, 2015; Epp, Fournet & Davoren, 2021; Indeck et al., 2021*). Given the wide range of contexts within which these calls were detected (different group types, from breeding areas to feeding areas), these social calls are probably among the most common in humpback whales, and they may have important social roles. These social calls may constitute a global repertoire shared by humpback whales around the world. Further studies are needed to determine their behavioral context and roles, especially for mother-calf pairs.

Social calls were detected even in mother-calf groups with neonate calf (C1 class), suggesting that vocal exchanges between mother and calf occur very soon right after birth. Such vocal interactions may be a way to reinforce the calf's social bond with the mother and to imprint the calf's voice on the mother. Calves have been reported to vocalize, and they can produce series of grunts, predominantly low-frequency sounds with a relatively narrow bandwidth (*Zoidis et al., 2008*). In our acoustic recordings, one call type, heek, is very similar to the amplitude modulated frequency sounds described by *Zoidis et al. (2008)*, and thus, heek may be potentially assigned to calves.

We identified calls that can be combined or mixed with a given call type. We can assume that the calls were not successive calls from different individuals vocalizing one after the other due to the quasi absence of silence (and absence of overlap) in all instances. Call combination has not been previously described in humpback whales. Composite or concatenated calls have only been documented for few species (*Koren & Geffen, 2009; Ouattara, Lemasson & Zuberbühler, 2009; Jansen, Cant & Manser, 2012, 2013; Déaux, Charrier & Clarke, 2016*). Concatenated calls often have different biological functions than calls produced separately, as shown for the bark-howl vocalizations in dingo (*Canis familiaris dingo*) (*Déaux, Charrier & Clarke, 2016*).

Compared to the East-Australian catalogue (*Dunlop et al., 2007*) for which recordings were performed on migrating humpback whales of different group compositions (*i.e.*, with or without calves), our repertoire contained fewer main categories (five *vs.* six), a similar number of call types (30 *vs.* 34, with eight shared call types), and a lower proportion of social calls also used in songs within the studied area (nine out of 32 in Madagascar *vs.* 22 out of 34 in Eastern Australia; *Dunlop et al., 2007*). A repertoire with 16 call types has been described for the Southeast Alaskan humpback whales, with three calls likely shared with our repertoire (*Fournet, Szabo & Mellinger, 2015*). The repertoire described in Newfoundland (Canada) consisted of 13 calls types and shared only one call type with our repertoire. A standardized comparative study using the same recording methods among these different areas is needed to accurately determine if a given call type is really unique to a population/area, as well as to confirm if the described call types are indeed new ones or a variation of one (previously described) call type. Our results, however, along with these previous descriptions of the repertoire of the humpback whale, support the existence of a highly diversified repertoire of social calls in a humpback whale. Our results also suggest

that there is likely as much call diversity in mother-calf groups as in other social groups. Other acoustic studies focusing on mother-calf pairs also support the occurrence of such diversity (Indeck *et al.*, 2021).

Regarding our analysis on received levels, we found that calls recorded in mother-calf groups (mother-calf pairs accompanied or not by an escort) were produced at a low amplitude level, as found previously (Tyack, 1983). The received levels ranged from 132 to 145 dB re 1 μ Pa RMS, which is lower compared to the estimated received level of songs produced by singers of 149 to 169 dB re 1 μ Pa (Au *et al.*, 2006) and from our own recordings of singers (>165 dB re 1 μ Pa, hydrophone clipped). Our results are consistent with a recent study on mother-calf pairs in Australia (136 to 141 dB re 1 μ Pa RMS; Videsen *et al.*, 2017). Such low-amplitude vocal production in a mother-offspring pair is quite common in mammals, such as in pinnipeds (walrus; Miller, 1966; Charrier, Aubin & Mathevon, 2010), sheep (low-pitch bleats; Sèbe *et al.*, 2010), and cats (purring sounds; Peters, 2002). Low amplitude level in the context of mother-offspring interactions is not surprising as the communication between the mother and her calf is short- to medium-range, and the purpose is likely to maintain social contact, to reinforce the social bond and maternal attachment with the calf, and to coordinate behaviors (*e.g.*, side by side swimming, nursing sessions, *etc.*). Social purpose includes specific role such as individual identification. In a short-range communication context, why yelling when talking is sufficient? Antipredator strategy and male escort avoidance may also be hypothesized to explain such low-amplitude calls (Videsen *et al.*, 2017).

CONCLUSIONS

Our study provides a first assessment of the vocal repertoire of humpback whale mother-calf groups off Sainte Marie island, Madagascar, South Western Indian Ocean. We found that social calls recorded in these mother-calf groups are highly diversified and may be as diverse as those previously described in social groups not including calves for instance. A low acoustic intensity level characterized these social calls. The results suggest important vocal interactions between mother-calf pair, and mother-calf pairs with escorts. Our study contributes to the global catalogue of humpback whale calls and is a starting point in investigating the role of acoustic communication in humpback whale mother-calf interactions.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Anjara Saloma conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Maevatiana N. Ratsimbazafindranahaka conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Mathilde Martin performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Aristide Andrianarimisa conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Chloé Huetz conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Olivier Adam conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Isabelle Charrier conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (*i.e.*, approving body and any reference numbers):

All methods and approaches were carried out in accordance with relevant national guidelines and regulations in force in Madagascar and were fully approved by the Ministry of Fisheries Resources, Madagascar (the approving body for all marine-related research in Madagascar) (National research and collect permits #44/13-MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #28/16- MRHP/SG/DGRHP, and #26/17-MRHP/SG/DGRHP).

The study complies with the European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU).

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Field studies were fully approved by the Ministry of Fisheries Resources, Madagascar.

Data Availability

The following information was supplied regarding data availability:

The raw measurements for all humpback whale social calls reported in the study are available in the [Supplemental File](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.13785#supplemental-information>.

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Appendix II. Related scientific paper produced in parallel to the main research (2/2)

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Morphometric study of humpback whale mother-calf pairs in the Sainte Marie channel, Madagascar, using a simple drone-based photogrammetric method

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Abstract

Morphometric studies of humpback whales (*Megaptera novaeangliae*) occurring in the Indian Ocean area have been limited by the technology currently available. In the Sainte Marie channel, Madagascar, straightforward aerial single-camera photogrammetry was tested on mother-calf pairs that combines standard Unoccupied Aerial Vehicle (UAV) with free, easy-to-access, and user-friendly software. The goals of the study were to estimate mother and calf body measurements and to investigate the effect of maternal parity (primiparous versus multiparous, based on length) on calf size. A mean length of 12.4±1.2 m for mothers ($N = 16$) and 5±0.9 m for calves ($N = 16$) was estimated. The size of calves did not depend significantly on maternal parity. The photogrammetry method used was simple and cost-effective, yet produced convincing morphometric measurements with acceptable precision and accuracy. The coefficients of variation (CVs) of repeated estimates and the level of error were relatively low (CV = 2.31 % for a known-sized object and average CV = 2.52 % for individual whales; average error = 1.8 % for a known-sized object). These results will encourage more teams to study the morphometry of large marine mammals despite limitations in terms of resources.

Keywords: aerial photogrammetry, breeding grounds, parity, Unoccupied Aerial Vehicle (UAV)

Introduction

Morphometric data is the numerical expression of an animal's morphological characteristics that can be used to address various biological questions (Schmidt-Nielsen and Knut, 1984). Previous studies have demonstrated the efficiency of using body length for determining growth rate, age-structures, and population demographics in cetaceans (Chittleborough, 1965; Perryman and Lynn, 1993). At the individual level, morphometric data can be examined to assess body condition and reproductive capacity (Perryman and Lynn, 2002; Miller *et al.*, 2012; Christiansen *et al.*, 2016; Fearnbach *et al.*, 2018). In addition, a time series

of morphometric data can be used to assess population responses to environmental and anthropogenic changes (Hanks, 1981). For example, long-term changes in size distribution can provide a signal of overexploitation of a population (Stevens *et al.*, 2000).

Live capture-release schemes are generally not applicable to large whales due to their size. Hence in the past, morphometric studies of large whales relied mainly on direct measurements on stranded or commercially harvested specimens (e.g., Chittleborough, 1955, 1958, 1965; Omura, 1955; Nishiwaki, 1959, 1962). Later, the development of photogrammetry for

studying whales allowed for the extension of morphometric studies to live animals. Known as the science of measuring objects using photographs, photogrammetry is better than direct measurements as it does not require physical capture of animals and is thus non-invasive and less opportunistic. Photogrammetry used in whale studies can be divided into two main approaches; either stereo-photogrammetry or single-camera photogrammetry. Stereo-photogrammetry uses overlapping photographs to estimate length (Cubbage and Calambokidis, 1987; Dawson *et al.*, 1995). It allows for accurate measurements of whales since the measurements are done in 3-dimensions. However, it requires a complex pre-configuration such as a precise and controlled stereo-camera mounting and synchronization. On the other hand, single-camera photogrammetry requires only a single photograph and uses either a known-size object in the frame for scale (Christiansen *et al.*, 2016) or a measurement of the range to the individual (Best and Rüther, 1992; Perryman and Lynn, 2002; Jaquet, 2006; Fearnbach *et al.*, 2011; Miller *et al.*, 2012; Durban *et al.*, 2015; Dawson *et al.*, 2017; Christiansen *et al.*, 2018; Burnett *et al.*, 2019). To achieve accurate measurements from single photographs while optimizing the cost, a variety of combinations of tools, detailed in Table 1, has been used in the field. One of the most notable advances is the use of Unoccupied Aerial Vehicles (UAVs) or small aerial drones to perform aerial photogrammetry.

UAVs have facilitated an array of methods for monitoring wildlife and studying spatial ecology. They provide an ideal solution if the studied animals are scared by the presence of humans in the area or if the animals are dangerous for human observers (Linchant *et al.*, 2015). UAVs allow researchers to observe animals in their environment from above, are less invasive than Occupied Aircrafts (OA), and are significantly much more cost-effective. UAVs have therefore been used for a number of marine mammal research applications (Goebel *et al.*, 2015; Fiori *et al.*, 2017), including measuring individual animals (Christiansen *et al.*, 2016, 2018; Durban *et al.*, 2016; Dawson *et al.*, 2017; Burnett *et al.*, 2019).

The models of UAVs commonly used in aerial photogrammetry of whales vary from standard UAVs, such as DJI Phantom 3, to the more expensive UAVs specifically designed for scientific research and/or above-water operations. To obtain an approximation of the range between the camera on the UAV and the whale,

researchers generally rely on an altimeter, i.e., an altitude measurements tool (as mentioned in Table 1). The altimeter can be a barometric one (Durban *et al.*, 2015, 2016; Burnett *et al.*, 2019) or an external customized tool such as Light Detection and Ranging technology or LIDAR (Dawson *et al.*, 2017; Christiansen *et al.*, 2018). LIDAR can provide very accurate and precise altitude measurements (Dawson *et al.*, 2017). However, the deployment of LIDAR on an UAV can incur additional cost. Therefore, although barometric altimeters are less accurate and less precise than LIDAR, they are still suitably reliable for photogrammetric purposes and are commonly integrated into most UAVs (Durban *et al.*, 2015, 2016; Burnett *et al.*, 2019). It should be noted that since the lens of the UAVs camera often distorts the images, some photogrammetric studies incorporate prior image correction to improve photo accuracy during the image processing step (Dawson *et al.*, 2017; Burnett *et al.*, 2019). Alternatively, other studies follow a set of specific framing rules in order to minimize the distortion effects on the image (Durban *et al.*, 2015, 2016; Christiansen *et al.*, 2016, 2018).

The logistical challenges in utilizing advanced research tools for studying whales may offer an explanation as to why comprehensive surveys on humpback whale morphometry in some regions is lacking. Adding elements to an existing UAV or designing a new UAV can be for example a complex task for teams lacking a Research & Development or electronics department. In this paper, the performance of a simple and cost-efficient single-camera photogrammetry approach is established and validated that combines a standard UAV (here a DJI Phantom 4) with open-source software to target mother-calf pairs from the Sainte Marie channel, Madagascar.

Humpback whales are a highly migratory species. They spend the majority of the summer in their mid- or high-latitude feeding grounds. In winter, they breed and give birth in warm tropical waters (Clapham, 2018). The Sainte Marie channel, located on the eastern coast of Madagascar, is part of the humpback whale's breeding grounds in the South Western Indian Ocean. It is an important breeding ground in terms of the presence of mother-calf pairs as the channel is relatively calm and shallow (Trudelle *et al.*, 2018). Humpback whales arrive here between June and September.

Female humpback whales start to calve between 5 to 9-years old (Clapham, 1992; Gabriele *et al.*, 2007) where they give birth to a single calf, approximately

Table 1. Non-exhaustive list of photogrammetric approaches used for measuring whales at sea. For Aerial vehicle: (***) expensive, time and resource consuming aerial vehicle. (**) efficient/specialized but expensive aerial vehicle. (*) Low price/standard vehicle. (.) Aerial vehicle not required. For Range measurement tool: (****) Efficient/specialized but expensive tool. (**) Moderate price/standard tool or pre-integrated in the vehicle. For Image measurement tool: (****) highly specialized scientific tool. (**) Paid software/Script available for free but requiring paid software. (*) Free software/Script and software available for free. (a) Based on linear measurements of a known-sized object. (b) Based on linear measurements of individual adult whales. (c) Based on measurements of the surface area of individual whales.

Reference	Aerial vehicle	Type	Range measurement tool	Scale basis	Lens distortion correction	Image measurement tool	CV (%)	Error (%)
Cubbage & Calambokidis (1987)	Airplane (OA) ***	Stereo-photogrammetry	Radar altimeter **	Independent reference object	No	Stereoplotter ***	1.7 (a)	0.5 (a)
Best and R��ther (1992)	Helicopter (OA) ****	Single-camera-photogrammetry	Radar altimeter ***	Independent reference object	No	Stereoplotter ****	1.3 (b)	-
Dawson <i>et al.</i> (1995)	(Not required)	Stereo-photogrammetry	(Not required)	Camera characteristics (obtained from calibration)	No	Stereoplotter ****	4.4 (b)	< 2.5 (a)
Spitz <i>et al.</i> (2000)	(Not required)	Single-camera-photogrammetry	Sonar **	Camera characteristics (obtained from calibration)	Yes	Adobe Photoshop software (Adobe) **	4.3 (a)	4.6 (a)
Perryman & Lynn (2002)	Airplane (OA) ****	Single-camera-photogrammetry	Radar altimeter ***	Camera characteristics (factory specifications)	No	Image Pro Plus (Media Cybernetics) **	2 (b)	1 (a)
Jaquet (2006)	(Not required)	Single-camera-photogrammetry	Laser range finder **	Independent reference object	No	Adobe Photoshop software (Adobe) **	1.3 (b)	0.27 (a)
Fearnbach <i>et al.</i> (2011)	Helicopter (OA) ****	Single-camera-photogrammetry	GPS ***	Camera characteristics (factory specifications)	No	ImageJ software (NIH) *	-	< 3.2 (a)
Miller <i>et al.</i> (2012)	Airplane (OA) ****	Single-camera-photogrammetry	Radar altimeter **	Independent reference object	No	Image Pro Plus (Media Cybernetics) **	1.7 (b)	-
Durban <i>et al.</i> (2015, 2016)	APH-22 hexacopter (UAV) **	Single-camera-photogrammetry	High precision barometer ***	Camera characteristics (factory specifications)	No	-	-	< 1 (a)
Christiansen <i>et al.</i> (2016)	Splashdrone quadcopter (UAV) **	Single-camera-photogrammetry	(Not required)	Reference object in the same frame as the target animal	No	Custom-written script in R *	< 12 (c)	-
Dawson <i>et al.</i> (2017)	DJI Inspire Pro (UAV) **	Single-camera-photogrammetry	LIDAR ***	Camera characteristics (obtained from calibration)	Yes	Custom-written script in MATLAB **	1.2 (b)	1 (a)
Christiansen <i>et al.</i> (2018)	DJI Inspire Pro (UAV) **	Single-camera-photogrammetry	LIDAR ***	Camera characteristics (factory specifications)	No	Custom-written script in R *	0.3 (b)	4.75 (b)
Burnett <i>et al.</i> (2019)	DJI Phantom 3 Pro/4/4 Pro (UAV) *	Single-camera-photogrammetry	Barometer ***	Independent reference object	Yes	Custom-written script in MATLAB **	< 5 (b)	-

every 2 years (Clapham, 2018). Humpback whale mothers are left with the responsibility of the survival of their young until the calf reach the age of approximately 1-year old (Clapham, 2018). The size of sexually mature females ranges between 11 m to 15 m (Omura, 1955; Nishiwaki, 1959, 1962). Christiansen *et al.* (2016) reported a mean length of 12 m for females accompanied by a calf off Australia. A similar measurement has been reported by Spitz *et al.* (2000) in Hawaii. The mean length of calves is about 4.2 m at birth (Chittleborough, 1965) and they have a growth rate of approximately 3 cm per day (Christiansen *et al.*, 2016).

In pinnipeds (Bowen, 2009) and some large whale species (Laws, 1961; Gambell, 1972; Best and Rüther, 1992), it has been found that primiparous mothers (females having their first young and thus inexperienced mothers) tend to produce smaller offspring compared to multiparous mothers (mothers that have previously calved and thus more experienced). This trend may be related to numerous factors, such as a physiological change in the mother following her first parturition that favours the development of future foetuses, a more favourable external environment for the mother, or a behavioural change in the mother gained through previous experiences (Ellis *et al.*, 2000). Female investment in offspring size can be considered as a form of maternal contribution to the survival of the offspring since larger offspring are known to have higher chances of survival in mammals (Ronget *et al.*, 2018). In humpback whales, the effect of the maternal parity on offspring size has not yet been investigated. Therefore, the goals of this study were to: 1) estimate mother and calf body measurements (standard length and maximum width), and 2) test whether the calf's size is related to the parity of the mother (primiparous or multiparous).

Materials and methods

Study site

Field studies were conducted in the Sainte Marie channel, in Madagascar (Indian Ocean). About 60 km long and 7 to 30 km wide (Trudelle *et al.*, 2018), the channel is located between Sainte Marie Island (between latitudes 17° 19' and 16° 42' South, and longitudes 49° 48' and 50° 01' East) and the East coast of Madagascar's mainland. The data collection, conducted in conjunction with an ongoing study on humpback whale mother-calf interactions, were completed between August and September 2018 under the national research permits #28/18 MRHP/SG/DGRHP.

UAV platform

The DJI Phantom 4 UAV is a quadcopter weighting 1380 g, with a diameter of 350 mm. It is equipped with a built-in barometer that provides real-time altitude measurements (in m), and a gimbal camera with a 3.61-mm focal length, infinite focus and 0.0015-mm pixel size. Within a centred radius equivalent to 60 % of the video frame height, the distortion-related displacement on an image from the camera is less than five pixels (Burnett *et al.*, 2019), which is low. In this study, the video resolution was set at 4096×2160-pixels (4K) with a framerate of 24 frames per seconds.

Whale visual searches protocol

All methods and approaches were carried out in accordance with relevant guidelines and regulations in force in Madagascar. Dedicated visual searches for humpback whale mother-calf pairs were conducted from a 6.40 m rigid motor boat during days with moderate weather conditions (Beaufort scale ≤ 3 , corresponding to gentle breeze, wind speed less than 12 km h⁻¹, and wave height not exceeding 0.5 m) between 0630 and 1730 hours. The crew consisted of at least 3 trained observers (one on an elevated platform at the back of the boat and two covering the lateral view) and 1 or 2 experienced drone pilots. When a mother-calf pair was spotted, it was approached at idle speed to a distance between 100 and 200 m. All mother-calf pairs were photo-identified to ensure that there was no double-sampling during the study period. The ventral face of the tail fluke (visible when the whale is about to dive) and/or the dorsal fin of each individual was/were photographed using a Nikon digital camera (model D5600) fitted with a 50-300 mm lens. The photographs obtained within the season were then manually compared in order to check that indeed no double-sampling of mother-calf pairs occurred. Depending on the degree of dorsal furl, the relative age of each calf was also estimated (neonate versus non-neonate, Cartwright and Sullivan, 2009; Faria *et al.*, 2013; Saloma, 2018). All sighting data were integrated into the local dataset CETANET (www.cetanel.org, managed by Cétamada Association) that gathers all marine mammal sighting information recorded in Madagascar since 2009.

UAV flight protocol for whale images acquisition

The UAV was deployed from the boat to video-record the spotted mother-calf pair vertically overhead from an altitude around 15 m to 60 m, at a vertical speed of approximately 0.5 m s⁻¹. Sometimes the mother and the calf were not close to each other or were not

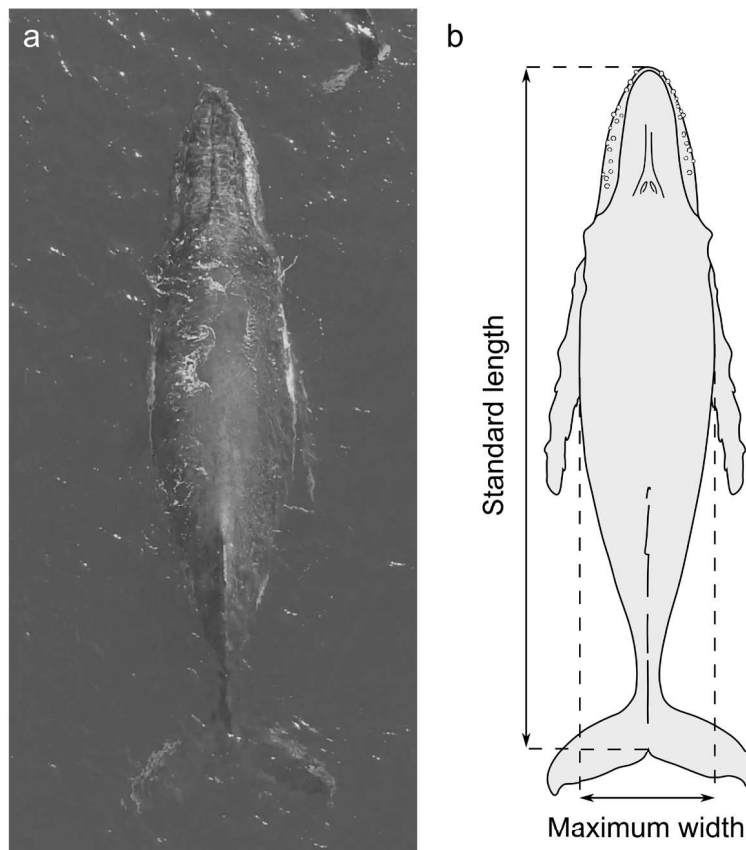


Figure 1. (a) Example of acceptable aerial photograph of humpback whale extracted from the video recording and used for photogrammetry. The original image was of 4096×2160-pixel but was cropped in this figure to highlight the fixed criteria. The whale must be flat at the surface, dorsal side facing up, emerged as much as possible, static or travelling at relatively slow speed, with a contour not masked by chops and with a non-arching body axis and peduncle. (b) Measurements in pixel recorded for each photograph.

at the surface at the same time. In these cases, they were filmed separately. The drone initialization (altitude zeroing) was performed before each flight on an on-boat platform 0.6 m above the sea level (the variation of the on-boat load between outings was fairly low and assumed to not have a very significant effect on this zeroing height). A maximum of two flight sessions was conducted for each pair (10-15 min duration per flight). Photographs were extracted afterward from the video recordings (see Images extraction and digitization).

Calibration images acquisition

To estimate the whales' dimension from photographs in the absence of known size scale markers in the frames and to account for systematic error in ranging, the camera needed to be calibrated. This can be done using images of an object with a known length taken at various distances between the object and the camera, i.e., ranges (Jaquet, 2006; Burnett *et al.*, 2019).

To perform calibration in this study, a static floating kayak of 2.75 m in length was video-recorded vertically overhead at altitudes between 5 m to 45 m at the end of the study period. In addition, for testing, a supplementary filming flight was performed to acquire video material that was independent to the one dedicated to the calibration. The equipment, settings used, and weather conditions present during calibration were consistent with the whale survey flights.

Image extraction and digitization

The photogrammetric method was based on 4096×2160-pixel photographs (no cropping) extracted from the collected nadir pointing video using the frame capture function in GOM Player v2.3.32.5292 (GOM & Company, www.gomlab.com). Video recordings were viewed frame by frame for the process. For each filmed individual, one photograph which was of the highest quality was extracted. A high quality

photograph is one which includes the whale lying flat at the surface, dorsal side facing up, emerged as much as possible, static or travelling at relatively slow speed, with contour not masked by chops, and with a non-arching body axis and peduncle (Fig. 1a). As the unadjusted lens is likely to distort images around the outside of the frame, a suitable high quality photograph was selected if the subject was positioned within the 60 % radius in the middle of the frame (see lens description in UAV platform). For each photograph, the standard length and the maximum width of the whale were measured in pixels using the software Inkscape v0.92 (www.inkscape.org) (Fig. 1b).

With respect to the kayak video dedicated to calibration, eight photographs were extracted at approximately 5 m altitude intervals (reference photographs). Only photos with clear, centred frames containing the entire kayak were selected. Additionally, from the supplementary independent kayak video, several photographs (tests hereafter) were taken at an altitude ranging from 5 to 45 m. The length of the kayak in all photographs was then measured in pixels.

Calibration process

For each of the reference photographs, the measured length from the photographs (in pixels) and the real length of the kayak (in m) were used to calculate the corresponding scale (in m pixel⁻¹):

$$\text{Scale} = \text{real length} / \text{length in pixels} \quad (1)$$

Then, the scale was regressed against the altitude at which the reference photographs were taken (Fig. 2):

$$\text{Scale} = 0.0004197 \times \text{altitude} + 0.0001814 \quad (2)$$

From (2), a formula was then derived with which the metric length could be estimated from vertical images taken at known altitudes:

$$\text{Estimated length} = \text{scale} \times \text{number of pixels} \quad (3)$$

Barometric altimeter accuracy evaluation

The UAV model used did not have a suitable alternate altitude measurement for comparison. Therefore, the accuracy of the barometric altimeter was assessed directly using the optical properties of the camera. All of the test photographs were used to back-calculate the expected distance between the camera and the object (in m) as done by Krause *et al.* (2017):

$$\text{Expected camera-object distance} = (\text{Real length} \times \text{Focal length}) / (\text{Number of pixels} \times \text{Pixel size}) \quad (4)$$

This was then compared with the barometric altitude reading while accounting for the zeroing height. To assess if the accuracy of the barometric altimeter varies with the expected altitude (expected camera-object distance minus zeroing height), a Spearman's correlation test was performed using the R statistical software v4.0.3 (R core team, www.R-project.org).

Measurement accuracy evaluation

It was not possible to directly address the accuracy of the measurements as it was impractical to include a scale object with a known size in each photograph of whales. However, as a proxy, the measurement error was evaluated based on the test photographs. From each photograph, the length of the kayak was estimated and the measurement error was then calculated as the percent difference as follows (Krause *et al.*, 2017):

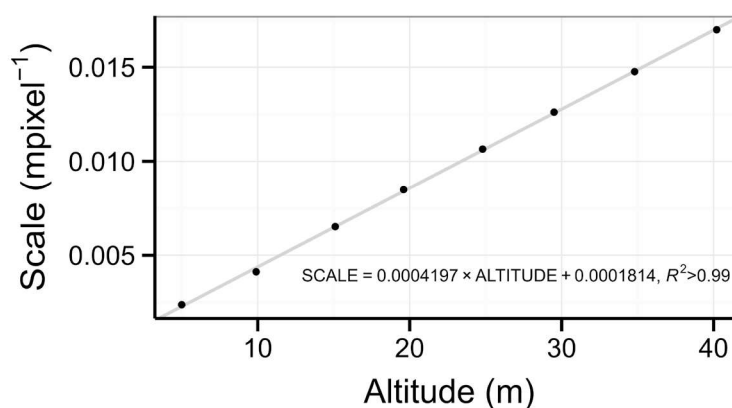


Figure 2. Relationship between photographic scale and height at which the photos were taken. Multiplied by the number of pixels, the regression equation gives length in meters.

$$\% \text{ Error} = | 1 - (\text{real length} / \text{estimated length}) \times 100 | \quad (5)$$

To investigate whether the error varies with the altitude at which the photographs were taken, a Spearman's correlation test and a Kruskal-Wallis test was used (using three altitude classes: 5 to 15 m, 15 to 25 m and > 25 m) in R.

Measurement precision evaluation

To indirectly assess the precision of the approach used, the coefficient of variation (CV) was calculated of the length estimations of the test object. Additionally, to address whether different observers consistently derive similar measurements, four independent observers estimated the length of the test object. The results were compared among observers using Kruskal-Wallis test in R.

Whale data analysis

The numbers of pixels of the whales were related to the estimated dimension in meters using the formula (2) and (3). Based on the estimated length and considering the life history of the humpback whale (Omura, 1955; Nishiwaki, 1959, 1962; Chittleborough, 1965; Clapham, 1992; Gabriele *et al.*, 2007; Clapham, 2018), the mothers were sorted into two categories: primiparous, i.e. likely accompanied by their first calf, for mothers < 13 m, and multiparous, likely already had previously one or more calves, for mothers \geq 13 m. To assess if the body lengths of calves differ between the two parity categories of mothers, a Wilcoxon test was performed in R.

Age has previously been used to categorize females as primiparous or multiparous when complete birth records for each individual were not available (Ellis

et al., 2000). Such an approach is possible when the life history of the species is known. As mentioned previously, the age at which female humpback whales have their first calf is between 5-9-years old (Clapham, 1992; Gabriele *et al.*, 2007) and the birth interval is about 2 years (Clapham, 2018). Based on these data, it can be assumed that females < 9-years old whom are accompanied by a calf are likely to be primiparous mothers, while those that are \geq 9 years old can be assumed to be multiparous. At age 9, a female humpback whale should reach 13 m (Chittleborough, 1965) and incidentally, this value is consistent with data obtained by whaling operations (i.e., data from direct measurements); the average size of sexually mature female humpback whales is 13 m (Omura, 1955; Nishiwaki, 1959, 1962). Therefore, 13 m was set as the threshold to define parity.

In some instances, it was possible to extract more than one suitable, high quality photograph of individual whales. Therefore, for these whales, it was possible to make additional length estimations. The CVs on individual whales was thus calculated as well to obtain a more direct precision assessment.

Results

Using a DJI Phantom 4, a total of 16 mother-calf pairs were photographed between August and September 2018. All calves had an unfurled dorsal fin, indicating that they were not neonates (yet aged less than 3 months). All photographs were obtained at an altitude ranging between 17 and 60 m (mean = 27 ± 11 m); the majority (29 out of 32) being obtained at an altitude < 45 m. The empirical calibration formulas (2) and (3) allowed estimation of the standard length and the maximum width of mothers and calves from these photographs.

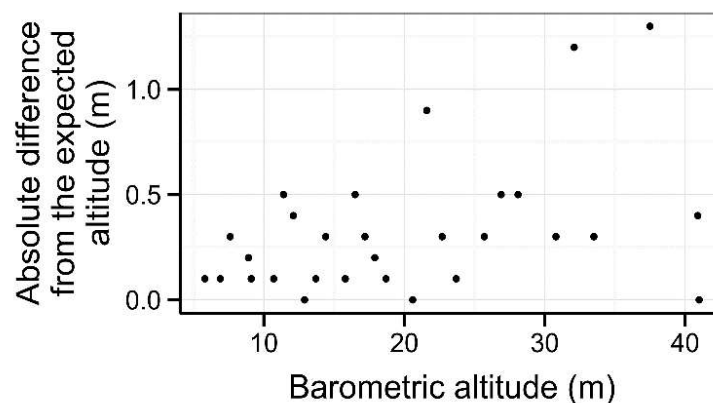


Figure 3. Barometric altitude reading versus its absolute difference from the expected altitude. The correlation was low and not statistically significant (Spearman's correlation test; $\rho = 0.354$, $S = 2624$ and $p = 0.06$).

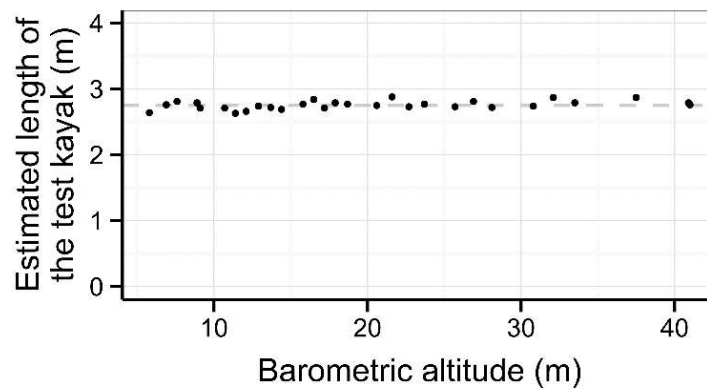


Figure 4. Repetitive estimation ($N = 29$) of the length of the test kayak at an altitude from 5.8 m to 40.9 m. The grey horizontal dashed line indicates the real length of the kayak (2.75 m). The coefficient of variation (CV) of the estimations was of 2.31 %.

Accuracy of the barometric altimeter

The absolute difference between the altitude reading provided by the barometric altimeter of the UAV and the expected altitude (expected camera-object distance minus zeroing height) was low (mean = 0.3 ± 0.3 m, min = 0 m, max = 1.3 m, $N = 29$; Fig. 3). Furthermore, the correlation between this difference and the barometric altitude was low and not statistically significant (Spearman's correlation test; $\rho = 0.354$, $S = 2624$ and $p = 0.06$).

Accuracy of the method using an object with a known size

The results of repetitive estimations of the length of an object with a known size, a 2.75-m test kayak, at an altitude between 5.8 and 40.9 m showed an average error of 1.8 ± 1.41 % with respect to the real length (min = 0 %, max = 4.56 %, $N = 29$). The errors showed no statistically significant variation with respect to altitude (Spearman's correlation test; $\rho = -0.16$,

$S = 4711$ and $p = 0.406$; Kruskal-Wallis test; $\chi^2 = 1.664$, $df = 2$ and $p = 0.435$; Fig. 4).

Precision of the method using an object with a known size

The repeated estimations of the length of an object with a known size showed a CV of 2.31 %. No statistically significant differences were detected for the estimated length of the object among four independent observers (Kruskal-Wallis test; $\chi^2 = 0.511$, $df = 3$ and $p = 0.916$; Fig. 5).

Morphometric measurements of whales

All estimations are presented in Table 2. The mothers showed a mean body length of 12.4 ± 1.2 m (min = 10.2 m, max = 14.7 m, $N = 16$). Their average maximum width was 2.8 ± 0.4 m (min = 2.1 m, max = 3.6 m, $N = 16$). The calves presented a mean body length of 5 ± 0.9 m (min = 3.6 m, max = 7.2 m, $N = 16$) and a mean maximum width of 1 ± 0.2 m (min = 0.7 m, max = 1.5 m, $N = 16$).

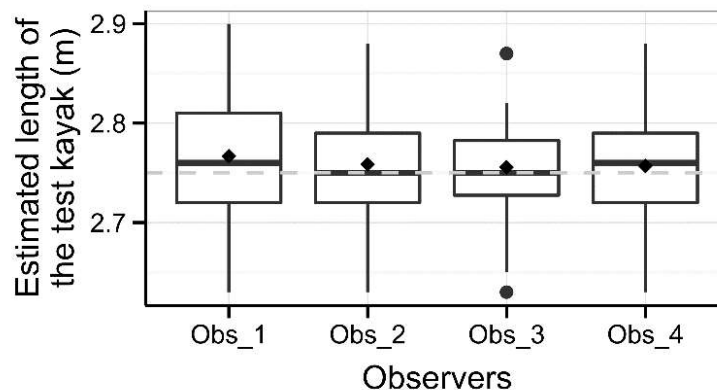


Figure 5. Repetitive estimation ($N = 29$) of the length of the test kayak compared between four independent observers. The grey horizontal dashed line indicates the real length of the kayak (2.75 m). The difference found was not statistically significant (Kruskal-Wallis test; $\chi^2 = 0.511$, $df = 3$ and $p = 0.916$).

Table 2. Morphometric measurements of mothers and calves from photogrammetry and reproductive category of the mothers based on their estimated length. Length corresponds to standard length, i.e., length from the tip of the snout to the notch of the tail fluke. Width represents the maximum body width.

Pair ID	Mother			Calf	
	Length (m)	Width (m)	Category	Length (m)	Width (m)
1	13.3	2.9	Multiparous	4.9	0.9
2	14	3.6	Multiparous	4.8	1.1
3	13.1	2.9	Multiparous	4.9	0.9
4	14.7	3.2	Multiparous	7.2	1.5
5	12.7	3.1	Primiparous	4.6	1
6	10.2	2.3	Primiparous	3.6	0.7
7	12.1	3	Primiparous	5	1.1
8	12.1	2.6	Primiparous	4.9	1
9	12.4	2.7	Primiparous	4.6	0.9
10	13.7	3	Multiparous	6.6	1.4
11	12.1	2.8	Primiparous	4.3	1
12	10.7	2.2	Primiparous	4.4	1
13	12.4	2.6	Primiparous	4.9	1
14	11.2	2.7	Primiparous	4.9	1
15	12.6	3	Primiparous	4.6	1
16	11	2.1	Primiparous	5.3	1

Relation between calf size and parity

The majority of the mothers (11 out of 16) were < 13 m in length and were classified into the primiparous category. The remaining 5 individuals were classified as multiparous mothers (≥ 13 m in length). The length of calves from primiparous mothers was smaller than those from multiparous ones on average (Fig. 6). However, there was no statistically significant difference (Wilcoxon test; $W = 12$ and $p = 0.084$).

Precision of the whale measurements

For most individual whales ($N = 24$), it was possible to extract supplementary photographs at different altitudes. Including the initial whale photographs, two length estimations for 23 individuals and three for one individual were obtained. With these estimations, an average CV of 2.52 ± 1.65 % (min = 0.02 %, max = 5 %) was found.

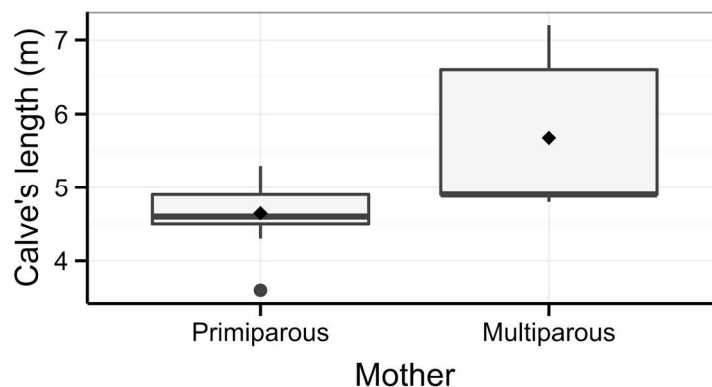


Figure 6. Calves' estimated standard body length according to the parity of their mother. The bold black lines represent the median and the diamonds represent the mean. The difference found was not statistically significant (Wilcoxon test; $W = 12$ and $p = 0.084$).

Discussion

The photogrammetric approach used relied on a formula which was based on several vertical-aerial photographs of a reference object with a known size (a 2.75-m kayak) placed on the sea surface. This empirical formula allowed assessment of morphometric data of both humpback whale mothers and their calves using nadir pointing aerial photographs taken at a known altitude with a DJI Phantom 4 UAV. In this method, errors are likely due to 1) the distortion of the lens, 2) the human error in the digitization process, 3) the accuracy of the UAV's barometric altimeter, and 4) the whales' body flex and varying submersion level. To minimise lens distortion, all the images were centred, with the targeted object avoiding the outer frames. With framing, the pixel displacement normally does not exceed 5 pixels (Burnett *et al.*, 2019). Thus, the associated error is likely to be relatively small. Also, the contribution of human error is likely to be negligible, as it was found that independent observers systematically derived similar estimations.

With the assumption that local environmental barometric pressure is relatively uniform within and between individual flights in a given site (Burnett *et al.*, 2019), the tests suggested that the measurements obtained with this method are relatively precise and accurate. Although higher than those reported by Dawson *et al.* (2017) and by Durban *et al.* (2015, 2016), the CVs of repeated estimates (2.31 % for an object with a known size and 2.52 % on average for individual whales) and the level of error (1.8 % on average, as calculated using an object with a known size) did not differ greatly from those reported in Christiansen *et al.* (2016) and in Burnett *et al.* (2019).

Regarding the barometric altimeter of the drone, the altitude it provided, used as a proxy for range, was accurate to within 1.3 m. Compared to the LIDAR altimeter like the one used by Dawson *et al.* (2017) which is accurate to < 0.06 m, the barometric altimeter of the drone was less accurate, which in turn, likely contributed greatly to the estimated errors and variation over repeated measurements.

With respect to the contribution of the body flex and varying body submersion of free-ranging whales, precise quantification is difficult as the true size of each individual is not known in advance for comparison. The dorso-ventral flexing of the body may result in underestimation of length if the method is based on nadir-pointing images (Cubbage and Calambokidis,

1987; Dawson *et al.*, 1995). Body submersion may also contribute to additional underestimation and variation because the altitude was used as a proxy for range (camera-object distance). As whales are always partially submerged (at least), the range is always slightly greater when photographing a whale than when photographing a kayak from the same altitude. Also, because the degree of submersion may vary slightly amongst photographs and individuals, there could be additional ranging imprecision which was not taken into account during this study. Incidentally, this may partially explain why the CV of repeated estimates is greater for whales than for the test kayak. Further studies involving this method and other alternatives at the same time that can take into account the whales' body flex and body submersion (e.g., stereo-photogrammetry, Cubbage and Calambokidis, 1987; Dawson *et al.*, 1995) would allow the quantification of these errors and are thus encouraged. In all cases, the method used in the present study ensured that only photographs of the whale lying flat at the surface, emerged as much as possible from the water, and with straight body axis and caudal peduncle were used. The authors are thus confident that these whale related issues were minimized.

The estimated standard lengths of the mothers were consistent with those obtained from underwater images by Spitz *et al.* (2000) in Hawaii and from aerial vertical photographs by Christiansen *et al.* (2016) off Australia. Using a threshold that was defined according to the known life history of humpback whales, the mothers were categorized as primiparous (< 13-m mothers) or multiparous (\geq 13-m mothers). The calves produced by mothers categorized as multiparous seemed larger than those produced by mothers categorized as primiparous. It has been reported that novice (primiparous) females generally produce smaller offspring (Clutton-Brock, 1991), while multiparous females are capable of producing larger offspring, as they are physically and physiologically more mature than primiparous females (Ellis *et al.*, 2000). For both fin whales (*Balaenoptera physalus*) and sperm whales (*Physeter macrocephalus*), it has been documented that the offspring of primiparous females are smaller than those of multiparous females examined at the same time (Laws, 1961; Gambell, 1972). For right whales (*Eubalaena australis*), calves from primiparous females have a smaller mean length than calves from older females (Best and R  ther, 1992). In this study, the difference in size between calves from multiparous mothers and primiparous mothers was however not statistically significant. It should be considered that

this study was conducted at the end of the breeding season, and all calves observed had an unfurled dorsal fin and were longer on average compared to the mean length at birth (4.3 m; Chittleborough, 1965). This means that the calves have already grown significantly since birth. The difference in size, while likely evident at birth, is likely less evident with time as calves may grow throughout the season at different rates depending on various external factors, as seen in pinnipeds (Bowen, 2009). Milk intake by humpback whale calves and the milk production from each mother may for example differ amongst mother-offspring pairs, meaning the postnatal growth rate may vary. Although the sample size was relatively small, the results provide a first assessment of the morphometry of the South Western Indian Ocean's female humpback whales and their calves.

In conclusion, this study allowed the estimation of the body measurements of humpback whale mother-calf pairs and the investigation of the effect of maternal parity on calf size using a relatively straightforward photogrammetric method that combined a standard UAV and free, easy-to-access, and user-friendly software. This method was not as precise and as accurate as methods involving more advanced equipment and tools such as drones equipped with an acute altimeter (Durban *et al.*, 2015, 2016; Dawson *et al.*, 2017) and paid software (Dawson *et al.*, 2017; Burnett *et al.*, 2019). However, it was demonstrated that the method presented in the present study produce convincing morphometric measurements with both satisfactory precision and accuracy. While the level of error limits the suitability of the method presented in the present study for comparing individuals, the method still has potential applications to study the global morphometric trend of a population. The method presented in the present study can be further adapted for studying population structures or for investigating population responses to a changing environment as has been done previously (Chittleborough, 1958; Hanks, 1981; Stevens *et al.*, 2000; Perryman and Lynn, 2002). It is hoped that this study will encourage more teams to study the morphometry of large marine mammals despite limitations in terms of resources. Such studies would especially help in conservation decision-making as it may help identifying environmental issues.

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Titre : Interactions mère-baleineau chez la baleine à bosse : étude des comportements d'allaitement, de nage, et de production vocale

Mots clés : Interactions mère-jeune, Cétacés, Habitat marin, Biotélémétrie, Ontogénèse

Résumé : Les mammifères présentent des formes sophistiquées de soins maternels indispensables à la survie des jeunes. Cette thèse a pour but de mieux comprendre les interactions mère-jeune dans le milieu aquatique en étudiant les couples mère-baleineau de baleine à bosse (*Megaptera novaeangliae*) dans les eaux côtières de Sainte Marie, Madagascar. La méthode utilisée se base sur l'utilisation de balises multi-capteurs embarquées.

Dans la première partie, une méthodologie a été développée pour étudier le comportement d'allaitement, révélant un schéma d'allaitement stéréotypé s'adaptant au besoin du baleineau à aller respirer en surface et à sa croissance, et se faisant sur une base de sessions régulières dans la journée. Dans la deuxième partie, la nage des baleineaux et de leur mère a été explorée, montrant comment leurs

activités évoluent avec l'âge et comment les mères aident les baleineaux. La dernière partie s'est penchée sur les vocalisations et leurs fonctions biologiques. Les cris des baleineaux ont été identifiés comme étant un moyen de contact acoustique avec la mère lors des séparations verticales et sont aussi impliqués dans l'initiation de comportements tel que l'allaitement.

Cette thèse fournit des informations cruciales sur les interactions mère-baleineau chez la baleine à bosse, offrant un aperçu unique des soins maternels, du développement des jeunes, et de l'utilisation des signaux acoustiques pour la communication dans un contexte assez différent du contexte terrestre. Ces résultats ont le potentiel d'informer les mesures de conservation et de stimuler des recherches futures.

Title : Humpback whale mother-calf interactions: investigating nursing, swimming, and vocal behaviors

Keywords : Mother-offspring interactions, Cetaceans, Marine habitat, Biologging, Ontogeny

Abstract : Mammals exhibit sophisticated forms of maternal care that are essential for the survival of their young. This thesis aims to better understand mother-calf interactions in aquatic environments by studying humpback whales (*Megaptera novaeangliae*) mother-calf pairs off Sainte Marie, Madagascar. The method used was based on animal-borne multi-sensor tags.

In the first part, a methodology was developed to study suckling behavior, revealing a stereotyped suckling pattern adjusted to the calf's need to breathe at the surface and its growth and occurring in regular sessions throughout the day. The second part explored the swimming behavior of the calves and their mothers, revealing how their activities

unwind with age and how the mothers help the calves. The final part examined the vocalizations and their biological functions. Calf calls have been identified as a means of acoustic contact with the mother during vertical separations and are also involved in initiating behaviors such as suckling.

This thesis provides crucial information on mother-calf interactions in humpback whales, offering a unique insight into maternal care, calf development, and the use of acoustic signals for communication in a context somewhat different from the terrestrial one. These results have the potential to inform conservation measures and stimulate future research.