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Acoustic Communication and Social Behavior in Bottlenose Dolphins (*Tursiops truncatus*)

Juliana Lopez Marulanda

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Juliana Lopez Marulanda. Acoustic Communication and Social Behavior in Bottlenose Dolphins (*Tursiops truncatus*). Vertebrate Zoology. Université Paris Saclay (COmUE), 2018. English. NNT : 2018SACLS016 . tel-02002939

HAL Id: tel-02002939

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Acoustic Communication and Social Behavior in Bottlenose Dolphins (*Tursiops truncatus*)

Thèse de doctorat de l'Université Paris-Saclay
préparée à l'Université Paris Sud

École doctorale n°568 Signalisations et Réseaux Intégratifs en
Biologie (Biosigne)
Spécialité de doctorat: Sciences de la vie et de la santé

Thèse présentée et soutenue à Orsay, le 18 janvier 2018, par

Juliana López Marulanda

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Communication acoustique et comportement social chez les grands dauphins (Tursiops truncatus)

Les grands dauphins sont des cétacés sociaux qui vivent dans un système social de fusion- fission. Ils se servent principalement du canal acoustique pour communiquer sur de longues distances ou dans des habitats dont la visibilité est limitée. Ils possèdent des capacités cognitives avancées. Par exemple, ils sont capables de rester vigilants pendant toute une journée, ils ont une mémoire de travail comparable à celle des primates non humains et une mémoire à long terme d'au moins 20 ans. Ils sont aussi capables d'apprentissage vocal et de comprendre des règles de syntaxe. Il y a un manque général d'information concernant l'utilisation de ces compétences au sein des groupes sociaux. Cependant, nous savons que la production vocale des grands dauphins comprend des sifflements, des clics et des sons pulsés en rafale, avec certains sifflements appelés « signatures sifflées » qui pourraient être utilisés pour s'adresser les uns aux autres.

Afin de comprendre comment ces animaux communiquent, il est nécessaire de combiner des méthodes de localisation acoustique avec des observations comportementales sous-marines, or pour l'instant les méthodologies actuelles ne sont pas satisfaisantes. Au cours de cette thèse, nous avons développé un système facile à déployer qui identifie l'animal produisant le son et permet des observations comportementales sous-marines simultanées. Nous avons testé cette méthodologie avec des grands dauphins en liberté et en captivité.

La présente thèse de doctorat vise à mieux comprendre la communication des grands dauphins au sein de leur groupe social. D'abord, j'ai développé deux études visant à décrire comment l'activité vocale des dauphins captifs varie en relation avec

le comportement et l'interaction avec les humains. Pour cela, je me suis d'abord concentré sur la production de signatures sifflées, puis sur la production de sifflements non signature liée aux comportements sous-marins observés. Ces deux études mettent en évidence la nécessité d'identifier l'émetteur de la production vocale.

Deuxièmement, je présente la conception et la mise en œuvre d'une méthodologie innovante (système BaBeL) qui permet de localiser un dauphin vocalisant dans un environnement tridimensionnel. Ce procédé peut être utilisé avec des dauphins en captivité et en liberté. Enfin, je présente deux applications de cette méthodologie de localisation pour aborder des questions de recherche concernant le comportement exploratoire d'un jeune dauphin et l'utilisation de vocalisations lors de mouvements coordonnés chez les grands dauphins.

Les résultats montrent que les séances d'entraînement avec des soigneurs modulent la production de sifflements de dauphins captifs. Cette modulation varie selon les groupes d'animaux et selon le management des différentes installations.

En captivité et dans la nature, les grands dauphins produisent abondamment des sifflements non signatures qui mériteraient d'être mieux examinés. L'étude de ces vocalisations avec des observations comportementales sous-marines simultanées devrait fournir l'information nécessaire pour interpréter le rôle des sifflements non signature dans le réseau de communication des grands dauphins.

Il est nécessaire d'identifier le dauphin émettant une vocalisation et la réponse comportementale de ses congénères afin de comprendre le rôle de cette vocalisation.

L'utilisation du système BaBeL m'a permis d'étudier la production de trains de clics lors de l'exploration de nouveaux objets dans la nature et leur rôle dans la synchronisation de la locomotion en captivité.

Ce travail montre enfin la possibilité d'énoncer de nouveaux paradigmes pour des recherches futures sur la communication sonore et sociale des mammifères marins.

Acknowledgments

First, I would like to give special thanks to Olivier Adam and Fabienne Delfour, my supervisors. The first, for answer to my request, trust me and gave me the chance to do this PhD, for opening me so many doors and supporting me. The second, for being there for me and never stop believing in my abilities (e.g. « harassing » me and giving me « lashes » to make be stop to procrastinate) and, guiding me step by step in the development of this four years' project.

This PhD would not have been possible without the financial support of Colciencias, Parc Asterix, Abyss Foundation and the CNRS (Centre Nationale pour la Recherche Scientifique). I am very grateful to those institutions. Also I would like to thank the all the members of the jury for taking my time to read this work and contribute to its improvement.

When I arrived to this lab (NeuroPSI) I found and amazing team of people (The Acoustic Communication Team) that received me very well: Isabelle, who became my mentor/academic therapist enduring the pain of all the interruptions I made to her work; Helene, who listened to me and gave me useful advices, Fanny; who taught me how to recognize the birds and their vocalizations; Thierry, who never stopped joking about my Colombian accent in French but always supported me; Chloé and

her “special service to the desperate PhD student”; Clément, who made me laugh so many times kidnapping my rabbits; Juliette, who was there to cheer me up; Anjara, who motivated me to arrive early to the lab; Kaja, that gave me company during my smoke breaks. I wanted you to know I’m very grateful and I consider you my friends.

During the construction of my database I counted with the help of many people that I would like to thank: Birgitta Mercera and the trainers’ team of Parc Asterix, especially Caroline, Stéphane, Fleur, Sully, Julien, Daphne and Juana which contributed directly to my observations. Marie Vallée and the Abyss association team members, Emmanuel Antongiorgi (DUOCEAN), Philippe Henry (Guadeloupe Plongée Evasion), the Boudewijn sea park team: Sander, Sabrina, Thomas, Gunter, Mathias, Olivia, Tyra and Nele, they received me in their facility as another team member. Torea Blanchard who made significant contributions to my methodology and Nikolaas Colpaert who helped me to analyze my data and make me feel in Brugges like in home.

I would like to thank “les colocs”, that accepted me in their house and were always so kind: Claire, Romain, Fabien, Mathieu. And the ones who came after: Stouphie, David, Michele and Thomas, it was a pleasure to share these years with you.

Also I would like to give special thanks to Isabella Clegg, for transporting me, listening to me, correcting my English, giving me gifts, eating sushi with me and competing against me for the “chouchou” place.

Special thanks to Denis, my partner, who supported during the last year of my PhD and made me eat vegetables and soup and to Dr. Gorog and Dr. Faucher who guided me through the difficulties.

Finally, I would like to thank my family for their support, my sister Sara and Jean Eudes who were there to listen to my complains and cheer me up, my sister Elizabeth and our super funny “cumbia dancing sessions” and my parents.

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GENERAL INTRODUCTION



Photo: Parc Astérix

1 Animal Communication.

Animal communication is defined as an exchange of information from one individual to another via a signal that typically elicits a response (Perrin *et al.*, 2009). Animal interactions facilitate information exchanges between individuals within the framework of communication systems. These communication systems are based on the chain of information transmission in which one individual (the emitter) produces a physical support of information (signal) that propagates in a medium (channel). During the process of transmission, the signal is subject to changes (noise) before it is perceived by another individual (receiver) who will then decode and interpret the signal and modify its behavior accordingly, giving some feedback to the emitter (Shannon and Weaver, 1949). Unlike cues, which are generated inadvertently or for purposes other than communication, the function of most signals is to provide information to another individual (Bradbury and Behrencamp, 2011).

Communication not only happens between individuals of the same species, it occurs between individuals of different species, such as with the case of inter-specific alarms (Bradbury and Vehrencamp, 2011). In a communication process, both the emitter and the receiver should benefit from the exchange of information (Simmons, 2003). The capacity of production and decoding a signal are dependent on the physiological and anatomical features of emitters and receivers (Johnstone, 1997). The message is what the emitter wants to transmit using a signal, and the meaning is what the receiver interprets from the signal and it depends on the receiver history of life (e.g. previous experiences) (Dudzinski and Hill, 2018). The message and the meaning of a signal are never identical because both the emitter and the receiver are different individuals with different histories (Dudzinski and Hill, 2018). Natural

selection will favor individuals that produce clearer signals and receivers that are capable of decoding information from them effectively (Maynard and Smith, 2003).

In many situations, such as the cooperative foraging, the search for a sexual partner, the defense of a territory, the relationship between mother-calf and the avoidance of potential predators, the implementation of communication systems is essential (Bradbury and Vehrencamp, 2011). According to the context, the emitter transmits an extensive set of information about itself, for example, its location, identity, sex, age, toxicity and/or palatability, social rank, size, health state, reproductive receptivity and/or emotional state. Information concerning the environment can also be exchanged, for example the presence of a predator, food, water, shelter or other resources (Bradbury and Vehrencamp, 2011).

Communication signals fall into five categories according to the channel of transmission: tactile, visual, chemical, electrical or acoustic (Bradbury and Vehrencamp, 2011). The different species in the animal kingdom may prioritise certain channels of transmission that are used independently or synergistically according to their sensory adaptations and depending on the content and function of the message.

2 Communication in cetaceans.

Cetaceans are genetically closely related to hippopotamus (*Hippopotamus amphibious*) (Geisler and Uhen, 2003, 2005); however, the phylogenetic evolution of these animals is very unique as they re-entered the aquatic environment at least seven times in the course of evolutionary history (Uhen, 2007). The last return to the ocean occurred in the early Eocene, approximately 50 m.y. ago (Gingerich *et al.*, 1983). Such a return to aquatic life implies strong adaptations, notably in terms of

behavior and anatomy. A review of evolution of aquatic mammals (Uhen, 2007; Lambert et al., 2017) explains that early cetaceans developed an elongated end of the rostrum with external nares posterior to the tip of it, and with the eyes in a high position on the lateral sides of the skull. The most representative adaptation of early cetaceans to aquatic life was the enlargement and inflation of the ectotympanic lobe into a tympanic bulla, a characteristic that seems to be an adaptation to aid in hearing sounds underwater rather than in air (Uhen, 2007).

The auditory channel of cetaceans is well adapted to aquatic life. In fact, sound travels five times faster through water than in the atmosphere, allowing for communication at long distances; this is very important for these animals, especially between mothers and calves, since their anatomy and habitat do not allow the mother to physically hold on to its offspring or to construct a den to leave the calves behind while foraging (Janik, 2009). In these highly mobile animals, individuals of the same group can be separated by hundreds of meters within a habitat of limited visibility (Connor *et al.*, 1998). Under these conditions, the use of acoustics signals seems to be the most effective strategy to assess their social and natural environment. Thus, communication in cetaceans relies mainly on the acoustic channel (Tyack, 1999), but can be also tactile (Sakai *et al.*, 2006; Dudzinski *et al.*, 2009), visual (reviewed in Tyack, 1999) and chemical (Kuznetsov, 1990; Kremers *et al.*, 2016). It may also involve several perceptive channels, in which case it would be described as multimodal communication (Harley *et al.*, 1996).

Communication is crucial for all social behaviors (Janik, 2009), and it is associated with the cognitive abilities of a species since this impacts the way in which the information flows (Tyack, 1999). Cognitive abilities of a species are in turn related to

the particular characteristics of the habitat, such as exposure to predators or food availability (Barret and Würsig, 2014).

Living cetaceans are divided in two suborders that differ in their social organization and communication strategies: *Mysticeti* and *Odontoceti*. There are about 70 species of odontocetes classified into six different families within which we find a wide variety of social systems. In this thesis, I am going to focus on the social organization and communication of delphinids, one of the most studied families of odontocetes.

2.1 Social organization in delphinids

Delphinids are social creatures and it is less common to find a lone individual in nature (Johnson and Norris, 1986). Within the 34 species that make up this family, there is a wide variety of social systems that are dependent on life history of animals.

For larger delphinids, such as killer whales (*Orcinus orca*), pilot whales (*Globicephala spp.*) and possibly Risso's dolphins (*Grampus griseus*) kinship appears to be very important in establishing the structure of groups (Wells *et al.*, 1999; Reisinger *et al.*, 2017). For instance, the most stable social organization found to date in the delphinids is that of killer whales, who live in stable extended family units called pods (Bigg *et al.*, 1987) that are composed of mothers and their offspring. The term pod, another word for group, is defined as the individuals that regularly swim together (Norris and Dohl, 1979). This definition excludes the possibility that delphinids swimming some distance apart may be in acoustic contact for as much as hundreds of meters. However, delphinids in close proximity interact in other ways; they communicate by using subtle signals of body movements, engage in cooperative herding of prey, or participate in the parental care of the young (Würsig and Pearson, 2015).

In killer whales, both sexes spend their lives within their natal group (Heimlich-Boran, 1986) where each pod develops its own acoustic dialect (Tyack, 1999). For pilot whales, pods are composed of related females with their offspring, with one or more unrelated adult males whose presence is temporary (Amos *et al.*, 1993). Killer whales, pilot whales and Risso's dolphins tend towards social matriarchies (Baird, 2000; Kasuya and Marsh, 1984) and are sexually dimorphic, where males are larger and have bigger dorsal fins. It is likely that these systems tend toward polygyny (Würsig and Pearson, 2015).

The stable associations found in these larger species are less evident in smaller delphinids. Societies of smaller delphinid species are built around repeated, but not constant associations among individuals or closely affiliated groups. This kind of society is called fission-fusion and has also been described for chimpanzees (Goodall, 1986). In fission-fusion societies, the amount of time that individuals spend together depends on their gender, age, reproductive conditions and genetic relationships (Wells *et al.*, 1999), as well habitat conditions, prey availability, mating opportunities and predation risk (Gowans *et al.*, 2008). For instance, small delphinids in nearshore areas tend to occur in small groups of a few individuals to several tens, while many offshore groups occur in hundreds to thousands (Würsig and Pearson, 2015).

Most pelagic, small delphinids exhibit polygynandry; males show polygynous mating attempts while females are polyandrous (Orbach *et al.*, 2014). These species also tend to be monomorphic, with only subtle morphological differences beyond the genital slit that differentiates males and females (Würsig and Pearson, 2015). The eastern spinner dolphin (*S. longirostris orientalis*) is probably an example of an exception to polygynandry. Males have a huge postanal keel and strongly backward-

canted dorsal fin, and authors have assumed that polygyny is the norm in this subspecies (Norris *et al.*, 1994; Perrin and Mesnick, 2003).

2.2 Communication in delphinids

2.2.1 Tactile communication

Delphinids have skin that is quite sensitive to even the lightest touch (Dudzinski and Hill, 2018) with most sensitive areas around the eyes, blowhole, rostrum, lower jaw, melon and the genital area (Wartzok and Ketten, 1999). Tactile communication plays an important role in the relationships between individuals (Dudzinski, 1998). For instance, Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas show 16 types of contacts behaviors with affiliative or aggressive functions (Dudzinski, 1998). This has also been reported for spinner dolphins (*Stenella longirostris*) (Norris and Würsig, 1994) and for other small delphinids (Pryor, 1990).

Delphinids are known to rub their bodies against each other and engage in rubbing behaviors using their pectoral fins (Dudzinski *et al.*, 2010; Dudzinski and Ribic, 2017). Most of the tactile behavior is thought to be affiliative and is often accompanied by preferences of partners and positions (Dudzinski and Hill, 2018). However, tactile behaviors are also observed during aggressive interactions, characterized by contacts that might cause pain, such as biting, raking, ramming, wrestling and butting (Dudzinski and Hill, 2018).

In bottlenose dolphins (*Tursiops truncatus*) and Atlantic spotted dolphins (*S. frontalis*) the genital regions might serve as a tactile receptor for low frequency echolocation trains called “buzzes” during mating and during mother-calf interactions (Herzing, 2000)

2.2.2 Visual communication

In clear water, visual signals might serve as a close-range complement to acoustic signals. In delphinids visual signals include actions and gestures such as open-jaw threat displays, aerial leaps, tail lobbs, flared pectoral fins and S-shaped postures (Dudzinski and Hill, 2018). Postures are used to synchronize actions among individuals or groups and can function as a signal for group coordination or social interaction (Connor and Krützen, 2015). Delphinids flare their pectoral fins and open their jaws as a threat signal to appear larger, and males adopt S-shaped postures during courtship encounters with females, presumably as a visual signal to indicate the male's interest (Hill *et al.*, 2015).

Bubbles appear to be an extra visual communication signal, and they take several forms: bubble streams, bubble clouds and bubble rings. They are often produced as a threat signal (Marten *et al.*, 1996) but are also used as a play signal in captive animals (Janik, 2015).

2.2.3 Chemical communication

The olfactory structures in delphinids have been lost in the course of evolution due to the several shifts of the nasal apparatus (Morgane and Jacobs, 1972). Although some olfactory structures are present during embryonic development, as has been shown in striped dolphins (*S. coeruleoalba*), they degenerate until birth (Kamiya and Pirlot, 1974; Sinclair, 1966).

In contrast, taste receptors have been confirmed in delphinids by behavioral experiments (Kuznetsov, 1990). Some studies have speculated about the role of taste reception in communication. For example, excretions of the perianal glands in male dolphins may serve as a chemical signal detected by conspecifics (Herman and

Tavolga, 1980). It has also been suggested that the “open mouth behavior” in solitary delphinids might serve to enhance taste reception (Herzing, 2000). Recent research suggests that dolphins might sample chemical signatures in the urine and feces of conspecifics for individual recognition (Kremers *et al.*, 2016). Further studies are needed to support the role of taste reception in delphinid communication.

2.2.4 Acoustic communication

The main adaptation of delphinids and all odontocetes to aquatic life may be the development of echolocation to assist locomotion in visually-limited habitats. This has been highlighted in fossils by the development of facial structures involved in the production of outgoing sound, and the modifications of the inner ear for the perception of very high frequencies (Uhen, 2007). Echolocation is the ability to produce high frequency clicks in order to obtain a sense of the surrounding environment from the echoes received (Au, 1993). In this process, the aim of echolocating signals does not seem to be the transfer information to another animal like in a communication process. While all delphinids produce click vocalizations, not all species whistle (Madsen *et al.*, 2012). For instance, it has been reported that Hector’s dolphins (*Cephalorhynchus hectori*) do not produce whistles, but might use echolocation clicks for communication (Dawson, 1991). Other species or non-whistling dolphins that might use clicks for communication are Commerson’s dolphins (*Cephalorhynchus sp*) and dusky dolphins (*Lagenorhynchus obscurus*) (Dziedzic and Buffrenil, 1989).

However, the most commonly investigated communication sounds produced by delphinids are whistles (Lammers and Oswald, 2015). Whistles are continuous, narrow-band, frequency-modulated signals (May-Collado *et al.*, 2007a) with a duration that range from tens of milliseconds to several seconds (Tyack and Clark,

2000). They are composed of a fundamental frequency and often one or more harmonics (Lammers and Oswald, 2015). The harmonic content of whistles is correlated with the orientation of the animal producing it, and this has led some researchers to suggest that the information carried in the harmonics of whistles might be used by other individuals to infer the direction of movement of the emitter (Miller, 2002; Lammers and Au, 2003).

Most delphinid species produce whistles with fundamental frequencies that range from 2 to 20 kHz (Lammers and Oswald, 2015). However, some delphinid species such as spinner dolphins (*Stenella longirostris*), Atlantic spotted dolphins (*S. frontalis*), white-beaked dolphins (*Lagenorhynchus albirostris*), Guiana dolphins (*Sotalia guianensis*) and killer whales (*Orcinus orca*) produce whistles beyond this range (Lammers *et al.*, 2003; Rasmussen and Miller, 2002; May-Collado and Wartzok, 2009). Whistles are believed to play an important role in the social communication of delphinids (Herzing, 2000).

Burst pulsed sounds are pulsed signals with short inter-pulse intervals (e.g. 200-1700 clicks per second) that do not seem to have an echolocation purpose (Dudzinski and Hill, 2018). Instead they have been associated with agonistic behavior and have been identified as communicating excitement, agitation and other emotions (Herzing, 1996). Delphinids of many species produce burst pulsed when they are excited or angry and thus it is thought that these kind of vocalizations transmit information about the emotional state of the animal producing them (Dudzinski and Hill, 2018).

Delphinids also engage in nonvocal acoustic communication (Dudzinski and Hill, 2018). For example, they display breaches, tail slaps, pectoral fin slaps and jaw claps, where these behaviors result in sounds that travel hundreds of meters and appear to be produced under the intentional control of the animal exhibiting them

(Dudzinski and Hill, 2018). In delphinids, fluke slaps are considered a sign of frustration or irritation (Mann, 2000), but have been also documented during play (Greene *et al.*, 2011).

2.2.4.1 Mechanisms of production of sounds

Delphinids have two bilateral sets of phonic lips, one associated with each nasal passage (Cranford, *et al.*, 1996) (Figure 1). These sets are different in size in nearly all species of the family, with the right side being larger than the left (Cranford *et al.*, 2015). Despite this bilateral configuration, there is a current debate in the literature about the existence of a single *versus* a multiple click generator in delphinids.

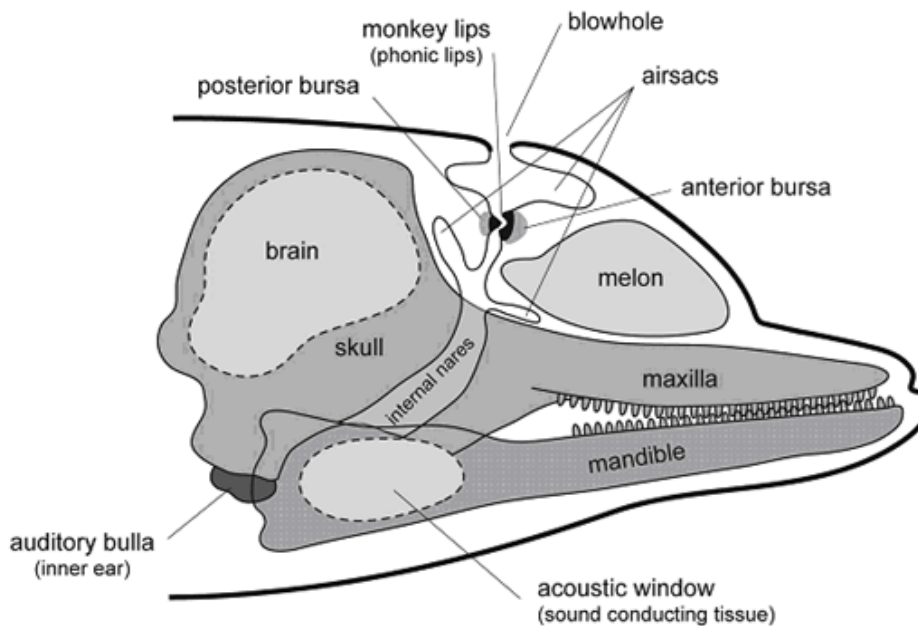


Figure 1: Schematic Illustration of a dolphin's head anatomy. Modified and adapted from Cranford *et al.*, (1996). Image taken from <https://matthewhardcastle.wordpress.com/2012/09/30/hello-world/>

For instance, a study conducted on two species of delphids, bottlenose dolphins (*Tursiops truncatus*) and false killer whales (*Pseudorca crassidens*) placed two contact hydrophones on the head of the animals, each one next to one pair of phonic lips. Then they asked the animals to perform a detection task of a target 2.6m away. By the observation of the time-of-arrival differences between both hydrophones, the authors suggested that not only the two studied species but all the delphinids click only with the right side phonic lips (Madsen *et al.*, 2013). This conclusion disregards with the observations of several authors in which the left-side phonic lips do indeed produce clicks but less frequently than the right-side (Cranford *et al.*, 2011; Mackay and Liaw, 1981). Madsen *et al.* (2013) suggested that highly trained animals could be biased by the simplicity of the detection task asked during their experiments and only

needed to produce clicks with the right side's phonic lips. However, all these studies have been conducted with animals in captivity and to date it is unknown how dolphins in the wild choose the parameters of their sound generation system (Cranford *et al.*, 2015).

Regarding whistle production, it was believed that they were generated by a resonance phenomenon in the air-filled cavities of the upper nasal pathways (Lilly, 1962; Mackay and Liaw, 1981). However, this idea was challenged by Murray *et al.*, (1998) who suggested that whistles were tissue-borne vocalizations. A more recent experiment validated this hypothesis (Madsen *et al.*, 2012): the authors analyzed recordings of a bottlenose dolphin that was given heliox to breathe. Since the speed of sound is higher in this mixture than in air, they expected to find an increase of the fundamental frequency. However, it remained unchanged and they suggested that the whistles were generated by vibrating tissues, as in the vocal chords of humans or the syrinx in birdsong (Madsen *et al.*, 2012).

2.2.4.2 Mechanism of reception of sounds

The auditory system of delphinids is adapted to the aquatic environment (Janik, 2009). In order to reduce the hydrodynamic drag while swimming, there is a lack of protruding parts associated with external ears. The middle and the inner ear are encased in a bony structure (tympanic bulla) that is connected to the skull by cartilage, connective tissue and fat, instead of bones (Figure 1). The absence of an external acoustic meatus is compensated by the presence of a thin region on each side of the mandible that is in intimate contact with the tissues that connect to the tympanic bulla. Through this connection between mandible and tympanic bulla, dolphins allow sound to enter into their auditory system while keeping a low

hydrodynamic drag. The physical isolation of the bulla from the skull allows the dolphin to localize sounds received by bone conduction (Reviewed in Au, 1993).

The hearing range of delphinids is 50 Hz to 150 kHz, with some variation between species (reviewed in Richardson *et al.*, 2013). This wide range allows the perception of several harmonics as well as large frequency modulations for communication with tonal acoustic signals. Behavioral experiments have shown that bottlenose dolphins spontaneously distinguish different whistle types even if they come from other dolphin species (Caldwell *et al.* 1973a in Janik, 2009). Furthermore, the frequency discrimination abilities of delphinids are exceptional as they discriminate tonal sounds that differ by only 0.2–0.8 % of the fundamental frequency of the tone (Thomson and Herman, 1975, in Janik, 2009).

Several experiments have been conducted in order to determine dolphins' echolocation limits. Using a 2.54 cm-diameter solid steel sphere and a 7.62cm-diameter stainless steel water-filled sphere, Au and Snyder (1980) measured the maximum detection range of the echolocation abilities in two bottlenose dolphin individuals. Results showed that dolphins could reach a 50% correct answer threshold at 75 m with the 2.54 cm-diameter sphere and at 113 m with the 7.62 cm-diameter sphere. The same results were registered in a false killer whale individual (*Pseudorca crassidens*) (Thomas and Turl, 1990). Delphinids also detect objects under noisy conditions. In fact, bottlenose dolphins present a generally unbiased detection of a target sphere (7.62 cm-diameter) at noise levels of 77 dB or lower (Au *et al.*, 1982). Delphinids are able to recognize differences of 1 dB in the amplitude of echoes, and to perceive subtle differences in targets with their sonar. This ability allows them to discriminate for example between a 6 cm cube and a 6 cm cylinder with a performance of 96 % accuracy (reviewed in Au, 1993).

3 Bottlenose dolphins

Bottlenose dolphins (*Tursiops truncatus*) are the most studied cetacean (Connor *et al.*, 2000). This is not only because of its large easily accessible range which includes coastal waters, but also because of its history of association with humans and the fact that they are the species of cetacean most commonly kept in aquariums (Connor *et al.*, 2000). As a model for the study of cetacean communication, bottlenose dolphins are very interesting because of their social structure, cognitive capacities and vocal production.

3.1 Bottlenose dolphins' Social structure

Bottlenose dolphins' social structure consists of highly dynamic fission-fusion groups, in which individuals associate in small groups that often vary in size and composition, and persists from minutes to hours or days at a time (Connor *et al.*, 1998; Connor *et al.*, 2000). Groups typically contain between five and seven individuals, but nursery groups tend to be larger for increased protection against predators (Mann *et al.*, 2000; Smolker *et al.*, 1992; Wells, 2003). Bottlenose dolphins express affiliation by proximity, physical contact such as pectoral or body rubbing (Sakai *et al.*, 2006; Dudzinski *et al.*, 2009) and synchronous movement (Fellner *et al.*, 2013).

There is a difference between the sexes concerning the nature of social bonds formed within the groups. Bonds between males tend to be stronger than those between females (Connor *et al.*, 1992; Connor *et al.*, 2001). In fact, adult males form consistent groups of two or three individuals called alliances that remain intact for years, and which is thought to optimize access to females in estrus (Connor *et al.*, 1992). The individuals from these alliances are not genetically related, but tend to be of similar age and were often raised in the same nursery group (Wells *et al.*, 1990).

In contrast, females tend to form weaker bonds with other females but have a wider social network, this is because their associations change according to their reproductive status (Pearson, 2011). Female bottlenose dolphins spend most of their time with other females at a similar point of their reproductive lives (Wells *et al.*, 1990). They rarely associate with males, except when cycling (Würsig and Pearson, 2015).

Calves remain with their mothers for an average of four years, during which they learn foraging techniques and social skills (Mann *et al.*, 2000). After this time, they form juvenile groups of mixed gender (Wells *et al.*, 1987).

Under human care, dolphins do not choose their group members; however preferential associations between individuals have been observed that resemble findings in free ranging bottlenose dolphins (Birgersson *et al.*, 2014).

3.2 Cognitive capacities of bottlenose dolphins

Several studies on cognition in bottlenose dolphins show that these animals have remarkable abilities which make them a very interesting model of study for understanding social cognition in the animal kingdom.

3.2.1 Attention

Bottlenose dolphins' brains are capable of remaining alert and attentive during the entire diurnal cycle (Pack, 2015). This was highlighted by research in which two captive dolphins were asked to press a paddle within 21 seconds of hearing a target sound. The dolphins were required to maintain their attention and press the paddle only when the target sound appeared and in order to get a reward. Mean performance levels in correct target detections across the sessions were over 94 percent for both animals. The dolphins sustained their attention over 120 hours (the

maximum duration tested) with no significant decrease in performance, with no differences between day and night (Ridgway *et al.*, 2006).

3.2.2 Working Memory

A study on working memory for sounds heard passively and objects inspected visually used a delayed matching-to-sample (MTS) procedure in which a stimulus was presented to a dolphin briefly, and after a delay interval, several comparison stimuli appeared. The dolphin was asked to indicate which comparison matched the sample. Herman and Gordon (1974) found that matching accuracy remained consistent across hundreds of pairs of novel sounds for nearly all time delays (they tested up to 120 seconds delay). For visually inspected objects, the matching accuracy of the dolphin was sustained above time delays of 30 seconds, and then gradually declined, remaining at 70 percent correct with delays up to 80 seconds (the longest delay tested) (Herman *et al.*, 1989). These experiments show that bottlenose dolphins' working memory is well developed, that it uses information arriving in different modalities, and that it is comparable to the visual working memory in nonhuman primates (Herman and Gordon, 1974).

3.2.3 Long term memory

Bottlenose dolphins' long-term memory has been tested with the recognition of familiar vs. non familiar "signature whistles", a kind of whistles that are unique for an individual (King and Janik, 2013). First a given dolphin was habituated to unfamiliar whistles, and then its behavior was observed for either a familiar or a non-familiar signature whistle. The results showed a greater responding to familiar signature whistles than to unfamiliar whistles even if the time of separation with its congeners was 20 years, the maximum separation time tested (Bruck, 2013).

3.2.4 Communication

Bottlenose dolphins have shown outstanding abilities in communication: they are capable of vocal learning and reference, where they have been known to copy novel sounds and use them to refer to objects (Richards *et al.*, 1984). They also understand syntactic rules of an artificial signaling system based on acoustic and hand signals (Herman *et al.*, 1986). Bottlenose dolphins naturally produce signature whistles when they are separated from their companions (Janik and Sayigh, 2013) and they appear to use signature whistles referentially to address each other (King and Janik, 2013). However, there is no evidence in wild for the referential use of non-signature whistles or non-whistle sounds, or for the use of syntax (Herman, 2010).

3.2.5 Social and self-knowledge and awareness

Social knowledge is defined as the possession of information about another and may include understanding another's actions, the networks of individuals and their associations in a society (Connor and Mann, 2006). Social awareness is the understanding of another's attention state and knowledge (Pack, 2015).

Bottlenose dolphins are capable of social imitation; they can be trained to imitate the behaviors of conspecifics (Herman, 2002). Also, they are capable of joint attention which allows a shared perception, occurring when a dolphin listens or eavesdrops to the clicks and echoes produced by another individual nearby (Xitco and Roitblat, 1996). However, there is a lack of studies on how much dolphin's guide each other's attention using echolocation.

Bottlenose dolphins are capable of mirror self-recognition (Reiss and Marino, 2001), a capacity that indicates self-awareness (Lewis, 1991). This ability is rare in the animal kingdom and was once thought to be unique to humans (Amsterdam, 1972)

and great apes (Gallup, 1970). However, more recently studies have shown that Asian elephants (*Elephas maximus*) (Plotnik *et al.*, 2006), and magpies (*Pica pica*) (Prior *et al.*, 2008) are able to recognize their image in the mirror.

3.2.6 Social learning and tool use

Bottlenose dolphins are capable of extensive and rich vocal and behavioral imitation, one of the forms of social learning (Marino *et al.*, 2007). We can find different types of social learning in the species: vertical, horizontal and obliquus.

Bottlenose dolphins in Shark Bay (Australia) have been observed breaking off sponges (*Echinodictyum mesenterinum*) and wearing them over their rostrum as a protection while foraging on the seafloor (Smolker *et al.*, 1997). This behavior is carried out by only some individuals of the population, most of them females (Mann and Patterson, 2013), calves learn this behavior from their mothers in their second or third year of life (Mann and Sargeant, 2003). This is not only an example of tool use in the species, but is also a vertical transmitted cultural behavior as individuals (mostly daughters) will only sponge if their mother also sponged (Mann *et al.*, 2008; Mann *et al.*, 2012).

Bottlenose dolphins are also capable of horizontal social learning, since in captivity young calves have been observed imitating other calves (Kuczaj *et al.*, 2006). In the wild, bottlenose dolphins' calves model their signature whistles (see section 3.3.1.2) on signature whistles of community members, possibly those with whom they associate only rarely; this is an example of obliquus learning.

3.3 Vocal production of bottlenose dolphins

Bottlenose dolphins are a highly mobile species, as individuals of the same group can be separated by hundreds of meters within a habitat of limited visibility (Connor

et al., 1998). Under these conditions, the use of acoustics signals seems to be the most effective strategy for animals to assess their social and natural environment. Therefore, bottlenose dolphins display a very complex and rich sound production.

The diversity of sounds emitted by this species has been classified in different ways by researchers and in addition the same names are given for types of vocalizations produced by different dolphin species; therefore it has been challenging to find a consensus for the range of *T. truncatus* vocalizations in the literature. Currently, the described vocalizations are categorized into three structural categories and two functional classes. Structurally, the sounds emitted by the bottlenose dolphins are found within: whistles or tonal sounds (reviewed in Janik, 2009), clicks or pulsed sounds (Au, 1993), and burst-pulsed sounds (Lopez and Bernal-Shirai, 2009) (Figure 2).

Functionally, sound emissions may be used for echolocation (used for orientation and navigation), or may have a role in communication and social interactions (reviewed in Herzing, 2000).

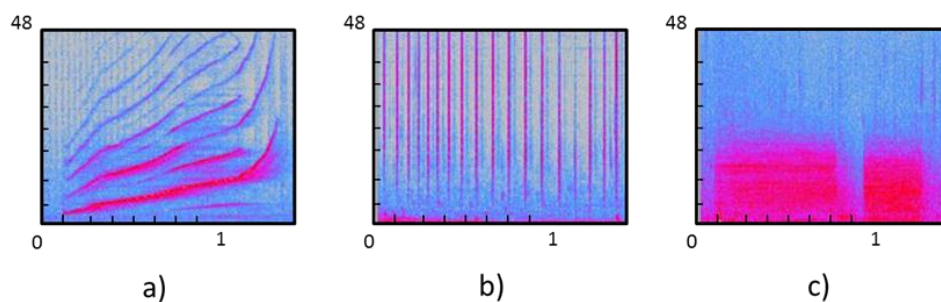


Figure 2: Spectrogram examples: a) whistle b) click train c) two burst-pulsed sounds. X axis represents the time in seconds and Y axis represents the frequency in kHz.

3.3.1 Whistles

Whistles are frequency modulated signals with fundamental frequencies from 800Hz to 28.5kHz and durations between 100ms and 4sec (reviewed in Janik, 2009). The term “whistle” is used to refer to a unit of one continuous contour (loop), two or more repeated contours (multiloops) that can be connected or separated by a period of silence lasting between 0.03 and 0.25 sec in duration (disconnected multi-loop whistle) (Esch *et al.*, 2009).

Dolphins produce signature and non-signature whistles that could be visually catalogued in six general categories with respect to the contour of its fundamental frequency (Figure 2): upsweep, down sweep, flat, convex, concave and continually modulated (Bazua-Duran, 2004; Akiyama and Ohta, 2006; Hickey *et al.*, 2008).

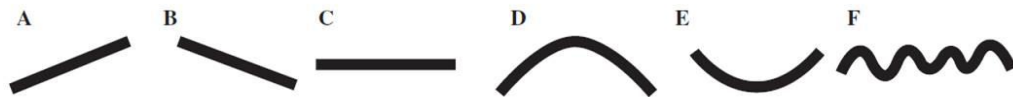


Figure 3: Categories of whistles with respect to the contour of its fundamental frequency a) Upsweep b) Down sweep c) flat d) convex e) concave f) continually modulated.

The upsweep whistle has been reported several times as the most frequently emitted (McCowan and Reiss, 1995; Hickey *et al.*, 2008; Diaz-Lopez, 2011), suggesting this kind of whistle plays an important role in the bottlenose dolphin whistle repertoire (Tyack, 1986; Janik *et al.*, 1994; Diaz-Lopez, 2011). However, the behavioural context description associated with this type of whistle remains vague and often behavioural observations are made from surface. In free ranging bottlenose dolphins the upsweep whistle type has been reported to be related to social behaviours (Diaz-Lopez, 2011), and in captivity this kind of whistle has been recorded when animals are fed by their caregivers (Akiyama and Ohta, 2006).

3.3.1.1 Non-signature whistles

Most studies on bottlenose dolphin communication focus on the production of signature whistles. However, signature whistles production corresponds only to 1% of produced whistles in captive dolphins (Janik and Slater, 1998), representing around 52% in free-ranging dolphins during social contexts (Cook *et al.*, 2004), and reaching values of more than 90% of whistles produced only during forced isolation (Sayigh *et al.*, 1990). Thus, non-signature whistles constitute a considerable percentage of the bottlenose dolphins' whistle repertoire. Despite this, there is a lack of information about the behavioral context of their production.

3.3.1.2 Signature whistles

Some individually specific whistles are called "signature whistles". These kind of whistles were discovered by Caldwell and Caldwell in 1965, who observed that during contexts of isolation, each individual produced one distinctive kind of whistle (Caldwell and Caldwell, 1965). Further studies showed that signature whistles are copied in captivity by other individuals of the group (Tyack, 1986). In free-ranging dolphins an increase of the signature whistle emission rate has been reported during capture-release procedures, suggesting that signature whistle emission rate could be considered as a potential indicator of stress in dolphins (Esch *et al.*, 2009b). Several authors reported signature whistle production in the context of forced isolation (Caldwell and Caldwell, 1965; Sayigh *et al.*, 1990, 1995; Janik *et al.*, 1994; Watwood *et al.*, 2005). However, outside this setting, signature whistles are more frequently emitted during social interactions than during other behavioral contexts, such as feeding or travelling (Cook *et al.*, 2004). It has been shown that signature whistles are emitted as a contact or cohesion call between mothers and calves (Smolker *et*

al., 1993) and between members of the same group when animals are out each other's visual range (Janik and Slater, 1998).

Signature whistles may be composed of single or multiple loop (Caldwell *et al.*, 1990). The number of loops produced in a signature whistle varies according to the behavioral context and it increases with age, which means that older individuals produce signature whistles with more loops (Caldwell *et al.*, 1990). More recently, a study on wild dolphins showed that signature whistles are also copied by other individuals of the group, possibly to label a particular individual (Janik, 2000). After several playback experiments in captivity, it has been suggested that signature whistle mimicry might be affiliative (King *et al.*, 2014) and the number of loops depends on whether it is produced by its owner or copied by another individual, with copies having more loops (King *et al.*, 2013).

There is an increase in signature whistle production during late-term pregnant mothers which suggests that the fetus might be susceptible to imprinting *in utero*, meaning that the new-born dolphin would recognize its mother's signature whistle right after birth (Mello and Amundin, 2005). The calves take one or two years to develop their own signature whistle (Fripp *et al.*, 2005; Sayigh *et al.*, 1990) and their frequency modulation pattern remains stable during their entire life (Sayigh *et al.*, 1990). However, males' signature whistles vary throughout life as a consequence of changing social relationships (Watwood *et al.*, 2004). Young males may use signature whistles similar to their mother's, while young females that tend to remain in their natal group are more likely to choose different frequency modulation patterns, probably to allow differentiation from their mothers (Sayigh *et al.*, 1990, 1995).

3.3.2 Clicks

Clicks are short broadband signals typically lasting 40-70 μ s with peak frequencies between 110 kHz and 130 kHz and peak-to-peak source levels between 210 and 228 dB at 1m re 1 μ Pa (reviewed in Au and Hastings, 2008). Clicks are typically used in echolocation, which is the projection of clicks in order to obtain a sense of the surrounding from the echoes received (Au, 1993). During target scanning, sequences of clicks (click trains) are produced. The inter-click interval (ICI) is the time of two-way travel of the sound (TWT) to and from a target plus an echo processing period between 19 and 45 ms long (Au, 1993). During target detection, *T. truncatus* modify the ICI in order to focus their attention to a particular distance (Penner, 1988). However, when the target is at close ranges (<40cm), the ICI decrease to 2.5ms (Evans and Powell, 1967), suggesting the dolphins may process several echoes at a time (Au, 1993).

Bottlenose dolphins use clicks as a sensory tool to navigate or hunt for prey (reviewed in Herzing and dos Santos 2004) and obtain information from their own returning signals (Au, 1993) and by eavesdropping on the echoes produced by other dolphins (Xitco and Roitblat 1996; Gregg *et al.*, 2007).

Bottlenose dolphins develop their ability to echolocate in the first one to three months of life (reviewed in Harder *et al.*, 2016). Before they are one month old, calves' clicks are of shorter duration (Reiss 1988) and lower frequency (Reiss 1988; Lindhard 1988) than adults. Additionally, at 14 days old, click trains have a shorter inter-click intervals (ICI) and shorter duration (Favaro *et al.* 2013) than adults.

3.3.3 Burst pulsed sounds

Burst-pulsed sounds are the least studied category and their definition is less clear in the literature (Herzing, 2000). They are often defined as rapid click trains (Janik, 2009), with many types of different sound emissions being labelled in this category (Herzing, 2000). In fact, the term is used for all the vocalizations that are not considered clicks or whistles (Janik, 2009) or, to be more precise, by all the pulsed sounds (clicks) for which no echolocation function is known (Lammers *et al.*, 2004). Burst-pulsed sounds have received several names in literature such as: cracks, pops, barks, squeaks, squawks, rasps or moans (reviewed in Herzing, 2000). However, a more recent study, classified the total repertoire of burst-pulsed sounds made by *T. truncatus* in two categories depending on duration and frequency: short burst pulsed vocalizations (impulsive emissions shorter than 200ms with most energy below 5kHz) and “long burst pulsed vocalizations” (a single or sequence of pulses longer than 200ms) (Diaz-Lopez and Bernal-Shirai, 2009).

Burst-pulsed sounds have been generally associated with aggressive behaviors (Overstrom, 1983; Herzing, 1996; Sayigh *et al.*, 2017). One kind of burst pulsed sound called “bray call” has been associated with foraging, apparently to facilitate the capture of prey (Janik, 2000).

3.4 Social behavior and vocal communication of bottlenose dolphins

Studies of bottlenose dolphins’ social behavior and communication rely on simultaneous descriptions of both visual and acoustic signals (Thomas *et al.*, 2002). However, the main pitfall in linking acoustic production and behavior is the difficulty in identifying which dolphin in a group is the vocalizer. This challenge is caused by two

reasons: first, dolphins do not open their mouth or display any external cues when producing a sound (Janik, 2009) and second, human hearing is not well-adapted to localize sound sources underwater (Hollien, 1973). In order to overcome these obstacles, several methodologies have been developed to accurately identify which dolphin is emitting the sound.

3.4.1 Forced Isolation

Forced isolation of bottlenose dolphins allowed scientists to discover the existence of signature whistles (Caldwell *et al.*, 1990) and enabled them to make the first descriptions about its use (Sayigh *et al.*, 1990; Janik *et al.*, 1994; Sayigh *et al.*, 1995; Sayig *et al.*, 1998). However, this methodology does not allow addressing research questions regarding how the bottlenose dolphins use their vocalizations while they are swimming freely within their social group.

3.4.2 Tagging

The principle describes attaching a suction cup with a built-in hydrophone to an animal. The use of a tag with an embedded hydrophone produced the first evidence of the mimicry of signature whistles (Tyack, 1986). However, the presence of such a tag could conceivably lead to modification of the subject's behaviors and its vocalization rate (Tyack, 1986).

3.4.3 Bubble stream emission.

Several authors use the production of bubbles streams concurrent with whistle production to identify the dolphin vocalizing (Mc Cowan and Reiss, 1995; Herzing, 1996). However, more recent studies showed that only some kind of whistles are accompanied by bubbles while being produced, and thus they are not representative of the entire whistle repertoire of the species (Fripp, 2005, 2006).

3.4.4 Hydrophone arrays

The use of hydrophones arrays is a non-intrusive method that uses the differences of arrival of sound to each hydrophone to calculate the direction of the source of sound. Hydrophones arrays can be fixed or mobile.

Fixed hydrophone arrays have been conceived with two (Lopez-Rivas and Bazua-Duran, 2010), three (Watkins and Schevill, 1974), four (Brensing *et al.*, 2001; Quick *et al.*, 2008) and eight hydrophones (Thomas *et al.*, 2002). With these kinds of arrays, the behavioral observations are obtained from surface, which allows collecting only a very small percentage of the dolphins' behavioral activity (Janik, 2009).

Mobile arrays consists of an underwater camera with a number of hydrophones, and are able to collect more details about the dolphin's behavior. They have been designed with two (Dudzinski *et al.*, 1995), three (Hoffman-Kuhnt *et al.*, 2016), four (Au and Herzing, 2003; Schotten *et al.*, 2004) and 16 hydrophones (Ball and Buck, 2005). Their main disadvantage is that dolphins are highly mobile species and the narrow angle of the underwater camera allows the localization of only those dolphins vocalizing right in front of it.

4 Aims of the thesis

To summarize, bottlenose dolphins are social cetaceans living in a fission-fusion groups. They rely mainly on the acoustic channel to communicate over long distances or in habitats of limited visibility. They possess advanced cognitive abilities, such as being able to remain alert during the entire day, and having a working memory comparable to nonhuman primates and a long term memory of at least 20 years. They are capable of vocal learning, referencing, and can be taught to

understand syntactic rules. There is a general lack of information about the use of these abilities within their social group. However, we know that bottlenose dolphins' vocal production includes whistles, clicks and burst-pulsed sounds, with some whistles called "signature whistles" potentially being used to address each other. In order to understand how these animals communicate, it is necessary to combine acoustic localization methods with underwater behavioral observations, and at the moment the current methodologies are not satisfactory. During this thesis, we developed an easily deployable system that identifies the animal producing the sound and allows concurrent underwater behavioral observations. We tested this methodology with free ranging and captive bottlenose dolphins.

The present PhD thesis aims to better understand the communication of bottlenose dolphins within their social group. First, I developed two studies aiming to describe how captive dolphin's vocal activity varies in relationship with behavior and interaction with humans. For this, I focused first on signature whistle production (Chapter 1) and then on non-signature whistle production linked to observed underwater behaviors (Chapter 2). These two studies highlight the necessity to link the vocal production to its owner.

Second, I present the conception and implementation of an innovative methodology that allows the localization of the dolphin vocalizing in a three-dimensional environment, and which can be used in captivity and with free-ranging dolphins. This methodology will be fully described in chapter 3.

Finally, I present two applications of this localization methodology to address research questions regarding the exploratory behavior of a dolphin calf (Chapter 4) and the use of vocalizations for coordinated movements in bottlenose dolphins (Chapter 5).

RESULTS



Photo: Emmanuel Antongiorgi

Chapter 1: Modulation of Whistle Production Related to Training Sessions in Bottlenose Dolphins (*Tursiops truncatus*) Under Human Care

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ZooBiology, 35(6), 495-504

Synthesis Chapter 1

Context

Bottlenose dolphins are highly social cetaceans that strongly rely on acoustic communication and signaling. The diversity of sounds emitted by the species has been structurally classified in whistles, clicks and burst-pulsed sounds. Whistles are continuous narrow-band frequency modulated signals. Some individually specific whistles are called “signature whistles” and are used as cohesion calls.

Research questions

The management of dolphins in captivity is largely based on several training/feeding sessions that are held per day. However, it remains unknown how the scheduled training/feeding sessions in bottlenose dolphins under human care modulate the emission rate of different whistles types (e.g., signature whistles). This study aims to describe the possible effects that training/feeding sessions, have on the emission rate of non- signature and signature whistles, in a group of captive bottlenose dolphins.

Analysis

The study was conducted on a group of 8 (in November 2014) and 9 (in May 2015) bottlenose dolphins at the Parc Asterix dolphinarium (Plailly, France). Whistles were recorded approximately 15 min before, during and 15 min after ten training sessions. We applied the SIGID method to identify signature whistles within our catalog of whistle types. Mean values of whistles emission rate and signature whistle emission rate per minute were calculated for the recordings before, during and after each training session.

Results

The dolphins' overall whistle emission rate did not significantly change before, during and after the training sessions. However, the non-signature emission rate was higher during and afterwards than before the training sessions and the signature whistle emission rate was significantly higher after than before the training sessions. The emission rate varied between the different signatures whistles types.

Conclusion

In conclusion, our study shows that non-signature and particular signature whistle emission rate increases after scheduled training sessions in Parc Asterix dolphinarium. We suggest that animals might have been seeking social interactions after the sessions. However, in order to validate this hypothesis, it is necessary to directly observe the animals' behaviors and to link the patterns of group association with whistle emissions.

RESEARCH ARTICLE

Modulation of Whistle Production Related to Training Sessions in Bottlenose Dolphins (*Tursiops truncatus*) Under Human Care

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Bottlenose dolphins are highly social cetaceans with an extensive sound production including clicks, burst-pulsed sounds, and whistles. Some whistles, known as signature whistles, are individually specific. These acoustic signatures are commonly described as being emitted in contexts of stress during forced isolation and as group cohesion calls. Interactions between humans and captive dolphins is largely based on positive reinforcement conditioning within several training/feeding sessions per day. Vocal behavior of dolphins during these interactions might vary. To investigate this, we recorded 10 bottlenose dolphins of Parc Asterix dolphinarium (France) before, during and after 10 training sessions for a total duration of 7 hr and 32 min. We detected 3,272 whistles with 2,884 presenting a quality good enough to be categorized. We created a catalog of whistle types by visual categorization verified by five naive judges (Fleiss' Kappa Test). We then applied the SIGID method to identify the signatures whistles present in our recordings. We found 279 whistles belonging to one of the four identified signature whistle types. The remaining 2,605 were classified as non-signature whistles. The non-signature whistles emission rate was higher during and after the training sessions than before. Emission rate of three signature whistles types significantly increased afterwards as compared to before the training sessions. We suggest that dolphins use their signature whistles when they return to their intraspecific social interactions succeeding scheduled and human-organized training sessions. More observations are needed to make conclusions about the function of signature whistles in relation to training sessions. *Zoo Biol.* XX: XX–XX, 2016. © 2016 Wiley Periodicals, Inc.

Keywords: signature whistle; whistle; communication; dolphinarium

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are highly social cetaceans that live in a fission–fusion society where individuals associate in small groups that can vary in composition according to age, sex, reproductive status, and activity [Connor et al., 2000; Mann et al., 2000; Gibson and Mann, 2008; Tsai and Mann, 2013]. In this extremely mobile species, group members can be separated by hundreds of meters within a habitat with limited visibility [Connor et al., 1998]. Interactions based on the use of acoustic signals seem to be the most effective communication strategy under these conditions [Janik, 1999a,b].

Consequently, bottlenose dolphins display an extensive sound production including clicks or pulsed

sounds [Au, 1993; Au and Fay, 2012], burst-pulsed sounds [López and Shirai, 2009], and whistles or tonal sounds (reviewed in Janik, 2009). The term “whistle” is used to refer to a unit of one continuous contour (loop), two or more

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Received 13 April 2016; Revised 05 September 2016; Accepted 20 September 2016

DOI: 10.1002/zoo.21328

Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

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repeated contours (multiloops) that can be connected or separated by a period of silence lasting between 0.03 and 0.25 sec in duration (disconnected multi-loop whistle) [Esch et al., 2009a]. The term “whistle type” describes all whistles showing specific frequency modulations as determined by visual categorization [Kriesell et al., 2014].

Some individually specific whistles are called “signature whistles” [Caldwell and Caldwell, 1965]. Signature whistles may be composed of a single or multiple loops [Caldwell et al., 1990]. The number of loops produced in a signature whistle varies according to the behavioral context and it increases with age [Caldwell et al., 1990]. It can also depend of whether it is produced by its owner or copied by another individual [King et al., 2013]. Signature whistles have been detected in dolphins as young as 1 or 2 years old [Fripp et al., 2005; Sayigh et al., 1990] and their frequency modulation pattern remains stable during the entire life of the individuals [Sayigh et al., 1990]. However, males’ signature whistles can vary throughout life as a consequence of changing social relationships [Watwood et al., 2004]. Young males may use signature whistles similar to their mother while young females are more likely to choose different frequency modulation patterns [Sayigh et al., 1990, 1995]. Signature whistles are emitted in context of forced isolation [Caldwell and Caldwell, 1965; Sayigh et al., 1990, 1995; Janik et al., 1994; Watwood et al., 2005] and as a contact or cohesion call between mothers and calves [Smolker et al., 1993] and between members of the same group [Janik and Slater, 1998]. During social interactions, signature whistles are more frequently emitted than during other behavioral contexts such as feeding or travelling [Cook et al., 2004]. These signals can also be copied [Janik, 2000; Tyack, 1986] by other individuals of the group, possibly to label a particular individual [Janik, 2000]. It has been suggested that signature whistle mimicry might be affiliative [King et al., 2014]. Finally, an increase of the signature whistle emission rate has been reported during capture-release procedures with free-ranging bottlenose dolphins, suggesting that signature whistle emission rate could be considered as a potential indicator of stress in dolphins [Esch et al., 2009b].

The management of dolphins in captivity is largely based on positive reinforcement training [Brando, 2010; Laule, 2003], and often several training/feeding sessions are held per day during which caregivers promote desired behaviors to facilitate husbandry and medical care and build a bond with the animals [Brando, 2010]. In the daily life of captive dolphins, training/feeding sessions could represent remarkable events that involve the development of cognitive skills and the modulation of the animals’ behaviors. In the case of Parc Asterix delphinarium, the dolphins are separated into sub-groups during each training session and each sub-group performs different exercises. Under these conditions, it is possible that the dolphins’ vocal repertoire and behavior may vary. For example, it has been reported that the number of whistle emissions in captive bottlenose dolphins increases

during interactions with people [Akiyama and Ohta, 2007]. Another study on a captive group of false killer whales (*Pseudorca crassidens*) reported that the highest vocalization rate was registered when animals were fed [Platto et al., 2015]. However, according to our knowledge, it remains unknown how the scheduled training/feeding sessions in bottlenose dolphins under human care modulate the emission rate of different whistles types (e.g., signature whistles).

This study aims to describe the possible effects that training/feeding sessions, have on the emission rate of non-signature and signature whistles, in a group of captive bottlenose dolphins.

METHODS

Study Subjects

The study was conducted in November 2014 and May 2015 at the Parc Asterix delphinarium (Plailly, France). At the time of the study, the delphinarium was closed to the public. The complex was first inhabited in November by nine Atlantic bottlenose dolphins (*T. truncatus*), four females aged 41, 34, 20, and 15 and years, and five males aged 32, 5, 4, 4, and 3 years. In January 2015, two males (4 and 5 years old) were transferred to another facility and one adult male (31 years old) arrived. Thus, the recordings in May were conducted on a group of eight individuals. All dolphins are subject to the same management schedule based on positive reinforcement training methods. Every day dolphins take part in at least five training sessions approximately at the same time during which their trainers feed them after they perform several exercises aimed to facilitate the husbandry and medical care procedures and to prepare for presentations to the public. Each dolphin knows around 100 behaviors to perform upon trainers’ command plus the new behaviors they are learning. Their sequence, their frequency and their duration change every day in every session. It could be underwater/aerial behaviors and solitary/group behaviors. Before and after the training sessions the trainers mainly stayed in the office and food preparation area and remained not visible but audible by the dolphins. At the beginning of each training session the trainers went out of the food preparation area at the same time carrying fish buckets and place themselves at the edge of the pool. During training sessions, the trainers divide the animals into sub-groups of the same two or three individuals. Each sub-group stays with one trainer and performs different exercises during the session which lasts around 15 min. This separation is never forced and it is achieved because animals are reinforced positively when they stay together in their assigned group. The trainers start and end their working day by feeding the dolphins ad-libitum without asking them to perform any kind of exercises.

Overall, this facility consists of one outdoor and two indoor pools not acoustically isolated. The outdoor pool has a volume of 3,246 m³ and a depth that varies from 2.5 m at the

shallowest point to 4.5 m at its deepest. The indoor part of the complex, divided into two sections, has a total volume of 550 m³ and a depth of 2.5 m. The dolphins have free access between the pools at all times.

Whistle Recordings

Whistles were recorded approximately 15 min before, during and 15 min after ten training sessions that took place on 6 days: five recording sessions were conducted over 4 days in November 2014 and five more over 2 days in May 2015. The recordings were carried out using a CRT hydrophone C54XRS (frequency response: 0.016–44 kHz \pm 3 dB) plugged in to a TASCAM HDP2 recorder at the acquisition rate of 96 kHz and samples were coded on 24 bits. In order to prevent the dolphins touching and grabbing the hydrophone, it was placed in a flexible floating tube inside an 18.9 L polycarbonate bottle with multiple perforations. The apparatus was fixed to a wooden stick at a distance of 50 cm from the edge of the pool and 50 cm deep near the small beach area (Fig. 1).

Visual Categorization Process

To create a whistle catalogue, spectrograms (FFT size: 1024, overlap 50%, Hanning window) of the recorded whistles were analyzed using Audacity 2.06 software (GNU General Public License, The Audacity Team, Pittsburg, PA). Graphs with standardized *x*- and *y*-axes (1 sec long, with a frequency range of 0 Hz to 48 kHz) of the frequency modulation of each whistle were used to prevent distortion of whistles caused by axes differing in length as this would have influenced the visual categorization process.

Whistles with a negative signal-to-noise ratio or overlapping with other whistles were registered but not included in the categorization. Once each whistle spectrogram was registered, a visual categorization of whistle types was carried out. We applied the SIGID method [Janik et al., 2013] to identify signature whistles within our catalog of whistle types based on two criteria: firstly, signature whistles were whistle types repeated at least four times in a recording session, and secondly, at least on one occasion the whistles were produced in a sequence in which 75% or more repetitions occur within 1–10 sec of one other. The whistle types that were not cataloged as signature whistle types using this method were cataloged as non-signature whistle types.

To verify the reliability of our classification method, five experts, all affiliated to the acoustic communication team of NeuroPSI laboratory (Orsay, France) and working on bioacoustics in classification of birds or cetacean sounds, performed two visual classification tasks using the identified signature whistles of our dataset [see Kriesell et al., 2014]. For each signature whistle type, six whistle repetitions were randomly selected: 1 to act as a template and 5 to be classified by the experts. Each signature whistle repetition was surrounded by the signature whistle templates and was presented to each expert on a Microsoft Power Point slide. In the first task, the experts were asked to compare each whistle repetition with each template and to rate the similarity in a scale from 1 (very different) to 5 (very similar). The second task was to assign to each whistle repetition the most similar template category. The ratings were compared between experts using Fleiss' Kappa statistic [Siegel and Castellan, 1988] to determine inter-observer agreement in whistle classification and consistency in categorization (with and

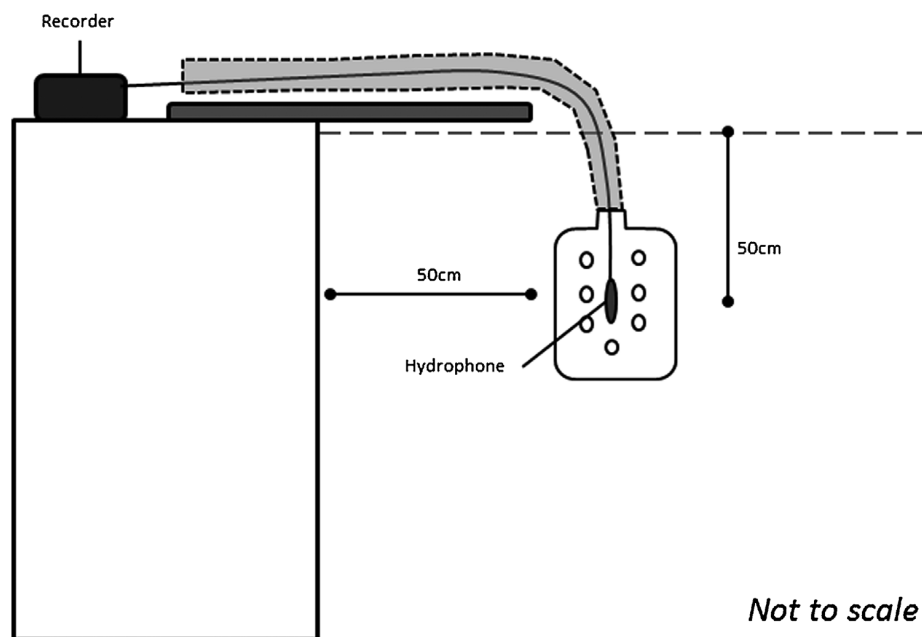


Fig. 1. Position of the recording set-up in the pool. Not to scale.

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without authors' classifications). When experts are in complete agreement Fleiss' Kappa statistics (k) is equal to 1 [Landis and Koch, 1977]. If agreement between experts is the same as expected by chance, then k is equal to 0.

Whistle Emission Analysis

Statistical tests were conducted using R statistical software version 3.02 [R Core Team, 2013]. Mean values of whistles emission rate and signature whistle emission rate per minute were calculated for the recordings before, during and after each training session. The Friedman Rank Test was used to compare the non-signature whistle emission rate and the signature whistle emission rate before, during and after each training session. Post hoc tests were performed to examine the variation in the tested variables.

RESULTS

A total of 7 hr 32 min (Table 1) were recorded among the ten training sessions (154 min before, 147 min during training sessions and 152 min after) in which 3,272 whistles were identified: 309 (9.44%) were classified as having too low signal-to-noise ratio whistles to be considered in this study and 79 (2.41%) were classified as overlapping whistles, the remaining 2,884 (88.14%) were classified in signature or non-signature whistle types. Most of the identified whistles were recorded during the first five recording sessions with nine individuals ($n = 1,946$; before training: 288, during training: 743, and after training: 915) while less of half of whistles was recorded during the last five recording sessions with eight individuals ($n = 938$; before training: 192; during training: 329, and after training: 417).

According to SIGID method, 279 (9.67%) signature whistles were identified belonging to four different signature whistles types (Fig. 2). The remaining 2,605 (90.32%) were classified as non-signature whistle types. The four signature whistles were present in the first five recording

sessions in November with nine individuals and in the last five recording sessions in May with eight individuals. We detected the occurrence of 210 signature whistles during the first recording sessions and the occurrence of 69 signature whistles during the last recording sessions.

The two visual classification tasks tested reliability of identifying whistle types. The first task showed a low inter-observer agreement (Fleiss' kappa statistic without author as judge: $k = 0.388$, n judges = 5, $z = 18.7$, $P = 0.00001$; with author as judge: $k = 0.408$, n judges = 6, $z = 24.2$, $P = 0.00001$). During the second task, the experts repeatedly chose the highest similarity rating for the first task as the most similar whistle to the template category. The inter-observer agreement was high in the second task (Fleiss' kappa statistic: $k = 0.956$, $z = 28.7$, $P = 0.00001$). These results show that clearly defined whistle types exist in the repertoire of Parc Asterix bottlenose dolphins and support the authors' visual categorization of the dataset.

The overall whistle emission rate during our recordings was 7.48 whistles per minute. We calculated this rate (including signature and non-signature whistles) by averaging the ten sessions before, during and after the training sessions. The rate did not change significantly from 4.72 ± 3.32 whistles per minute before the training sessions, to 8.14 ± 2.74 whistles per minute during the training sessions and 9.84 ± 7.44 whistles per minute after the training sessions (Friedman Rank Test: $\chi^2 = 2.6$, $df = 2$, $P = 0.2725$) (Fig. 3).

When comparing non-signature and signature whistles separately, we found that dolphins emitted more non-signature whistles during and afterwards (respectively Wilcoxon signed Rank Test: $V = 4$, $P = 0.0137$ and $V = 2$, $P = 0.0058$ with Bonferroni-adjusted significance level of $P < 0.0167$) than before the training sessions. No significant differences were found between the non-signature whistle emission rate during and after the training sessions (Wilcoxon signed Rank Test: $V = 25$, $P = 0.8457$ with Bonferroni-adjusted significance level of $P < 0.0167$) (Fig. 4).

TABLE 1. Time of recording of the 10 sessions: Before, during and after the training

Session and social grouping	Duration (hh:mm:ss)			
	Before	During	After	Total
1st social grouping, session 1	00:02:09	00:24:21	00:14:32	00:41:02
2	00:04:17	00:20:42	00:15:59	00:40:58
3	00:06:49	00:17:50	00:14:26	00:39:05
4	00:16:23	00:13:18	00:14:29	00:44:10
5	00:15:00	00:11:08	00:16:33	00:42:41
Sub-total	00:44:38	01:27:19	01:15:59	03:27:56
2nd social grouping, session 1	00:30:07	00:13:29	00:15:00	00:58:36
2	00:35:39	00:15:33	00:15:08	01:06:20
3	00:14:58	00:11:18	00:15:00	00:41:16
4	00:12:38	00:11:30	00:15:00	00:39:08
5	00:16:01	00:08:13	00:15:00	00:39:14
Sub-total	01:49:23	01:00:03	01:15:08	04:04:34
Total	02:34:01	02:27:22	02:32:07	07:32:30

The first five recording sessions were carried out with the first social group (nine animals) and the last five recording sessions were carried out with a second social group (eight animals).

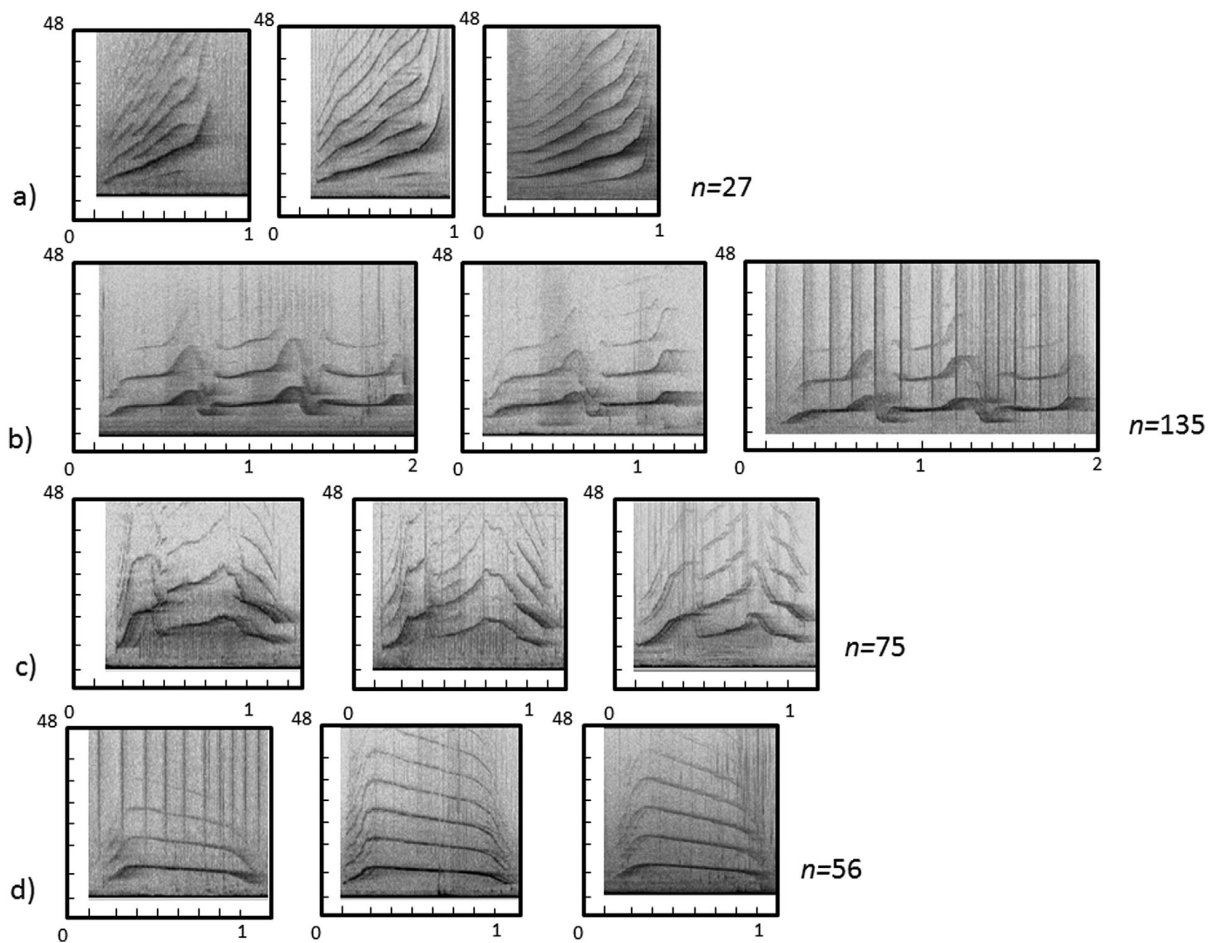


Fig. 2. Three randomly chosen spectrograms of each of the identified signature whistles emitted by Parc Astérix bottlenose dolphins (Plailly, France): (a) Signature whistle type 1 (SW1); (b) Signature whistle type 2 (SW2) which can be identified as variably loopy based on the final loop which is consistent from whistle to whistle; (c) Signature whistle type 3 (SW3); (d) Signature whistle type 4 (SW4). The numbers in the right are the total occurrences of the whistle type found in the acoustic recordings ($n=293$ signature whistles). Spectrograms are all presented in the same scaling. Frequency (kHz) is on the y-axis and ranges from 0 to 48 kHz. Time (s) is on the x-axis. FFT 1,024, Hanning window, overlap 50%.

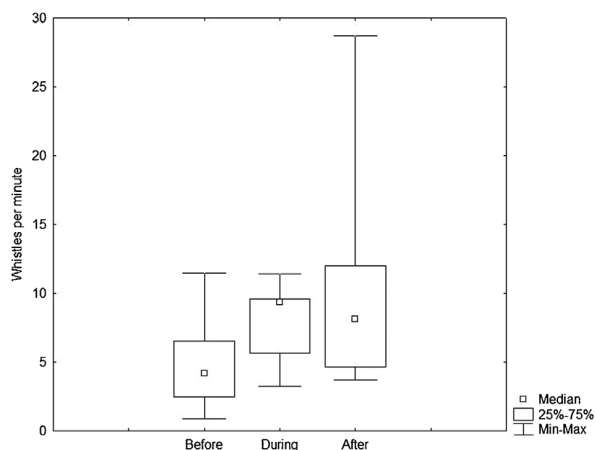


Fig. 3. Boxplot of bottlenose dolphins' whistle (all types) emission rate before, during and after training sessions ($n=10$). Friedman Rank Test: $\chi^2=2.6$, $df=2$, $P>0.05$.

When we pooled the four types of signature whistles, we found that signature whistle emission rate varied significantly before, during and after training sessions (Friedman Rank Test: $\chi^2=12.2$, $df=2$, $P=0.0022$): dolphins emitted significantly more signature whistles afterwards than before the training sessions (Wilcoxon signed Rank Test: $V=0$, $P=0.0019$ with Bonferroni-adjusted significance level of $P<0.0167$), but the animals' signature whistle emission rate before and during the training sessions did not show any significant variation (Wilcoxon signed Rank Test: $V=30$, $P=0.8457$ with Bonferroni-adjusted significance level of $P<0.0167$) nor between periods during and after the training sessions (Wilcoxon signed Rank Test: $V=0$, $P=0.0195$ with Bonferroni-adjusted significance level of $P<0.0167$) (Fig. 5).

The four different signature whistle types were not present in all the recording sessions making it impossible to statistically compare the whistle emission rate of each kind of

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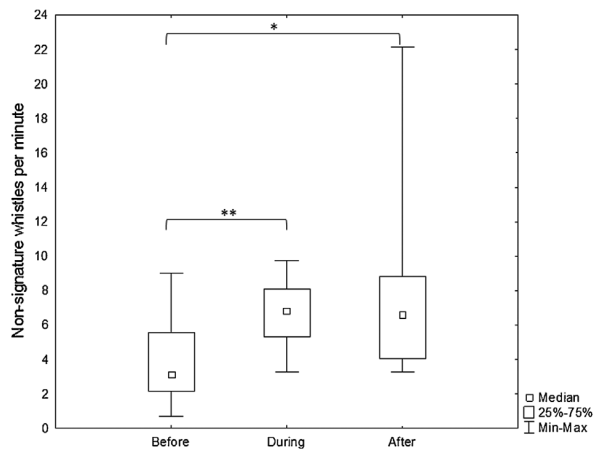


Fig. 4. Boxplot of bottlenose dolphins' non-signature whistle emission rate before, during and after training sessions ($n = 10$). *Wilcoxon signed Rank Test: $V = 2$, $P < 0.0167$ (with Bonferroni correction). **Wilcoxon signed Rank Test: $V = 4$, $P < 0.0167$ (with Bonferroni correction).

signature whistle between the sessions. However, we calculated the emission rate of each signature whistle type for the 10 sessions before, during and after the training. Whistle rate increased after the training sessions for signatures whistles type 1 (SW1), type 2 (SW2), and type 3 (SW3). The whistle emission rate of the signature whistle type 4 (SW4) was higher before than after the training sessions (Fig. 6).

To summarize, the dolphins' overall whistle emission rate did not significantly change before, during and after the training sessions. However, the non-signature emission rate was higher during and afterwards than before the training sessions and the signature whistle emission rate was significantly higher after than before the training sessions. The emission rate varied between the different

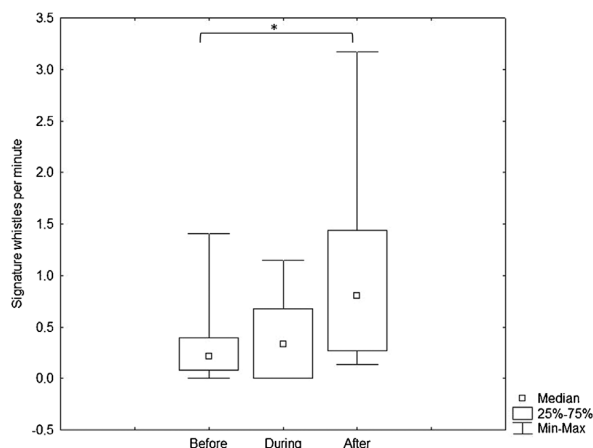


Fig. 5. Boxplot of bottlenose dolphins' signature whistle (all types) emission rate before, during and after training sessions ($n = 10$). *Wilcoxon signed Rank Test: $V = 0$, $P < 0.0167$ (with Bonferroni correction).

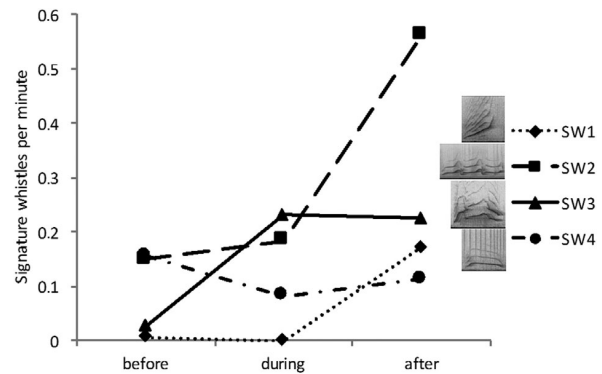


Fig. 6. Signature whistle emission rate for each type of signature whistle (SW) before, during and after the training sessions.

signatures whistles types, increasing for types 1, 2, and 3 and decreasing for type 4.

DISCUSSION

Dolphin whistle emission rate is highly variable and depends on several parameters: groups size [Jones and Sayigh, 2002; Cook et al., 2004; Quick and Janik, 2008], group composition [Hawkins and Gartside, 2010] and behavioral context [Dos Santos et al., 1990; Jacobs et al., 1993; Acevedo-Gutiérrez and Stienessen, 2004; Cook et al., 2004]. Most of the whistles detected occurred during the first five recording sessions: in November the nine dolphins whistled and produced signature whistles two times more frequently than the eight individuals in May. It is comprehensible to have more whistles and signature whistles produced when the group size increases [Van Parijs et al., 2002], but here, the difference in occurrence of whistles was not proportional to the number of individuals. Instead, it is possible that the group composition impacted the dolphins' vocal productions, and in particular the age of the individuals might also have been an important variable. The first recording sessions in November were carried out in a group with four young dolphins out of nine individuals while the second set of recordings in May occurred in a group of two young dolphins and six adults. Mother-offspring interactions include various behaviors (i.e., teaching behaviors) [Bender et al., 2009] and involve vocalizations (i.e., during periods of separation) [Smolker et al., 1993]. The nature of the intraspecific social interactions conducted within the groups might have influenced the number of whistles and signature whistles recorded. We suggest that the presence of young dolphins might have increased the number of affiliative, play and discipline behaviors within the group and these behaviors could be correlated to a high production of whistles.

The SIGID method [Janik et al., 2013] allowed us to identify four signature whistles within the bottlenose dolphins at Parc Asterix dolphinarium. If signature whistles are individually specific [Caldwell et al., 1990] we could

expect to find nine signature whistles in the first half of our recording sessions and eight in the second half. However, the SIGID method was conceived to be very conservative so that false positives were eliminated. This precaution means the SIGID method did not consider about half of the signature whistles present in the sample [Janik et al., 2013]. We recorded a total of 7 hr and 32 min. It is probable that signature whistles of all the individuals were present in our samples but we only identified less than 50% of them using the SIGID method. In this case, some of the non-signature whistles that were used in our analyses are signature whistles that were not detected by the method and in this terms the results we obtained on the non-signature whistle emission rate are influenced by the signature whistle emission rate. However, the emission of signature whistles in captivity is very scarce and for some individuals can be less than 1% of whistle emission rate [Janik and Slater, 1998]. Thus, it is highly probable that signature whistles of all the individuals were not present in our acoustic recordings. It would be necessary to record the animals during forced [Esch et al., 2009a] or voluntary isolation [Janik and Slater, 1998] or using a hydrophone array [López-Rivas and Bazúa-Durán, 2010], to link the whistle emission to individual dolphins in order to find the signature whistle for each member of the group.

The first classification task allows our study to be comparable to previous studies that use visual categorization of bottlenose dolphins' whistles as Janik [2000] and Kriesell et al. [2014]. The low inter observer agreement obtained on the first classification task has also been reported by these authors and might be due to the fact that we asked judges to classify whistles on a scale of discrimination that is too fine and leads to subjectivity. In fact when one of the authors redid the first classification task several months later, the inter observer agreement with herself was low ($K = 0.133$, $z = 1.9$, $P = 0.0581$). However, the second classification task that asked the judges to choose the most similar whistles showed a high inter observer agreement, which supports the author's visual categorization of the data set.

When we compared signature and non-signature whistles, the total emission rate did not significantly change before, during and after the training sessions. Our results differ from previous findings on other groups of cetaceans under human care: for instance, bottlenose dolphins increased whistle production during interactions with humans [Akiyama and Ohta, 2007; Therrien et al., 2012]. Akiyama and Ohta [2007] measured the number of whistles emitted by three captive bottlenose dolphins (one male and two females, all less than 8 years old) during several situations in a facility in Muroto (Japan): immediately before feeding, during feeding, during the animals' free-time without the presence of people, and during interactions with people on a float and in the water. They found that most of the whistles were emitted during the period preceding feeding (which is analog to the period before trainings in our study), and whistle emission was higher during various interactions with humans (including feeding) than during

their free-time in absence of people (which is analog to the period after training session in our study). Therrien et al. [2012] measured the whistle production of a group of eight bottlenose dolphins (four adult females, two adult males, and two young males) and found increased whistle production to coincide with increased interactions with humans during feeding/training sessions. Recently, a study carried out on five captive false killer whales (*P. crassidens*) (three adult females, one adult male, and one male calf) also found an increase in their acoustic emissions (including whistles) upon trainers' arrival [Platto et al., 2015]. The high rate was maintained during feeding sessions and reduced immediately after the animals were fed. In contrast, we found that non-signature whistles increased during the training sessions but their rate was higher afterwards, and signature whistle rate was higher after the training sessions compared to before.

Dolphins' behaviors and vocalizations can be modulated by trainings [Kuczaj and Xitco, 2002]. Since no information could be found about the influence of the nature and content of trainings in the related papers, we cannot comment on the impact they have on whistle emission rate. Moreover, in Akiyama and Ohta's [2007] study, dolphins spent less than 2 years under human care; this is in contrast to Parc Astérix dolphins, where six out of nine dolphins are born in the dolphinarium and the other three have been in captivity for over 2 decades. It has been shown that free-ranging dolphins increase their whistle emission rate during feedings probably to recruit more members to the group [Acevedo-Gutiérrez and Stienessen, 2004], and this behavior is likely not necessary, or less present, in captivity where feeding is less cooperative than in the wild. In Akiyama and Ohta's [2007] study, the dolphins might interact (e.g., to cooperate) while feeding. Unfortunately, Therrien et al. [2012] and Platto et al. [2015] do not specify for how long their studied animals have been in captivity.

Our study shows that overall, signature whistle emission significantly increased after the training sessions. However this was not the case for all the signature whistles types we detected, suggesting that depending upon the situation dolphins' signature whistles production varies, and consequently they might be used for various functions. Context of emissions of signature whistles varies from stress calls during forced isolation [Esch et al., 2009a] to cohesion calls [Smolker et al., 1993; Janik and Slater, 1998; Quick and Janik, 2012]. In Parc Asterix, during training sessions the trainers divide the animals into groups of the same two or three individuals. Each sub-group remains with one trainer and performs different exercises during the session. This division is never forced and it is achieved by using positive reinforcement. The training session by itself can be considered as rewarding for the animals [Laule and Desmond, 1998], since they are positively reinforced when they perform exercises. A previous study conducted in this facility measured the breathing rate of animals before and after the training sessions [Jensen et al., 2013] as a possible indicator of stress [Broom and Johnson, 1993; Dierauf,

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2001]. The results showed that the animals maintained the same breathing rate before and after the sessions [Jensen et al., 2013], indicating that the exercises they were asked to perform did not affect their level of stress. The increase in signature and non-signature whistle emission rates therefore is not likely to be explained by the animals being stressed during the training sessions. We suggest that the increase in non-signature and some signature whistle emission after training sessions is due to an augmentation of social behaviors. Before training sessions, dolphins can freely interact displaying affiliative, agonistic, and sexual behaviors [Herzing, 1996; Samuels and Gifford, 1997]. Since training sessions occur consistently approximately at the same hour, dolphins can perform anticipatory behaviors [Jensen et al., 2013] which could have an influence in their vocal production as has been found in captive false killer whales (*P. crassidens*) [Platto et al., 2015] and bottlenose dolphins in other facilities [Akiyama and Ohta, 2007]. Training sessions occur consistently approximately at the same hour and before these dolphins can perform anticipatory behaviors [Jensen et al., 2013] which could have an influence in their vocal production as has been found in captive false killer whales (*P. crassidens*) [Platto et al., 2015] and bottlenose dolphins in other facilities [Akiyama and Ohta, 2007]. During training sessions, the groups are subdivided and dolphins are asked to perform several exercises, where these activities modulate social interactions between animals. Finally, after the training sessions individuals are free to regroup as they want and the signature whistles might then be used as cohesion calls and copied as affiliative signals [King et al., 2014].

When comparing the emission rate of signature whistles before and after the training sessions we found that SW1, SW2, and SW3 emission rates increased after the training session and SW4 emission rate decreased after the training session. Signature whistles are individually specific [Caldwell et al., 1990], so it is highly probable that the four signature whistles identified were mostly emitted by four particular individuals with the exception of the cases where the signature whistles are copied [Janik, 2000; Tyack, 1986]. If this is the case, the signature whistles detected are not from the three males that were transferred between facilities because they are present before and after the transfer. One of the signature whistles (SW2) consists of several connected loops. Since the number of loops increases with the age of the individual [Caldwell et al., 1990], we suggest that SW2 probably belongs to one of the oldest animals in the group.

The differences found between the emission rates of each signature whistle type might be due to individual differences, meaning that the three individuals that emitted more signature whistles after the training sessions were probably seeking group cohesion or at least looking for social interactions. In contrast, one individual emitted more signature whistles before the training sessions probably looking for social interactions in a different moment.

These individual differences could be explained by the presence of different personalities in dolphins [Birgersson et al., 2014; Highfill and Kuczaj, 2007] that leads to individual variation in vocal activity. Since group composition and behavioral contexts influence dolphins' vocalization rate [Dos Santos et al., 1990; Jacobs et al., 1993; Cook et al., 2004; Hawkins and Gartside 2010], it would be necessary to identify the vocalizing dolphins and to observe the animals' behaviors during signature whistle emissions to explain the particular behavioral context that caused these individual differences. As a hypothesis, we suggest that non-signature whistles are intended to give information to listener dolphins, while signature whistles are used to give information about the emitter. The copy of signature whistles might play a role in spreading the information and letting the emitter know that the information has correctly been received. Vocal mimicry is an important part of communication in all species of mammals, but this is higher for cetacean species, in particular for toothed whales. These prolific vocal exchanges might probably be due to the development of their personalities, the features of their social structure and also the large diversity of their sound emissions.

In conclusion, our study shows that non-signature and particular signature whistle emission rate increases after scheduled training sessions in Parc Asterix dolphinarium. We suggest that animals might have been seeking social interactions after the sessions. We suppose that before the sessions, animals are free to interact, or not interact, with the partner(s) they choose, during the training sessions the group structure changes due to human intervention (trainers regroup particular dolphins into groups of 2–3 individuals), and after the training sessions dolphins freely regroup using signature whistles as cohesion calls. However, in order to validate this hypothesis, it is necessary to directly observe the animals' behaviors and to link the patterns of group association with whistle emissions. Moreover, during training sessions the trainers ask the dolphins to perform solitary and coordinated exercises, and their vocalization rate might also depend on the task the trainers ask them to perform. We can expect higher sound production rates during coordinated exercises and cooperative tasks [Eskelinen et al., 2016]. Linking whistle emissions to particular behaviors will be the next step to better understand how dolphins under human care communicate.

ACKNOWLEDGMENTS

We are very grateful to the Parc Asterix Dolphinarium curator, Birgitta Mercera, and her trainers for their help during the recording sessions. We would like to thank to the acoustic communication team (NeuroPsi) members for their constructive comments and for carrying out the classification tasks and Isabella Clegg for revising the English of this manuscript.

REFERENCES

- Acevedo-Gutiérrez A, Stienessen SC. 2004. Bottlenose dolphins (*Tursiops truncatus*) increase number of whistles when feeding. *Aquat Mamm* 30:357–362. Available online at: <http://doi.org/10.1578/AM.30.3.2004.357>
- Akiyama J, Ohta M. 2007. Increased number of whistles of bottlenose dolphins, *Tursiops truncatus*, arising from interaction with people. *J Vet Med Sci* 69:165–170.
- Au WWL. 1993. The sonar of dolphins. New York, NY: Springer-Verlag.
- Au WWW, Fay RR. 2012. Hearing by whales and dolphins. NY, USA: Springer.
- Bender CE, Herzog DL, Bjorklund DF. 2009. Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Anim Cogn* 12:43–53.
- Birgersson S, Birot de la Pommeraye S, Delfour F. 2014. Dolphin personality study based on ethology and social network theory. Saarbrücken, Germany: Lambert Academic Publishing. p 60.
- Brando SI. 2010. Advances in husbandry training in marine mammal care programs. *Int J Comp Psychol* 23:777–791.
- Broom DM, Johnson KG. 1993. Stress and animal welfare. London, UK: Chapman & Hall.
- Caldwell MC, Caldwell DK. 1965. Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). *Nature* 207:434–435.
- Caldwell MC, Caldwell DK, Tyack PL. 1990. Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood, Reeves RR, editors. The bottlenose dolphin: recent progress in research. San Diego: Academic Press. p 199–234.
- Connor RC, Mann J, Tyack PL, Whitehead H. 1998. Social evolution in toothed whales. *Trends Ecol Evol* 13:228–232.
- Connor RC, Wells RS, Mann J, Read AJ. 2000. The bottlenose dolphin. Social relationships in a fission-fusion society. In: Mann J, Connor RC, Tyack PL, Whitehead H, editors. Cetacean societies: field studies of dolphins and whales. Chicago: University of Chicago Press. p 91–126.
- Cook MLH, Sayigh LS, Blum JE, Wells RS. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proc Biol Sci* 271:1043–1049. Available online at: <http://doi.org/10.1098/rspb.2003.2610>.
- Dierauf LA. 2001. Stress. In: Dierauf LA, Gulland FMD, editors. CRC handbook of marine mammal medicine. 2nd edition. Boca Raton, FL: CRC Press.
- Dos Santos ME, Caporin G, Moreira HO, Ferreira AJ, Coelho JB. 1990. Acoustic behavior in a local population of bottlenose dolphins. In: Thomas JA, Kastelein RA, editors. Sensory abilities of cetaceans. New York: Springer USA. p 585–598.
- Esch HC, Sayigh LS, Wells RS. 2009a. Quantifying parameters of bottlenose dolphin signature whistles. *Mar Mamm Sci* 25:976–986.
- Esch HC, Sayigh LS, Blum JE, Wells RS. 2009b. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *J Mammal* 90:638–650.
- Eskelinen HC, Winship KA, Jones BL, Ames AE, Kuczaj SA, II. 2016. Acoustic behavior associated with cooperative task success in bottlenose dolphins (*Tursiops truncatus*). *Anim Cogn* 19:789–797.
- Fripp D, Owen C, Quintana-Rizzo E, et al. 2005. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Anim Cogn* 8:17–26. Available online at: <http://doi.org/10.1007/s10071-004-0225-z>
- Gibson QA, Mann J. 2008. The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother-calf groups in Shark Bay, Australia. *Anim Behav* 76:389–405.
- Hawkins ER, Gartside DF. 2010. Whistle emissions of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) differ with group composition and surface behaviors. *J Acoust Soc Am* 127:2652–2663.
- Herzong DL. 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquat Mamm* 22:61–80.
- Highfill LE, Kuczaj SA, II. 2007. Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquat Mamm* 33:380.
- Jacobs M, Nowacek DP, Gerhart DJ, et al. 1993. Seasonal changes in vocalization during behavior of the Atlantic bottlenose dolphin. *Estuaries* 16:241–246.
- Janik VM. 1999a. Origins and implications of vocal learning in bottlenose dolphins. In: Box HO, Gibson KR, editors. Mammalian social learning: comparative and ecological perspectives. Cambridge, UK: Cambridge University Press. p 308–326.
- Janik VM. 1999b. Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. *Anim Behav* 57:133–143.
- Janik VM. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* 289:1355–1357. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10958783>
- Janik VM. 2009. Acoustic communication in delphinids. In: Naguib M, Janik VM, editors. Advances in the study of behavior. Burlington: Academic Press. p 123–157.
- Janik VM, King SL, Sayigh LS, Wells RS. 2013. Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). *Mar Mamm Sci* 29:109–122.
- Janik V, Slater P. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim Behav* 56:829–838. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9790693>
- Janik VM, Todt D, Dehnhardt G. 1994. Signature whistle variations in a bottlenose dolphin, *Tursiops truncatus*. *Behav Ecol Sociobiol* 35:243–248.
- Jensen ALM, Delfour F, Carter T. 2013. Anticipatory behavior in captive bottlenose dolphins (*Tursiops truncatus*): a preliminary study. *Zoo Biol* 32:436–444.
- Jones GJ, Sayigh LS. 2002. Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Mar Mamm Sci* 18:374–393.
- King SL, Harley HE, Janik VM. 2014. The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. *Anim Behav* 96:79–86. Available online at: <http://doi.org/10.1016/j.anbehav.2014.07.019>
- King SL, Sayigh LS, Wells RS, Fellner W, Janik VM. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proc Biol Sci* 280:20130053.
- Kriesell HJ, Elwen SH, Nastasi A, Gridley T, Russo D. 2014. Identification and characteristics of signature whistles in wild bottlenose dolphins (*Tursiops truncatus*) from Namibia. *PLoS ONE* 9:e106317.
- Kuczaj SA, II, Xitco MJ. 2002. It takes more than fish: the comparative psychology of marine mammal training. *Int J Comp Psychol* 15:186–200.
- Landis JR, Koch GG. 1977. The measurement of observer agreement for categorical data. *Biometrics* 33:159–174.
- Laule GE. 2003. Positive reinforcement training and environmental enrichment: enhancing animal well-being. *J Am Vet Med Assoc* 223:969–972.
- Laule G, Desmond T. 1998. Positive reinforcement training as an enrichment strategy. In: Sheperdson DH, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington, DC, USA: Smithsonian Institution Press. p 302–313.
- López BD, Shirai JAB. 2009. Mediterranean common bottlenose dolphin's repertoire and communication use. In: Pearce AG, Correa LM, editors. Dolphins: anatomy, behavior, and threats. New York, NY: Nova Science Publishers, Inc. p 129–148.
- López-Rivas RM, Bazúa-Durán C. 2010. Who is whistling? Localizing and identifying phonating dolphins in captivity. *Appl Acoust* 71:1057–1062.
- Mann J, Connor RC, Barre LM, Heithaus MR. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav Ecol* 11:210–219.
- Platto S, Ding W, Kexiong W. 2015. Variation in the emission rate of sounds in a captive group of false killer whales *Pseudorca crassidens* during feedings: possible food anticipatory vocal activity? *Chinese J Oceanol Limnol* 31:1218–1237.
- Quick NJ, Janik VM. 2008. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. *J Comp Psychol* 122:305–311. Available online at: <http://doi.org/10.1037/0735-7036.122.3.305>
- R Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Samuels A, Gifford T. 1997. A quantitative assessment of dominance relations among bottlenose dolphins. *Mar Mamm Sci* 13:70–99.
- Sayigh L, Tyack P, Wells R, Scott M. 1990. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behav Ecol Sociobiol* 26:247–260. Available online at: <http://doi.org/10.1007/BF00178318>
- Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB. 1995. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behav Ecol Sociobiol* 36:171–177.
- Siegel S, Castellan NJ, Jr. 1988. Nonparametric statistics for the behavioral sciences. 2nd edition New York, NY: McGraw-Hill.

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- Smolker RA, Mann J, Smuts BB. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav Ecol Sociobiol* 33:393–402. Available online at: <http://doi.org/10.1007/BF00170254>
- Therrien SC, Thomas JA, Therrien RE, Stacey R. 2012. Time of day and social change affect underwater sound production by bottlenose dolphins (*Tursiops truncatus*) at the Brookfield Zoo. *Aquat Mamm* 38:65.
- Tsai Y-JJ, Mann J. 2013. Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar Mamm Sci* 29:261–279.
- Tyack P. 1986. Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles?. *Behav Ecol Sociobiol* 18:251–257. Available online at: <http://doi.org/10.1007/BF00300001>
- Van Parijs SM, Smith J, Corkeron PJ. 2002. Using calls to estimate the abundance of inshore dolphins: a case study with Pacific humpback dolphins *Sousa chinensis*. *J Appl Ecol* 39:853–864.
- Watwood SL, Tyack PL, Wells RS. 2004. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behav Ecol Sociobiol* 55:531–543. Available online at: <http://doi.org/10.1007/s00265-003-0724-y>
- Watwood SL, Owen EC, Tyack PL, Wells RS. 2005. Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. *Anim Behav* 69:1373–1386.

Chapter 2: Non-signature whistles are possible used as cohesion calls in bottlenose dolphins (*Tursiops truncatus*) under human care

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Article in preparation

Synthesis Chapter 2

Context

Although signature whistles have been largely studied, not much is known about non-signature whistles, which are the most frequently produced whistles by the species in captivity.

Research questions

The behavioral context of emission of non-signature whistles has been poorly studied in detail and often behavioral observations are done from surface taking into account only general behavioral categories such as travel, rest, socializing and foraging.

The aim of this study was to determine if there is an association between the non-signature whistle production and the underwater behaviors of a group of eight bottlenose dolphins under human care.

Analysis

The study was conducted in a group of 8 bottlenose dolphins (*T. truncatus*) during six days in February 2017 at the Boudewijn Seapark (Bruges, Belgium). Audio-video recordings were made 15 minutes before and after 10 training sessions. The behavioral analysis was made by focal follows on each individual based on six behavioral categories. The acoustical analysis was made at the group level, and non-signature whistles recorded (N=661) were visually classified in six categories according to their frequency modulation.

Results

Multifactorial analysis showed that the occurrence of the six categories of whistles were highly collinear. Non-signature whistle production was positively correlated with the slow swimming alone behavior and negatively with the affiliative body contact.

Conclusion

Our results suggest that non-signature whistle production plays a role in the cohesion of animals when they are in the same range of vision. This is the first analysis that links the production of non-signature whistles with particular underwater behaviors in the species. However, in order to test our hypothesis, it will be necessary to localize and identify the animal producing a whistle and the behavioral response of its congeners.

ABSTRACT

Bottlenose dolphins are highly social cetaceans that strongly rely on acoustic communication and signaling. The diversity of sounds emitted by the species has been structurally classified in whistles, clicks and burst-pulsed sounds. Although click sounds and individually-specific signature whistles have been largely studied, not much is known about non-signature whistles, which are the most frequently produced whistles by the species in captivity. Most studies that link behavior and whistle production conduct aerial behavioral observations and link the production of whistles to the general category of social interactions. The aim of this study was to determine if there was a correlation between the non-signature whistle production and the underwater behaviors of a group of eight bottlenose dolphins in Boudewijn Sea Park (Belgium). In order to do this we made audio-video recordings 15 minutes before and after 10 training sessions. For the behavioral analysis we made focal follows on each individual based on six behavioral categories. For the acoustical analysis, made at the group level, we visually classified the non-signature whistles recorded (N=661) in six categories according to their frequency modulation. Multifactorial analysis showed that the occurrence of the six categories of whistles were highly collinear. Non-signature whistle production was positively correlated with the slow swimming alone behavior and negatively with the positive affiliative body contacts. Our results suggest that non-signature whistle production plays a role in the cohesion of animals when they are in the same range of vision. This is the first analysis that links the production of non-signature whistles with particular underwater behaviors in the species.

Key words: vocalizations, underwater observations, captivity

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are highly social cetacean that exhibit a system of fission-fusion grouping pattern, in which the individuals associate in small groups that often vary in composition according to age, sex, reproductive status and activity (Connor et al., 2000; Mann et al., 2000; Gibson and Mann, 2008; Tsai and Mann, 2013). In this highly mobile species, individuals of the same group can be distant by hundreds of meters within a habitat of limited visibility (Connor et al., 1998). Under these conditions, individual interactions based on the use of acoustics signals seems to be the most effective strategy in order to assess their social and natural environments (Janik, 2009).

The diversity of the sounds emitted by the species has been classified into three structural categories and two functional classes. Structurally, the sounds emitted by the bottlenose dolphins are categorized in whistles or tonal sounds (Reviewed in Janik, 2009), clicks or pulsed sounds (Au, 2012), and burst-pulsed sounds (Diaz-Lopez and Bernal-Shirai, 2009). Functionally, sound emissions may be used for echolocation (involved in orientation and navigation), or may have a role in communication and social interactions (Herzing, 2000).

Whistles are continuous narrow-band frequency modulated signals that range from 800 Hz to 28.5 kHz and have duration between 100ms and over 4s (Evans and Prescott, 1962). This kind of sounds is associated with many social situations, with some whistles being individually specific (Caldwell et al., 1990) and functioning to maintain group cohesion (Janik and Slater, 1998). These whistles, also called “signature whistles”, have been largely studied (Caldwell et al., 1990; Janik, 2000;

Janik and Sayigh, 2013; King et al., 2014). Their production rate varies with the contexts: signature whistles can represent more than 90% of whistles produced by temporally restrained dolphins (Caldwell and Caldwell, 1965; Sayigh et al., 1990), between 30-70% of free ranging dolphins (Cook et al., 2004) and less than 1% in dolphins under human care (Janik and Slater, 1998). Thus, most of the whistles produced by unrestrained dolphins are not-signature whistles.

One common method for describing non-signature whistles is to qualitatively classify them based on their contour shape. Shape categories include upsweep, downsweep, convex, concave and sinusoid (Bazua-Duran and Au, 2002; Hickey et al., 2009; Lopez, 2011). The behavioral context of emission of non-signature whistles has been poorly studied in detail and often behavioral observations are done from surface taking into account only general behavioral categories such as travel, rest, socializing and foraging (Herzing, 2015). For instance, in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean foraging behavior was associated with sinusoid whistles, while upsweep whistles were associated with social behaviors (Lopez, 2011). Underwater behavioral observations allow the creation of more detailed ethograms (Herzing, 2015).

The management of bottlenose dolphins in captivity is largely based on positive reinforcement training (Laule, 2003; Brando, 2010), and often several training or feeding sessions are held per day. These trainings can be rewarding, as animals voluntarily take part and must work in order to obtain rewards and develop cognitive skills (Laule and Desmond, 1998). In the daily life of captive dolphins, training sessions could represent outstanding events that involve feeding and interaction with humans. The schedule of human-controlled periods modulates the behavior of animals during their free time (Clegg et al., 2017). It has been observed that

anticipatory behaviors are higher before training sessions (Jensen et al., 2013; Clegg et al., 2017), while synchronized swimming peaks shortly after training sessions (Clegg et al., 2017). With respect to the non-signature whistle vocalization rate, it has been found that upsweep whistles are mainly produced during feeding sessions, while convex and sinusoid whistles are more frequent during the time before the feeding session (Akiyama and Ohta, 2006).

The aim of this study was to determine if there is an association between the non-signature whistle production and the underwater behaviors of a group of eight bottlenose dolphins under human care. For instance we assessed if specific social contexts (e.g. alone vs. synchronous swimming) induce particular non-signature whistle types production.

METHODOLOGY

Study subjects

The study was conducted during six days in February 2017 at the Boudewijn Seapark (Bruges, Belgium). The complex was inhabited by eight Atlantic bottlenose dolphins (*T. truncatus*), six adult females aged 51, 41, 32, 19 and 14, one adult male aged 12 years, and two calves, one male and one female that were born at the park in the summer of 2015. Two of the adult females were born at the park, the adult male was born at another facility and the three oldest females originated from wild. All dolphins are subject to the same management schedule based on positive reinforcement training methods. Every day dolphins take part in six to eight training sessions approximately at the same time during which their trainers feed them after they perform several exercises aimed to facilitate the husbandry and medical care procedures and to prepare for presentations to the public. The adult animals know to

perform 100 to 130 behaviors upon trainers' command plus the new behaviors they are learning. Their sequence, their frequency and their duration change every day in every session. It could be underwater/aerial behaviors and solitary/group behaviors. Before and after the training sessions the trainers mainly stayed in the office and food preparation area and remained not visible or audible by the dolphins. At the beginning of each training session the trainers went out of the food area at the same time carrying fish buckets and place themselves at the edge of the pool. During training sessions the animals are divided into subgroups that goes to different pools depending on whether they were performing exercises or not. Separations into subgroups are obtained by positive reinforcements and the animals remain within acoustical reach of one another at all times.

Overall this facility consists of five connected pools: a main show pool, two holding pens, a medical pool and quarantine pool (Figure 1). The quarantine pool and main show pool are connected by a channel. The depth of the pools is at least 3m in the shallowest areas and 5,6m at its deepest point in the main show pool. The total volume is 2896m³ or approximately 3millions liters. Training sessions with caregivers can take place in all of the pools. During the recordings, the audio-video device was placed in the main pool and the animals could move freely between the five pools. The facility was closed to the public at the time of the recordings. Between the recording sessions the animals were provided with enrichment items that were alternated on a daily basis.

Recording device

Simultaneous audio and video recordings were collected using an improved waterproof 360° audio-video system, named BaBeL (BioAcoustique, Bien-être et Langage) (Lopez-Marulanda et al., 2017). Video data were collected using one

GIROPTIC 360° camera consisting in three objectives that allowed a 360° range of view. This camera was positioned under the waterproof housing of a digital recorder ZOOM H6, plugged to four calibrated and automatically synchronized Aquarian H2a-XLR hydrophones. Audio recordings were conducted at a 96kHz sampling frequency and coded on 24 bits.

Two claps were made at the beginning of the recording session in order to manually synchronize video with audio recordings during the a posteriori analysis with specific video editing software (Final Cut Pro X 10.1.3 © Apple Inc.). A single video file was created from the GIROPTIC camera and was associated with one of the four audio tracks and its corresponding turning spectrogram (FFT size: 1024, overlap 50%, Hanning window) provided by the free software Audacity 2.0.6 (GNU General Public License). For this study the localization of dolphin producing a whistle was not possible using our hydrophone array due to the reverberation on the walls of the pool. We chose then to add only one track in the video as a reference.

Desensitization process

During four weeks prior to the recording sessions, animal caregivers were provided with BaBeL to desensitize the animals to the presence of the device in the water. The desensitization process carried out by the trainers consisted of 6 steps which were gradually built up over the weeks prior to our recordings. The first step involved placing the device on the side of the main pool, out of the water, but within sight of the animals. For the second step, an animal caregiver took the device into the water, standing on the underwater platform in the channel that connected the main show pool to the quarantine pool, holding the device in the main show pool. During this phase, the animals could see the device in the water, but were kept under control by other trainers. Thirdly, the animals were allowed to swim freely for limited times in the

presence of the device which was held by a trainer as described in step 2. These times were gradually prolonged and animals were rewarded when ignoring the device. For the fourth step, the device was placed in the water without a trainer while the animals were kept under control. In step five, the device was left in the water while the animals swam freely with enrichment items to distract them from showing interest in BaBeL. Finally, during the last phase, the device was frequently placed in the water by the animal trainers at different times of the day, with or without the presence of enrichment items.

Audio-video recordings

Recording sessions were carried out approximately 15min before and 15min after ten training sessions that took place on six days. During the recordings, the device was suspended from a buoy and kept in place at the side of the tank by two ropes and a pole manipulated by one observer who remained at the edge of the pool avoiding visual contact with the animals. The location of the device during the recordings is marked by a red dot in Figure 1.

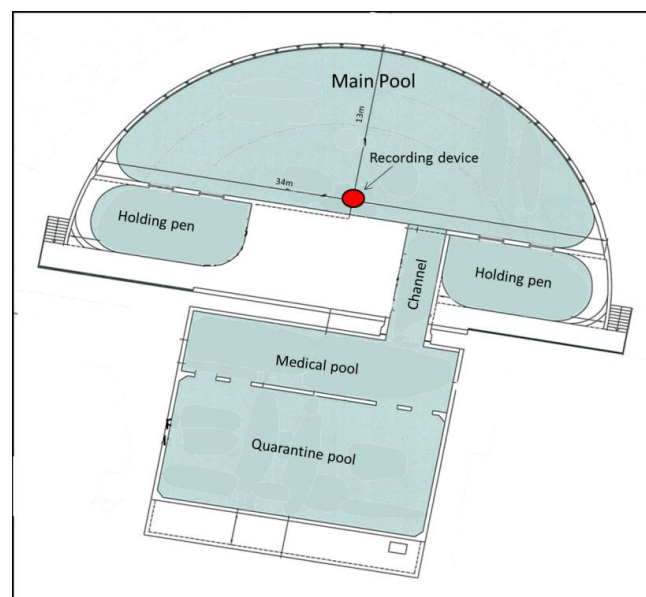


Figure 1: Top view of the enclosure at the Boudewijn Seapark (Belgium). The location of the BaBeL device during the recordings is marked by a red dot. Animals have access to all the pools except the two holding pens.

Whistle categorization

Recorded whistles were analyzed by inspecting the spectrograms (FFT size: 1024, overlap 50%, Hamming window) in Audacity 2.06 software (GNU General Public License). A graph of the spectrogram of each whistle was registered giving special attention to standardize the x- and y-axes of (1second long, with a frequency range of 0Hz to 48 kHz) to prevent distortion of whistles caused by axes of differing length influencing the categorizing process. Whistles with a negative signal-to-noise ratio or overlapping with other whistles were registered but not included in the categorization.

To categorize the whistles we first applied the SIGID method (Janik et al., 2013) to identify signature whistles within our recordings based on two criteria: firstly, signature whistles were whistles repeated at least four times in a recording session, and secondly, at least on one occasion the whistles were produced in a sequence in which 75% or more repetitions occur within 1–10 sec of one other. The whistles that were not cataloged as signature whistles using this method were cataloged as non-signature whistles. Non-signature whistles were visually categorized into one of six fundamental shapes: upsweep, downsweep, flat, convex, concave and sinusoid (with more than one inflection point).

Behavioral analysis

For each video, a focal-animal sampling technique was conducted to note the occurrence and duration of the most frequent social and anticipatory behaviors

displayed by the animals (Altmann, 1974; Mann, 1999). The behaviors were adapted from a published repertoire built to analyze the effect of training sessions on the behavior of dolphins under human care (Clegg et al., 2017). We took into account the swim style (alone or synchronous), the different speeds of swim (slow: around 2m/s or less, minimal tail beats; fast: more than 2m/s and stronger tail beats), play, positive social body contact, agonistic, sexual and anticipatory behaviors (Table 1). For each individual we calculated the total time spent within the range of view of the camera.

Table 1: Behavioral catalogue used for this study, based on an ethogram proposed by Clegg et al. (2017).

Behavior	Description
Alone swimming	Dolphin swims at more than one body length of any other dolphin in the pool and shows no synchronous movements with its conspecifics. (slow: around 2m/s or less, minimal tail beats; fast: more than 2m/s and stronger tail beats)
Synchronize swimming	Dolphin swims in synchronous manner within one body length of another dolphin, showing parallel movements and body axes. Breathing can be separated maximum by 2 sec. (slow: around 2m/s or less, minimal tail beats; fast: more than 2m/s and stronger tail beats)
Play ¹	Dolphin engages with another dolphin in a sequence of chase, bite and/or hit behaviors that end with one of the dolphins swimming erratically in the vicinity of its conspecific (Serres and Delfour, 2017)
Positive social contact	Dolphin touches or rubs another dolphin with its rostrum, its pectoral fin or any other part of its body.
Agonistic ¹	Dolphin engages with another dolphin in a sequence of chase, bite and/or hit behaviors that end with the abrupt flee of one of the individuals (Serres and Delfour, 2017)
Sexual ¹	Dolphin touches other dolphin genitals with any part of its body or with its own genitals.

Anticipatory

Dolphin directs its look out of the water towards the arrival point of the trainers by a simple surface look, spy hopping, jumping or body slapping close to the edge of the pool.

[†] These behaviors did not occur during the observations of the present study.

No individual marking was used. Each dolphin could be recognized by the use of patterns as the general coloration of the body, patches of permanent skin discoloration, body size, body shape and notches on the dorsal fin and tail. Before the data collection began, we verified that the observer (JLM) could identify dolphins with 100% accuracy.

Data analysis and sample sizes

Individual-based behavioral data were collected during 10 sessions prior to and 9 sessions after the training sessions. As some dolphins were not present during the observations, the total number of observations (individual observations during different sessions) was $n = 75$ prior to the training and $n = 66$ after the training. Always at least six individuals were present in the main pool during the recordings; in four sessions, two individuals were absent from the main pool. However, when excluding these data and re-running all analysis the principally same results were obtained. All statistical analyses were done with R, version 3.4.1. (R Core Team, 2017). Except for the principal component analysis PCA, we always used permutation tests for the calculation of P -values. Permutation tests for linear models are well adjusted for moderate sample sizes and do not require normal distribution of model residuals (Good, 2005). However, we verified homogeneity of variances for all models (linear models LM or linear mixed-effects models LMM) by plotting residuals versus fitted values (Faraway, 2006).

We run a PCA (R package *prcomp*; Venables and Ripley, 2002), based on the different non-signature whistles, which were found to be highly collinear (see Table 2). The resulting first axis was used as non-signature whistle score in further statistical analyses. See more details in results.

Correlations at the group level, i.e. between the number of occurrences of the different non-signature whistle types and comparisons of the whistle score (dependent variable) recorded before and after the training sessions (factor with 2 levels) were tested by linear models LM.

Table 2: Correlations between the different non-signature whistle types, calculated by linear models. All models included the interaction with timing (factor with 2 level), i.e. whether the whistles were recorded before or after the training sessions. These interactions were never significant (all $P > 0.10$) and were removed from the models before these were re-calculated. P values were calculated by 1000 Monte Carlo permutations. The adjusted R^2 is provided. Upsweep whistle: A, downsweep whistles: B, flat whistles: C, convex whistles: D, concave whistles: E, sinusoid whistles: F. All the analysis was made for 8 individuals, 10 sessions prior to the training and 9 sessions after.

Dependent variable	Independent variable	R^2	P
A	B	0.616	< 0.001
A	C	0.669	< 0.001
A	D	0.579	< 0.001
A	E	0.502	< 0.001
A	F	0.568	0.001
B	C	0.499	0.001
B	D	0.243	0.020
B	E	0.142	0.064
B	F	0.184	0.032
C	D	0.647	< 0.001
C	E	0.222	0.024
C	F	0.277	0.021
D	E	0.321	0.008
D	F	0.447	0.003
E	F	0.863	< 0.001

Comparisons at the individual level, i.e. between the duration (% time) of the different behaviors before and after the training session were tested by linear mixed-effects models (LMM) based on restricted maximum likelihood estimates by using the *lme* function of the R package *nlme* (Pinheiro et al., 2015). Furthermore, we used LMM to test for associations between the group-level pattern of non-signature whistles a (using the whistle score as obtained by PCA) and the individual-level % time the individuals spent showing the different behaviors recorded. This analysis was done separately during the period prior to and after the training sessions. Training-session identity (thus pairing together observation sessions before and after a particular training session) and individual dolphin identity (thus allowing for repeated measurements at the individual level across different observation sessions) were used as random factors (random intercepts) in all LMM. We used a nested random effects structure, i.e. individual identity was nested within training-session identity. *P*-values for LMM as well as for LM were calculated by Monte Carlo sampling with 1000 permutations, using the *PermTest* function of the R package *pgirmess* (Giraudeau, 2016).

For all significant covariate effects of LMM and GLMM, we provide the slopes (β ; based on scaled values) including their standard errors as a measure of (standardized) effects size.

RESULTS

Patterns of whistles of the group

A total of 4hr 26 min (Table A, supplementary material) were recorded during the ten training sessions (2hr 30 min before and 1 hr 56 min after) in which 776 whistles were identified: 95 (12.24%) were classified as having too low signal-to-noise ratio to

be considered in this study, 9 (1.16%) were classified as overlapping whistles, 11 (1.42%) whistles were classified as signature whistles belonging to two different whistles types according to the SIGID method (Janik et al., 2013) and 661 (85.18%) were classified as non-signature whistles and visually categorized in the six categories mentioned in the methods section.

Associations between different whistles

The most frequent category of non-signature whistle recorded in our study was the sinusoid whistle F with an occurrence of 1.12 min^{-1} , followed by the upsweep whistle A (0.52 min^{-1}), the concave whistle E (0.31 min^{-1}), the flat whistle C (0.19 min^{-1}), the convex whistle D (0.17 min^{-1}), and the downsweep whistle B (0.15 min^{-1}).

The occurrences of these different types of non-signature whistles recorded at the group level were statistically not independent, since there were various significant and positive correlations between them (Table 2). The non-significant interactions with the factor timing (factor with 2 levels; either before or after the training) indicate that these significant correlations were not modulated by the timing of recording, i.e. whether the whistles were recorded before or after the training sessions.

Due to this high level of collinearity between the different non-signature whistle types, we decided to express the variation in whistle patterns by a single score (from here on referred to as 'whistle score'), calculated by the first axis of a principal component analysis PCA. This first axis explained 75.1% of the variation of the data, and the eigenvalue of this axis was 4.5. Further axes had eigenvalues of > 1 and thus were not considered for further analyses. The loadings of all whistle types included in the analysis were all positive (A: +0.450; B: +0.375; C: +0.409; D: +0.405; E: +0.394; F: +0.412).

Comparison of non-signature whistles production before and after training sessions

The whistle score, reflecting the totality of different non-signature whistles emitted by the group, was significantly higher prior to the training sessions than after the session

(LM with 1000 permutations: $P < 0.001$; Fig. 3). That is, the dolphin group produced more non-signature whistles before than after the training sessions.

Individual-level behaviors

Comparison of individual-level behaviors before and after training sessions

A comparison of all observed individual-level behaviors revealed that only the % time of positive social body contacts differed significantly during the observations prior to and after the training sessions (LMM with 1000 permutations: $P = 0.027$). That is, the dolphins showed significantly more positive social body contacts after than before the training sessions.

There were some tendencies indicating that the % time the animals spent swimming alone differed between the observations before and after the training session; however, this difference was modulated by the speed of swimming (Fig. 2). Fast swimming tended to be more frequent prior to the training sessions ($P = 0.051$), whereas slow swimming tended to be more frequent after the training sessions ($P = 0.055$). There were no significant differences with respect to the % time the dolphins showed synchronous swimming, either slow ($P = 0.283$) or fast ($P = 0.544$), and the time they spent showing anticipatory behaviors ($P = 0.663$; see Fig. 3). There were no significant effects of sex or of age class with respect to any of the behaviors tested (all $P > 0.10$; see details on statistics in Table B of the supplementary material).

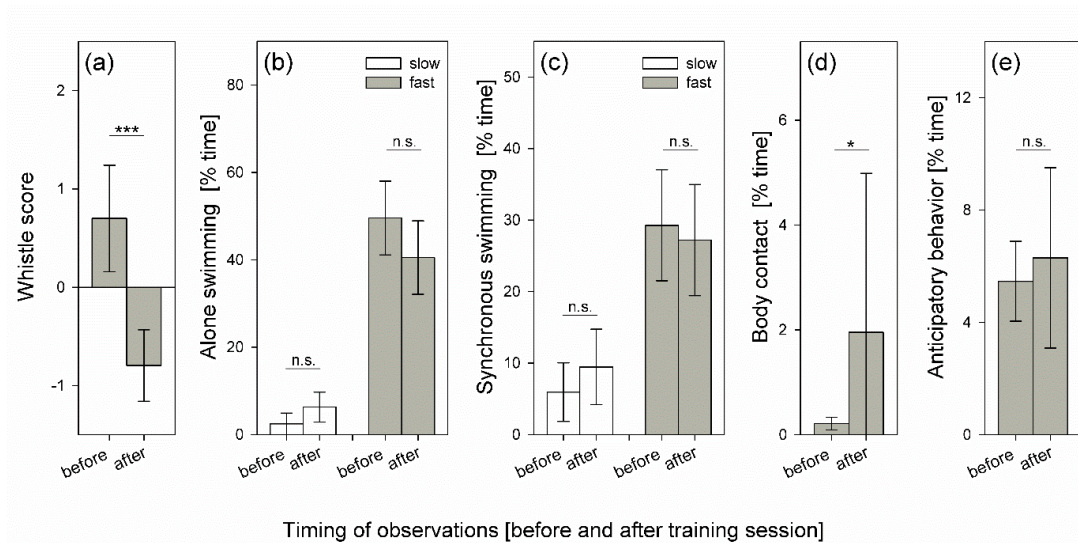


Figure 2: Comparison between (a) the pattern of non-signature whistles at the group level (whistle score obtained by PCA, see text) and (b-e) individual-based behaviors prior to and after training sessions of bottlenose dolphins ($n = 8$ individuals, although not all individuals were observed in all sessions). Means with 95% confidence intervals are given. Observation sessions ($n_{\text{before}} = 10$; $n_{\text{after}} = 9$) were around 15 min. Statistical comparisons by linear mixed-effects models; see text for details. Significant differences are indicated by asterisks (** $P < 0.001$, * $P < 0.050$).

Associations between vocalization patterns and individual behaviors

There were significant associations between the group-level pattern of non-signature whistles (as assessed by a PCA-based whistle score) and certain of the different individual-level behaviors recorded, but only during the observations prior to the training sessions. The % time the animals spent swimming alone in a slow mode was significantly increased when more non-signature whistles were emitted by the group, as indicated by the significant and positive correlation between the % time spent

swimming alone and the whistle score (LMM with 1000 permutations: $\beta = +0.387 \pm 0.179$ SE, $P = 0.017$; Fig. 3a). Furthermore, the % time the animals spent showing positive social body contacts was significantly decreased when more non-signature whistles were emitted by the group $\beta = -0.286 \pm 0.120$ SE, $P = 0.014$; Fig. 3b).

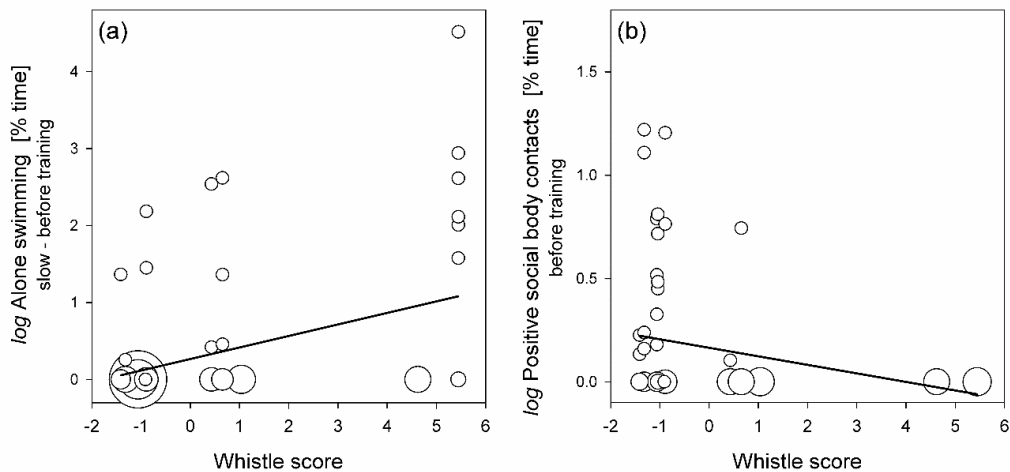


Figure 3: Comparison between the pattern of non-signature whistles at the group level (whistle score obtained by PCA, see text) and the % time individuals (a) spent swimming alone or (b) showed positive social contacts with conspecifics. Data from 6 bottlenose dolphins observed during 10 sessions prior to training sessions ($n_{total} = 75$ observations). The size of dots indicate the number of overlapping cases.

Parameters of regression lines obtained by linear mixed-effects models using log-transformation of dependent variables; see text for details.

Associations between the whistle score and any other behavior recorded prior to or after the training sessions were not statistically significant (all $P > 0.10$; see details in Table C in the supplementary material). However, there were significant differences

for the alone swim fast behavior between males and females ($\beta = -0.842 \pm 0.270$ SE, $P = 0.003$) and for the anticipatory behavior between young and older dolphins ($\beta = +1.093 \pm 0.232$ SE, $P = 0.001$). That is, the females showed significant more alone swim fast behavior than males and the young showed significant more anticipatory behavior than adults.

To summarize, bottlenose dolphins produced more non-signature whistles before than after the training sessions. These whistles were mostly sinusoid whistles and upsweep whistles; however there was a strong correlation between all the non-signature whistles types.

We observed significantly more positive body contacts in the periods after the training sessions. The fast swimming behavior was most frequent before the training sessions and the slow swimming behavior was most frequent after the training sessions.

With respect to the correlations between non-signature whistle emission and the different behaviors, we found that during the time prior to the training sessions more non-signature whistles were produced when animals were swimming slow and alone. In contrast less non-signature whistles were emitted when animals showed positive social body contacts.

Finally, young dolphins showed more anticipatory behaviors than adults and females showed more fast swimming alone behavior than males.

DISCUSSION

Bottlenose dolphins produced more non-signature whistles during the time prior to than after the training sessions. As traditionally whistle emission has been linked with communication and social interactions (Herzing, 2000), we suggest that during the

time prior to training sessions the animals invest more time in actively communicating and interacting socially than after the training sessions that could be devoted to rest. This result contrast with what has been found in other facility, in which dolphins produce more non-signature whistles in the period after than before the training sessions (Lopez-Marulanda et al., 2016). Several factors could explain these differences in the vocal activity: differences in group composition (Hawkins and Gartside, 2010; Heiler et al., 2016), different personalities of the animals (Bigersson *et al.*, 2014; Highfill and Kuczaj, 2007), and differences in management between both facilities. In fact, both facilities differ in the procedure during the training sessions. In Boudewjin SeaPark, the animals are separated in different pools during each training, while in Parc Asterix (France), the animals are never isolated (Lopez-Marulanda et al., 2016). The isolation of animals might increase the production of whistles (Esch *et al.*, 2009) and subsequently modulate the production of whistles before and after the training sessions. As a consequence of this, in Boudewjin SeaPark, most of the whistles are produced during the training sessions (Colpaert, 2017). It is possible that in this case, the period prior to training sessions elicited the production of more non-signature whistles, probably as an anticipatory behavior to the isolation. We did not found differences in the anticipatory behavior before than after the training sessions. This is probable due to the fact that the presence of the observers during the recording sessions elicited surface looking behaviors in the dolphins before and after the training sessions. These behaviors were classified as anticipatory as it was impossible to distinguish between the surface looking behavior directed to inspect the trainers arrival and the surface looking behavior directed to observe the experimenters keeping the BaBeL device in the right position. Thus, we consider this result as a bias.

Sinusoid and upsweep whistle types were the most frequent non-signature whistle types produced during the recordings. These two kinds of whistles have been reported by several authors as the most common produced by the animals, both in captivity (Akiyama and Ohta, 2006) and in the wild (Hickey et al., 2009; Diaz Lopez, 2011). Our results confirm that these kinds of whistles play an important role in the natural communication system of bottlenose dolphins (Diaz Lopez, 2011). However, we also found that all the non-signature whistle types were highly correlated, which means that the production of non-signature whistles elicit the emission of other non-signature whistles.

With respect to the behaviors, we found that positive social body contacts were more frequent after than before the training sessions. Positive social body contacts play a role in restoring the friendly relationships and reduce conflicts between bottlenose dolphins in captivity (Tamaki et al., 2006) and spotted dolphins (*Stenella frontalis*) in the wild (Dudzinski, 1998). According to this, we could suggest that the time after the training session plays a role in maintaining positive social relationships between the individuals of this group of dolphins. Moreover, during our recordings these behaviors were only observed between mothers and calves, an interaction that has been also reported as frequent for free ranging Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Sakai et al., 2006).

The fast swimming behaviors were also more frequent in the time prior to the training sessions than after. This result matches with what has been described for bottlenose dolphins in captivity; in which high-speed swimming was concurrent with periods of high production of vocalizations (Sekiguchi and Kohshima, 2003). However, this contrast with what has been found for the behaviors of the animals with respect to the training sessions in other facilities, in which the speed of swim did not differ

between the time prior and after the training sessions (Clegg et al., 2017). We suggest that different groups of dolphins might differ in their expression of behaviors according to group composition, personalities and management. In the case of Boudewijn Sea Park, the separation of animals during the training sessions may cause the excitation of the animals which is reflected in the increase of fast swimming and non-signature whistle emission.

Our results show strong correlations between the non-signature whistle production and some behaviors. During the time prior to training sessions, dolphins produced significantly more non-signature whistles while swimming slowly alone. Also, they produced less non-signature whistles during the positive social body contacts. Even if this strong correlation cannot be interpreted as a causality, we suggest that non-signature whistles might play a role in the cohesion of the animals as when they swim slow and alone they produce more non-signature whistles probably to search for proximity or contact and when they are already in contact they do not need to produce these vocalizations which reflects the decrease in their production. The fact that the animals do not use instead signature whistles as cohesion calls (Janik and Slater, 1998) under these circumstances, could be explained because the animals are placed in the same pool and are in visual contact to each other, so they do not need to transfer information about their identity to regroup. However, in order to test our hypothesis it will be necessary to localize and identify the animal producing a whistle and the behavioral response of its congeners. Moreover it will be necessary to observe these behaviors and vocalizations in other groups of dolphins under human care and in the wild to determine the role of different non-signature whistles.

BIBLIOGRAPHY

- Akiyama, J., & Ohta, M. (2007). Increased number of whistles of bottlenose dolphins, *Tursiops truncatus*, arising from interaction with people. *Journal of Veterinary Medical Science*, 69(2), 165-170.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3), 227-266.
- Au, W. W. (2012). *The sonar of dolphins*. Springer Science & Business Media.
- Bazúa-Durán, C., & Au, W. W. (2002). The whistles of Hawaiian spinner dolphins. *The Journal of the Acoustical Society of America*, 112(6), 3064-3072.
- Birgersson S, Birot de la Pommeraye S, Delfour F. 2014. Dolphin personality study based on ethology and social network theory. Saarbrücken, Germany: Lambert Academic Publishing. p 60.
- Brando SI. 2010. Advances in husbandry training in marine mammal careprograms. *Int J Comp Psychol* 23:777–791.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature*, 207(4995), 434-435.
- Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. *The bottlenose dolphin*, 199-234.
- Clegg, I. L., Rödel, H. G., Cellier, M., Vink, D., Michaud, I., Mercera, B., ... & Delfour, F. (2017). Schedule of human-controlled periods structures bottlenose dolphin (*Tursiops truncatus*) behavior in their free-time. *Journal of Comparative Psychology*, 131(3), 214.

- Colpaert, N. Emission Of Signature Whistles By 8 Bottlenose Dolphins (*Tursiops Truncatus*) Under Human Care. Master Thesis. University of Ghent. Belgium.
- Connor, R. C., Wells, R. S., Mann, J. A. N. E. T., & Read, A. J. (2000). The bottlenose dolphin. *Cetacean societies*, 91-125.
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in ecology & evolution*, 13(6), 228-232.
- Cook, M. L., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2004). Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B: Biological Sciences*, 271(1543), 1043.
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella fimmntalis*). *Aquatic Mammals*, 24, 129-142.
- Esch HC, Sayigh LS, Blum JE, Wells RS. 2009b. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *J Mammal* 90:638–650.
- Evans, W. E., & Prescott, J. H. (1962). Observations of the sound production capabilities of the bottlenose porpoise: a study of whistles and clicks. *Zoologica*, 47(11), 121-128.
- Faraway, J. J. (2005). *Linear models with R*. Boca Raton, USA: Chapman & Hall.
- Giraudoux, P. (2016). pgirmess: Data analysis in ecology. R package version 1.6.4. <https://CRAN.R-project.org/package=pgirmess>.
- Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Animal Behaviour*, 76(2), 375-387.

- Good, P. I. (2005). *Permutation, parametric, and bootstrap tests of hypotheses*. New York, USA: Springer.
- Hawkins, E. R., & Gartside, D. F. (2010). Whistle emissions of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) differ with group composition and surface behaviors. *The Journal of the Acoustical Society of America*, 127(4), 2652-2663.
- Heiler, J., Elwen, S. H., Kriesell, H. J., & Gridley, T. (2016). Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition. *Animal behaviour*, 117, 167-177.
- Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: implications for a sound society. In *Hearing by whales and dolphins* (pp. 225-272). Springer New York.
- Herzing, D. L. (2015). 6 Making Sense of It All: Multimodal Dolphin Communication. *Dolphin Communication and Cognition: Past, Present, and Future*, 139.
- Hickey, R., Berrow, S., & Goold, J. (2009, September). Towards a bottlenose dolphin whistle ethogram from the Shannon Estuary, Ireland. In *Biology and Environment: Proceedings of the Royal Irish Academy* (pp. 89-94). Royal Irish Academy.
- Highfill LE, Kuczaj SA, II. 2007. Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquat Mamm* 33:380.
- Janik, V. M., & Slater, P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal behaviour*, 56(4), 829-838.

- Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*, 289(5483), 1355-1357.
- Janik, V. M. (2009). Acoustic communication in delphinids. *Advances in the Study of Behavior*, 40, 123-157.
- Janik, V. M., & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology A*, 199(6), 479-489.
- Janik, V. M., King, S. L., Sayigh, L. S., & Wells, R. S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 29(1), 109-122.
- Jensen, A. L. M., Delfour, F., & Carter, T. (2013). Anticipatory behavior in captive bottlenose dolphins (*Tursiops truncatus*): a preliminary study. *Zoo biology*, 32(4), 436-444.
- King, S. L., Harley, H. E., & Janik, V. M. (2014). The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 96, 79-86.
- Laule GE. 2003. Positive reinforcement training and environmental enrichment: enhancing animal well-being. *J Am Vet Med Assoc* 223: 969–972.
- Laule G, Desmond T. 1998. Positive reinforcement training as an enrichment strategy. In: Sheperdson DH, Mellen JD, Hutchins M. editors. *Second nature: environmental enrichment for captive animals*. Washington, DC, USA: Smithsonian Institute Press. p 302–313.

- López, B. D., & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. *Dolphins: Anatomy, behavior, and threats*, 129-148.
- López, B. D. (2011). Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: influence of behaviour. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 76(2), 180-189.
- Lopez Marulanda, J., Adam, O., & Delfour, F. (2016). Modulation of whistle production related to training sessions in bottlenose dolphins (*Tursiops truncatus*) under human care. *Zoo biology*, 35(6), 495-504.
- Lopez-Marulanda, J., Adam, O., Blanchard, T., Vallée, M., Cazau, D., & Delfour, F. (2017). First Results of an Underwater 360° HD Audio-Video Device for Etho-Acoustical Studies on Bottlenose Dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 43(2), 162.
- Mann, J. (1999). Behavioral sampling methods for cetaceans: a review and critique. *Marine mammal science*, 15(1), 102-122.
- Mann, J. (Ed.). (2000). *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2015).nlme: Linear and Nonlinear Mixed Effects Models.R package version3.1–122. <http://CRAN.R-project.org/package=nlme>.
- R Core Team (2017). *R: A Language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing, www.R-project.org.

- Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, 22(4), 966-978.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26(4), 247-260.
- Sekiguchi, Y., & Kohshima, S. (2003). Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). *Physiology & behavior*, 79(4), 643-653.
- Tamaki, N., Morisaka, T., & Taki, M. (2006). Does body contact contribute towards repairing relationships?: The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioural processes*, 73(2), 209-215.
- Tsai, Y. J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science*, 29(2), 261-279.
- Venables WN, Ripley BD. (2002). *Modern Applied Statistics with S*, 4th edition ed. Berlin: Springer.

Supplementary material

Table A: Time of recording sessions: Before and after 10 training sessions.

Session	Duration (hh:mm:ss)		
	Before	After	Total
1	00:19:04	0	00:19:04
2	00:15:57	00:01:45	00:17:42
3	00:16:21	00:15:54	00:32:15
4	00:15:18	00:02:34	00:17:52
5	00:14:55	00:15:29	00:30:24
6	00:07:42	00:15:19	00:23:01
7	00:15:56	00:03:41	00:19:37
8	00:15:48	00:16:02	00:31:50
9	00:14:04	00:15:40	00:29:44
10	00:15:02	00:12:11	00:27:13
Total	02:30:07	01:38:35	04:08:42

Table B: Comparison of different individual-level behaviors before and after the training sessions (timing: factor with 2 levels), tested by a linear mixed-effects models. *P*-values were calculated by 1000 Monte Carlo permutations. The slope parameters (based on scaled data) of the effects of all independent variables are provided. Significant effects are given in bold.

Dependent variable	Independent variables	Slope (SE)	β	\pm	<i>df</i>	<i>P</i>
Alone swim - slow	Timing	-0.327 0.156		\pm	1	0.051
	Age class (juv)	-0.343 0.210		\pm	1	0.108
	Sex (m)	-0.119 0.216		\pm	1	0.584
Alone swim - fast	Timing	+0.214 0.109		\pm	1	0.055
	Age class (juv)	-0.313 0.677		\pm	1	0.616
	Sex (m)	-0.937 0.677		\pm	1	0.165
Synchronous swim - slow	Timing	-0.159 0.142		\pm	1	0.263
	Age class (juv)	-0.551 0.554		\pm	1	0.274
	Sex (m)	-0.637 0.556		\pm	1	0.219
Synchronous swim - fast	Timing	+0.087± 0.135			1	0.536
	Age class (juv)	-0.025 0.580		\pm	1	0.967
	Sex (m)	+0.747 0.581		\pm	1	0.161
Positive	Timing	-0.214		\pm	1	0.027

social body contacts		0.168		
	Age class (juv)	-0.043 0.244	± 1	0.984
	Sex (m)	-0.121 0.248	± 1	0.433
Anticipatory behavior				
	Timing	-0.071 0.166	± 1	0.695
	Age class (juv)	+0.047 0.272	± 1	0.864
	Sex (m)	+0.374 0.276	± 1	0.153

Table C: Correlations between non -signature whistles recorded at the group level (whistle score) and the occurrence of different individual-level behaviors, tested by a linear mixed-effects models. *P*-values were calculated by 1000 Monte Carlo permutations. Analyses were calculated separately for recordings during a 15-min time window (a) prior to and (b) after training sessions. The slope parameters (based on scaled data) of the effects of all independent variables are provided. Significant effects are given in bold and are shown in Figure 4.

Timing of observation	Dependent variable	Independent variables	Slope (β ± SE)	<i>df</i>	<i>P</i>
(a) Before training	Alone swim - slow	Whistle score	+0.387 ± 0.179	1	0.017
		Age class (juv)	-0.140 ± 0.230	1	0.545
		Sex (m)	+0.070 ± 0.238	1	0.763
	Alone swim - fast	Whistle score	+0.097 ± 0.102	1	0.334
		Age class (juv)	-0.299 ± 0.247	1	0.247
		Sex (m)	-1.019 ± 0.256	1	< 0.001
	Synchronous swim - slow	Whistle score	-0.138 ± 0.141	1	0.374
		Age class (juv)	-0.436 ± 0.266	1	0.107
		Sex (m)	+0.540 ± 0.276	1	0.151
Synchronous swim - fast	Whistle score	-0.076 ± 0.172	1	0.640	
	Age class (juv)	+0.349 ± 0.240	1	0.158	

			Sex (m)	+0.923 0.248	± 1	0.001
		Positive social body contacts	Whistle score	-0.286 0.120	± 1	0.014
			Age class (juv)	+0.447 0.266	± 1	0.098
			Sex (m)	-0.281 0.276	± 1	0.666
		Anticipatory behavior	Whistle score	-0.189 0.150	± 1	0.183
			Age class (juv)	+1.093 0.232	± 1	< 0.001
			Sex (m)	-0.217 0.240	± 1	0.367
(b) training	After	Alone swim - slow	Whistle score	-0.019 0.123	± 1	0.875
			Age class (juv)	-0.499 0.291	± 1	0.101
			Sex (m)	-0.178 0.296	± 1	0.572
		Alone swim - fast	Whistle score	+0.107 0.112	± 1	0.314
			Age class (juv)	-0.390 0.266	± 1	0.160
			Sex (m)	-0.842 0.270	± 1	0.003
		Synchronous swim - slow	Whistle score	-0.106 0.125	± 1	0.382
			Age class (juv)	-0.558 0.282	± 1	0.081
			Sex (m)	+0.671 0.287	± 1	0.053
		Synchronous swim - fast	Whistle score	-0.087 0.128	± 1	0.477

	Age class (juv)	+0.318 0.279	± 1	0.275
	Sex (m)	+0.598 0.284	± 1	0.058
Positive social body contacts	Whistle score	-0.044 0.128	± 1	0.864
	Age class (juv)	-0.075 0.300	± 1	0.961
	Sex (m)	-0.154 0.305	± 1	0.507
Anticipatory behavior	Whistle score	+0.106 0.143	± 1	0.544
	Age class (juv)	-0.494 0.278	± 1	0.086
	Sex (m)	+0.665 0.282	± 1	0.068

Chapter 3: First Results of an Underwater 360° HD Audio-Video Device for Etho-Acoustical Studies on Bottlenose Dolphins (*Tursiops truncatus*)

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Aquatic Mammals, 43(2), 162-176

Synthesis Chapter 3

Context

Studies of dolphin social behavior and communication rely on simultaneous descriptions of both visual and acoustic signals (Thomas et al., 2002). However, the main obstacle associated with completing these descriptions is the difficulty in identifying which dolphin in a group is the vocalizer.

Research questions

An audio-video system (called BaBeL: *Bioacoustique, Bien-être, Langage*) that was non-intrusive and compact enough to be deployed from a small boat was developed. This underwater device includes five hydrophones and a 360° HD video recording system with a limited blind spot that allows localization of sounds to free-swimming, vocalizing dolphins coming from almost every direction. In this article, details about this system's design and the software developed to localize sounds and to link them to individually identified dolphins are provided.

Analysis

Data from a population of bottlenose dolphins were collected during 14 boat surveys along the northwest coast of Reunion Island (France) by following a strict pre-established protocol to standardize data collection. Three audio-video sequences of free-ranging bottlenose dolphins have been analyzed to illustrate the benefits of this system in dolphin ethological and acoustical research.

Results

A total of 21 min of audio-video were recorded when dolphins were present, and 42 click trains and 42 whistles were detected from these data. Dolphins identified as vocalizers were also present for 17% (n = 7) of emitted click trains and 33% (n = 14) of emitted whistles on the videos. When the observers stayed ahead and avoided the direct path of groups of five to nine dolphins, only one animal emitted click trains while swimming towards the observers or after turning its rostrum in the humans' direction, and this dolphin was never the one leading the group.

Conclusion

The BaBeL system offers a method of data collection to conduct an etho-acoustical analysis of bottlenose dolphin sound emissions potentially to be associated with individual dolphins and their underwater behaviors. The BaBeL and the associated software algorithms for data analysis represent an improved tool for ethologists to record and collect data on all dolphins present in a 360° space via focal and group follows.

First Results of an Underwater 360° HD Audio-Video Device for Etho-Acoustical Studies on Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

Bottlenose dolphins (*Tursiops truncatus*) are highly social odontocetes that live in a fission-fusion society and demonstrate production of a varied sound repertoire, including clicks, whistles, and burst-pulsed sounds, as well as a diverse behavioral repertoire. To better understand the species' behavior, it is necessary to compare visual and acoustic observations and link vocalizations to individuals and their specific actions. However, the task of linking sounds to individual dolphins is challenging for human observers because dolphins do not always display specific visual cues when producing a sound, and also because human hearing is not naturally adapted to locate underwater sound sources. To respond to these challenges, a new underwater 360° HD audio-video device, the BaBeL, was designed and built. This device consists of a five-hydrophone array attached to two wide-angle video cameras that together cover a 360° field of vision. Acoustic recordings were analyzed with a customized program to detect and localize sound sources and to identify individual vocalizing dolphins. Data from a population of bottlenose dolphins were collected during 14 boat surveys along the northwest coast of Reunion Island (France) by following a strict pre-established protocol to standardize data collection. A total of 21 min of audio-video were recorded when dolphins were present, and 42 click trains and 42 whistles were detected from these data. Dolphins identified as vocalizers were also present for 17% ($n = 7$) of emitted click trains and 33% ($n = 14$) of emitted whistles on the videos. Therefore, an analysis of three video sequences as examples of the scope of this methodology is

presented. The results show that when the observers stayed ahead and avoided the direct path of groups of five to nine dolphins, only one animal emitted click trains while swimming towards the observers or after turning its rostrum in the humans' direction, and this dolphin was never the one leading the group. The benefits of using this audio-video device for underwater observations of dolphins in clear water with good visibility are discussed.

Key Words: behavior, acoustics, hydrophone array, acoustic localization, bottlenose dolphin, *Tursiops truncatus*

Introduction

Bottlenose dolphins (*Tursiops truncatus*) are highly social odontocetes with a fission-fusion social structure (Connor et al., 2000; Mann et al., 2000; Gibson & Mann, 2008; Tsai & Mann, 2013). Group members may travel very short or very long distances within a habitat of limited visibility (Connor et al., 1998). As such, communication via acoustic signals is the most effective strategy for sharing information under water (Janik, 1999). Bottlenose dolphins display a complex and extensive repertoire of sounds such as clicks or pulsed sounds (Au, 1993; Au & Fay, 2012), burst-pulsed sounds (Lopez & Bernal-Shirai, 2009), and whistles or tonal sounds (reviewed in Janik, 2009).

Dolphin sound production is enriched by non-acoustic communication signals during social interactions when individuals are within visual range of one another. These animals display various body postures (Pryor, 1990), contacts (Sakai et al., 2006; Dudzinski et al., 2009), and bubble

emissions (Marten et al., 1996). Several dolphin vocalizations are associated with behavioral contexts; for example, burst-pulsed sounds (squawks and whines) have been associated with agonistic behaviors (Herzing, 1996), and low-frequency bray calls are related to feeding (Janik, 2000; King & Janik, 2015).

Studies of dolphin social behavior and communication rely on simultaneous descriptions of both visual and acoustic signals (Thomas et al., 2002). However, the main obstacle associated with completing these descriptions is the difficulty in identifying which dolphin in a group is the vocalizer. This challenge is caused by two factors: (1) human hearing is not adapted to localize to sound sources underwater; and (2) dolphins do not show visible, regular signs when emitting sounds, like opening their mouths or displaying external clues (Janik, 2009). To overcome these obstacles, several methodologies have been developed. Animals have been isolated (Caldwell et al., 1990; Sayigh et al., 1990) or tagged (Tyack, 1991; Nowacek et al., 1998); however, these approaches can be considered invasive and might lead to modification of the subjects' behaviors and vocalizations. Emission of bubble streams concurrent with vocalizations has been used to identify a vocal animal because sometimes dolphins emit bubbles while whistling (McCowan & Reiss, 1995; Herzing, 1996); however, whistles with bubble streams are not representative of the entire whistle repertoire of bottlenose dolphins (Fripp, 2005, 2006).

As a non-intrusive method to identify the vocalizing animal, different hydrophone arrays have been designed. These arrays allow for processing of the differences in time of arrival of the sound to each hydrophone to determine where the call originated. The position of the sound source is linked to the video recordings to confirm which animal is in the same position as the sound source, thereby identifying the vocalizer. Fixed arrays using two (López-Rivas & Bazuá-Durán, 2010), three (Watkins & Schevill, 1974), four (Brensing et al., 2001; Quick et al., 2008), and eight (Thomas et al., 2002) hydrophones have been used to link audio recordings to behavioral observations or video recordings; however, fixed arrays are not well adapted to study highly mobile, free-ranging dolphins, and the video recordings were often obtained from a fixed point at the surface. The main problem with acquiring behavioral information from the surface is that the documented behaviors could possibly represent only a very small percentage of an animal's behavioral activity (Janik, 2009). Moreover, an array with two hydrophones (Lopez-Rivas & Bazuá-Durán, 2010) allows data to be obtained only on the angle of arrival and not the real position of the emitting

dolphin. Four hydrophones are needed to localize a moving dolphin in 3D (Watkins & Schevill, 1972; Wahlberg et al., 2001)

Mobile arrays of two (Dudzinski et al., 1995), four (Au & Herzing, 2003; Schotten et al., 2004), and 16 (Ball & Buck, 2005) hydrophones have been used to study dolphin vocalizations and their associated underwater behaviors, but they, too, presented several disadvantages. Dudzinski et al.'s (1995) system did not allow localization in the vertical axis, and the systems with four hydrophones were used only for localization of click emitters (Au & Herzing, 2003; Schotten et al., 2004). The 16-hydrophone array had elements separated by 3.2 cm (Ball & Buck, 2005) but did not allow the confirmation of the emitter's identity if animals were located outside of the narrow angle of the video camera.

As part of this study, an audio-video system that was non-intrusive and compact enough to be deployed from a small boat was developed. This underwater device includes five hydrophones and a 360° HD video recording system with a limited blind spot that allows localization of sounds to free-swimming, vocalizing dolphins coming from almost every direction. In this article, details about this system's design and the software developed to localize to sounds and to link them to individually identified dolphins are provided. Three audio-video sequences of free-ranging bottlenose dolphins have been analyzed to illustrate the benefits of this system in dolphin ethological and acoustical research.

Methods

Recording Device

Simultaneous audio and video recordings were collected using a waterproof audio-video system named BaBeL (BioAcoustique, Bien Être et Langage) (Figure 1). The acoustic set-up was comprised of five calibrated Aquarian H2a-XLR hydrophones connected and synchronized to a ZOOM H6 digital audio recorder. Audio recordings were made at a 96-kHz sampling frequency and coded on 24 bits. The recorder was placed in a waterproof housing rated to 60 m depth. The architectural design of the hydrophone array was a compromise between a large aperture between hydrophones and maneuverability since the system needed to be deployed from small boats with limited space and to be controllable by one observer when submerged. The synchronized hydrophones were positioned to obtain the time delay of arrival to provide the 3D estimations of dolphin positions.

The video portion of the BaBeL system was comprised of two Kodak SP360 video cameras

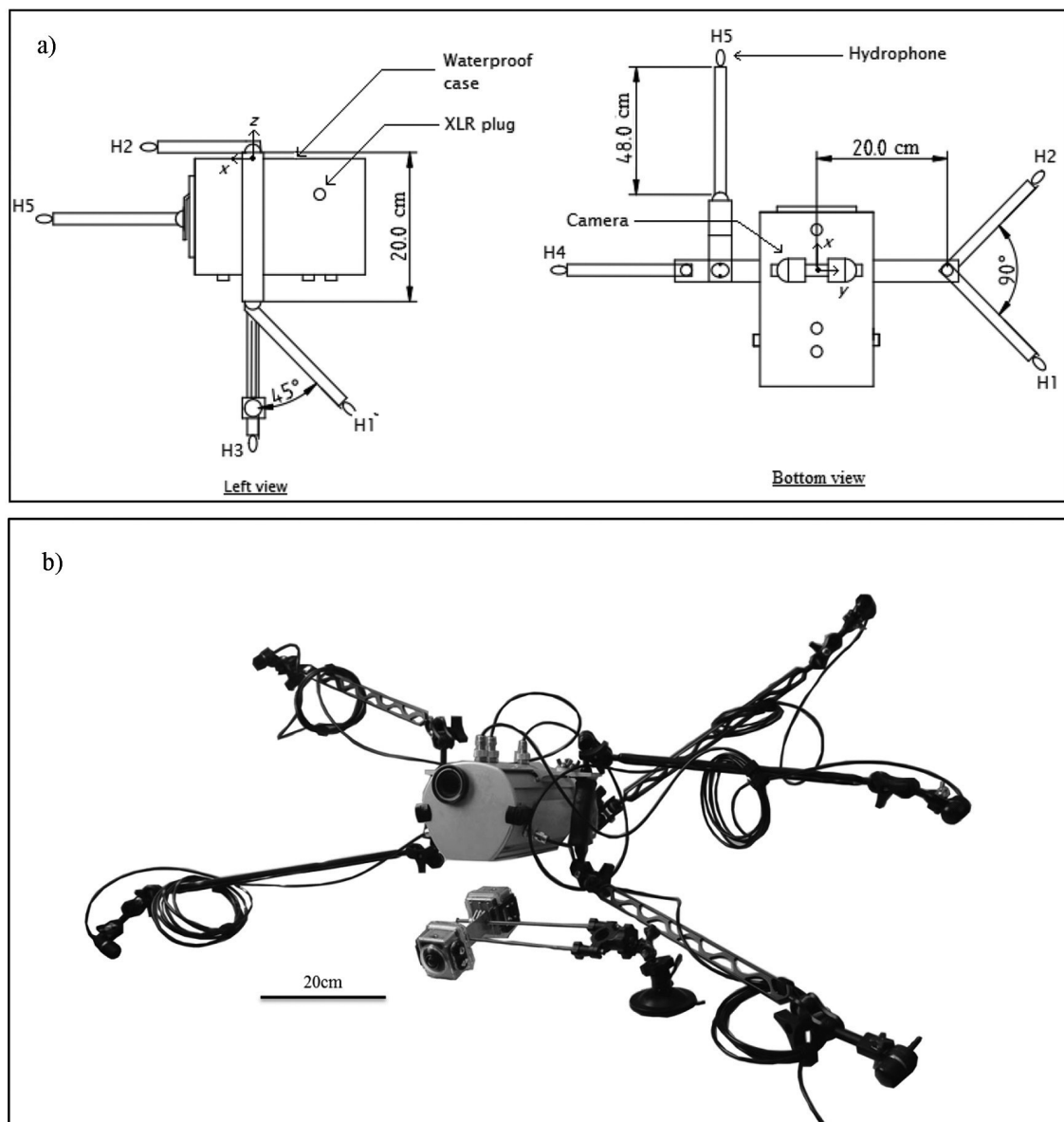


Figure 1. BaBeL (BioAcoustique, Bien Être et Langage) device: (a) Diagram and orientation of hydrophones (H); and (b) picture of the device with 360° cameras unattached—five hydrophones installed on five deployable arms and plugged to a ZOOM H6 (inside the adapted waterproof case).

both with a wide-angle field of view (214°); the cameras were placed opposite of each other to the left and the right to allow for 360° field of vision for the system. These cameras were positioned below the waterproof housing of the acoustic recorder (Figure 2). Video and audio files were stored for *a posteriori* analysis.

Custom-Made Program for Data Analysis

A geometrical localization method was used to estimate the position of an acoustic source. This

method used the spatial distribution of hydrophones, the acoustic properties of the source (e.g., propagation speed and spherical propagation model), and the measure of the time differences of arrival (TDOA) of the acoustic wave from the source to the different hydrophones (Alameda-Pineda & Horaud, 2014). The aim was to estimate the differences in time of arrival of emitted sounds; the cross-correlation function method for whistle detection (Van Lancker, 2001) and the threshold time energy for click detection

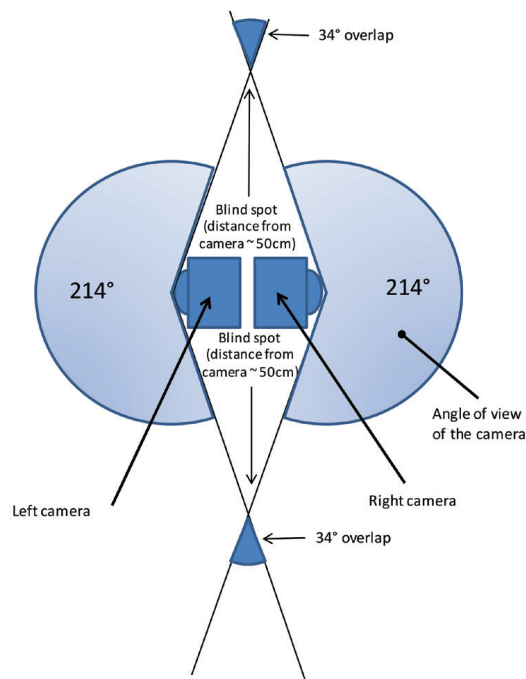


Figure 2. Disposition of two Kodak SP360 video cameras. Each camera has a 360° (N-S-E-W) plus 214° angle of view. As both cameras are placed opposite to each other, there is a 34° overlap in the images and a ≈ 50 -cm blind spot between the cameras.

(Blanchard, 2015) were used. To display the estimated position of the acoustic source in the video image, a conversion position-pixel that took into account the deformations of the image because of the spherical curved lens of the Kodak SP360 video cameras was used. With these considerations, a customized program to analyze data obtained with the BaBeL system was created in *MATLAB*[®], Version 2013a (Mathworks, Natick, MA, USA) to synchronize the video and audio recordings and then to estimate the localization(s) of each vocalizing dolphin (Blanchard, 2015) (Figure 3). After identifying the location of the vocalizing dolphin, video analysis allowed for the identification of the dolphin based on recognizable scars and marks.

Tests with Artificial Sounds

Two simulated whistles to test this approach with different signal-to-noise ratios (SNRs) (Figure 4) were created. The objective of this test was to confirm performance of the time correlation for acoustic signals deteriorated by underwater acoustic propagation or when ambient noise is present in the marine area. To verify our localization method, the system was tested in a 3.1×8.2 m² rectangular freshwater swimming pool. The BaBeL was immersed in the center of the

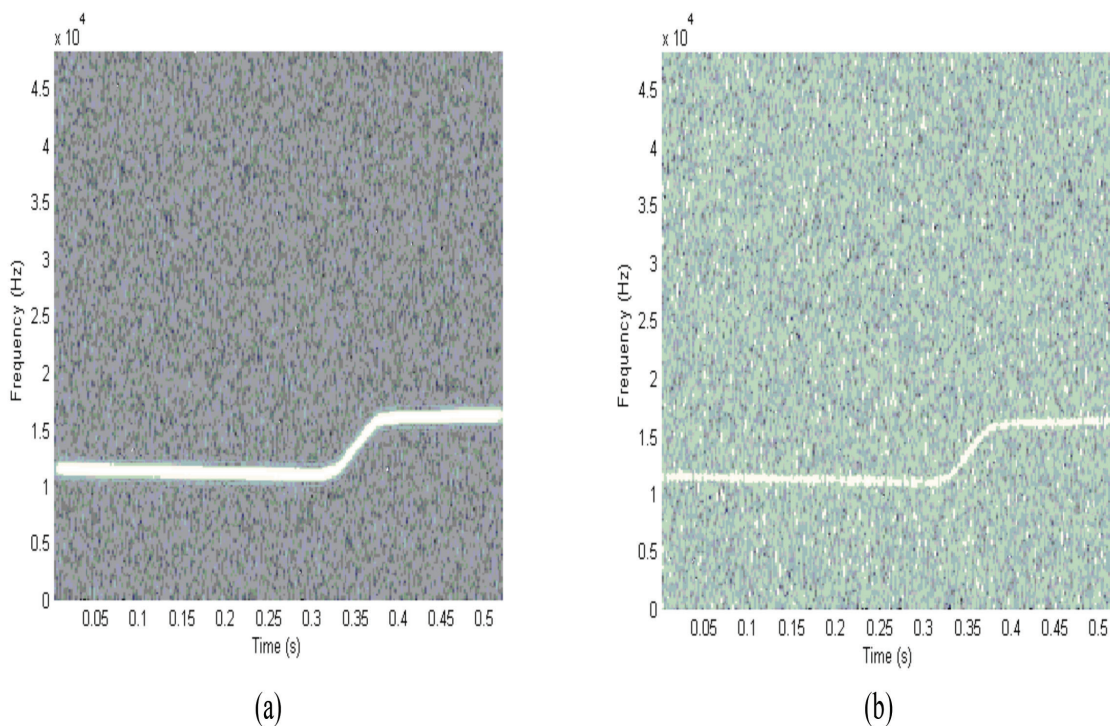


Figure 4. Simulated whistles with two signal-to-noise ratios (SNRs): (a) +20 dB and (b) -10 dB.

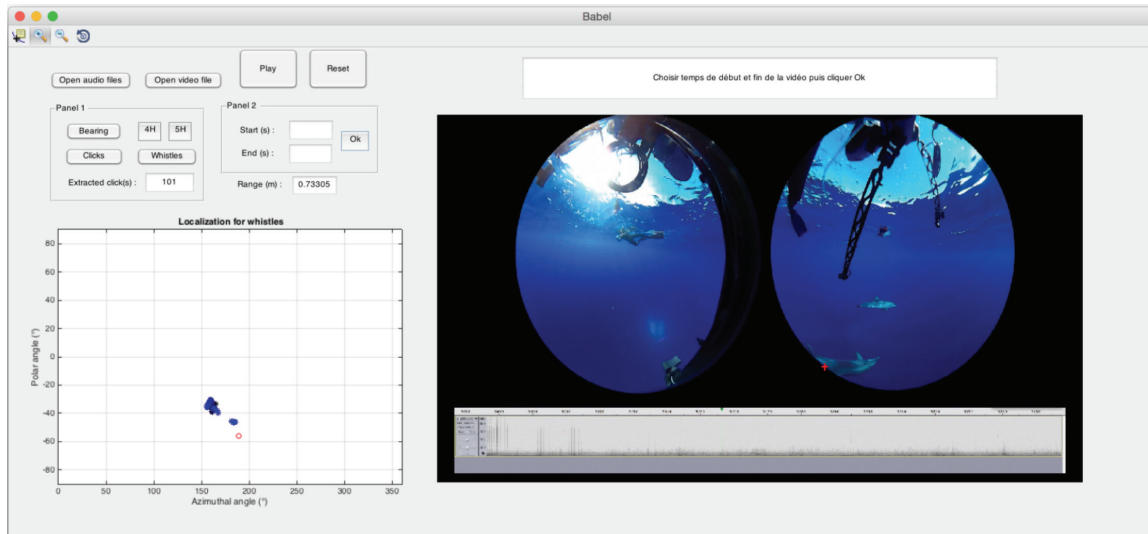


Figure 4. Screen display to track dolphins by videos and passive acoustics. On the bottom left, estimations of the angles from the successive clicks (in blue) and the whistle (in red). On the right, the red cross points to the emitter dolphin.

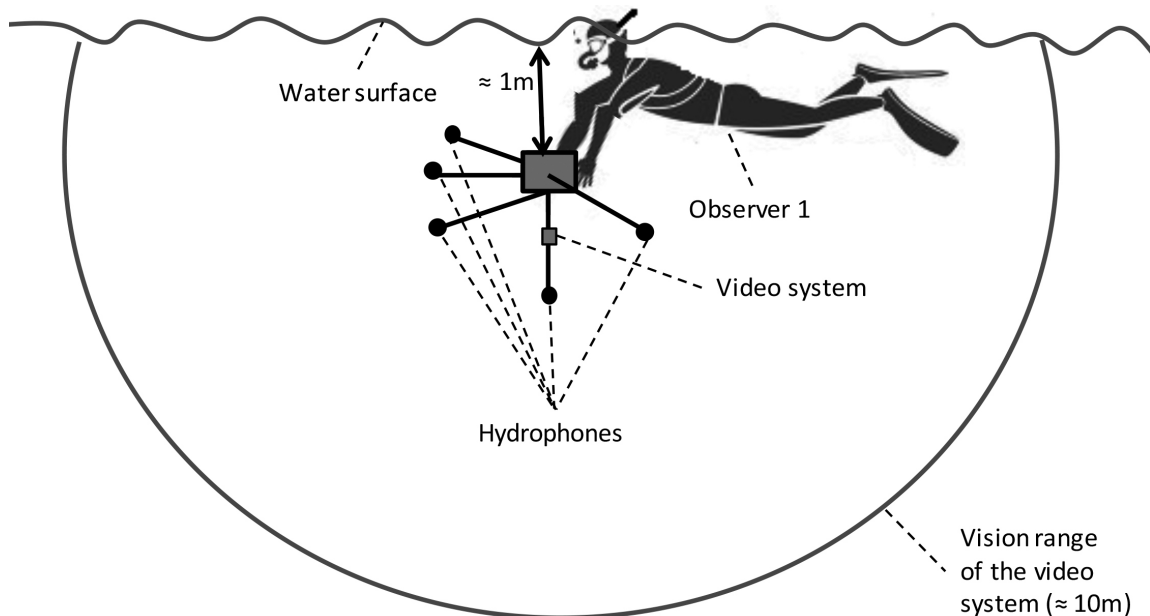


Figure 5. Disposition of BaBeL device in the water; the whole system is controlled by Observer 1. The vision range of the camera depends on water clarity. For the Reunion Island, it is ≈ 10 m. The real scales are not represented in the figure.

pool at 2.5 m from the edge. Percussive sounds were generated by knocking together two steel bars from nine different known places in the horizontal plane of the device's gravity center. Using the position-pixel conversion, the position of each percussive sound source in the video image was estimated and compared to the location estimated by the custom program.

Bottlenose Dolphin Data Collection

Acoustic and video data were collected on free-ranging bottlenose dolphins along the northwest coast off Reunion Island, a French territory in the Mascarene Islands in the Southwest Indian Ocean. The species is observed in this location throughout the year in groups of 10 to 100 individuals (48 individuals on average) and occurs in deeper water

(425.6 m on average) and further offshore (1.2 to 6 km from the coast) than other cetacean species in this area (Dulau-Drouot et al., 2008).

Fourteen boat surveys were conducted from 21–29 May 2015 and from 6–18 June 2015 to search for bottlenose dolphins and collect etho-acoustical data. When a group of dolphins was sighted, a strict pre-established protocol was followed (see *Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area* [ACCOBAMS], Resolution 4.18) to decide if observers would enter the water to start a recording session. First, the boat was positioned parallel to the animals' travel direction at a distance of more than 50 m. The behavioral response of the dolphin group was recorded into one of three categories: (1) "avoidance," (2) "indifference," and (3) "oncoming" (see ACCOBAMS for definitions). If the behavioral response was cataloged as "indifference" or "oncoming," the boat was slowly positioned 100 m ahead of the first animal of the group, never interfering with the travel direction of the animals. Once in this position, two observers slipped into the water.

Procedure in Water—One observer swam with the BaBeL device submerged below the sea surface (≈ 1 m under the surface) (Figure 5), while the other observer recorded the animals on a backup SONY HDR-GW66 video camera. Date and time on all video cameras were synchronized for a *posteriori* analysis. Since BaBeL was being operated for the first time, the intent was to document all the events. The backup video sequences might be used later to confirm what was observed on the BaBeL wide-angle cameras, and the recorded sequences might be replayed to document the BaBeL operator's position and behavior in the water.

At the beginning of the recording session, two successive claps were made—one in front of each camera in order to synchronize both videos with audio recordings during the *a posteriori* analysis. Both observers remained floating at the surface with their bodies oriented perpendicular to the group's travel direction, avoiding the direct path of the dolphins and letting the animals choose at what speed and distance they approached. When dolphins slowly moved along the observers, they swam calmly in parallel with the animals. Depending on whether the dolphins stayed around the observers or departed, recording sessions were repeated several times on the same group by carefully re-orienting the boat and by informing the observers each time the dolphins swam by. A recording session finished when dolphins were not visible for 5 min or when weather conditions prevented continued observations.

Audio-Video Analysis

The claps at the beginning of each recording session were used to manually synchronize acoustic and video data with video editing software (*Final Cut Pro X*, Version 10.1.3®, Apple Inc.). A single video file was created displaying the videos of the two Kodak SP360 video cameras in the same window, as well as one of the five audio tracks and its corresponding turning spectrogram (FFT size: 1,024, overlap 50%, Hanning window) obtained with *Audacity*, Version 2.0.6 (GNU General Public License). We chose only one track in the video as a referent since the five audio tracks were used for our custom-made acoustical analysis in *MATLAB*® (Blanchard, 2015).

The location of the vocalizing dolphin was noted as "visible" when our program was able to point out one of the dolphins in the video, "ambiguous" when the program pointed out two dolphins that were close to each other or in the same direction, and "not visible" when the program pointed to another direction indicating that the emitter dolphin was far outside the range of vision of the video cameras, estimated at further than 10 m away in all directions but also dependent on the wide-angle lens (reduces the size of objects) and water clarity.

To conduct our etho-analysis, the sequences in which we could locate with no doubt at least one vocalizing dolphin were selected (see Appendix 2, Figure 1); a focal-animal sampling technique was used to note occurrence and duration of body postures, tactile contacts, and other behaviors displayed during intraspecific interactions and during interactions towards humans in video sequences (Altmann, 1974; Mann, 1999). Since all sightings were mainly "swim by" wherein the dolphins did not remain near the observers for long, individual dolphins in each sequence were listed in order of appearance in the video. The "all occurrences" recording sampling method focused on frequencies, and durations of occurring behaviors was used (Martin et al., 1993). The analyzed sequences allowed the researchers to create a behavioral catalog (Tinbergen, 1963), which included nonsocial and social (intraspecific and human-dolphin interactions) behaviors and sounds produced (Table 1).

Results

Tests with Artificial Sounds

As this study is dedicated to the analysis of behaviors, only situations when at least one dolphin was visible in the videos, at a distance of less than 10 m, were taken into account. If this dolphin emitted clicks and/or whistles during a period with no underwater noise, then the SNR ratio

Table 1. Behavioral catalog of the dolphins observed while swimming by observers and documented with the BaBeL device

Behaviors	Code	Definition
Pectoral rubbing	PR	The dolphin touches another dolphin.
Synchronized swimming	SyS	Dolphins swim in synchronous manner within one body length of another dolphin, showing parallel movements and body axes.
Swim upside down	SUD	The dolphin swims with its belly turned up.
Swim upside down underneath	SUDU	The dolphin swims with its belly turned up underneath a conspecific.
Side swimming	SS	The dolphin swims with its belly turned to the right or the left next to a conspecific.
Approach	APP	The dolphin approaches the observers by leaving the direction axis of its group.
Swim towards observers	STO	The dolphin swims towards the BaBeL device and the observers.
Turn rostrum	TR	The dolphin turns its rostrum in the direction of an observer.
Leave	L	The dolphin stops swimming towards the observers and starts to move away.
Whistle	W	The dolphin whistles.
Click train	C	The dolphin emits a click train.

Table 2. Accuracy of the time correlation on simulated signals

Simulated signal	Features	SNR = 20 dB	SNR = -10 dB
Whistle #1	Duration: 0.1 s Fundamental: 11 kHz	Δ TDOA = 0	Δ TDOA = 1.8 ms
Whistle #2	Duration: 0.5 s Fundamental frequency 11 kHz switch to 16 kHz at 0.35 s	Δ TDOA = 0	Δ TDOA = 0

was higher than 20 dB. If the dolphin vocalizes further away, SNR decreased and could be negative. We performed our approach for positive and negative SNR (Table 2). The time differences of arrival (TDOAs) were still correctly estimated for SNR larger than -10 dB, which is acceptable for our study because underwater noise was low compared to dolphin sounds. (SNR was always positive in our acoustic recordings.)

Results of the first test comparing estimations of positions in video and audio show that differences in estimation for azimuthal localizations are less than 12° except for in positions 3 and 4 (Table 3). For elevation localizations, the difference is less than 10°, except for in position 8. Positions 3, 4, and 8 can only be seen right on the edge of the image, making estimations more difficult due to image compression. Taking into account that the maximal vision range of the BaBeL is estimated to be 10 m depending on water clarity, a 10° difference in estimations from video and audio means that localization at 10 m from the BaBeL can have a maximum difference of 1.7 m from the position of the source in the video, which is less than

one bottlenose dolphin body length. For distances from the device, the error of the custom program was 1.1 to 3.9 m (Table 3).

Data Description

During 14 boat surveys, dolphins were sighted four times, allowing collection of 21.03 min of 360° HD audio-video data with dolphins present. Recordings allowed the detection of 42 click trains and 42 whistles. The vocalizing dolphin was localized and visible on the video for seven click trains (17%). The vocalizer was not visible for 25 click trains (59%); and for 10 click trains (24%), localization of the vocalizer was ambiguous. For whistles, localization analysis was not possible for five whistles (12%) because of a low SNR ratio. The vocalizing dolphin was visible on the video for 14 whistles (33%), the vocalizer was not visible on the video for 18 whistles (43%), and the localization of the vocalizer was ambiguous for five whistles (12%).

Three recording sessions (24 May at 0937 and 0949 h, and 27 May at 1316 h) were chosen during which it was possible to localize the

Table 3. Localization performance of our custom-made program using the sound produced by two bars of steel during tests in a pool

Position	Position estimated from the videos			Position estimated from the acoustic recordings			Difference in estimation		
	Azimuth (°)	Elevation (°)	Distance (m)	Azimuth (°)	Elevation (°)	Distance (m)	Azimuth (°)	Elevation (°)	Distance (m)
1	33.0	5.3	4.7	21.4	3.4	6.3	11.6	1.9	-1.6
2	5.7	1.2	4.5	6.2	-2.6	0.8	-0.5	3.8	3.7
3	328.8	3.5	4.7	349.6	1.1	0.8	-20.8	2.4	3.9
4	315	3.1	3.3	349.3	-3.1	1.5	-34.3	6.2	1.8
5	8.0	-6.1	3.0	2.9	-7.9	0.8	5.1	1.8	2.2
6	43.6	2.3	3.3	36.3	4.2	1.3	7.3	-1.9	2.0
7	61.6	5.6	2.1	55.4	-2.8	0.7	6.2	8.4	1.4
8	6.8	0.7	1.5	0.6	12.5	0.4	6.2	-11.8	1.1
9	304.4	-0.7	2.1	303.1	-7.7	0.5	1.3	7.0	1.6
						Mean	-2.0	2.0	1.8
						SD	15.2	6.0	1.6

dolphin vocalizing to facilitate completion of detailed analyses of dolphin behavior according to the behavioral catalog (Table 1; see Appendix 1). Results show that the first animal of the group to approach the observers did not produce click trains. A click train was made after an approach and/or movement of the rostrum towards the device: in the first observation, the click train was emitted by the second individual after it turned its rostrum towards the device (see Appendix 1, Figure 1). In the second observation, the click train was emitted by the last individual after it approached the device (see Appendix 1, Figure 2; video available on the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). In the third observation, the click train was emitted by the second individual after it approached the device (see Appendix 1, Figure 3). The same individual produced the four whistles presented in our second sequence; the first whistle was emitted before the approach, and the three others were emitted after leaving. This animal produced no whistles while swimming towards the observers.

Discussion

The results with the BaBeL system are promising for the study of dolphin behavior. Its accuracy using simulated underwater sounds in a pool was validated. The BaBeL design during field testing was verified: the device achieved

neutral buoyancy, maneuverability, and simplicity of deployment simultaneously. The BaBeL is relatively easy to deploy from small boats to record behavior and acoustic data on free-ranging dolphins and can also be used with delphinids under human care. Contrary to other hydrophone arrays, the BaBeL system can be used to detect, locate, and track dolphins emitting sounds in a 3D space. The hydrophone arrays of Au & Herzing (2003), Schotten et al. (2004), and Ball & Buck (2005) all present hydrophones in the same plane, making it impossible to discriminate from the audio recording if the emitter dolphin was in front of or behind the device. The design of our system places hydrophones in different planes, allowing us to determine the position of the vocalizing dolphin regardless of its direction of approach to the observers, and the wide-angle HD 360° video cameras provide information to localize to an identified vocalizing dolphin visually. When animals are in the visual range of the camera, this 360° audio-video system could greatly increase the number of vocalizations that can be attributed to an individual dolphin.

Simultaneous visual and acoustic recordings are necessary for localizing to a vocalizing dolphin. This system is mainly limited by visual detection, which depends not only on water clarity but also on the wide-angle video cameras. Wide-angle lenses affect the perspective by exaggerating the distance between objects. They make subjects at moderate and far distances seem further away than they really are. Consequently, only

dolphins vocalizing near BaBeL (within 10 m) were visually and acoustically detected. As previously demonstrated by Watkins & Shevill (1974), the accuracy of this acoustic localization system should decrease as the distance of dolphins from the device increases. To improve accuracy, the distance between the hydrophones can be increased, but this would reduce system maneuverability. Therefore, it is recommended that this device only be used in clear water and preferably with dolphin populations habituated to the presence of human swimmers, or with dolphins under human care.

The five possible situations that observers might encounter while using BaBeL are summarized in Appendix 2. Contrary to using a regular camera, an observer using such a 360° video system increases the possibility of capturing ongoing behaviors regardless of his position with respect to the animals and his concentration level, thus reducing human error. In 59% of the detected click trains and in 43% of detected whistles, this device could acoustically and visually detect dolphins, but the customized program did not point to one of the dolphins present on the video, meaning that the dolphin emitting the sound was out of our range or vision. Therefore, in these cases, assigning the recorded sound to any of the dolphins present on the video would have been a mistake, demonstrating the necessity of the use of hydrophone arrays to aid in interpreting dolphins' vocal behavior location to avoid erroneous assumptions about the identity of the vocalizer. When dolphins were detected visually and acoustically, and the customized program pointed to one individual dolphin present in the video, it was found that the echolocating dolphin was never the first one of the group. Moreover, in one case, it was found that one dolphin emitted a click train while its conspecific swimming behind turned its head to observers. This particular dolphin might have been eavesdropping on the returning echoes of its echolocating conspecific (Gregg et al., 2007). Finally, echolocating dolphins swam dorsal side up or ventral side up, suggesting that the animals use different body postures while producing acoustic signals. Further investigations of the body postures dolphins display while vocalizing would enable better understanding of their sound production and their communication system.

The BaBeL system offers a method of data collection to conduct an etho-acoustical analysis of bottlenose dolphin sound emissions potentially to be associated with individual dolphins and their underwater behaviors. The BaBeL and the associated software algorithms for data analysis represent an improved tool for ethologists to record and collect data on all dolphins present in a 360° space via focal and group follows.

Acknowledgments

FD's contribution was partially funded by Focused on Nature. Parc Asterix funded previous preliminary fieldwork of FD and JLM and funded TB's work. Materials and fieldwork were financed by the CERECAR project from Abyss Foundation (La Réunion, France). We are very grateful to the Parc Asterix Dolphinarium curator, Birgitta Mercera, and her trainers for their help in testing previous versions of our device within their group of dolphins. We would like to thank Abyss Foundation volunteers and Emmanuel Antongiorgi for their support in collecting data, and Isabelle Charrier and the Bioacoustic Communication Team of NeuroPSI for her constructive comments during the development of this work. We thank Isabella Clegg for revising the English of this manuscript. Finally, we would like to give special thanks to editor Dr. Kathleen Dudzinski for her advice and encouragement to improve this manuscript.

Literature Cited

- Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS), Resolution 4.18. (n.d.). *Guidelines on the granting of exceptions to Article II, paragraph 1, for the purpose of non-lethal in situ research in the agreement area*. Retrieved from www.accobams.org
- Alameda-Pineda, X., & Horaud, R. (2014). A geometric approach to sound source localization from time-delay estimates. *IEEE/ACM Transactions on Audio, Speech, and Language Processing*, 22(6), 1082-1095. <https://doi.org/10.1109/TASLP.2014.2317989>
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227-265. <https://doi.org/10.1163/156853974X00534>
- Au, W. W. L. (1993). *The sonar of dolphins*. New York: Springer-Verlag. <https://doi.org/10.1007/978-1-4612-4356-4>
- Au, W. W. L., & Fay, R. R. (Eds.). (2012). *Hearing by whales and dolphins* (Vol. 12). New York: Springer Science & Business Media.
- Au, W. W. L., & Herzing, D. L. (2003). Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*). *The Journal of the Acoustical Society of America*, 113(1), 598-604. <https://doi.org/10.1121/1.1518980>
- Ball, K. R., & Buck, J. R. (2005). A beamforming video recorder for integrated observations of dolphin behavior and vocalizations. *The Journal of the Acoustical Society of America*, 117(3, Pt 1), 1005-1008. <https://doi.org/10.1121/1.1831284>
- Blanchard, T. (2015). *Innovation audio-visuel pour le suivi des grands dauphins* [Audio-visual innovation for monitoring bottlenose dolphins] (Master's thesis). Ecole

- Nationale Supérieure d'Ingenieurs du Mans, Le Mans, France.
- Brensing, K., Linke, K., & Todt, D. (2001). Sound source location by difference of phase, on a hydrophone array with small dimensions. *The Journal of the Acoustical Society of America*, *109*(1), 430-433. <https://doi.org/10.1121/1.1333421>
- Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin: Recent progress in research* (pp. 199-234). San Diego: Academic Press.
- Connor, R. C., Mann, J., & Watson-Capps, J. (2006). A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, *112*(7), 631-638. <https://doi.org/10.1111/j.1439-0310.2006.01203.x>
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology and Evolution*, *13*(6), 228-232. [https://doi.org/10.1016/S0169-5347\(98\)01326-3](https://doi.org/10.1016/S0169-5347(98)01326-3)
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91-126). Chicago: University of Chicago Press.
- Dulau-Drouot, V., Boucaud, V., & Rota, B. (2008). Cetacean diversity off La Réunion Island (France). *Journal of the Marine Biological Association of the United Kingdom*, *88*(6), 1263-1272. <https://doi.org/10.1017/S0025315408001069>
- Dudzinski, K. A., Clark, C. W., & Würsig, B. (1995). A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals*, *21*(3), 187-194.
- Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj II, S. A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioural Processes*, *80*(2), 182-190. <https://doi.org/10.1016/j.beproc.2008.11.011>
- Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *29*(3), E203-E225. <https://doi.org/10.1111/j.1748-7692.2012.00609.x>
- Fripp, D. (2005). Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, *21*, 29-44. <https://doi.org/10.1111/j.1748-7692.2005.tb01206.x>
- Fripp, D. (2006). Bubblestream whistles are not representative of bottlenose dolphin whistle repertoires reply to McCowan. *Marine Mammal Science*, *22*, 496-501. <https://doi.org/10.1111/j.1748-7692.2006.00028.x>
- Gibson, Q. A., & Mann, J. (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother-calf groups in Shark Bay, Australia. *Animal Behaviour*, *76*, 389-405. <https://doi.org/10.1016/j.anbehav.2008.01.022>
- Gregg, J. D., Dudzinski, K. M., & Smith, H. V. (2007). Do dolphins eavesdrop on the echolocation signals of conspecifics? *International Journal of Comparative Psychology*, *20*(1), 65-88.
- Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, *22*(2), 61-79.
- Janik, V. M. (1999). Origins and implications of vocal learning in bottlenose dolphins. In H. O. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 308-326). Cambridge, UK: Cambridge University Press.
- Janik, V. M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B: Biological Sciences*, *267*(1446), 923-927. <https://doi.org/10.1098/rspb.2000.1091>
- Janik, V. M. (2009). Acoustic communication in delphinids. In M. Naguib & V. M. Janik (Eds.), *Advances in the study of behavior* (1st ed., Vol. 40, pp. 123-157). New York: Academic Press. [https://doi.org/10.1016/S0065-3454\(09\)40004-4](https://doi.org/10.1016/S0065-3454(09)40004-4)
- King, S. L., & Janik, V. M. (2015). Come dine with me: Food-associated social signaling in wild bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *18*(4), 969-974. <https://doi.org/10.1007/s10071-015-0851-7>
- López, B. D., & Bernal-Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. In *Dolphins: Anatomy, behavior, and threats* (pp. 129-148). New York: Nova Science Publishers, Inc.
- López-Rivas, R. M., & Bazúa-Durán, C. (2010). Who is whistling? Localizing and identifying phonating dolphins in captivity. *Applied Acoustics*, *71*(11), 1057-1062. <https://doi.org/10.1016/j.apacoust.2010.05.006>
- Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, *15*(1), 102-122. <https://doi.org/10.1111/j.1748-7692.1999.tb00784.x>
- Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*, 210-219. <https://doi.org/10.1093/beheco/11.2.210>
- Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996). Ring bubbles of dolphins. *Scientific American*, *275*(2), 82-87. <https://doi.org/10.1038/scientificamerican0896-82>
- Martin, P., Bateson, P. P. G., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/cbo9781139168342>
- McCowan, B., & Reiss, D. (1995). Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): Wide-band, low-frequency signals during mother/aunt-infant interactions. *Zoo Biology*, *14*(4), 293-309. <https://doi.org/10.1002/zoo.14301404022>

- Nowacek, D. P., Tyack, P. L., Wells, R. S., & Johnson, M. P. (1998). An onboard acoustic data logger to record biosonar of free-ranging bottlenose dolphins. *The Journal of the Acoustical Society of America*, 103(5), 2908. <https://doi.org/10.1121/1.422063>
- Pryor, K. W. (1990). Non-acoustic communication in small cetaceans: Glimpse, touch, position, gesture, and bubbles. In J. A. Thomas & R. A. Kastelein (Eds.), *Sensory abilities of cetaceans* (pp. 537-544). New York: Springer. https://doi.org/10.1007/978-1-4899-0858-2_37
- Quick, N. J., Rendell, L. E., & Janik, V. M. (2008). A mobile acoustic localization system for the study of free-ranging dolphins during focal follows. *Marine Mammal Science*, 24(4), 979-989. <https://doi.org/10.1111/j.1748-7692.2008.00231.x>
- Sakai, M., Hishii, T., Takeda, S., & Konshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, 22(4), 966-978. <https://doi.org/10.1111/j.1748-7692.2006.00082.x>
- Sakai, M., Morisaka, T., Kogi, K., Hishii, T., & Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes*, 83(1), 48-53. <https://doi.org/10.1016/j.beproc.2009.10.001>
- Sayigh, L., Tyack, P., Wells, R., & Scott, M. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26(4), 247-260. <https://doi.org/10.1007/BF00178318>
- Schotten, M., Au, W. W. L., Lammers, M. O., & Aubauer, R. (2004). Echolocation recordings and localization of wild spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*S. attenuata*) using a four-hydrophone array. In J. A. Thomas, C. F. Moss, & M. Vater (Eds.), *Echolocation in bats and dolphins* (pp. 393-399). Chicago: The University of Chicago Press.
- Thomas, R. E., Fristrup, K. M., & Tyack, P. L. (2002). Linking the sounds of dolphins to their locations and behavior using video and multichannel acoustic recordings. *The Journal of the Acoustical Society of America*, 112(4), 1692-1701. <https://doi.org/10.1121/1.1494805>
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410-433. <https://doi.org/10.1111/j.1439-0310.1963.tb01161.x>
- Tsai, Y.-J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science*, 29(2), 261-279. <https://doi.org/10.1111/j.1748-7692.2011.00559.x>
- Tyack, P. L. (1991). Use of a telemetry device to identify which dolphin produces a sound. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies* (pp. 319-344). Berkeley: University of California Press.
- Van Lancker, E. (2002). *Acoustic goniometry: A spatio-temporal approach* (Doctoral dissertation). Faculté Polytechnique de Mons.
- Wahlberg, M., Mohl, B., & Madsen, P. (2001). Estimating source position accuracy of a large aperture hydrophone array for bioacoustics. *The Journal of the Acoustical Society of America*, 109, 397-406. <https://doi.org/10.1121/1.1329619>
- Watkins, W. A., & Schevill, W. (1972). Sound source location with a three-dimensional hydrophone array. *Deep-Sea Research*, 19, 691-706. [https://doi.org/10.1016/0011-7471\(72\)90061-7](https://doi.org/10.1016/0011-7471(72)90061-7)
- Watkins, W. A., & Schevill, W. E. (1974). Listening to Hawaiian spinner porpoises, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *Journal of Mammalogy*, 55(2), 319-328. <https://doi.org/10.2307/1379001>

Appendix 1

Etho-Acoustical Description

First Observation—In this sequence (34 s), we analyzed the behaviors of nine adult dolphins (Ind1 to Ind9) and one calf (Ind10) (Figure 1). The first dolphin (Ind1) approached and swam towards the BaBeL for 15 s; and at 7 and 9 s, Ind1 turned its rostrum towards the BaBeL and continued swimming towards the observers for 6 s more before leaving. Ind2 approached and swam towards the device for 11 s before leaving, emitting a click train at 4 s. Ind3 swam by the device. Ind4 swam upside down underneath Ind5 for 15 s then moved to a synchronized swimming position above Ind 5. Ind5 swam synchronously for 14 s above Ind4 and then moved to a side swimming posture for 1 s before returning to synchronized swimming below Ind4. Ind6 swam synchronously below Ind7 for 14 s; at 11 s, Ind6 turned its head to observers and continued swimming synchronously below Ind7. At 19 s, Ind6 swam upside down underneath Ind7; at 20 s, Ind6 conducted pectoral fin-to-pectoral fin rubbing to Ind7 for 7 s. At 27 s, Ind6 continued swimming synchronously below Ind7, and Ind7 swam synchronously with Ind6 and touched Ind6 with its pectoral fin on two occasions for 2 s at 14 s on the body and then for 1 s at 26 s on the belly. At 27 s, Ind6 and Ind7 stopped body contact and started synchronized swimming next to each other. Ind8 swam by the observers. Finally, Ind9 and Ind10 swam synchronously by the BaBeL next to each other.

Second Observation—In the second sequence (40 s), five adult dolphins passed in front of the BaBeL system. The first and second dolphin (Ind1 and Ind2) approached synchronously. Ind1 swam towards the observers for 4 s, pointed its rostrum towards the recording system with no sound being detected, and left. Ind2 also swam towards the observers for 5 s, pointed its rostrum towards the observers with no sound being detected, and left. Following behind the first two dolphins, Ind3 whistled, swam towards the observers for 2 s, and left. After leaving, Ind3 emitted three more

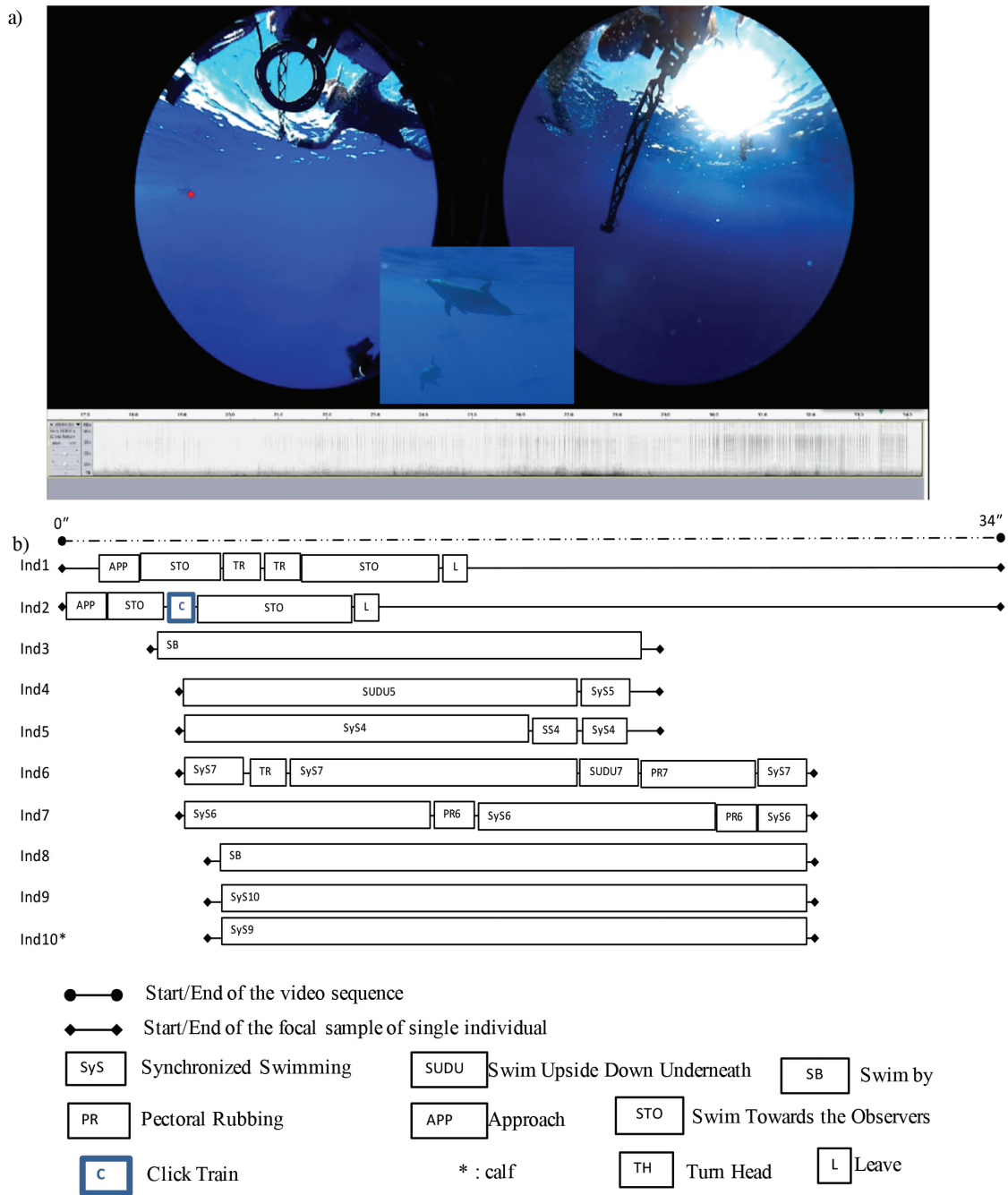


Figure 1. First observation: (a) Screenshot of the location of the clicking dolphin (Ind2) in 360° video and backup video with the red cross pointing to the source of the sound emission; and (b) timelines for ten individuals.

whistles before disappearing out of the range of vision of the video system. Ind4 swam by the BaBeL, while Ind5 approached and swam towards the observers for 4 s, emitted a click train, and continued swimming towards the observers for 5 s before leaving (Figure 2).

Third Observation—In this 22 s sequence, six adult dolphins passed from left to right in front of the BaBeL (Figure 8). Ind1 swam less than 50 cm distance above Ind2. Ind2 swam upside down underneath Ind1 for 16 s; at 3 s, Ind2 turned its rostrum towards the observers and, at 8 s, emitted

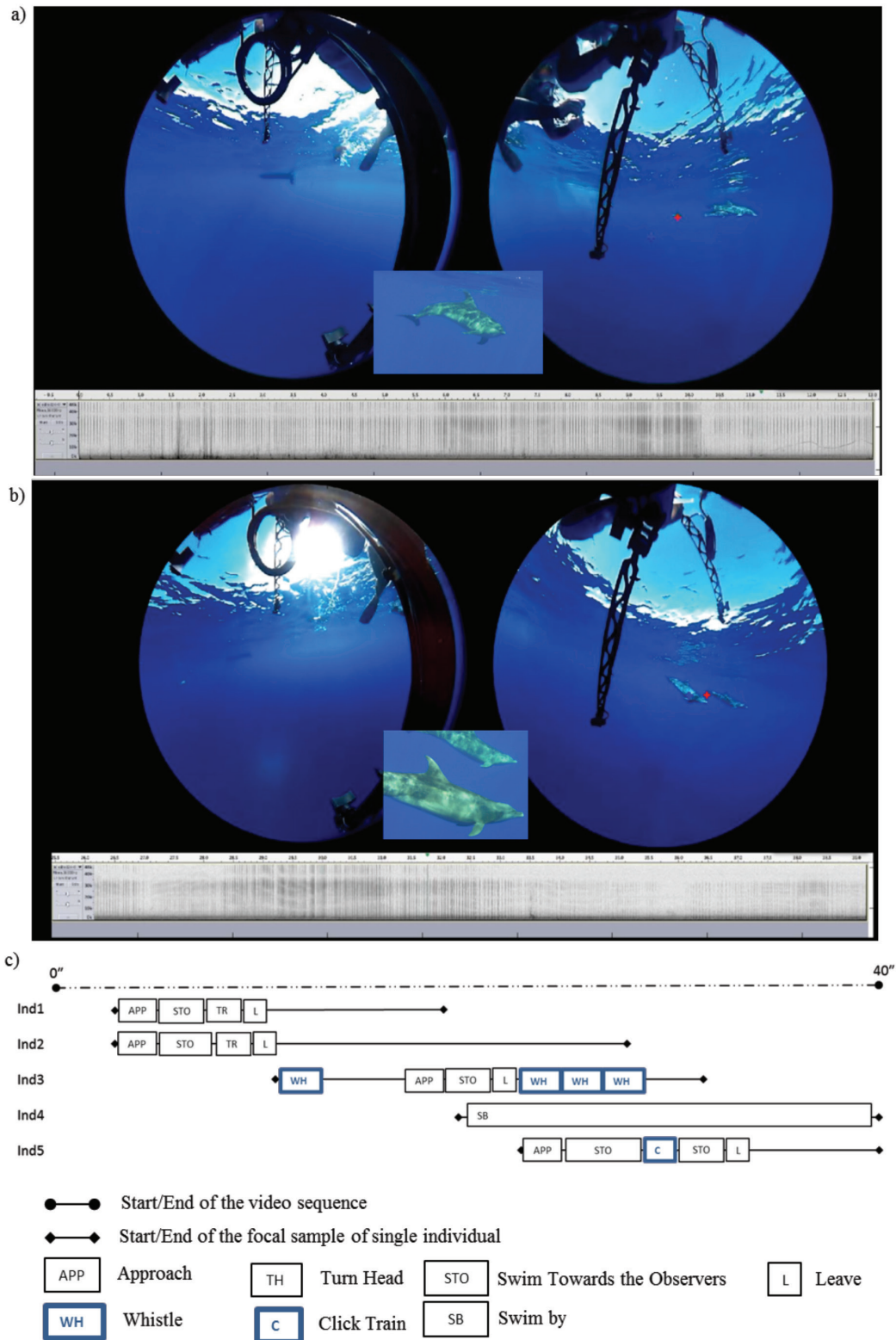


Figure 2. *Second observation:* (a) Screenshot of the location of the whistling dolphin (Ind3) in 360° video and backup video with the red cross pointing to the source of the sound emission; (b) screenshot of the location of the clicking dolphin (Ind5) in 360° video and backup video; and (c) timelines for five individuals (Ind1 to Ind5).

a click train. At 11 s, Ind2 rubbed Ind1’s belly with its pectoral fin for 8 s. At 19 s, Ind2 stopped its contact with Ind1 and swam synchronously above it until the end of the sequence.

Ind3 swam by the BaBel, and Ind4 synchronously swam next to Ind5 and Ind6. Ind5 swam

upside down underneath Ind4 for 4 s and then continued swimming synchronously with Ind4. Ind4 pectoral fin rubbed Ind5’s belly for 1 s at 3 s and then continued swimming synchronously with Ind5 and Ind6 (Figure 3).

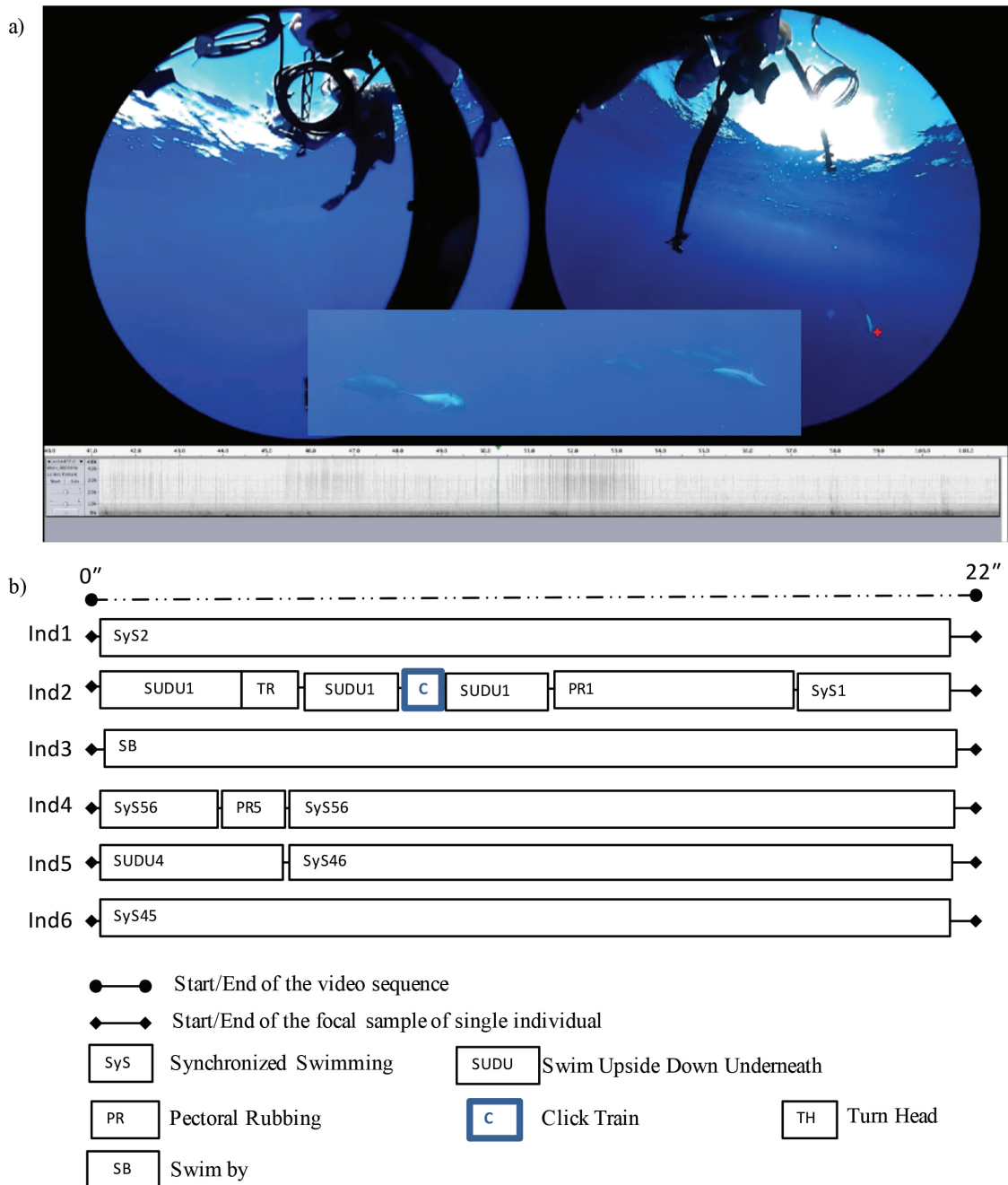


Figure 3. *Third observation:* (a) Screenshot of the location of the clicking dolphin (Ind3) in 360° video and backup video with the red cross pointing to the source of the sound emission; and (b) timelines for six individuals.

Appendix 2

The five possible situations observers could encounter while operating the BaBeL.

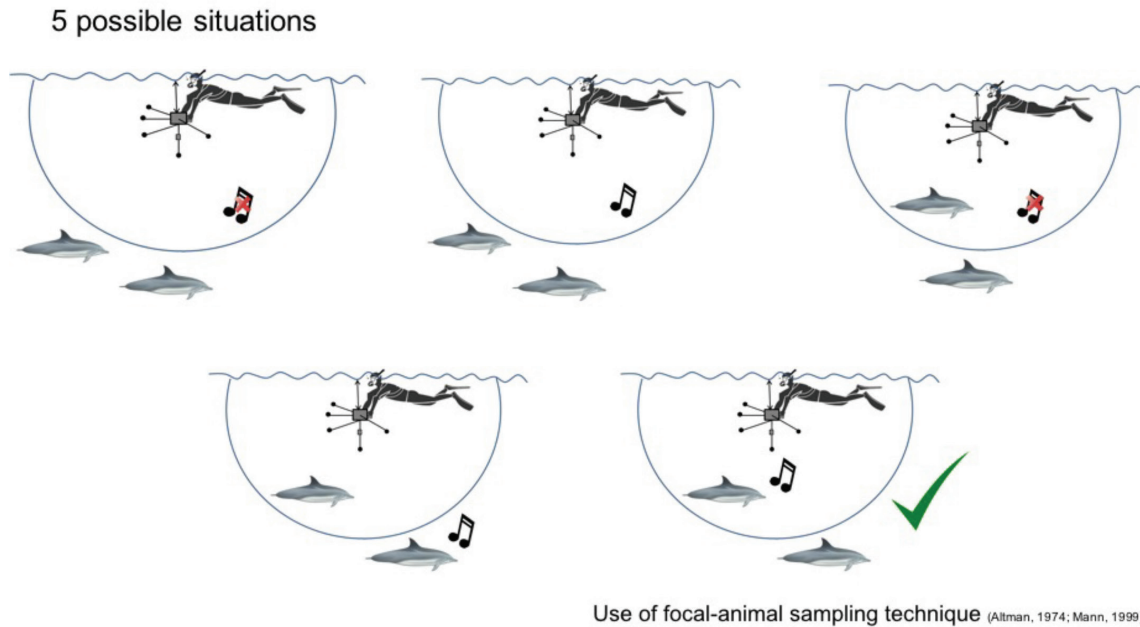


Figure 1. Use of focal-animal sampling technique. *Top left:* No sound detected and dolphins out of the camera's visual range; *Top middle:* Sound detected but dolphins out of the camera's visual range; *Top right:* No sound detected but dolphins in the visual range of the camera; *Bottom left:* Dolphin in the visual range of the camera and sound detected, but the dolphin vocalizing is not present in the video; and *Bottom right:* Dolphin in the visual range of the camera, with the sound detected and the vocalizing dolphin present in the video.

Chapter 4: Description Of a Bottlenose Dolphin Calf's Acoustic And Visual Exploratory Behaviour Towards A Non-Alimentary Complex Object

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Submitted to International Journal of Comparative Psychology

Synthesis Chapter 4

Context

Exploratory behavior includes all the actions that an animal performs to obtain information about a new object, environment or individual through using its different senses of perception. Bottlenose dolphins explore their environment through visual perception and through echolocation. They develop their ability to echolocate in the first to three months of life. Individual of the species have shown to have a visual lateralization when exploring a new object.

Research questions

The birth of a dolphin offers a great opportunity to study how the exploratory behaviour regarding an immersed object evolves in the calf. In this study, we focused on the development of the exploratory behavior of a calf aged from 39 to 169 days, by measuring its acoustic productions and visual laterality when investigating an immersed complex object.

Analysis

Simultaneous audio and video recordings were collected using a waterproof 360° audio-video system named BaBeL that allows localization of the dolphin that is producing sounds. During 6 hours 55 minutes of audio-video recordings, 46 click trains were attached to an individual dolphin: 18 times to the calf, 11 times to its mother and 17 times to another dolphin in the pool. The acoustic parameters of the click trains were measured and compared between the calf and its mother. The visual and spatial laterality were tested.

Results

The calf's click train acoustic parameters did not differ significantly from its mother. However, the calf showed an augmentation of click rate with age and a decrease in ICI. During click train emission and when accompanied, the calf used mostly its right eye. The two situations when the calf used its left eye coincided with the emission of click trains while the calf was swimming alone. The accompanying dolphin was mostly placed to the right of the calf.

Conclusion

At the age of 39 days, a bottlenose dolphins' calf's acoustic parameters regarding its click trains did not differ from that of an adult. However, click rate was shown to increase with age of the calf. When visually and acoustically exploring an immersed non-alimentary object, the calf showed a right eye preference. This study used a new methodology that allowed us to describe not only the acoustic parameters of the subjects' click trains but also the position of the calf during exploratory behavior with respect to the object explored and to its conspecifics.

ABSTRACT

Exploratory behaviour includes all the actions that an animal performs to obtain information about a new object, environment or individual through using its different senses of perception. Here, we studied the development of the exploratory behaviour of a bottlenose dolphin (*Tursiops truncatus*) calf aged from 39 to 169 days, by investigating its acoustic productions and visual laterality in relation to an immersed object. The study was conducted between July 2015 and January 2016 at Parc Asterix dolphinarium (Plailly, France). Simultaneous audio and video recordings were collected using a waterproof 360° audio-video system named BaBeL that allows localization of the dolphin that is producing sounds. During 6 hours 55 minutes of audio-video recordings, 46 click trains were attached to an individual dolphin: 18 times to the calf, 11 times to its mother and 17 times to another dolphin in the pool. No significant differences were found when comparing the calf's click rate; mean click duration and mean interclick interval (ICI) with these parameters from its mother. However, linear regression showed that calf's click rate increased with age, mean ICI decreased with age. In 11 situations the calf produced a click train while being accompanied and in 7 situations the click train was emitted while it was swimming alone. Visual lateralization analysis showed the calf's preference for the use of its right eye (binomial test, $p = 0,007$) while echolocating. The accompanying dolphin was mostly placed at the right of the calf. This is the first study that simultaneously describes the acoustic parameters and exploratory behaviour of a calf within its social group.

Key words: echolocation, laterality, *Tursiops truncatus*, hydrophone array, ontogenesis

INTRODUCTION

Exploratory behaviour includes the actions that an animal performs to obtain information about a new object, environment or individual by using its different senses of perception (Keller *et al.* 2012). Exploratory behaviour is differentiated into extrinsic and intrinsic exploration (Berlyne 1960): extrinsic exploration is a behaviour primarily directed towards an external goal in response to some specific requirement, and intrinsic exploration, named also “novelty seeking” (McReynolds 1962), “reactive curiosity” (Penney and McCann 1964) or “stimulus seeking” (Hoyenga and Hoyenga, 1984) facilitates investigation of a stimulus mainly in response to an interest in the stimulus itself (Berlyne 1960). Intrinsic exploration has been studied in a diverse number of species. For example, in captive jackdaws (*Corvus monedula*), social structure (Katzir 1982) and heritage (Dingemans *et al.* 2002) modulate the individuals’ novelty seeking behaviour. In mammals, intrinsic exploration has been mostly studied in rodents (reviewed in Belzung 1999) and primates (Rubenstein 1967; Miller *et al.* 1986; Parker *et al.* 2007), and its development in captive species has been shown to depend on multiple factors, including sex (Lynn and Brown 2009), environmental enrichment (Zimmermann *et al.* 2001) and maternal care (Rubenstein 1967).

For marine mammals, exploratory behaviour has been little studied. Under human care, environmental enrichment was found to promote exploratory behaviour in harbour seals (*Phoca vitulina concolor*), gray seals (*Halichoerus grypus*) (Hunter *et al.*, 2002) and bottlenose dolphins (*Tursiops truncatus*), with some inter-individual variation seen in relation to their different personalities (Kuczaj *et al.*, 2006; Birgersson *et al.*, 2014), the type of introduced objects (Delfour and Beyer 2012; Delfour, Faulkner and Carter, in press), as well as the sex and/or age of the

individuals (Eskelinen *et al.* 2015). In wild Delphinids, this behaviour has been reported in rough-toothed dolphins (*Steno bredanensis*) (Kuczaj and Yeater 2007). The study of exploratory behaviour in bottlenose dolphins is of particular interest for two principal reasons. Firstly, these cetaceans are social mammals living in a fission-fusion social structure (Connor 2000; Mann *et al.* 2000) that could influence the development of exploratory behaviours (Katzir 1982). Secondly, bottlenose dolphins explore their environment through visual perception (Pack and Herman, 1996) and through echolocation by projecting clicks in order to obtain a sense of their surrounding from the echoes they receive (Au, 1993). Bottlenose dolphins' clicks are directional, forward-projecting, brief pulsed sounds of high intensity and broadband (Richardson *et al.* 1995). They use clicks as a sensory tool to navigate or hunt for prey (reviewed in Herzing and dos Santos 2004) and obtain information from their own returning signals (Au, 1993) and by eavesdropping on the echoes produced by another dolphin (Xitco and Roitblat 1996; Gregg *et al.*, 2007). The ontogenesis of bottlenose dolphins' echolocation has been described elsewhere: these cetaceans develop their ability to echolocate in the first to three months of life (reviewed in Harder *et al.*, 2016). Before they are one month old, calves' clicks are of shorter duration (Reiss 1988) and lower frequency (Reiss 1988; Lindhard 1988) than adults. Additionally, at 14 days old, calves' sequences of clicks (click trains) have a shorter inter click intervals (ICI) and shorter duration (Favaro *et al.* 2013) than adults. Bottlenose dolphins integrate echoic and visual information to perceive their environment (Harley *et al.* 1996). The visual exploration in dolphins is conducted mostly with one eye at a time, although they do use two eyes simultaneously when their heads are out of water or when they swim upside down, in which case the direction of view is naso-ventral (Dral. 1972). These mammals have been shown to

have visual lateralizations; the right eye is mostly used in daily activities (Yaman *et al.* 2002) and performs better in spatial and visual discrimination tasks than the left eye (Kilian *et al.* 2000; Yaman *et al.* 2002; Delfour and Marten 2006).

The birth of a dolphin offers a great opportunity to study how the exploratory behaviour regarding an immersed object evolves in the calf. In this study, we focused on the development of the exploratory behaviour of a calf aged from 39 to 169 days, by measuring its acoustic productions and visual laterality when investigating an immersed complex object. We were interested in comparing the calf's and accompanying dolphin's click trains parameters, and our aim was to describe how exploratory behaviour using acoustic and visual modalities simultaneously evolved with age. In order to analyse exploratory behaviour in a social context, we took into account the presence, the position and the click train emissions of the dolphin accompanying the calf.

METHODS

Study subjects and facility

The study was conducted between July 2015 and January 2016 at Parc Asterix dolphinarium (Plailly, France) where nine Atlantic bottlenose dolphins (*T. truncatus*) lived together in 3 inter-connected pools. In the group, there were four females aged 42, 34, 20 and 15 years old, and four males aged 33, 31, 4 and 3 years old. The 15 year old female gave birth to a female calf on July 3th, 2015.

Overall, this facility is composed of one outdoor and two indoor pools which are not acoustically isolated. The outdoor pool has volume of 3,246m³ and a depth that varies from 2.5m at the shallowest point to 4.5m at its deepest. The indoor part of the

complex, divided into two sections, has a total volume of 550m³ and a depth of 2.5 m. The dolphins have free access between the pools at all times.

Every day the dolphins take part in at least five training sessions, starting approximately at the same time each day, during which their trainers feed them after they perform several exercises aiming to facilitate the husbandry and medical care procedures and to prepare for presentations to the public.

Recording Device

Simultaneous audio and video recordings were collected using a waterproof 360° audio-video system, named BaBeL (BioAcoustique, Bien-Être et Langage) (López Marulanda *et al.* 2017). Video data were collected using two Kodak SP360 video cameras (wide angle of 214°), one on each side of BaBeL to allow a 360° view. These cameras were positioned under the waterproof housing of a digital audio recorder ZOOM H6, plugged to five calibrated and automatically synchronized Aquarian H2a-XLR hydrophones. The synchronized hydrophones were positioned to obtain the time delay of arrival in order to provide the 3D estimations of dolphin positions. Audio recordings were conducted at a 96 kHz sampling frequency and coded on 24 bits. All the details about the geometry of the hydrophone array are described in Lopez-Marulanda *et al.* (2017).

Two successive claps were made at the beginning of the recording session: one in front of each camera, in order to manually synchronize videos with audio recordings during the *a posteriori* analysis with specific video editing software (*Final Cut Pro X 10.1.3* © Apple Inc.). A single video file was created from the two Kodak SP360 video cameras in the same window, which was associated with one of the five audio tracks and its corresponding turning spectrogram (FFT size: 1024, overlap 50%, Hanning window) provided by the free software *Audacity 2.0.6* (GNU General Public License). We chose to add only one track in the video as a reference.

Recording sessions

During the first days after the calf's birth, special efforts were made to not disturb the animals in order to preserve the mother and new born dolphin's health and relationship. Mother and calf were never isolated from their social group and could

freely move between the three pools. As a person was needed to operate BaBeL, we chose an experienced trainer that was known by all the members of the group of dolphins and we waited thirty-nine days after the calf's birth to make recording sessions of maximum 15min, which were scheduled every week, two times per day, at 11:30am and 3:30pm after a training session. All the recording sessions were made from the outdoor pool. From July 2016 to January 2016 we conducted a total of 32 recording sessions lasting 6 hours and 55 minutes.

The familiar trainer immersed himself/herself with the BaBeL device below the water surface (≈ 1 m under the surface), and remained floating near the edge of the pool, so the animals could choose the speed and distance to approach to the trainer.

Data analysis

The five audio tracks from each recording were used for the acoustical analysis, conducted by a custom-made program in MATLAB® version 2013a (Mathworks, Natick, MA) (Blanchard 2015). This custom-made program is based on a geometrical localization method that estimates the position of the vocalising dolphin. This method used the spatial distribution of hydrophones, the acoustic properties of the acoustic source (propagation speed and spherical propagation model), and the evaluation of the time differences of arrival (T.D.O.A.) of acoustic waves from the source to each hydrophone (Alameda-Pineda and Horaud, 2014). The localization given by the T.D.O.A. was linked to the video using a conversion position-pixel (Lopez-Marulanda *et al.*, 2017). The localized dolphin was identified using body size and colour and any particular body marks.

We selected sequences where the calf was present in the video, a click train was emitted and our customized program localized the emitter of the vocalization. For

these sequences, we used using the pulse train analysis function of Avisoft-SASLab Pro version 5.2.07 (Raymond Specht, Berlin, Germany) to measure click rate, mean duration of click and mean ICI for comparative purposes with previous studies (Reiss, 1988; Lindhard, 1988; Favaro *et al.*, 2013; Harder *et al.*, 2016). A hysteresis of 10 dB and a start/end threshold of -2 dB were the parameters used to analyze all the click sequences. Linear regressions evaluated changes in the calf's click train parameters with age. Mann-Whitney tests were used to compare calf's click train parameters with its mother's. When the producer of the click train was the calf, we registered its visual laterality when approaching BaBeL and the spatial position of the dolphin accompanying it when present, binomial test was used to test the significance of the differences found. Statistical tests were conducted using R statistical software version 3.02 (R Core Team 2013). We considered that a dolphin was accompanying the calf when it was positioned at 1m or less and its movements were in synchrony with the calf with less than 2 sec intervals. When the click trains were produced by another dolphin, we noted their temporal distribution with respect to the click trains produced by the calf in order to determine if there was a pattern of imitation.

RESULTS

Localization process

During the study, 32 recording sessions were carried out for a total of 6 hours 55 minutes of audio-video recordings. Dolphins were present in the videos for 5 hours and 7 minutes and the calf for 27 minutes and 20 seconds. During this time, the calf swam by the BaBeL device while a click train was recorded 188 times. The localization of the vocalizing dolphin was catalogued as ambiguous because of the proximity of two dolphins on 40 occasions (21.28%). In 9 occasions (4.79%) the dolphin emitting the vocalization was out of the range of vision of BaBeL (in indoor

pools). In 37 situations (19.68%) the low signal to noise ratio or the overlapping nature of the recorded click trains did not allow the localization of the vocalizing dolphin. For 56 click trains (29.79%) the localization of the source pointed to the wall of the pool, probably due to acoustic reverberation. Finally, in 46 situations (24.46%), the click train was linked to a dolphin present in the video (Figure 1): 18 times to the calf (Table 1), 11 times to its mother (Table 1) and 17 times to another dolphin.

1 Table 1: Acoustic parameters of localized calf's and mother's click trains

Age (days)	Click rate (clicks/sec)		Mean duration (msec)		Mean ICI (msec)	
	Calf	Mother	Calf	Mother	Calf	Mother
39	99.13		0.28±0.01		10.08±1.74	
46	57.45	45.94	0.31±0.01	0.31±0.02	17.39±2.74	21.75±10.48
	98.26	86.05	0.32±0.04	2.29±0.97	6.72±3.26	11.59±6.95
	79.71		0.32±0.02		12.53±0.24	
62	91.21	156.6	0.32±0.03	0.36±0.03	10.95±6.80	6.53±2.47
		86.61		0.31±0.04		11.54±4.45
		97.52		0.35±0.04		10.25±4.76
67	85.68	86.99	0.35±0.04	0.31±0.03	10.25±4.76	11.49±1.45

	97.94	80.77	0.29±0.01	0.32±0.06	10.20±1.37	12.37±3.48
81	85.76	124.8	0.30±0.02	0.30±0.01	11.65±10.83	8.00±5.20
138	144.8		0.31±0.05		6.90±5.42	
145	89.96	145.3	0.31±0.06	0.28±0.01	11.11±1.14	6.87±1.03
	72.92		0.32±0.02		13.70±2.81	
	126.5		0.29±0.02		6.38±11.71	
	89.55		0.28±0.01		11.16±9.14	
	186		0.28±0.01		5.37±1.17	
	167.7		0.30±0.03		5.95±2.57	
	111.6		0.29±0.01		8.95±2.15	
166	144.7		0.29±0.01		6.90±2.60	
159		39.7		0.81±0.22		25.17±9.41
166	195		0.288±0.010		5.121±1.156	

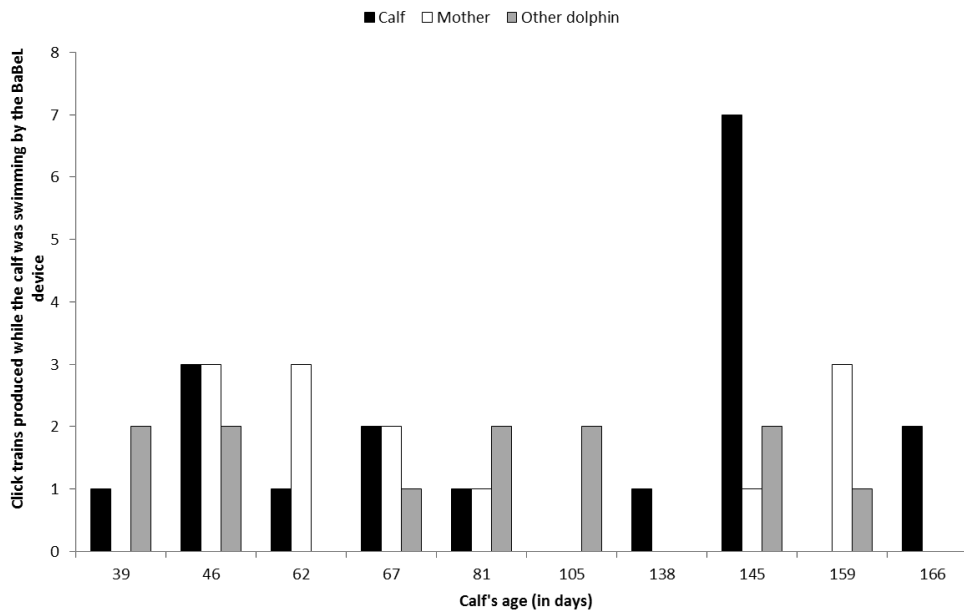


Figure 1: Number of click trains produced per individual, regarding the calf's age (N = 46)

Click parameters of mother and calf

No significant differences were found when comparing the calf's click rate (Mann-Whitney U-test, U=73, P=0.256), mean duration of click (Mann-Whitney U-test, U=142.5, P=0.053) and mean ICI (Mann-Whitney U-test, U=133.5, P=0.126) with its mother.

Calf's echolocation production according to its age

Linear regressions showed that calf's click rates increased with age ($R^2=0.79$, $P=0.003$) (Figure 2a), mean ICI decreased with age ($R^2=0.72$, $P=0.007$) and mean duration of clicks showed no significant changes ($R^2=0.2$, $P=0.26$) (Figure 2b).

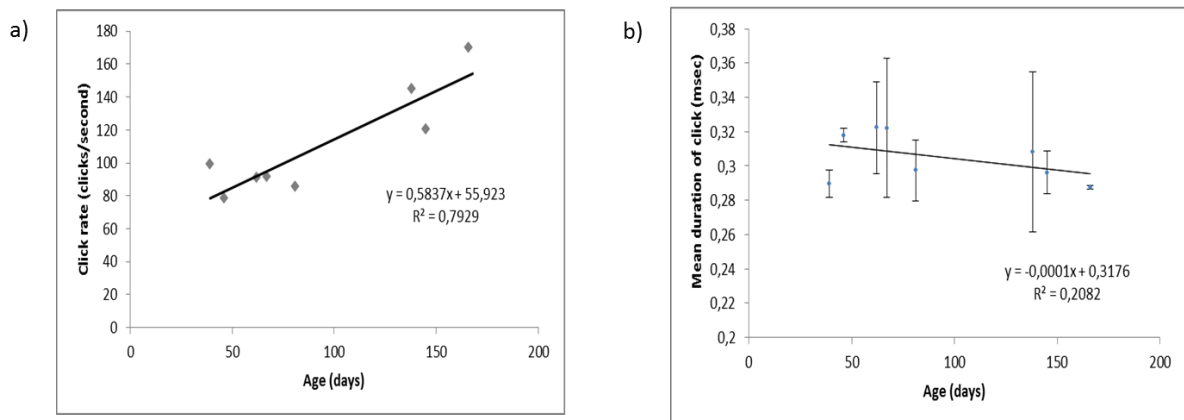


Figure 2: Linear regressions of acoustic parameters of calf's click trains: a) Click rate
b) Mean duration of click.

Calf and accompanying dolphin's click trains

Analyzing other dolphins' click train productions, we found that in five situations the calf emitted click trains after its mother (between 7 and 168 seconds after mother's click train emission, mean= 63, 8 sec, s = 72.64 sec) while they were swimming together. In another situation, the calf emitted a click train shortly after the youngest male dolphin (+24sec). Those events were spread out during the entire experiment period, not concentrated during a specific period, or age of the calf.

Considering the calf's click trains, they occurred 11 times (61%) when another dolphin accompanied the calf. The dolphin accompanying was its mother on seven occasions, and another dolphin on four occasions (one time its grandmother, one time the 4-year-old male and two times the youngest male). At 145 days old, we recorded seven occasions (39%) in which the calf emitted a click train when she was swimming by BaBeL alone. At 166 days old, we recorded her first tactile exploration of the device (i.e., touching with the rostrum).

Calf's visual lateralization and mother's spatial position in relation to the calf

When analyzing the visual lateralization of the calf while swimming by BaBeL, only 15 click train emissions out of 18 were taken into account, since in three click train productions the calf remained static facing the BaBeL device head-on, without clearly choosing a side for its visual exploration. During 13 click trains out of 15 the calf swam by with its right eye towards BaBeL (binomial test, $p = 0,007$) (Figure 3). It was positioned along another dolphin's flank for all of the 13 right approaches. The 2 left click train emissions occurred when the 145 days old calf swam by alone.

In six situations (40% $N = 18$), the calf swam in an upside-down position while emitting a click train with its lower jaw directed towards the device. This happened once at 39 days old, once at 46 days old, and four times at 145 days old when it was swimming by the device alone.

Regarding the spatial position of the accompanying dolphin, during the calf's click trains emissions, the accompanying dolphin was at the right of the calf 7 times *versus* 4 times at its left ($P=0.05$, binomial test) (Figure 3).

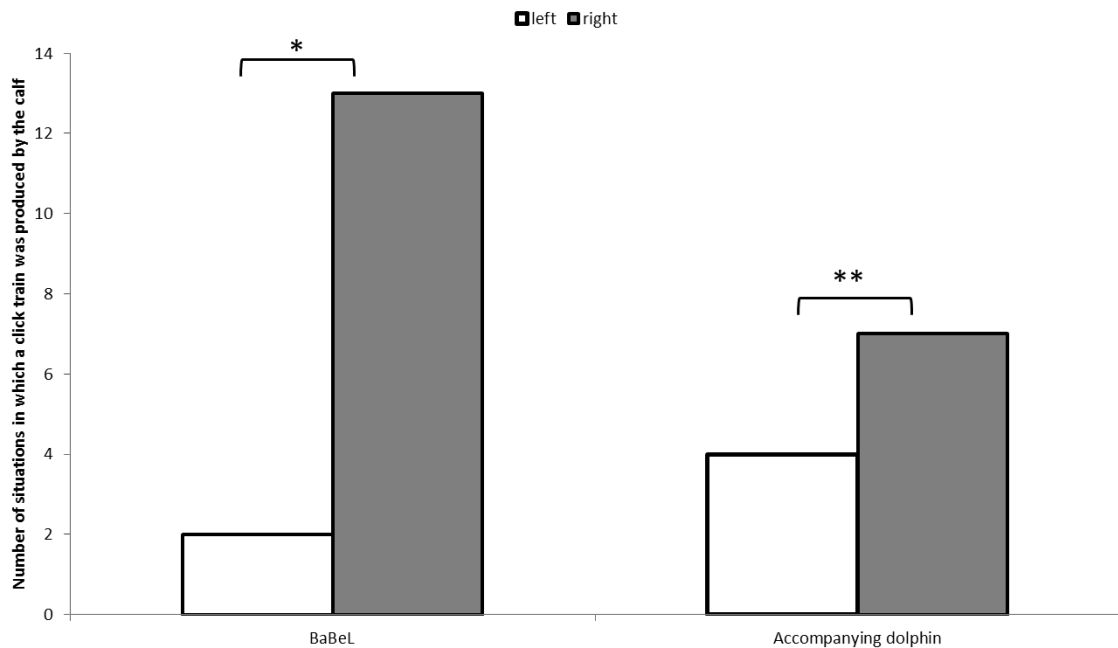


Figure 3: Calf's behavioral laterality while swimming by BaBeL (N = 15) *: (P = 0.007, binomial test) and accompanying dolphin's spatial position with respect to the calf (N = 11) **: (P = 0.05, binomial test)

To summarize, the calf's click train acoustic parameters did not differ significantly from its mother. However, the calf showed an augmentation of click rate with age and a decrease in ICI. During click train emission, the calf used mostly its right eye. The two situations when the calf used its left eye coincided with the emission of click trains while the calf was swimming alone. The accompanying dolphin was mostly placed to the right of the calf.

DISCUSSION

The study of development of exploratory behaviour in dolphins presents several difficulties. First, following and recording the vocalizations of a dolphin from early age in the wild is almost impossible and thus is only feasible with studies in captivity, where the birth of a calf occurs on average every 28 months per female (Cornell *et al.*

1987). As a consequence, to our knowledge there are only six studies focused on the development of dolphins' echolocation, and all carried out in captive conditions (Carder and Ridgway 1983; Reiss 1988; Linhard 1988; Manoukian *et al.* 2002; Favaro *et al.* 2013; Harder *et al.* 2016). Second, all the studies focused on the development of echolocation faced the difficulty of determining which dolphin is emitting a click train and thus used several indicators: the production of bubblestreams (Reiss 1988; Favaro *et al.* 2013), the intensity of the signal and the position of the calves with respect to the hydrophone (Lindhard 1988), the presence of head scanning behaviours at the same time as click recordings (Favaro *et al.* 2013), and the distraction of mothers in activities with trainers and the proximity, orientation and relative position of calves (Harder *et al.* 2016). All these indicators are subject to uncertainty and allow accurate analysis of click trains only during specific behavioural circumstances (ex: mothers distracted by trainers (Harder *et al.* 2016) or with their blowhole outside the water (Favaro *et al.* 2013)). The use of BaBeL system and a geometrical localization methodology allowed us to analyse a click trains occurring in varied circumstances, with the presence of other dolphins around the calf and regardless of its relative position. For the first time, the development of a calf's exploratory behaviour as well as the acoustic parameters of its concurrent click trains were analysed.

Nevertheless, our methodology presents several limitations. First, the wall of the pool caused reverberations, making our custom-made program identify the wall as the source of sound in 29.79% of the analysed sequences. Second, the identification of the vocalizing dolphin is only possible if the animal is in the range of vision of the video camera (Lopez Marulanda *et al.* 2017). If dolphins were vocalizing from the inside pools, they were no longer visible to allow the identification of the emitter.

Third, because of the dolphins' interest in the device, sometimes our recordings showed a general cacophony of clicks in which click trains mostly overlapped, making impossible to determine the initial and end time of click trains, and thus, to compare the click train duration as it was done in previous studies (Favaro *et al.* 2013; Harder *et al.* 2016).

Our results showed that the calf presented an increase in click rate and a decrease in ICI with age. The minimum value for the click rate was found at 46 days old (57.45Hz) and the maximum value at 166 days old (195 Hz). This contrast with a previous study (Harder *et al.* 2016) that analysed click train production in six calves during their first six months of life and found that mean click rate increased during the first month, decreased during the second month and remained constant between the third and the sixth month. With respect to the ICIs, the values for the six calves remained consistent with a mean value of 25.32ms (SD=10.35) (Harder *et al.* 2016). In our study, the ICI values from the calf's click trains varied from a mean value of 17.39ms (SD=2.74) at 46 days old to a mean value of 5.12ms (SD=1.15) at 166 days old. The calf in our study showed higher click rates and lower ICIs than the six calves analysed by Harder *et al.* (2016). These differences might be explained by the nature of the object explored. Contrary to Harder *et al.* (2016) where the calves were in presence of a simple object (a single hydrophone), in our study, the calf was exposed to a complex object consisting in five arms with attached hydrophones and two video cameras, that was handled by a familiar person in water. The physical parameters of the object offered the possibility to perceive various different densities and shapes. Moreover, the presence of a trainer in the water could have generated an increased interest by the calf. It might have increased its click production per second for two reasons: as a response to the complexity of the device that is known to arouse

curiosity (Berline *et al.* 1965; Studnitz *et al.* 2007) and/or due to the presence of a human in water, which can modify the behavioural response of animals, (Brensing *et al.* 2005; Akiyama and Ohta 2007).

The lack of difference between click rate, mean duration of click and mean ICI of the calf and its mother supports the finding that infant and adult pulses are indistinguishable at 40 days old (Reiss 1988). As our recordings started at 39 days old, it is possible that the calf could already produce click trains similar to those of an adult, at least regarding the measured acoustic parameters in this study. This does not exclude the possibility that other acoustical parameters of the calf's click train not measured here could differ from adults.

Our results showed the calf's had a right eye preference while echolocating. Bottlenose dolphins demonstrate this eye preference (Yaman *et al.* 2002) associated with a better performance in discrimination tasks (von Fersen. 2000; Kilian *et al.* 2000; Yaman *et al.* 2002; Delfour and Marten 2005). This right orientation has been found also with free ranging Atlantic Spotted Dolphins (*Stenella frontalis*) when exposed for the first time to a mirror that swimmers hold (Delfour and Herzing 2013). However, no sound recordings were conducted during those experiments, making impossible to link vision and echolocation. It is possible that our results were impacted by the dolphins' swimming patterns. A previous study showed that dolphins in captivity tend to swim counter-clockwise (Sobel *et al.* 1994). In our study, 188 times the calf swam by the device and we found that for 150 (79.78%) "swim by" situations, the calf swam counter-clockwise and for 38 (20.22%) situations it swam clockwise. However, it is not clear if dolphin's swims counter-clockwise because they have a visual lateralization of the right eye or *vice-versa*.

Perceptual laterality is influenced by the emotional value (Rogers *et al.* 1994; Quaranta *et al.* 2007) and the novelty of an object (Cantalupo *et al.*, 1995; Basile *et al.*, 2009). Bottlenose dolphins preferentially use their left eye to explore familiar objects and their right to explore unfamiliar objects (Blois-Heulin *et al.* 2012). We suggest that BaBeL was probably perceived as an unfamiliar object until 145 days old when BaBeL was immersed for the 15th time, and when for the first time the calf explored the device alone and used its left eye twice.

We found that the calf was positioned mostly at the left side of the accompanying dolphin while echolocating. This contrast with what has been found in free ranging (Karenina *et al.* 2010; Hill *et al.* 2017) and captive belugas (*Delphinapterus leucas*) (Hill *et al.* 2017) and in free ranging killer whales (*Orcinus orca*), where calves mostly swim at the right side of their mothers (Karenina *et al.* 2013). It might be possible that these species differ in their lateralization tendencies. However, it is also possible that the mother placed herself between her calf and the device. As we only analyzed the behavior of one individual, no conclusions can be made about the spatial lateralization of the species: for this, more observations about the lateralization of calves with respect to the accompanying dolphin are needed in wild and captivity.

To conclude, at the age of 39 days, a bottlenose dolphins' calf's acoustic parameters regarding its click trains did not differ from that of an adult. However, click rate was shown to increase with age of the calf. When visually and acoustically exploring an immersed non-alimentary object, the calf showed a right eye preference. This study used a new methodology that allowed us to describe not only the acoustic parameters of the subjects' click trains but also the position of the calf during exploratory behavior with respect to the object explored and to its conspecifics. Further studies using the same technology and methodology would reveal unknown

aspects of the dolphins' perception of their world and allow scientists to build new paradigms.

BIBLIOGRAPHIC REFERENCES

- Alameda-Pineda X, Horaud R (2014) A geometric approach to sound source localization from time-delay estimates. *IEEE/ACM Transactions on Audio, Speech and Language Processing* 22:1082-1095
- Akiyama J, Ohta M (2007) Increased number of whistles of bottlenose dolphins, *Tursiops truncatus*, arising from interaction with people. *J Vet Med Sci* 69:165–170
- Au WWL (1997) Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics* 8:137–162
- Basile M, Boivin S, Boutin A, Blois-Heulin C, Hausberger M, Lemasson A (2009) Socially dependent auditory laterality in domestic horses (*Equus caballus*). *Animal Cognition* 12:611-619
- Belzung C (1999) Measuring rodent exploratory behavior. *Techniques in the Behavioral and Neural Sciences* 13:738-749
- Berlyne DE (1960) Conflict, arousal, and curiosity. McGraw-Hill, New York
- Berlyne DE, Borsa DM, Craw MA, Gelman RS, Mandell EE (1965) Effects of stimulus complexity and induced arousal on paired-associate learning. *Journal of verbal Learning and verbal Behavior* 4:291-299
- Birgersson S, Birot de la Pommeraye S, Delfour F (2014) Dolphin personality study based on ethology and social network theory. Lambert Academic Publishing, Sarrebruck

- Blanchard T (2015) Innovation audio-visuel pour le suivi des Grands Dauphins [Audio-visual innovation for monitoring Bottlenose Dolphins]. Master's thesis, Ecole Nationale Supérieure d'Ingenieurs du Mans, Le Mans, France
- Blois-Heulin C, Crével M, Böye M, Lemasson A (2012) Visual laterality in dolphins: importance of the familiarity of stimuli. *BMC neuroscience* 13:9
- Brensing K, Linke K, Busch M, Matthes I, Van der Woude SE (2005) Impact of different groups of swimmers on dolphins in swim-with-the-dolphin programs in two settings. *Anthrozoös* 18:409-429
- Cantalupo C, Bisazza A, Vallortigara G (1995) Lateralization of predator evasion response in a teleost fish (*Girardinus falcatus: Poeciliidae*). *Neuropsychologia*, 33:1637-1646
- Delfour F, Beyer B (2012) Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo biology*, 31(2), 137-150
- Delfour F, Faulkner C, Carter T (in press). Object manipulation and play behaviour in Bottlenose Dolphins (*Tursiops truncatus*) under Human Care. *International journal of comparative psychology*.
- Delfour F, Marten K (2006) Lateralized visual behavior in bottlenose dolphins (*Tursiops truncatus*) performing audio-visual tasks: The right visual field advantage. *Behavioural processes* 71:41-50
- Dingemanse NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal behaviour* 64:929-938
- Dudzinski K.M., Hill H.M. (2018) Cetacean Communication. In: Vonk J., Shackelford T. (eds) *Encyclopedia of Animal Cognition and Behavior*. Springer, Cham

- Eskelinen HC, Winship KA, & Borger-Turner JL (2015) Sex, age, and individual differences in bottlenose dolphins (*Tursiops truncatus*) in response to environmental enrichment. *Animal Behavior and Cognition* 2:241-253
- Harder JH, Hill HM, Dudzinski KM, Sanabria KT, Guarino S, Kuczaj II, Stan A (2016) The Development of Echolocation in Bottlenose Dolphins. *International Journal of Comparative Psychology* 29(1)
- Hill HM, Guarino S, Calvillo A, Gonzalez III A, Zuniga K, Bellows C, Polasek L, Sims C (2017) Lateralized Swim Positions are Conserved across Environments for Beluga (*Delphinapterus leucas*) Mother-Calf Pairs. *Behavioural Processes* 138:22-28. doi: 10.1016/j.beproc.2017.01.018
- Hunter SA, Bay MS, Martin ML, Hatfield JS (2002) Behavioral effects of environmental enrichment on harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*). *Zoo Biology* 21: 375-387
- Karenina K, Giljov A, Baranov V, Osipova L, Krasnova V, Malashichev Y (2010) Visual laterality of calf–mother interactions in wild whales. *PLoS One* 5(11): e13787. doi:10.1371/journal.pone.0013787
- Karenina K, Giljov A, Ivkovich T, Burdin A, Malashichev Y (2013) Lateralization of spatial relationships between wild mother and infant orcas, *Orcinus orca*. *Animal Behaviour*, 86:1225-1231
- Kilian A, Von Fersen L, Güntürkün O (2000) Lateralization of visuospatial processing in the bottlenose dolphin (*Tursiops truncatus*). *Behavioural brain research* 116:211-215

- Keller H, Schneider K, Henderson B (eds) (2012) Curiosity and exploration. Springer Science & Business Media, Berlin
- Kuczaj SA, Makecha R, Trone M, Paulos RD, Ramos JA (2006) Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology* 19(2)
- Kuczaj li SA, Yeater DB (2007) Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *Journal of the Marine Biological Association of the United Kingdom* 87:141-148
- Katzir G (1982) Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L. I. Response to novel space. *Behaviour* 81:231-263
- Lambert, O., Bianucci, G., Urbina, M., & Geisler, J. H. (2017). A new inioid (Cetacea, Odontoceti, Delphinida) from the Miocene of Peru and the origin of modern dolphin and porpoise families. *Zoological Journal of the Linnean Society*, 179(4), 919-946.
- Lynn DA, Brown GR (2009) The ontogeny of exploratory behavior in male and female adolescent rats (*Rattus norvegicus*). *Developmental psychobiology* 51:513-520
- Lindhard M (1988) Apparent sonar clicks from a captive bottlenosed dolphin, *Tursiops truncatus*, when 2, 7 and 38 weeks old. In Nachtigall PE, Moore PW (eds) *Animal sonar: processes and performance*. Plenum Press, New York, vol 156 pp 109-113

- Lopez-Marulanda J, Adam O, Delfour F (*in press*). First results of an underwater audio-video device for etho-acoustical studies on bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 43(2), 162-176
- Miller LC, Bard KA, Juno CJ, Nadler RD (1986) Behavioral responsiveness of young chimpanzees (*Pan troglodytes*) to a novel environment. *Folia primatologica* 47:128-142
- Pack AA, Herman LM (1995) Sensory integration in the bottlenosed dolphin: Immediate recognition of complex shapes across the senses of echolocation and vision. *The Journal of the Acoustical Society of America* 98:722-733
- Parker KJ, Rainwater KL, Buckmaster CL, Schatzberg AF, Lindley SE, Lyons DM (2007) Early life stress and novelty seeking behavior in adolescent monkeys. *Psychoneuroendocrinology* 32:785-792
- Quaranta A, Siniscalchi M, Vallortigara G (2007) Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology* 17:199-201
- Reiss D (1988) Observations on the development of echolocation in young bottlenose dolphins. In Nachtigall PR, Moore PWB (eds) *Animal sonar: Processes and performance*. Plenum Publishing Corporation, New York, pp 121-127
- Richardson WJ, Green CR, Malme CI, Thomson DH (1995) *Marine mammals and noise*. Academic press, New York
- Rogers LJ, Ward JP, Stanford D (1994) Eye-dominance in the small-eared bushbaby, *Otolemur garnettii*. *Neuropsychologia* 32:257-264
- Rubenstein J (1967) Maternal attentiveness and subsequent exploratory behavior in the infant. *Child Development* 1089-1100

- Schwab C, Huber L (2006) Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology* 120:169
- Studnitz M, Jensen MB, Pedersen LJ (2007) Why do pigs root and in what will they root? A review on the exploratory behaviour of pigs in relation to environmental enrichment. *Applied Animal Behaviour Science* 107:183-197
- Van Lancker E (2002) Acoustic goniometry: a spatio-temporal approach. Doctoral dissertation, Faculté Polytechnique de Mons
- Von Fersen L, Schall U, Güntürkün O (2000) Visual lateralization of pattern discrimination in the bottlenose dolphin (*Tursiops truncatus*). *Behavioural brain research*, 107:177-181
- Yaman S, Von Fersen L, Dehnhardt G, Güntürkün O (2003) Visual lateralization in the bottlenose dolphin (*Tursiops truncatus*): evidence for a population asymmetry? *Behavioural brain research* 142:109-114
- Zimmermann A, Stauffacher M, Langhans W, Würbel H (2001) Enrichment-dependent differences in novelty exploration in rats can be explained by habituation. *Behavioural brain research* 121:11

Chapter 5: Bottlenose Dolphins Under Human Care

Acoustically Coordinate Their Aerial Jumps.

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Synthesis Chapter 5

Context

Synchronous behaviors occur when two or more animals perform the same behavior at the same time and they have been described for free ranging dolphins of several populations. Dolphins' communication relies mainly on the acoustic channel (Tyack, 1999), and as these marine mammals live in habitats of limited visibility (Connor et al., 1998), we can assume that the mechanism of communication to perform simultaneous behaviors may involve acoustic cues.

Research questions

It is unknown if dolphins use acoustic cues to perform simultaneous movements and this is difficult to highlight in free ranging dolphins. The management of dolphins in captivity provides an excellent opportunity to study the mechanism underlying synchronous behavior. The first aim of this study was to experimentally determine whether dolphins use acoustic cues when performing a known simultaneous exercise following a gestural command from their caregivers. The second aim, if they do use acoustic cues, was to identify the emitters.

Analysis

A coordination experiment was conducted with three bottlenose dolphins (2 females and 1 male). Random trials of a target exercise (jump) were carried out with the animals alone or by pairs. The acoustical parameters of their vocalizations during the jumps were compared when they were performed individually or collectively. The BaBeL system was used to localize and identify the dolphin producing vocalization.

Results

Results indicated that dolphins managed to spontaneously synchronize their jumps 100% of times when paired. Whether they jumped alone or in pairs, they produced click trains before and after 92% of jumps. During the jumps performed in pairs these click trains were emitted by only one individual 98% of times. The acoustic localization processing allowed the successful identification of the vocalizing dolphin in 19.8% of cases. Our study also showed that in all but one successful localizations, the click trains were produced by the same individual. Noteworthy, this individual appeared to be the oldest female of the group.

Conclusion

In conclusion, this paper provides the first evidence that dolphins use acoustic cues, and more particularly click trains, to synchronize their movements possibly by eavesdropping the echoes produced by one individual that leads the navigation.

ABSTRACT

Synchronous behaviors occur when two or more animals perform the same behavior at the same time and they have been described for free ranging dolphins of several populations. However, the mechanism underlying the synchrony is not well understood. In this study we implemented audio and video recordings on three captive bottlenose dolphins performing aerial jumps, either individually or in pairs, in order to determine if they use acoustic cues to synchronize their movements. Experiments were recorded with an hydrophone array and a 360° underwater camera allowing to localize precisely the sound source and thus the identity of the individual producing the sound. Results indicated that dolphins managed to spontaneously synchronize their jumps 100% of times when paired. Whether they jumped alone or in pairs, they produced click trains before and after 92% of jumps. During the jumps performed in pairs these click trains were emitted by only one individual 98% of times. The acoustic localization processing allowed the successful identification of the vocalizing dolphin in 19.8% of cases. Our study also showed that in all but one successful localizations, the click trains were produced by the same individual. Noteworthy, this individual appeared to be the oldest female of the group. This paper provides the first evidence that dolphins could use acoustic cues, and more particularly click trains, to synchronize their movements possibly by eavesdropping the echoes produced by one individual that leads the navigation.

INTRODUCTION

Synchronous behaviors occur when two or more animals perform the same behavior at the same time (Connor et al., 2006) and have been described for several animal species in different modalities (eg. visual, acoustic) (reviewed in Herzing, 2015). The degree of synchronization can vary from time intervals of less than one second to several minutes (Sakai et al., 2010). For example, visual synchrony occurs between fireflies (*Pteroptyx* spp.) that synchronize their bioluminescent flashing during the night (Buck, 1988) and between male fiddler crabs (*Uca annulipes*) that wave their major claw in synchrony to attract females (Blackwell et al., 1999). Acoustic synchrony has been described for example in the vocalizations of male long-tailed manakins (*Chiroxiphia linearis*) (Trainer and McDonald, 1993) and in male frogs (*Kassina kuvangensis*) (Grafe, 2003). Synchronous behaviors might have several functions, for example, they might be used as an adaptive response to avoid predators or to cope with novel objects and situations (Norris and Schilt, 1988; Pryor and Shallenverger, 1991), as a way to receive some aero- or hydrodynamic advantage in movement (Herskin & Steffensen, 1998), as means to facilitate shared attention (Sebanz et al., 2006) and foraging success (Tremblay and Cherel, 1999).

In odontocetes, the term “synchrony” has been used in two different ways: first, to describe group members that perform nonrandom grouping behaviors, swimming and breathing in synchrony (Hastie et al., 2003; Fellner et al., 2013); and second, behaviors that are performed ‘simultaneously’ or ‘in unison’ (Mann and Smuts, 1999; Connor et al., 2006). Visual simultaneous behavior has been described in several dolphin species. Pantropical spotted dolphins (*Stenella attenuata*) synchronize their movements as a defensive response while being herded in tuna nets (Pryor and

Kang-Shallenberger, 1991). Synchronous behavior has been reported in Atlantic spotted dolphins (*Stenella frontalis*) in aggressive contexts during interspecific interactions with bottlenose dolphins (*Tursiops truncatus*) as a way to dominate a larger size opponent (Cusick and Herzing, 2014). Male Indian Ocean bottlenose dolphins (*Tursiops aduncus*) have been observed synchronizing their surfacing behavior during social behavior with female consorts (Connor et al., 2006; Sakai et al., 2010), and during herding behavior of females (Connor et al, 1992; Connor and Smolker, 1996).

Vocal synchrony has been also described in these animals. Spinner dolphins (*Stenella longirostris*) synchronize their vocalizations while dispersing from bays (Brownlee and Norris, 1994). Offshore populations of bottlenose dolphins (*T.truncatus*) showed vocal synchrony apparently to maintain contact in a large home range (Janik et al., 2011). Finally, simultaneous vocal and visual signals have been reported for this species during intraspecific aggressions (Herzing, 2015).

Sounds emitted by dolphins are classified into three structural categories and two functional classes. Structurally, sounds productions are thus categorized in: whistles or tonal sounds (reviewed in Janik, 2009), clicks or pulsed sounds (Au et al., 1974), and burst-pulsed sounds (Diaz-Lopez and Bernal-Shirai, 2009). Functionally, sound emissions may be used for echolocation, which could be defined as the acoustic representation of the surroundings obtained by the projection of clicks and the subsequent nervous integration of the perceived echoes (Au, 1993). Sound emissions may also play a role in communication and social interactions (reviewed in Herzing, 2000).

When two or more dolphins engage in a synchronous behavior, information might flow between them that can involve a communication process (Johnson, 2015). Dolphins' communication relies mainly on the acoustic channel (Tyack, 1999), and as these marine mammals live in habitats of limited visibility (Connor et al., 1998), we can assume that the mechanism of communication to perform simultaneous behaviors may involve acoustic cues. The use of acoustic cues to perform simultaneous movements are difficult to highlight in free ranging dolphins for several reasons: first, the occurrence of synchronous behaviors and the individuals performing them cannot be controlled by the experimenter; second, the low visibility underwater in most of the habitats of this species (Würsig and Pearson, 2015) do not allow the clear determination of the degree of synchronization, neither the localization of the individual emitting the sound.

The management of dolphins in captivity provides an excellent opportunity to study this mechanism because the synchronous behaviour can be requested to the target animals and replicated several times. The clarity of water allows a direct observation of the behavioural sequence and allows the identification of the individual emitting a vocalization by the use of a hydrophone array. Dolphins under human care are often engaged in simultaneous behaviors (e.g. jumps) promoted by their caregivers by positive reinforcement (Brando, 2010). However, it is unknown how animals manage to synchronize their actions and if they use acoustic cues to coordinate their simultaneous behaviors. The first aim of this study was then to experimentally determine whether dolphins use acoustic cues when performing a known simultaneous exercise following a gestural command from their caregivers. The second aim, if they do use acoustic cues, was to identify the emitters.

METHODS

Studied Subjects and facility

The coordination experiment was conducted in February and March 2017 at the Boudewijn Seapark (Bruges, Belgium). Three individuals were selected for the experiment: two adult females named Puck and Linda aged respectively 51 and 41 years, and one adult male named Kite aged 12 years. The females originated from wild and the male was born in another facility. This choice was based on two criteria: first, the three animals were trained to perform the same exercise individually and collectively and second, two animals were known to work together very well (Puck and Linda) and two animals were known to work together with difficulty (Puck and Kite) (Vanderheul, pers. Comm.).

Overall this facility consists of five connected pools not acoustically isolated: a main show pool, two holding pens, a medical pool and a quarantine pool. The depth of the pools is at least 3 m in the shallowest areas and 5.6 m at its deepest point in the main show pool. The training sessions with caregivers take place in all pools. During the experiment, the target animals were placed in the main pool with the recording device. The other animals were placed in the two holding pens and a trainer was responsible for maintaining their head out of the water to avoid the propagation of their potential acoustic emissions through the pools. This procedure prevented from erroneous estimated positions of the emitting individual as vocalizations originating from outside the experimental pool could produce false alarms during acoustic processing.

Recording device

Simultaneous audio and video recordings were collected using a waterproof 360° audio-video system, named BaBeL (BioAcoustique, Bien-Être et Langage) (López Marulanda et al. 2017). Underwater video data were collected using GIROPTIC 360 ° video camera with 3 objectives covering each one 120° and allowing a 360° view of the main pool. This 360° camera was positioned under the waterproof housing of a digital audio recorder ZOOM H6, connected to four calibrated and automatically synchronized Aquarian H2a-XLR hydrophones. The hydrophones were asymmetrically positioned at the extremities of a virtual square distant from 1.5m to each other. This allowed us to determine the time differences of arrival (TDOA) of the sound to each hydrophone and thus to estimate the 3D position of the dolphin producing the sound. Audio recordings were conducted at a 96 kHz sampling frequency and coded on 24 bits. Details about the function of this hydrophone array are described in Lopez-Marulanda et al. (2017). In addition, we used a GoPro hero 3+ to record a video back up of the experience from the surface. Videos and audio recording were synchronized. A single video file was created from the video cameras and was associated with one of the four audio tracks and its corresponding turning spectrogram (FFT size: 1024, overlap 50%, Hanning window) provided by the free software Audacity 2.0.6 (GNU General Public License).

Habituation process

Before experiments, dolphins were gradually habituated to the presence of the BaBeL device in the water. The habituation procedure involved 6 steps which were gradually built up over the four weeks prior to the recording session. The first step consisted in positioning the device on the side of the main pool, out of the water, but

within sight of the animals. In the second step, an animal caregiver held the device on the underwater platform in the channel that connected the main show pool to the quarantine pool. Thus, during this phase, the animals could see the device into the water, but were kept under control by other trainers. Thirdly, the animals were allowed to swim freely for a limited time in the presence of the device which was held by a trainer as described in step 2. Exploration time was gradually prolonged and animals were rewarded to ignore the device. In the fourth step, the device was placed alone in the water while the animals were kept under control. In the step five, the device was left in the water while the animals swam freely with enrichment items to distract them from showing interest in BaBeL. Finally, during the last phase, the device was randomly placed in the water, with or without the presence of enrichment items.

Coordination experiment

Before the beginning of each training session, the audio-video recording device was placed in the main pool suspended from a buoy and kept in place at the side of the tank by two ropes and a pole manipulated by one observer who remained at the edge of the pool. We carried out 30 training sessions (max. two per day) in which animals were asked to perform “back jump” exercise, which consisted in jumping with the dorsal part of the animal pointing towards the water surface. The dolphins were trained to perform the back-jump many times until the trainers blew their whistle to indicate that the task was well performed and they can come back to get a reward (fish). For the experiment, the trainers decided, according to the motivation of the animal, to let it jump between one to five times before blowing the whistle.

During each training session the trainers asked the animals to perform the “back jump” five non-consecutive times, other exercises were inserted in between in order to maintain the dolphins’ motivation. The trials were randomly distributed in order to get at the end of the experiment 30 trials for each dolphin individually performing the back jump, 30 trials for Kite and Puck together, and 30 trials for Linda and Puck together. For the trials collectively performed, two trainers were placed one at each side of the pool. Each dolphin was placed facing one trainer, in a way that they could not see the trainer’s gestural command given to the other dolphin. Once in this position, the trainers simultaneously produced the command to perform the back jump.

Behavioral analysis

We analysed the videos taken from BaBeL and the backup video to determine if animals jumped synchronously. We defined a synchronous jump as a jump performed by two animals with a time difference of less than 0.5 seconds.

Acoustical analysis

No whistles or burst-pulsed sounds were emitted by the animals during the exercises. Accordingly, all the acoustical analysis was based on their click trains production.

Click trains produced by the animals were analyzed using the pulse train analysis function of Avisoft-SASLab Pro version 5.2.07 (Raymond Specht, Berlin, Germany) to measure click rate for each trial. Click trains produced after the last jump of each trial were not taken into account for the statistical analysis because animals do not need to synchronize after the last jump of each trial to go back to the trainer and get the

reward. A visual inspection of the click trains allowed us to determine whether the click train was produced by one animal (regular click train, with inter-click interval (ICI) increasing, decreasing or constant) or more than one animal (irregular click train with no pattern of change in ICI as a consequence of a presumable overlapping of more than one click train).

Localization processing

For all the trials made by pairs a localization processing of the click trains was performed to identify which dolphin(s) emitted the vocalizations. A customized program was created in MATLAB®, Version 2013a (Mathworks, Natick, MA, USA) to analyze the data obtained with BaBeL (Blanchard, 2015). This program used a geometrical localization method to estimate the position of an acoustic source. More specifically this method relies on the spatial distribution of the hydrophones and the measure of TDOA of the acoustic wave from its source to the different hydrophones to calculate the sound source position. The localization is then displayed in the 360° video by a conversion position-pixel (Lopez-Marulanda et al., 2017).

Statistical analysis

Comparisons between the 3 individuals click rates were performed using a Kruskal-Wallis test and post hoc comparisons with Mann-Whitney tests. To compare if the click rates differed between the exercises performed individually vs. by pairs we used a Wilcoxon signed rank test for each individual. All the statistical tests were conducted using R statistical software version 3.02 (R Core Team, 2013).

RESULTS

Synchronous behavior

Videos analyses showed that 100% of the “back jumps” performed by pairs were synchronous. The inspection of the videos with the synchronized spectrogram also indicated that dolphins produced a click train before and after 92% of the jumps performed (Table 1).

Differences in click rates

A total of 331 click trains were extracted and analysed from the recordings (Table 1). In some situations, the click trains were not detected before or after a jump or its signal to noise ratio was too low to allow a pulse rate analysis. The table 1 summarizes the number of trials, jumps and analysed click trains for each individual or combination of individuals.

Table 1: Number of trials, jumps, detected click trains and analysed click trains for each individual

Individual	Trials	Jumps	Detected		Successfully Localized sound source
			Click trains	Analyzed click trains	
Kite	30	84	74	63	
Linda	30	75	72	64	
Puck	30	68	65	63	
Kite with Puck	30	79	64	64	10
Linda with Puck	30	77	77	77	18
Total	150	383	352	331 (141 collective)	28

Click rates between the individuals differed significantly (Kruskall-Wallis test: $\chi=24.16$, $df=2$, $P<0.0001$). Post hoc comparisons showed that there were no significant difference between the click rate of Kite and Linda (Mann-Whitney test, $W= 2961.5$, $P=0.1398$ with Bonferroni correction). However click rates of Puck were significantly inferior to click rates of Kite (Mann-Whitney test, $W= 3720$, $P<0.0001$ with Bonferroni correction) and Linda (Mann-Whitney test, $W= 3191$, $P=0.002$ with Bonferroni correction).

When comparing the click rate values for each individual alone and by pairs, we found no significant differences in the click rate for Kite (Wilcoxon signed Rank Test: $W=2952$ $P=0.802$; median click rate alone = 23.34 clicks.sec-1; median click rate by pair = 21.82 clicks.sec-1) and Linda (Wilcoxon signed Rank Test: $W=2574$ $P=0.5417$; median click rate alone = 21.27 clicks.sec-1; median click rate by pair = 22.97 clicks.sec-1). However, click rates of Puck alone were significantly inferior to click rates of the pair Kite-Puck (Wilcoxon signed Rank Test: $W=1495.6$ $P<0.0001$; median click rate alone = 17.6 clicks.sec-1; median click rate by pair = 21.82 clicks.sec-1) and the pair Linda-Puck (Wilcoxon signed Rank Test: $W=1682$, $P=0.0001$; median click rate alone = 17.6 clicks.sec-1; median click rate by pair = 22.97 clicks.sec-1) (Figure 1).

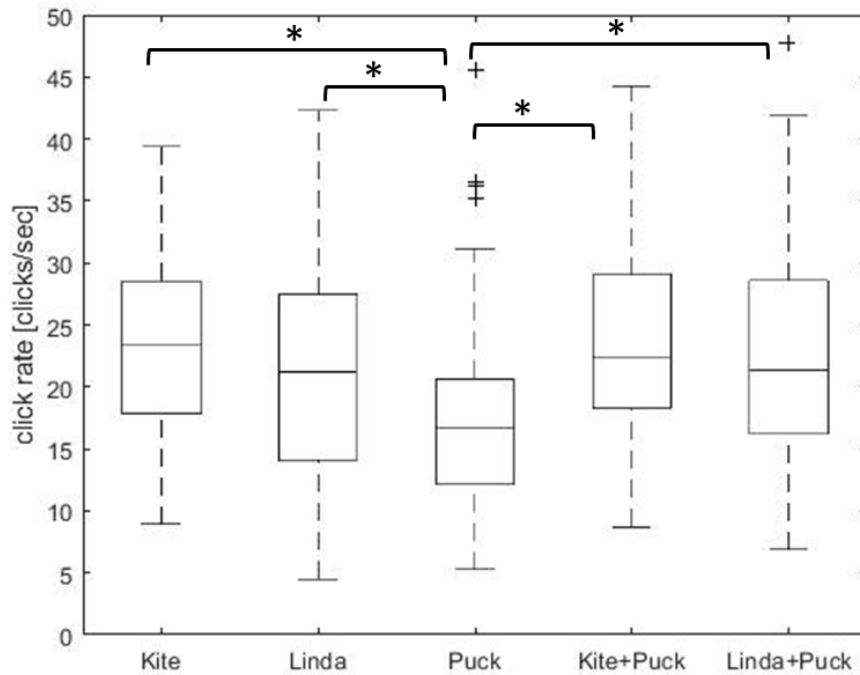


Figure 1: Click rate of the different individuals performing the exercise alone or by pairs. Boxes represent 25th and 75th percentiles. Whiskers correspond to the 1st and 99th centiles. + represents the outliers. * indicates P values ≤ 0.001

At this stage, the click trains produced during the exercise performed by pairs cannot be associated to one individual and are thus susceptible to be produced either by both individuals performing the exercise or by only one of them. A visual inspection showed that 98% (N=141) of the click trains emitted during collective jump performance did not overlap (see methods), therefore they were considered as produced by only one individual.

Localization

The localization processing was carried out with 141 click trains produced during the collective exercises in order to assess the emitter's identity. In 103 situations (73.1%), the localization was not achieved due to the noise caused by the reverberation of the sounds against the walls of the pool. In 10 situations (7,1%) the localization was ambiguous because the two dolphins were placed one behind the other with respect to the camera. Finally the localization was possible for 28 (19.8%) click trains, 10 times during the jumps of Kite with Puck, and 18 times during the jumps of Linda with Puck. In both pairs, Puck was identified as the individual producing the clicks, for 100% of the synchronized jumps with Linda and for 90% of the synchronized jumps with Kite (Figure 2).

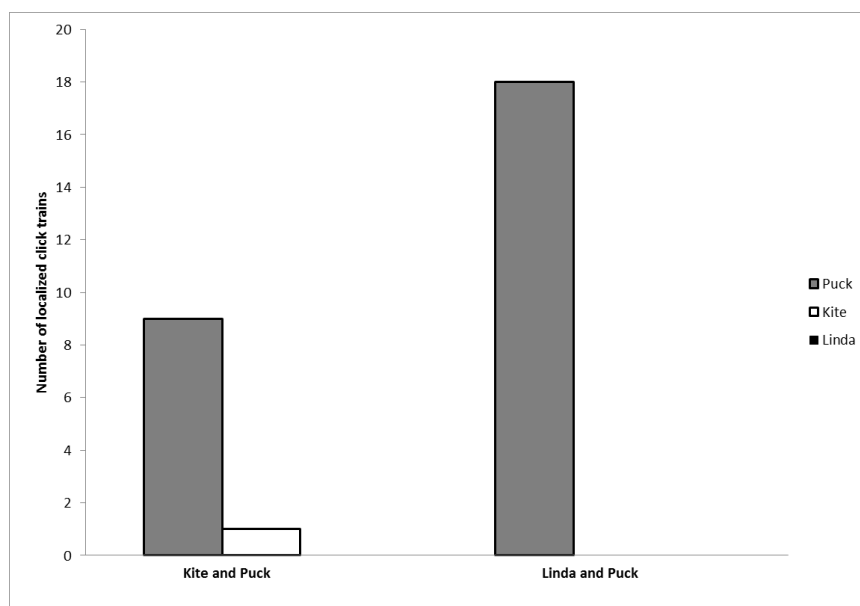


Figure 2: Number of localized click trains for each pair of individuals

Comparison of click rates of localized click trains

Localization processing allowed the identification of the click train emitter. Comparison between pair and alone conditions revealed that the click rates produced by Puck were significantly higher when jumping accompanied (median: 20.77 clicks.sec-1) than when jumping alone (median: 17.6 clicks. sec-1) (Wilcoxon signed Rank Test: $W=626$ $P=0.043$) (Figure 3)

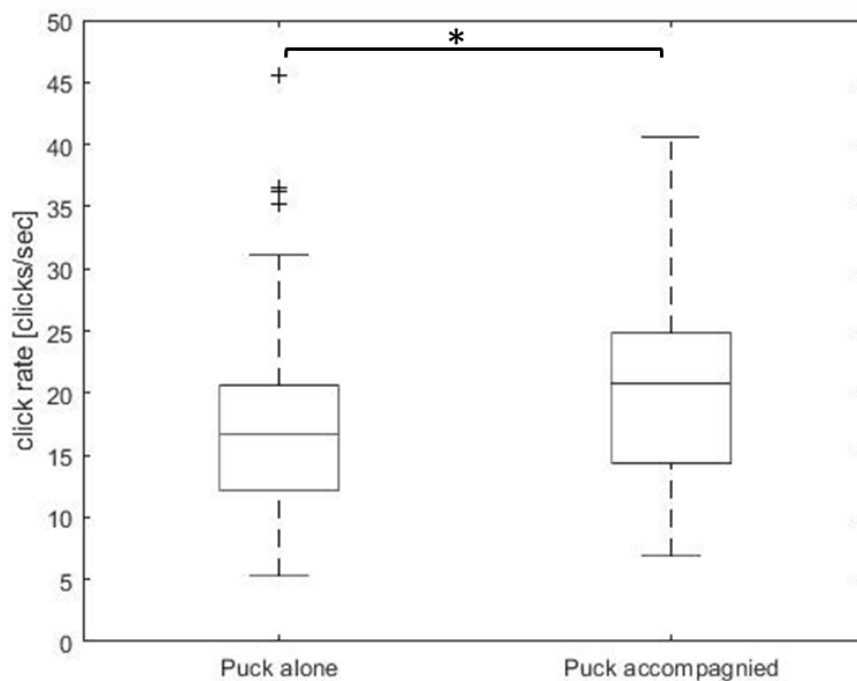


Figure 3: Comparison of click rates of click trains produced by Puck alone and accompanied. Boxes represent 25th and 75th percentiles. Whiskers correspond to the 1st and 99th centiles. + represents the outliers. * indicates P values < 0.05

DISCUSSION

Our results showed that dolphins performed the exercise all the time in synchrony despite the absence of any synchronization instruction; they produced click trains both when jumping alone and in pairs. When jumping alone, click rates of Puck were inferior to those of Kite and Linda. Click trains produced when jumping by pairs were presumably produced by only one individual. The click rates of these click trains did not significantly differ for Kite and Linda when jumping alone vs. when jumping by pairs. However, click trains produced by Puck when accompanied had a higher rate than the ones produced when jumping alone. The localization processing showed that the individual producing the click trains was Puck for 90%-100% of the successful localizations (Figure 2). Detailed analyses exclusively based on Puck clicks production confirmed a significant increase of her click rate when performing the exercise accompanied.

The results obtained from this study should be interpreted cautiously for several reasons: first, because of the schedule of the facility, we could only test three individuals and two different combinations of them for the collective jumps. Also, we wanted to let the animals move freely in the main pool and chose an appropriate location for the dolphins to perform their jump in order to do not interfere with their spontaneous acoustic behavior during the exercise, this measure has as a consequence a reduction of the efficiency of the localization processing to 19.8% of the total detected click trains. Our recording device was placed next to the wall of the pool to facilitate its deployment and control from the edge. The noise caused by the reverberation of the sounds against the walls of the pool made difficult the localization. In fact, during the emission of the click trains the animals could face the

opposite wall and their highly directional clicks bounce against it before reaching our hydrophones, these make the result of the localization point at the wall or appear as impossible in 80.2% times.

Animals spontaneously showed synchrony when performing the target exercise by pairs even if the gestural order given by the trainers was sent separately. This can be explained by the fact the dolphins have been performing the same exercise for more than ten years and spontaneously perform different exercises in synchrony without the need of being positively reinforced to do it (Vanderheul pers. com.). Such a spontaneous synchronization is also observed in the wild and it is already well known that free ranging dolphins spontaneously synchronize their movements and postures (Pryor and Kang-Shallenberger, 1991; Cusick and Herzing, 2014; Connor et al., 2006; Sakai et al., 2010; Connor et al, 1992; Connor and Smolker, 1996). The next question is now to highlight the kind of cues used by the animals to synchronize themselves. It may be assumed that dolphins use visual cues to produce simultaneous movements, which is possible in the clear waters of the facility. However, in nature these animals live often in habitats of limited visibility (Connor et al., 1998) in which visual cues cannot be sufficiently accurate to allow a perfect synchronization of behaviors. Although we do not exclude the possibility that visual cues were used to perform the synchronized exercise in this study, our results shows that the acoustic cues might also be relevant.

Surprisingly, no whistles or burst pulsed sounds were produced during the achievement of the jump exercise whether performed alone or by pair. Such kinds of sounds have been reported to play a role in communication and social interactions

(Herzing, 2000). The exercise asked to the animals might have needed vocalizations that serve mainly to navigate (as clicks). Moreover the animals know each other for a long time and they are used to perform this known exercise together . During the exercises there were only two animals in the pool, making easy for them to know with whom to perform the jump with. Under these conditions dolphins might have no need to socially interact during the exercise.

We observed that click trains are produced almost systematically before and after a jump (90% of time). This finding is not surprising given the navigation function of echolocation (Au, 1993). Thus, dolphins may use their sonar to orientate their bodies in the pool and choose the right moment to perform the jumps. The visual inspection of the click trains produced by the animals when jumping by pairs allowed us to deduce that they were produced by one single individual. A possible explanation is that one of the dolphins remains quiet to eavesdrop the clicks produced by the other, and uses this acoustic information (likely in combination with visual cues) to navigate and perform the jump as efficiently as it does when jumping alone. Supporting this hypothesis, an experimental study showed that dolphins can perform object recognition through echoic eavesdropping (Xitco and Roitblat, 1996). Our results then suggest that echoic eavesdropping might also be used for navigation. Now, the key question that may be raised is whether this role allocation is done randomly or depends on the dolphin's identity with specific animals tending to remain silent while others tend to produce the click trains.

The localization processing allowed us to identify the dolphin producing the click train only for 19.8% of detected click trains. Most localizations were not possible due to the

reverberation of the walls of the pool. However, we could assume that the probability of each click train to be localized is the same, and the reverberation acts in a random way. Thus, we could consider that our results constitute a representative sample and reflect what happens in most cases. We showed that in all but one successful localization, the click trains were produced by the same individual suggesting that one individual could acoustically lead the other during the exercises by pairs. Noteworthy, this individual appeared to be the oldest of the group. This female is probably the individual with the most experience in performing the jump exercise. Another hypothesis could be advanced to explain these results: Puck could be the most dominant female of the group as it has been described in captive females of bottlenose dolphins, in which the oldest ones (i.e. the most experienced) are also the most dominant (Samuels and Gifford, 1997). In our study, the dominant status of Puck may be expressed through her predominant acoustic activity when paired with a dominated individual. Moreover, Puck was the animal that produced lower click rate during the exercises when alone, probably because of the experience it had doing the exercise, which makes it needed less clicks to orientate and navigate while performing the jump.

Leadership has been defined as the situations when an individual steers the behavior of others (King et al., 2009) and it has been reported in highly dynamic fission-fusion species as free ranging bottlenose dolphins when travelling (Lewis et al., 2010). This study supports this theory and gives the first possible explanation for the mechanism used to synchronize movements. However more studies are needed to evidence which factors influence this leadership.

Finally, the leading dolphin, Puck, increases its click rate when performing the exercise accompanied, this changing in the click rate might serve to facilitate the coordinated movements. Nonetheless, it is necessary to test with other leader animals if the increase of the click rate occurs systematically during synchronous exercises.

In conclusion, this paper provides the first evidence that dolphins use acoustic cues, and more particularly click trains, to synchronize their movements possibly by eavesdropping the echoes produced by one individual that leads the navigation.

Acknowledgments

We would like to thank to the Boudewijn Sea Park (Bruges, Belgium) trainers and Nikolaas Colpaert for its invaluable collaboration with the development of this experiment, as well as Isabelle Charrier and the members of the Bioacoustics team (NeuroPSI) for its advice and support during the analysis of the data.

BIBLIOGRAPHY

Au, W. W., Floyd, R. W., Penner, R. H., & Murchison, A. E. (1974). Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *The Journal of the Acoustical Society of America*, 56(4), 1280-1290.

Au WWL. 1993. *The sonar of dolphins*. New York, NY: Springer-Verlag.

- Backwell, P. R. Y., Christy, J. H., & Passmore, N. I. (1999). Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology*, 105(5), 415-421.
- Blanchard, T. (2015). Innovation audio-visuel pour le suivi des grands dauphins [Audio-visual innovation for collect data on all dolphins present in a 360° space monitoring bottlenose dolphins] (Master's thesis). Ecole Nationale Supérieure d'Ingenieurs du Mans, Le Mans. France.
- Brando SI. 2010. Advances in husbandry training in marine mammal care programs. *Int J Comp Psychol* 23:777–791.
- Brownlee, S. M., & Norris, K. S. (1994). The acoustic domain. In K. S. Norris, B. Würsig, R. S. Wells, & M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 161-185). Berkeley, CA: University of California Press.
- Buck, J. (1988). Synchronous rhythmic flashing of fireflies. II. *The Quarterly review of biology*, 63(3), 265-289.
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceeding of the National Academy of Science USA*, 89, 987-990.
- Connor, R. C., & Smolker, R. A. (1996). 'Pop' goes the dolphins: A vocalization male bottlenose dolphins produce during consortships. *Behaviour*, 133, 643-662.
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in ecology & evolution*, 13(6), 228-232.

- Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour*, 72(6), 1371-1378.
- Cusick, J. A., & Herzing, D. L. (2014). The dynamic of aggression: How individual and group factors affect the long-term interspecific aggression between two sympatric species of dolphin. *Ethology*, 120, 287-303.
- López, B. D., & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. *Dolphins: Anatomy, behavior, and threats*, 129-148.
- Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 29(3).
- Grafe, T. U. (2003). Synchronized interdigitated calling in the Kuvangu running frog, *Kassina kuvangensis*. *Animal Behaviour*, 66(1), 127-136.
- Hastie, G. D., Wilson, B., Tufft, L. H., & Thompson, P. M. (2003). Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science*, 19(1), 74.
- Herskin, J., & Steffensen, J. F. (1998). Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. *Journal of Fish Biology*, 53(2), 366-376.
- Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: implications for a sound society. In *Hearing by whales and dolphins* (pp. 225-272). Springer New York.

- Herzing, D. L. (2015). Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas. *Anim Behav Cogn*, 2(1), 14-29.
- Janik, V. M. (2009). Acoustic communication in delphinids. *Advances in the Study of Behavior*, 40, 123-157.
- Janik, V. M., Simard, P., Sayigh, L. S., Mann, D., & Frankel, A. (2011). Chorussing in delphinids. *The Journal of the Acoustical Society of America*, 130, 2322.
- Johnson, C. M. (2015). The cognitive ecology of dolphin social engagement. *Dolphin communication and cognition*, 229-256.
- King, A. J., Johnson, D. D., & Van Vugt, M. (2009). The origins and evolution of leadership. *Current biology*, 19(19), R911-R916.
- Lewis, J. S., Wartzok, D., & Heithaus, M. R. (2011). Highly dynamic fission–fusion species can exhibit leadership when traveling. *Behavioral Ecology and Sociobiology*, 65(5), 1061-1069.
- Lopez-Marulanda, J., Adam, O., Blanchard, T., Vallée, M., Cazau, D., & Delfour, F. (2017). First Results of an Underwater 360° HD Audio-Video Device for Etho-Acoustical Studies on Bottlenose Dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 43(2), 162.
- Mann, J. & Smuts, B. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, 136, 529e566.

- Norris, K. S., & Schilt, C. R. (1988). Cooperative societies in three-dimensional space: on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. *Ethology and Sociobiology*, 9(2-4), 149-179.
- Pryor, K., & Shallenberger, I. K. (1991). Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the eastern tropical Pacific. *Dolphin societies: Discoveries and puzzles*, 161-196.
- Tremblay, Y., & Cherel, Y. (1999). Synchronous underwater foraging behavior in penguins. *Condor*, 179-185.
- Samuels, A., & Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science*, 13(1), 70-99.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: bodies and minds moving together. *Trends in cognitive sciences*, 10(2), 70-76.
- Sakai, M., Morisaka, T., Kogi, K., Hishii, T., & Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes*, 83(1), 48-53.
- Trainer, J. M., & McDonald, D. B. (1993). Vocal repertoire of the Long-tailed Manakin and its relation to male-male cooperation. *Condor*, 769-781.
- Tyack, P. L. (1999). Communication and cognition. *Biology of marine mammals*, 287-323.
- Xitco, M. J., & Roitblat, H. L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Learning & behavior*, 24(4), 355-365.

DISCUSSION

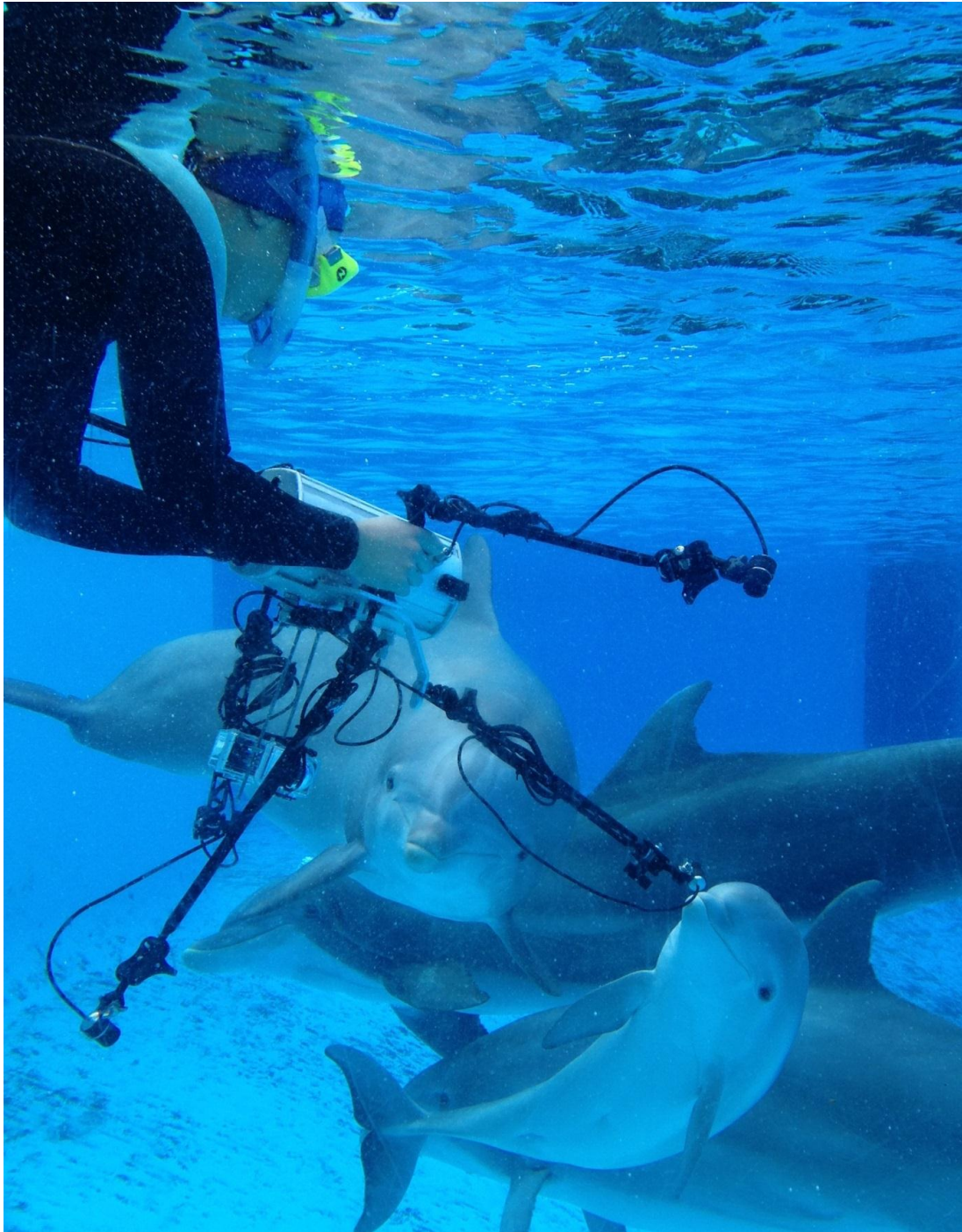


Photo: Parc Astérix

The studies conducted during my PhD thesis aims to contribute to the understanding of the acoustic communication and social behaviors of bottlenose dolphins. I initially described how the vocal activity and behavior varied in relationship with scheduled interactions with trainers. This led me to understand the need for new technologies that could identify the dolphin producing a sound allowing a fine-scale analysis of vocal behavior within the social group. The implementation of the BaBeL system allowed me to address such new research questions about dolphins' behaviors and more specifically their exploratory and synchronous behaviors.

1. How do dolphins under human care modulate their whistle repertoire according to human activity?

Chapter 1 and **2** revealed that dolphins modulate their whistle production as a function of their interactions with humans and this modulation varies between social groups. In the case of the dolphins in Parc Asterix (France), the whistle emission was higher after the training sessions than before; in contrast the dolphins from Boudewijn Sea Park (Belgium) produced more whistles before than after the training sessions. This variation could be explained by several differences between the two studied groups.

First, the group composition differed between the facilities (Table 1), which leads to different types of interactions between the animals: this might conceivably lead to the different use of vocalizations. Group composition has been reported as a factor influencing whistle emission in free-ranging dolphins (Hawkins and Gartside, 2010; Heiler *et al.*, 2016). For instance, mother–offspring interactions include various behaviors (e.g., teaching behaviors) (Bender *et al.*, 2009) and involve specific vocalizations (e.g., during periods of separation) (Smolker *et al.*, 1993). However, as

both studied groups had young dolphins at the time of the study, we cannot conclude that the differences found in the modulation of vocalizations are due to mother-offspring interactions. However, the two facilities present other group differences: during the second part of the study in Parc Asterix (France) the group included two adult males of 32 and 31 years old, while in Boudewijn Sea Park (Belgium) only one male (12 years old) was part of the group. As males can compete among themselves or form alliances to facilitate access to females in estrus (Connor *et al.*, 19921), it is possible that the presence of two adult males in Parc Asterix elicited more social interactions and vocalizations.

Table 1: Comparison of dolphins' group composition between Parc Asterix and Boudewijn Sea Parc facilities

Group Categories	Parc Astérix (November 2014)	Parc Astérix (May 2015)	Boudewijn Sea Park (February 2017)
Adult Females	4	4	5
Adult Males	1	2	1
Young females	0	0	1
Young males	4	2	1

Second, the animals might show different personalities that can also lead to differences in vocal activity (Bigersson *et al.*, 2014; Highfill and Kuczaj, 2007). Moreover, because the groups in captivity are formed artificially, social communication between individuals may or may not take place depending on their personality.

Third, there is one difference in the management of dolphins in these facilities: Parc Asterix's animals are never isolated, while Boudewijn Sea Park's dolphins are placed in different pools during the training sessions. The isolation of animals might increase the production of whistles (Esch *et al.*, 2009) and subsequently modulate the production of whistles before and after the training sessions. In chapter 2, I did not report the vocalizations produced during the training sessions themselves, but this work was conducted and the results showed that in Boudewijn Sea Park, most of the whistles are produced during the training sessions (Colpaert, 2017). Consequently, I suggest that the separation of the animals during the training sessions in Boudewijn Sea Park might increase the production of whistles and modulate the acoustic communication process between the animals in a way that they produce more whistles before than after the training sessions. In contrast, dolphins from Parc Asterix, that are never isolated, might prefer to communicate acoustically in the periods after the training sessions.

Despite these differences, a common result found in both facilities is the higher production of non-signature whistles with respect to signature whistles. This confirms what has been found previously in captivity, where dolphins' production of signature whistles is around 1% of total recorded whistles (Janik and Slater, 1998). This highlights the importance of focusing future research efforts on non-signature whistle production, which has received much less attention by the scientific community in comparison to signature whistles (Caldwell *et al.*, 1990; Janik, 2000; Janik and Sayigh, 2013; King *et al.*, 2014). Non-signature whistles are thought to have a role in bottlenose dolphin communication since they may transfer information: probably not the identity information seemingly contained in signature whistles, but more likely the emotional state of the animal or the behavioral context.

The observations carried out underwater in this project (**Chapter 2**) made it possible to establish the association between the non-signature whistle emission and some detailed behaviors. A positive correlation was found between the production of non-signature whistles and the slow swimming alone behavior, and a negative interaction was found between the non-signature whistle production and affiliative body contacts. These interactions cannot be interpreted as a causal relationship, but our results suggest that somehow non-signature whistle production might modulate or be modulated by some behaviors. Again, the localization of the dolphin emitting the non-signature whistle is necessary to better understand these interactions. I suggest that non-signature whistles might play a role in the cohesion of the animals as when they swim slowly and alone they produce more non-signature whistles probably to search for proximity or contact and when they are already in contact they do not need to produce these vocalizations, which reflects the decrease in their production. The fact that the animals do not use instead signature whistles as cohesion calls (Janik and Slater, 1998) under these circumstances, could be explained because the animals are placed in the same pool and are in visual contact to each other, so they do not need to transfer information about their identity to regroup.

This study's underwater behavioral observations allowed me to highlight the importance of this approach in starting to detail the behaviors occurring in conjunction with non-signature whistles. In the wild, it is rare to find the necessary water clarity and sea conditions to be able to conduct these detailed descriptions of behavior (Würsig and Pearson, 2015). Such conditions have been found during several studies in particular spots of the world in which the water clarity water allows a proper behavioral observation (Dudzinski, 1998; Herzing, 1996; Marten *et al* 2001). Dudzinski (1998) described specific affiliative contact or agonistic behaviors and

showed that the concurrent vocalizations (whistles and burst pulsed sounds) probably served to emphasize the message in Atlantic spotted dolphins (*Stenella frontalis*) in Bahamas. Also in the same area and with the same species, Herzing (1996) found that signature whistles were produced mostly during mother-calf interactions and alloparental care while burst-pulsed sounds were produced mostly during agonistic interactions. Marten *et al.* (2001) provided observations that supported the acoustic predation hypothesis, in which killer whales (*Orcinus orca*) and bottlenose dolphins (*T. truncatus*) are thought to kill their prey with high amplitude sounds. All these studies provide valuable information about the behavior of the animals underwater, and with the aim of supplementing this, Chapter 2 supplies a first approach to the study of non-signature whistles and their concurrent underwater behaviors.

In order to reveal the role of the different non-signature whistles in the communication of bottlenose dolphins it is necessary to identify the dolphin producing the vocalization and to note the behavioral response of the animals surrounding the emitter. This need prompted the development of a system to identify the dolphin emitting a vocalization in a 3D environment.

2. Applications of the BaBeL system to better understand acoustic communication in a social group of dolphins.

With the implementation of the BaBeL system I aimed to localize the dolphin producing a vocalization. However, with the actual BaBeL device and software we created, in captive conditions this method worked only for click trains due to the reverberation caused by the walls of the pool. In the wild, the method worked both for whistles and click trains, but unfortunately, my dataset on wild bottlenose dolphins

was too restricted since I was not lucky enough to find and record a substantial number of highly vocalizing free-ranging animals. Despite this, the BaBeL system allowed me to find interesting results regarding the click train production both in the wild and in captivity.

Chapter 3 addresses the implementation of the BaBeL system in the wild. I recorded bottlenose dolphins' exploratory behavior through echolocation in three situations in which the group spontaneously approached the BaBeL device. In each case, this behavior was carried out by only one individual of the group, and interestingly this animal was never the first to enter in visual contact with the observers. This lead me to suggest that dolphins might eavesdrop on the returning echoes of their conspecific (Gregg *et al.*, 2007) and that exploratory behavior might only be carried out by some individuals in the group. The fact that the echolocating individuals were never the first leading the movement of the group, i.e., the first in visual contact with the observers, enabled me to suggest that the exploratory activity towards a new object might be distributed between some individuals that are not the same that lead the movement of the group when travelling (Lewis *et al.*, 2010). Nonetheless, more observations in the wild are needed to provide more information about this phenomenon.

The immersion of BaBeL among a group of captive dolphins elicited exploratory behavior from the animals through echolocation clicks, for which the returning echoes could be perceived both by the producer and by any other individual in the pool through eavesdropping (Gregg *et al.*, 2007). This exploratory response towards a new object, allowed me to analyze the exploratory behavior of a dolphin calf within its social group (**Chapter 4**). Previous studies have used several indicators to identify when calves produce click trains, including bubblestream production (Reiss, 1988; Favaro *et al.*, 2013), the intensity of the signal and the position of the calves with

respect to the hydrophone (Lindhard 1988), the presence of head scanning behaviors at the same time as click recordings (Favaro *et al.* 2013) and the orientation and relative position of calves when their mothers were distracted by the trainers (Harder *et al.*, 2016). All these methods are dependent on the position of the calves with respect to the hydrophone and localize the vocalizing dolphin using inexact approaches, resulting in the analysis of click trains only emitted under certain conditions. In **chapter 4**, using the BaBeL system we were able to accurately identify the clicks as produced by the calf, and clicks were recorded regardless the position of the calf or its relative position to its mother, allowing us to observe the spontaneous production of echolocation clicks under several circumstances. We therefore were able to correlate the visual laterality concurrent with click production, to determine whether the calf produced a click train while accompanied by its mother or alone. In fact, the calf used mostly its right eye while echolocating. This result is consistent with previous studies in visual laterality (von Fersen, 2000; Kilian *et al.* 2000; Yaman *et al.* 2002; Delfour and Marten 2005). Also, the calf was positioned mostly at its mothers' left side while approaching to BaBeL, in contrast with what has been found for free ranging belugas and killer whales (Karenina *et al.*, 2010; Karenina *et al.*, 2013; Hill *et al.*, 2017). This may be due to differences in the lateralization tendencies between these species, or because the mother chose to place herself between her calf and the device.

Finally, the implementation of BaBeL allowed me to better understand the mechanism of synchronization of dolphins during a training task (Chapter 5). At the beginning I expected to detect not only echolocation clicks but whistles and burst-pulsed sounds during the synchronization tasks. The absence of whistles and burst-pulsed sounds during my recordings suggests that these dolphins, and perhaps

others, do not use these kind of vocalizations to synchronize their movements but instead rely on the production of click trains.

The fact that only one dolphin produced these click trains during the performance of the pair exercise, suggests one more time the animals probably eavesdrop on the echoes produced by the clicks of their congeners, in order to adapt their movements and achieve synchrony. Moreover, the leader of the synchronous movements was the oldest female of the group. This female is the most experienced individual in performing the exercise and it is also the most dominant female of the group. Older females are often found to be highly dominant in captive bottlenose dolphins (Samuels and Gifford, 1997). According to this, I suggest that during my experiments, the oldest and probably the most dominant female of the group carried out the echolocation task for navigate and orientate herself and the other animals performing the target exercise.

If click trains are used to transfer information from one individual to another in order to coordinate their behavior, these vocalizations should therefore be considered as a way to communicate in this species. This opens a new paradigm in the understanding of the communication network of bottlenose dolphins. Traditionally, clicks have been described to have an echolocation function (Au, 1993) while whistles and burst pulsed sounds are used in social interactions (reviewed in Herzing, 2000). However, my results suggest clicks play also a role in the communication of the species.

In delphinid species that do not produce whistles, such as Hector's Dolphin (*Cephalorhynchus hectorii*) and dusky dolphins (*Lagenorhynchus obscurus*) it has been suggested that clicks are used for communication (Dawson, 1991; Würsig and Würsig, 2010). However, as click train production is present in all odontocetes, we

can consider it an ancestral character of whistle production in regards to delphinid evolution. If some species of delphinids use this ancestral character to communicate, it could be that whistling delphinids might also use the information contained in click trains to communicate, at least under some circumstances, such as the needed to synchronize movements, which is the case with bottlenose dolphins. Future research should therefore investigate the likely communicative function of clicks in whistling cetacean species.

The BaBeL system is limited by several factors. Firstly, it needs sufficient water clarity to guarantee good visibility underwater, and this is only possible in captivity or in a few places in the world (Würsig and Pearson, 2015). Secondly, the system works well for click train localization but is less accurate for whistle localization; moreover, due to the reverberation of the walls of the pool, the system in its current state cannot be used for whistles of dolphins under human care. Thirdly, the sampling frequency in the current version of the system is limited to 96 kHz, which restricts the information we can obtain from click trains (e.g. peak frequency), that are found to be above this value. However, most of the vocalizations produced by the animals (e.g. whistles and burst pulsed sounds) can be recorded at this sampling frequency.

3. Conclusions

To conclude, human scheduled training sessions modulate whistle production of dolphins under human care. This modulation varies with different groups according to the management practices of in different facilities.

More importance should be given to the study of non-signature whistles both in captivity and in the wild. Studying these vocalizations with concurrent underwater

behavioral observations should provide the information needed to interpret the role of non-signature whistles in the bottlenose dolphins' communication network.

It is necessary to identify the dolphin emitting a vocalization and the behavioral response of its congeners in order to understand the role of this vocalization.

The use of BaBeL system allowed me to investigate about the use of click trains to explore novel objects in the wild, and their role in synchronizing locomotion in captivity. This uncovers a new paradigm with many future lines of research regarding the use of echolocation clicks for communication in this species and beyond.

4. Perspectives

The use of the BaBeL system provides valuable information about the localization and identification of the individual producing a vocalization. This should be used on wild delphinids for example to inquire about their exploratory behavior and the cooperative foraging strategies in clear waters.

Some improvements could be made to the BaBeL system. First, the 360° camera will be replaced by a higher performing device (e.g. Kolor) that gives a better image quality, enabling better identification of the animals and fewer blind angles. Second, the current recorder could be replaced by a sound card that enables recording at sampling frequencies above 96 kHz, which will allow to the recording and analyzing other aspects of click trains, such as the peak frequencies. Third, the entire system could have its own low-noise propulsion system with a remote control; this would facilitate its use without an observer in the water, which may modify the animal's behavior.

The use of BaBeL system can be extended to other cetacean species. For instance, as the system functions well for analyzing click production, it would be interesting to

test it with sperm whales (*Physeter macrocephalus*) since they are known to communicate through pulsed signals (Madsen *et al.*, 2002).

BIBLIOGRAPHY



Photo: Parc Astérix

- Akiyama, J., & Ohta, M. (2007). Increased number of whistles of bottlenose dolphins, *Tursiops truncatus*, arising from interaction with people. *Journal of Veterinary Medical Science*, 69(2), 165-170.
- Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental psychobiology*, 5(4), 297-305.
- Andre, M., & Kamminga, C. (2000). Rhythmic dimension in the echolocation click trains of sperm whales: A possible function of identification and communication. *Journal of the Marine Biological Association of the United Kingdom*, 80(1), 163-169.
- Amos, B., Schloetterer, C., & Tautz, D. (1993). Social structure of pilot whales revealed by analytical DNA profiling. *SCIENCE-NEW YORK THEN WASHINGTON-*, 260, 670-670.
- Au, W. W., & Snyder, K. J. (1980). Long-range target detection in open waters by an echolocating Atlantic Bottlenose dolphin (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, 68(4), 1077-1084.
- Au, W. W., Penner, R. H., & Kadane, J. (1982). Acoustic behavior of echolocating Atlantic bottlenose dolphins. *The Journal of the Acoustical Society of America*, 71(5), 1269-1275.
- Au, W.W.L. (1993). *The Sonar of Dolphins*. New York: Springer-Verlag. 277 pp.
- Au, W. W., & Hastings, M. C. (2008). *Principles of marine bioacoustics* (pp. 121-174). New York: Springer.
- Baird, R. W., & Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, 78(12), 2096-2105.

- Barrett, L., & Würsig, B. (2014). Why dolphins are not aquatic apes. *Animal Behavior and Cognition*, 1(1), 1-18.
- Bazúa-Durán, C. (2004). Differences in the whistle characteristics and repertoire of bottlenose and spinner dolphins. *Anais da Academia Brasileira de Ciências*, 76(2), 386-392.
- Bigg, M. A. (1987). Killer whales: a study of their identification, genealogy, and natural history in British Columbia and Washington State. Nanaimo, BC: Phantom.
- Birgersson, S., Birot de la Pommeraye, S., & Delfour, F. (2014) Dolphin personality study based on ethology and social network theory. Germany: Lambert Academic Publishing.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). Principles of animal communication.
- Bruck, J. N. (2013). Decades-long social memory in bottlenose dolphins. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1768), 20131726.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature*, 207(4995), 434-435.
- Caldwell MC, Caldwell DK, Tyack PL. 1990. Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood, Reeves RR, editors. *The bottlenose dolphin: recent progress in research*. San Diego: Academic Press. p 199–234.
- Colpaert, N. Emission Of Signature Whistles By 8 Bottlenose Dolphins (*Tursiops Truncatus*) Under Human Care. Master Thesis. University of Ghent. Belgium.

- Clapham, P. J. (1993). Social organization of humpback whales on a North Atlantic feeding ground. In *Symposia of the Zoological Society of London* (Vol. 66, pp. 131-145).
- Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Animal Behaviour*, 103, 223-235.
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in ecology & evolution*, 13(6), 228-232.
- Connor, R. C., Wells, R. S., Mann, J. A. N. E. T., & Read, A. J. (2000). The bottlenose dolphin. *Cetacean societies*, 91-125.
- Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H. (1998). Social evolution in toothed whales. *Trends Ecol.Evol.* 13, 228–232.
- Connor, R. C., & Mann, J. (2006). Social cognition in the wild: Machiavellian dolphins. *Rational animals*, 329-367.
- Cook MLH, Sayigh LS, Blum JE, Wells RS. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proc Biol Sci* 271:1043–1049. Available online at: <http://doi.org/10.1098/rspb.2003.2610>.
- Cranford, T. W., Amundin, M., & Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *Journal of morphology*, 228(3), 223-285.
- Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., ... & Ridgway, S. H. (2011). Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*):

- evidence for two sonar sources. *Journal of Experimental Marine Biology and Ecology*, 407(1), 81-96.
- Cranford, T. W., Amundin, M., & Krysl, P. (2015). Sound production and sound reception in delphinoids. *Dolphin Communication and Cognition: Past, Present, and Future*, 328.
- Dawson, S. M. (1991). Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology*, 88(4), 265-276.
- Dudzinski, K. A., Clark, C. W., & Würsig, B. (1995). A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals*, 21, 187-194.
- Dudzinski, K. M., & Ribic, C. A. (2017). Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal Behavior and Cognition*, 4(1), 30-48.
- Dudzinski K.M., Hill H.M. (2018) Cetacean Communication. In: Vonk J., Shackelford T. (eds) *Encyclopedia of Animal Cognition and Behavior*. Springer, Cham
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella fimntalis*). *Aquatic Mammals*, 24, 129-142.
- Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj, S. A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioural processes*, 80(2), 182-190.
- Dudzinski, K. M., Gregg, J. D., Paulos, R. D., & Kuczaj, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. *Behavioural processes*, 84(2), 559-567.

- Dziedzic, A., & De Buffrenil, V. (1989). Acoustic signals of the Commerson's dolphin, *Cephalorhynchus commersonii*, in the Kerguelen Islands. *Journal of Mammalogy*, 70(2), 449-452.
- Esch, H. C., Sayigh, L. S., & Wells, R. S. (2009a). Quantifying parameters of bottlenose dolphin signature whistles.
- Evans, W. E., and Powell, B. A. (1967). "Discrimination of Different Metallic Plates by an Echolocating Delphinid," in *Animal Sonar Systems: Biology and Bionics*, edited by R. G. Busnel (Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France), pp. 363-383.
- Esch, H. C., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, 90(3), 638-650.
- Favaro, L., Gnone, G., & Pessani, D. (2013). Postnatal development of echolocation abilities in a bottlenose dolphin (*Tursiops truncatus*): Temporal organization. *Zoo biology*, 32(2), 210-215.
- Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 29(3).
- Fripp D, Owen C, Quintana-Rizzo E, *et al.* 2005. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Anim Cogn* 8:17–26.
- Fripp, D. (2005), Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, 21: 29–44. doi: 10.1111/j.1748-7692.2005.tb01206.x

- Fripp, D. (2006), Bubblestream whistles are not representative of bottlenose dolphin whistle repertoires reply to McCowan. *Marine Mammal Science*, 22: 496–501.
doi: 10.1111/j.1748-7692.2006.00028.x
- Gallup, G. G. (1970). Chimpanzees: self-recognition. *Science*, 167(3914), 86-87.
- Geisler JH, Uhen MD. (2003). Morphological support for a close relationship between hippos and whales. *J. Vertebrate Paleontol.* 23, 991–996.
- Geisler JH, Uhen MD. (2005). Phylogenetic relationships of extinct Cetartiodactyls: results of simultaneous analyses of molecular, morphological, and stratigraphic data. *J. Mammal. Evol.* 12, 145– 160.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior.*
- Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Advances in Marine Biology*, 53, 195-294.
- Gregg, J. D., Dudzinski, K. M., & Smith, H. V. (2007). Do dolphins eavesdrop on the echolocation signals of conspecifics?. *International Journal of Comparative Psychology*, 20(1).
- Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology*, 24(3).
- Harder, J. H., Hill, H. M., Dudzinski, K. M., Sanabria, K. T., Guarino, S., Kuczaj, I. I., & Stan, A. (2016). The Development of Echolocation in Bottlenose Dolphins. *International Journal of Comparative Psychology*, 29(1).

- Harley, H. E., Roitblat, H. L., & Nachtigall, P. E. (1996). Object representation in the bottlenose dolphin (*Tursiops truncatus*): Integration of visual and echoic information. *Journal of Experimental Psychology: Animal Behavior Processes*, 22(2), 164.
- Heimlich-Boran, S. L. (1986). Cohesive relationships among Puget Sound killer whales. *Behavioral biology of killer whales*. Alan R. Liss, New York, New York, 251-284.
- Herman, L. M. (1986). Cognition and language competencies of bottlenosed dolphins. *Dolphin cognition and behavior: A comparative approach*, 221-252.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins.
- Herman, L. M., Hovancik, J. R., Gory, J. D., & Bradshaw, G. L. (1989). Generalization of visual matching by a bottlenosed dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual and auditory materials. *Journal of Experimental Psychology: Animal Behavior Processes*, 15(2), 124.
- Herman, L. M., & Gordon, J. A. (1974). Auditory delayed matching in the bottlenose dolphin. *Journal of the Experimental Analysis of Behavior*, 21(1), 19-26.
- Herman LM, Tavolga WN (1980) The communication systems of cetaceans. In: Herman LM (ed) *Cetacean behavior: mechanisms and functions*. Wiley, New York, pp 149–209
- Herman, L. M. (2010). What laboratory research has told us about dolphin cognition. *International Journal of Comparative Psychology*, 23(3).
- Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: implications for a sound society. In *Hearing by whales and dolphins* (pp. 225-272). Springer New York.

- Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, 22, 61-80.
- Hickey, R., Berrow, S., & Goold, J. (2009, September). Towards a bottlenose dolphin whistle ethogram from the Shannon Estuary, Ireland. In *Biology and Environment: Proceedings of the Royal Irish Academy* (pp. 89-94). Royal Irish Academy.
- Hill, H. M., Dietrich, S., Yeater, D., McKinnon, M., Miller, M., Aibel, S., & Dove, A. (2015). Developing a catalog of socio-sexual behaviors of beluga whales (*Delphinapterus leucas*) in the care of humans.
- Janik, V. M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1446), 923-927.
- Janik VM. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* 289:1355–1357. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10958783>
- Janik, V. M. (2015). Play in dolphins. *Current Biology*, 25(1), R7-R8.
- Janik VM, Todt D, Dehnhardt G. (1994). Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. *Behav Ecol Sociobiol* 35:243–248.
- Janik V, Slater P. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim Behav* 56:829–838.
- Janik, V.M. (2009). Acoustic communication in delphinids. In: *Advances in the Study of Behavior* (Naguib, M.&Janik, V.M., eds). Academic Press, Burlington, pp. 123—157.

- Janik, V. M., & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology A*, 199(6), 479-489.
- Jefferson, T. A., Webber, M. A., & Pitman, R. L. (2011). *Marine mammals of the world: a comprehensive guide to their identification*. Academic Press.
- Johnson, C. M., & Norris, K. S. (1986). Delphinid social organization and social behavior. *Dolphin cognition and behavior: A comparative approach*, 335-346.
- Johnstone, R.A. 1997. The evolution of animal signals. In: *Behavioral Ecology. An Evolutionary Approach*. 4th eds. (Eds., Krebs, J.R. and Davies, N.B.) pp.155-178. Wiley-Blackwell Science, Oxford.
- Kamiya, T. O. S. H. I. R. O., & Pirlot, P. A. U. L. (1974). Brain morphogenesis in *Stenella coeruleoalba*. *Sci. Rep. Whales Res. Inst*, 26, 245-253.
- King SL, Sayigh LS, Wells RS, Fellner W, Janik VM. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proc Biol Sci* 280:20130053.
- King, S. L., & Janik, V. M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences*, 110(32), 13216-13221.
- King SL, Harley HE, JanikVM. 2014. The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. *Anim Behav* 96:79–86.
- Kremers, D., Célérier, A., Schaal, B., Campagna, S., Trabalon, M., Böye, M., ... & Lemasson, A. (2016). Sensory perception in cetaceans: Part II—Promising experimental approaches to study chemoreception in dolphins. *Frontiers in Ecology and Evolution*, 4, 50.

- Kuczaj II, S. A., & Yeater, D. B. (2006). Dolphin imitation: Who, what, when, and why?. *Aquatic Mammals*, 32(4), 413.
- Kuznetzov, V. B. (1990) Chemical sense of dolphins: Quasi olfaction. In: *Sensory Abilities of Cetaceans* (eds J.A. Thomas & R. A. Kastelein). Plenum Press, New York, 481-504.
- Lammers, M. O., & Au, W. W. (2003). Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): A signal feature to cue direction of movement?. *Marine Mammal Science*, 19(2), 249-264.
- Lammers, M. O., Au, W. W. L., Aubauer, R., & Nachtigall, P. E. (2004). A comparative analysis of the pulsed emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). *Echolocation in bats and dolphins*, 414-419.
- Lammers, M. O., & Oswald, J. N. (2015). Analyzing the acoustic communication of dolphins. *Dolphin communication and cognition: Past, present, and future*, 107.
- Lewis, M. (1991). Ways of knowing: Objective self-awareness or consciousness. *Developmental review*, 11(3), 231-243.
- Lilly, J. C. (1962). Vocal behavior of the bottlenose dolphin. *Proceedings of the American Philosophical Society*, 106(6), 520-529.
- Lindhard M (1988) Apparent sonar clicks from a captive bottlenosed dolphin, *Tursiops truncatus*, when 2, 7 and 38 weeks old. In Nachtigall PE, Moore PW (eds) *Animal sonar: processes and performance*. Plenum Press, New York, vol 156 pp 109-113

- Ljungblad, D. K., Thompson, P. O., & Moore, S. E. (1982). Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. *The Journal of the Acoustical Society of America*, 71(2), 477-482.
- López, B. D. (2011). Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: influence of behaviour. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 76(2), 180-189.
- López, B. D., & Shirai, J. A. B. (2009). Mediterranean common bottlenose dolphin's repertoire and communication use. *Dolphins: Anatomy, behavior, and threats*, 129-148.
- Mackay, R. S., & Liaw, H. M. (1981). Dolphin vocalization mechanisms. *Science*, 212(4495), 676-678.
- Madsen, P., Wahlberg, M., & Møhl, B. (2002). Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology*, 53(1), 31-41.
- Madsen, P. T., Jensen, F. H., Carder, D., & Ridgway, S. (2012). Dolphin whistles: a functional misnomer revealed by heliox breathing. *Biology letters*, 8(2), 211-213.
- Madsen, P. T., Lammers, M., Wisniewska, D., & Beedholm, K. (2013). Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: clicking on the right side and whistling on the left side. *Journal of experimental biology*, 216(21), 4091-4102.
- Mann, J. (Ed.). (2000). *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press.

- Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Phil. Trans. R. Soc. B*, 368(1630), 20120424.
- Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature communications*, 3, 980.
- Mann, J. A. N. E. T., & Sargeant, B. R. O. O. K. E. (2003). Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). *The biology of traditions: Models and evidence*, 236-266.
- Marino, L., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., ... & Rendell, L. (2007). Cetaceans have complex brains for complex cognition. *PLoS biology*, 5(5), e139.
- Marten, K., Shariff, K., Psarakos, S., & White, D. J. (1996). Ring bubbles of dolphins. *Scientific American*, 275(2), 82-87.
- May-Collado, L. J., Agnarsson, I., & Wartzok, D. (2007). Reexamining the relationship between body size and tonal signals frequency in whales: a comparative approach using a novel phylogeny. *Marine Mammal Science*, 23(3), 524-552.
- May-Collado, L. J., & Wartzok, D. (2008). A comparison of bottlenose dolphin whistles in the Atlantic Ocean: factors promoting whistle variation. *Journal of Mammalogy*, 89(5), 1229-1240.
- Maynard Smith, J. and Harper, D. (2003). *Animal Signals*. Oxford University Press, Oxford.

- McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, 109(3), 242.
- Miller, P. J. (2002). Mixed-directionality of killer whale stereotyped calls: a direction of movement cue?. *Behavioral Ecology and Sociobiology*, 52(3), 262-270.
- Morgane, P. J., & Jacobs, M. S. (1972). Comparative anatomy of the cetacean nervous system. *Functional anatomy of marine mammals*, 1, 117-244.
- Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *The Journal of the Acoustical Society of America*, 104(3), 1679-1688.
- Norris, K. S., & Dohl, T. P. (1979). The structure and functions of cetacean schools. CALIFORNIA UNIV SANTA CRUZ CENTER FOR COASTAL MARINE STUDIES.
- Norris, K. S., Wursig, B., Wells, R. S., & Wursig, M. (1994). The Hawaiian spinner dolphin. Univ of California Press.
- Orbach, D. N., Packard, J. M., & Würsig, B. (2014). Mating group size in dusky dolphins (*Lagenorhynchus obscurus*): costs and benefits of scramble competition. *Ethology*, 120(8), 804-815.
- Overstrom, N. A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biology*, 2(2), 93-103.
- Pack, A. A. (2015). Experimental studies of dolphin cognitive abilities. *Dolphin communication and cognition*, 175-200.

- Payne, R., & Webb, D. (1971). Orientation by means of long range acoustic signaling in baleen whales. *Annals of the New York Academy of Sciences*, 188(1), 110-141.
- Pearson, H. C. (2011). Sociability of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*): understanding evolutionary pathways toward social convergence. *Evolutionary Anthropology: Issues, News, and Reviews*, 20(3), 85-95.
- Penner, R. H. (1988). Attention and detection in dolphin echolocation. In *Animal Sonar* (pp. 707-713). Springer US.
- Perrin, W. F., & Mesnick, S. L. (2003). Sexual ecology of the spinner dolphin, *Stenella longirostris*: geographic variation in mating system. *Marine Mammal Science*, 19(3), 462-483.
- Perrin, W. F., Würsig, B., & Thewissen, J. G. M. (Eds.). (2009). *Encyclopedia of marine mammals*. Academic Press.
- Plotnik, J. M., De Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences*, 103(45), 17053-17057.
- Pryor, K. W. (1990). Non-acoustic communication in small cetaceans: glance, touch, position, gesture, and bubbles. In *Sensory abilities of cetaceans* (pp. 537-544). Springer US.
- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS biology*, 6(8), e202.

- Rasmussen, M. H., & Miller, L. A. (2002). Whistles and clicks from white-beaked dolphins, *Lagenorhynchus albirostris*, recorded in Faxaflói Bay, Iceland. *Aquatic Mammals*, 28(1), 78-89.
- Reiss D (1988) Observations on the development of echolocation in young bottlenose dolphins. In Nachtigall PR, Moore PWB (eds) *Animal sonar: Processes and performance*. Plenum Publishing Corporation, New York, pp 121-127
- Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences*, 98(10), 5937-5942.
- Reisinger, R. R., Hoelzel, A. R., & de Bruyn, P. J. (2017). Kinship and association in a highly social apex predator population, killer whales at Marion Island. *Behavioral Ecology*, 28(3), 750-759.
- Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*.. *Journal of Comparative Psychology*, 98(1), 10.
- Richardson, W. J., Greene Jr, C. R., Malme, C. I., & Thomson, D. H. (2013). *Marine mammals and noise*. Academic press.
- Ridgway, S., Carder, D., Finneran, J., Keogh, M., Kamolnick, T., Todd, M., & Goldblatt, A. (2006). Dolphin continuous auditory vigilance for five days. *Journal of Experimental Biology*, 209(18), 3621-3628.
- Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, 22(4), 966-978.

- Sayigh L, Tyack P, Wells R, Scott M. 1990. Signature whistles of freeranging bottlenose dolphins *Tursiops truncatus*: stability and motheroffspring comparisons. *Behav Ecol Sociobiol* 26:247–260. Available online at: <http://doi.org/10.1007/BF00178318>
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D., & Irvine, A. B. (1999). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal behaviour*, 57(1), 41-50.
- Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB. 1995. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behav Ecol Sociobiol* 36:171–177
- Sayigh, L., Dziki, A., Janik, V., Kim, E., McHugh, K., Tyack, P. L., ... & Jensen, F. H. (2017). Non-whistle sounds used in bottlenose dolphin aggressive interactions recorded on digital acoustic tags. *The Journal of the Acoustical Society of America*, 141(5), 3947-3947.
- Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of information*. University Illinois Press, Urbana.
- Simmons, A.M. 2003. Perspectives an progress in animal acoustic communication. In: *Acousit communication* (Eds., Simmons, A.M., Popper, A.N. and Fay, R.R.) pp.1-4. Springer, New York.
- Sinclair, J. G. (1966). The olfactory complex of dolphin embryos. *Texas reports on biology and medicine*, 24(3), 426.
- Smolker RA, Mann J, Smuts BB. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav Ecol Sociobiol* 33:393–402. Available online at: <http://doi.org/10.1007/BF00170254>

- Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, 123(1), 38-69.
- Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (*Delphinidae*, *Tursiops* sp.): a foraging specialization involving tool use?. *Ethology*, 103(6), 454-465.
- Thomas, R. E., Fristrup, K. M., & Tyack, P. L. (2002). Linking the sounds of dolphins to their locations and behavior using video and multichannel acoustic recordings. *The Journal of the Acoustical Society of America*, 112(4), 1692-1701.
- Thomas, J. A., & Turl, C. W. (1990). Echolocation characteristics and range detection threshold of a false killer whale (*Pseudorca crassidens*). In *Sensory abilities of cetaceans* (pp. 321-334). Springer, Boston, MA.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). In search of the uniquely human. *Behavioral and brain sciences*, 28(5), 721-727.
- Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral ecology and sociobiology*, 8(2), 105-116.
- Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles?. *Behavioral Ecology and Sociobiology*, 18(4), 251-257.
- Tyack, P. L. (1999). Communication and cognition. In: *Biology of marine mammals*, 287-323.

- Tyack, P. L., & Clark, C. W. (2000). Communication and acoustic behavior of dolphins and whales. In *Hearing by whales and dolphins* (pp. 156-224). Springer, New York, NY.
- Uhen, M. D. (2007). Evolution of marine mammals: back to the sea after 300 million years. *Anat. Rec.* 290(6), 514–22. doi:10.1002/ar.20545
- Wartzok, D. O. U. G. L. A. S., & Ketten, D. R. (1999). Marine mammal sensory systems. *Biology of marine mammals*, 1, 117.
- Watkins, W. A., & Schevill, W. E. (1974). Listening to Hawaiian spinner porpoises, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *Journal of Mammalogy*, 55(2), 319-328. doi: <http://dx.doi.org/10.2307/1379001>
- Watwood SL, Tyack PL, Wells RS. 2004. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behav Ecol Sociobiol* 55:531–543.
- Watwood SL, Owen EC, Tyack PL, Wells RS. 2005. Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. *Anim Behav* 69:1373–1386.
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In *Current mammalogy* (pp. 247-305). Springer, Boston, MA.
- Wells, S., Boness D.J., and Rathbun, G.B. (1999) Behavior. In: *Biology of Marine Mammals* (Eds., Reynolds, J.E. and Rommel S.A.). pp 324-422. Smithsonian Institution.
- Wells, R. S. (2003). Dolphin social complexity: Lessons from long-term study and life history.

- Wells, R. S., & Scott, M. D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Report of the International Whaling Commission, (12).
- Würsig, B., & Pearson, H. C. (2015). Dolphin societies: structure and function. *Dolphin Communications and Cognition: Past, Present, and Future*. DL Herzing and CM Johnson (eds.). MIT Press, Cambridge, Massachusetts, 77-105.
- Xitco, M. J., & Roitblat, H. L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Learning & behavior*, 24(4), 355-365.

Titre : Communication acoustique et comportement social chez les grands dauphins (*Tursiops truncatus*)

Mots clés : sifflements, clics, comportements, localisation

Résumé : Les grands dauphins sont des cétacés sociaux qui se servent principalement du canal acoustique pour communiquer sur de longues distances ou dans des habitats dont la visibilité est limitée. Il y a un manque général d'information concernant l'utilisation de cette communication acoustique au sein de son groupe social. Cependant, la production vocale des grands dauphins comprend des sifflements, des clics et des sons pulsés en rafale, avec certains sifflements appelés « signatures sifflées » qui pourraient être utilisés pour s'adresser les uns aux autres.

Au cours de cette thèse, nous avons développé un système facilement déployable qui identifie l'animal produisant le son et permet des observations comportementales sous-marines simultanées. Nous avons testé cette méthodologie avec des grands dauphins en liberté et en captivité.

La présente thèse de doctorat vise à mieux comprendre la communication des grands dauphins au sein de leur groupe social.

D'abord, j'ai développé deux études visant à décrire comment l'activité vocale des dauphins captifs varie en relation avec le comportement et l'interaction avec les humains.

Deuxièmement, je présente la conception et la mise en œuvre d'une méthodologie innovante (système BaBeL) qui permet la localisation du dauphin vocalisant dans un environnement tridimensionnel, et qui peut être utilisé en captivité et avec des dauphins en liberté. Enfin, je présente deux applications de cette méthodologie de localisation pour aborder des questions de recherche concernant le comportement exploratoire d'une jeune dauphin et l'utilisation de vocalisations pour des mouvements coordonnés chez les grands dauphins.

Title: Acoustic Communication and Social Behavior in Bottlenose Dolphins (*Tursiops truncatus*)

Keywords: whistles, click train, behaviors, localization

Abstract: Bottlenose dolphins are highly social cetaceans that strongly rely on acoustic communication and signaling. The diversity of sounds emitted by the species has been structurally classified in whistles, clicks and burst-pulsed sounds, with some whistles called « signature whistles » that are used as cohesion calls.

During this thesis, we developed an easily deployable system that identifies the animal producing sound and allows simultaneous underwater behavioral observations. We tested this methodology with bottlenose dolphins in freedom and in captivity.

The present doctoral thesis aims to better understand the communication of bottlenose dolphins within their social group.

First, I developed two studies to describe how the signature and non-signature whistle rate of captive dolphins varies in relation to behavior and interaction with humans.

Secondly, I present the design and implementation of an innovative methodology (BaBeL system) that allows the localization of vocalizing dolphins in a three-dimensional environment, and which can be used in captivity and with free-range dolphins.

Finally, I present two applications of this location methodology to address research questions regarding the exploratory behavior of a young dolphin and the use of vocalizations for coordinated movements in bottlenose dolphins.