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# Production and perception of acoustic signals in captive bottlenose dolphins (*Tursiops truncatus*): contextual use of social signals and recognition of artificial labels

Alice de Moura Lima

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**THÈSE / UNIVERSITÉ DE RENNES 1**

*sous le sceau de l'Université Bretagne Loire*

pour le grade de

**DOCTEUR DE L'UNIVERSITÉ DE RENNES 1**

*Mention : Biologie*

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présentée par

**Alice de Moura Lima**

Préparée à l'unité de recherche UMR 6552 EthoS  
Laboratoire d'Ethologie Animale et Humaine  
UFR S.V.E.

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**Production and  
perception of  
acoustic signals in  
captive bottlenose  
dolphins (*Tursiops  
truncatus*):  
Contextual use of  
social signals and  
recognition of  
artificial labels**

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devant le jury composé de :

**Hugo COUSILLAS**

Professeur, Université de Rennes 1 / *président du jury / examinateur*

**Manuel DOS SANTOS**

Professeur associé, Instituto Universitario ISPA /  
rapporteur

**Elisabetta PALAGI**

Chercheuse associée, Università di Pisa /  
rapporteuse

**Florence LEVRERO**

Maître de conférences, Université Jean Monnet /  
*examinateur*

**Alban LEMASSON**

Professeur, Université de Rennes 1 / *directeur de thèse*

**Martine HAUSBERGER**

Directrice de Recherche, C.N.R.S. / *co-directrice de thèse*



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# **CHAPTER 1: INTRODUCTION**



The keys to understand the vocal behaviour of a species rely on the understanding of contexts of use and production of signals (Smith, 1965). Most of studies on this issue have been done on terrestrial mammals and birds (e.g. Adret-Hausberger, 1982; Arnold and Zuberbühler, 2013), showing that some calls can be more or less specific to their context of production. It has been known for a long time that dolphins are very vocal animals, but systematic study of their acoustic signals still deserves be deepen (Janik and Sayigh, 2013), since underwater life adds difficulties in collecting data on cetaceans. In this perspective, it is crucial to dedicate efforts in the sampling and discussion of cetacean vocal emissions.

This thesis intent to add knowledge on the use and perception of acoustic signals in the bottlenose dolphin. We introduce the extent of communication ability of these animals putting them in perspective in relation to the study of animal communication as a discipline. We introduce the definition and functions of communication based on classic and modern literature. Then, we introduce what is historically known about vocal communication in cetaceans, and, specifically, in Delphinidae family. We present their diversity of known signals and show some background information on their auditory perception abilities. Finally, as we have chosen to work on a group of captive dolphins, we discuss the advantages and disadvantages of such a study.

To conclude the Introduction section, the study species, *Tursiops truncatus* is briefly presented, together with the objectives of the thesis.

# 1. ANIMAL COMMUNICATION, VOCALIZATIONS AND CONTEXTUAL USE OF CALLS

## 1.1. *Communication: definition and functions*

Communication is a process by which an individual produces a signal, to convey information to a receiver, altering the probability of the subsequent behavior of the receiver(s), often facilitating social behaviour (Bradbury & Vehrencamp, 2011; Perrin et al., 2008). The study of animal communication is thus fundamental for the study of animal behaviour and for the understanding of the social dynamics of a species. Acoustic communication, found in many taxa, allows to communicate to conspecifics out of range (where other sensory modalities fail to transmit the message) and can be propagated to three dimensions.

Dawkins and Guilford (1997) argue that in order to explain the diversity of signal design among animals, a wide range of selection pressures must be taken into account. Variation in acoustic signals can be impacted by several factors (Fischer et al., 2016). Signals have to adapt to many selective pressures, for example the quality of the habitat including level of visibility (Marler, 1960), sound propagation (Marten et al., 1977) and background noise (e. g. Mathevon, 1997); the risk of predation (e.g. Elgar, 1986; Manser et al., 2002); the mode of reproduction (e.g., relation between size of vocal tracts and sperm production in howler monkey species, Dunn et al., 2015; and male koala's use of formant frequencies to assess rivals, Charlton et al., 2013) and the social system (see reviews in Blumstein and Armitage, 1997; Freeberg et al., 2012; McComb and Semple, 2005; Wilkinson, 2003), involving mobility, stability, group size (Freeberg and Harvey, 2008) and social organization (Bouchet et al., 2013). All of these selective pressures bring morphoanatomical and behavioural adaptations affecting the three most important facets of the study of communication: production (e.g. vocal fold viscoelastic properties in *Panthera*; Klemuk et al., 2011), use (e.g.

vibrational communication in insects; Cocroft and Rodríguez, 2005) and perception of signals (e.g. structural specializations in sand cat ears; Huang et al., 2002).

Communicative complexity is the product of an intricate evolutionary process that cannot be explained by a single isolated factor (Ord and Garcia-Porta, 2012), and that participates in the emergence of vocal signals with different functions within a species repertoire. Smith (1965) draws attention to the fact that any definition of communication is limited if concepts of message and meaning are not considered, as well as of historical and immediate context and function. Message may refer in some way to the state of the central nervous system of the communicator, as an emotional state; while meaning, being considered with reference to the context (anything that accompanies a signal: combined influences of sensory inputs, genetic program and memories of the individual, e. g. see review on alarm calls by Macedonia and Evans, 1993), may be identified as the response selected by the recipient (Smith, 1965). In this scenario, abundant evidence indicates that communicative signals may convey information about signaller's identity (size, sex, age, species, individual identity and social or sexual status, see review by Fernald, 2014), the external environment (food, danger, nest site, see review by Suzuki, 2016), or express its emotional state and motivation (e. g. Jürgens, 1979). As a result, there are contexts more or less broad or precise depending on the function of the signal. Referential vocal communication is typically associated with precise contexts of emission. Support for urgency-based and functionally referential signals comes from studies on various species of mammals and birds' alarm and food calls, which investigated the context of anti-predator behaviour and searching for food. Vervet monkeys, for example, emit acoustically different alarm calls in the presence of different predators (leopard, snake or eagle, Seyfarth et al., 1980) and chimpanzees produce acoustically distinct "rough grunts" according to the type of food (Slocombe and Zuberbühler, 2005). A similar phenomenon has been described in suricates (Manser et al., 2002), prairie dogs (Slobodchikoff et al., 1991) and

chicken (Evans et al., 1993). Other call types are rather associated with broad contexts. An example of call emitted in more general circumstances are the calls that display identity and callers' location (for example, contact calls in parakeets, Cortopassi and Bradbury, 2006). At the individual level, identity information can be encoded in differences in voice characteristics (Cheney and Seyfarth, 1982; Keenan et al., 2016), facilitating individual recognition (Bee and Gerhardt, 2002). Some species also show call sharing patterns reflecting social affinities (e. g. Lemasson and Hausberger, 2004).

Particular states of emotion may be accompanied by specific behaviours, with vocalization being one of them (Manteuffel et al, 2004). This view of vocalizations as indicators of emotions have been more explored in farm animals thus far. It has been suggested in pigs for example, that vocal production is strongly related to their level of excitement (Kiley, 1972; Manteuffel et al., 2004).

Manteuffel et al. (2004) proposed that a particular animal vocalization can be clearly associated with a distinct internal state (or a class of internal states) that may define the subjective meaning of the emission. This issue was widely discussed by Altenmüller et al. (2013), presenting numerous examples of how emotions can be reflected in vocalizations. For example, affiliative and play behaviours, and the vocalizations associated to these contexts have been proposed as indicators of positive emotional states (Boissy et al., 2007, but see Blois-heulin et al., 2015). In some cases, emotional encoding is clearly associated with the acoustic structure of a given vocalization. For example, some acoustic signals of domestic cats are considered to be produced in contexts of positive state, as purring in mother-kitten or familiar partners' interactions, being considered as a potential indicator of "pleasure" (Kiley-Worthington, 1984). In adult rats, two distinct and non-overlapping calls ensure unambiguous recognition of the state of the emitter, with negative states linked to 22-kHz calls and positive states with 50-kHz calls (Brudzynski, 2007). Some effort has also been done to associate call

structures to motivational states in primates (e.g. Jürgens, 1979; Morton, 1977). In other cases, vocalizations can accompany behaviours involving more subtle emotional channels, as yawning in gelada baboons (Palagi et al., 2009). Being relatively easy to record, acoustic signals have even been proposed as potential indicators of the welfare state by some authors (Dawkins, 1998; Manteuffel et al., 2004, Schön et al, 2004). Such an approach first developed for farm animals could expand to other groups of animals, as those housed in zoos, for example.

### **1.2. *Vocal communication of cetaceans***

Historically, the study of acoustic communication has first focused especially on songbirds and nonhuman primates (e. g. Adret-Hausberger and Jenkins, 1988; Bouchet et al., 2013; Ouattara et al., 2009) because they present great levels of complexity and plasticity: dialects (e. g. starlings, Adret-Hausberger, 1986), sensitive periods of learning (e.g. birds, Bateson, 1979), semantics (e.g. red-capped mangabeys, Bouchet et al., 2010), syntax (e.g. forest-dwelling guenons, Lemasson, 2011), conversational rules (e.g. Campbell's monkeys, Lemasson et al., 2011). These evidences of vocal plasticity put them in a special position as models to address evolutionary questions on the complexity of communication (Janik, 2009). Looking from this perspective, other taxa are also interesting, notably bats (Carter et al., 2012), elephants (Poole et al., 2005), pinnipeds (Schusterman et al., 2001) and cetaceans (Janik, 2014). Apparently vocal learning evolved independently in each of these animal groups. So, it is interesting to ask if there is a common factor that could have produced a convergent evolution of vocal learning (Janik, 2009). Among marine mammals, cetaceans and pinnipeds have shown vocal learning, meaning modifications in sound generation as a result of experience (review by Janik and Slater, 1997). At the same time, cetaceans present drastic differences compared to terrestrial mammals due to their aquatic life, and thus can provide

information on the evolution of communication complexity on a wider scale than if we focus only on terrestrial species (Janik, 2013).

The transmission of behaviours through advanced social learning skills is an attribute present in cetaceans that distinguishes them from most other non-human species (Rendell and Whitehead, 2001). Cetaceans show one of the most remarkable interests as a model for the study of communication: the vocal plasticity present in different species with different patterns. Sperm whales (*Physeter microcephalus*) and killer whales (*Orcinus orca*) have culturally transmitted group vocalizations, maintained during decades (Deecke et al., 2000; Ford, 1991; Rendell and Whitehead, 2003). These two species form clans, living in stable populations, sharing a unique repertoire of discrete call types (Whitehead et al., 2004; Yurk et al., 2002). In killer whales, it is known that calves adopt the call repertoire of their matrilineal unit, and may have a completely different repertoire from their fathers, these last belonging to another matrilineal unit (Filatova and Miller, 2015). The songs of humpback whales (*Megaptera novaeangliae*) are another striking example of the transmission of a cultural trait and social learning in a cetacean. Males of this species sing songs shared between thousands of individuals, in an analogous way to the colony or locale-specific birdsongs (Cerchio, 1993; Hausberger et al., 1995). Songs are organized within a nested hierarchy, with groups of units forming phrases and themes (set of repeated phrases) forming song types shared in one population (Garland et al., 2011). However, the song of the population changes each breeding season, with slow and gradual alterations being incorporated by males. Garland et al. (2017) studied rare hybrid songs, when parts of an existing song are spliced in a new one, providing insights into the mechanism governing song change and learning. Another strong evidence of vocal plasticity in cetaceans is their demonstration of interspecific vocal mimicry. White whales (*Delphinapterus leucas*) have been reported spontaneous mimicking human voice (Murayama et al., 2014; Ridgway et al., 2012) and killer whales demonstrated mimicry of

California sea lion (*Zalophus californianus*) barks (Foote et al., 2006). Also, bottlenose dolphins can imitate computer-generated artificial sounds (Reiss and McCowan, 1993; Richards et al., 1984) and whale sounds broadcast during shows (Kremers et al., 2011).

Also, as marine mammals are very social animals, the study of communication is crucial to understand their behaviour. In addition to this, as very mobile animals, they developed a communication system allowing them to maintain or regain contact with members of their group at the distances over which they separate (Tyack, 2000). Cetaceans exhibit a considerable diversity of social systems, with two species showing strong evidence for stable groups: killer whales and sperm whales (Tyack, 2000). The adaptive solution found by these species to keep contact was to develop group-distinctive contact calls. Other cetacean species, as the bottlenose dolphins, have a dynamic social structure, organized in a fission-fusion system, and rely on individual-specific signals to communicate, especially between strong individual social bonds (Tyack, 2000).

Complex social behaviour and the necessities of maintaining social relationships and negotiating in a large society have boosted the development of vocal learning and other cognitive skills, notably in toothed whales (Janik, 2014). More studied in bottlenose dolphin (Herman, 2006; Janik, 2013), these cognitive skills include different domains of intellectual functioning: declarative, procedural, social and self (Herman, 2006). They also present social learning and highly developed memory skills. Concerning those relevant for communication, we can cite understanding complex syntax (Herman et al., 1984), vocal learning and referential labelling (see review in Janik, 2013).

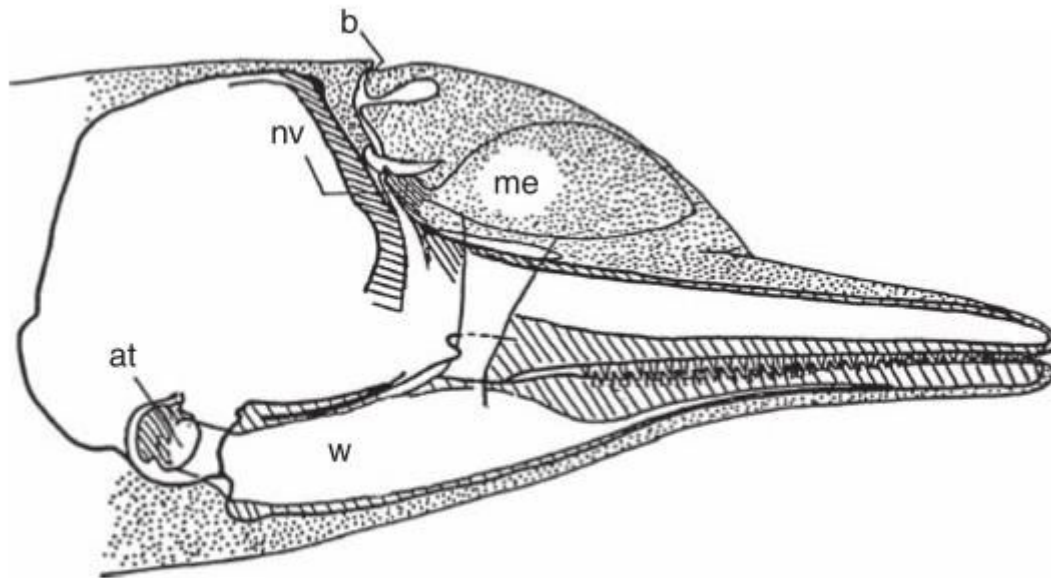
For underwater communication, the acoustic channel is the most efficient means, for both long-range and near distances (Herman and Tavolga, 1980). Due to their exclusively aquatic life and its specific constraints, such as low light conditions (specially night feeders, deep divers and species living in turbid rivers), cetaceans evolved complex acoustic systems to

communicate and explore their environment (Janik, 2009). However, life in water required a series of morph-anatomical adaptations for production and perception of sounds. The evolutionary transition from land to water, started about 50 millions of years ago, involved a great number of changes in individual organ systems until the modern cetacean body plan (Nummela et al., 2007; Thewissen and Williams, 2002). First, the characteristic impedance of soft mammalian tissues is similar to that of water, and so a "sound beam" is not reflected or refracted in the passage from the surrounding water to tissues such as skin or fat (Hemilä et al., 2010). When a cetacean vocalizes, sound vibrates in their soft tissues, transferring well to the surrounding medium, so they do not need to open their mouths or blowholes underwater (Tyack, 2000). Dolphins evolved a complex sound-generation system, which relies on the independent work of the right and left parts of the nasal passage, and a well-developed musculature, allowing the production of whistles and pulsed signals simultaneously (Solntseva and Rodionov, 2012). To detect prey, odontocete cetaceans evolved a method that can detect relatively small objects in considerable distance: echolocation (Perrin et al., 2008). Echolocation signals are projected from a dolphin's head in a beam, and through listening the echoes of dolphin waves reflecting off different objects/preys, the animal obtains an assessment of its environment (Au, 2004b; Kassewitz and Hyson, 2016).

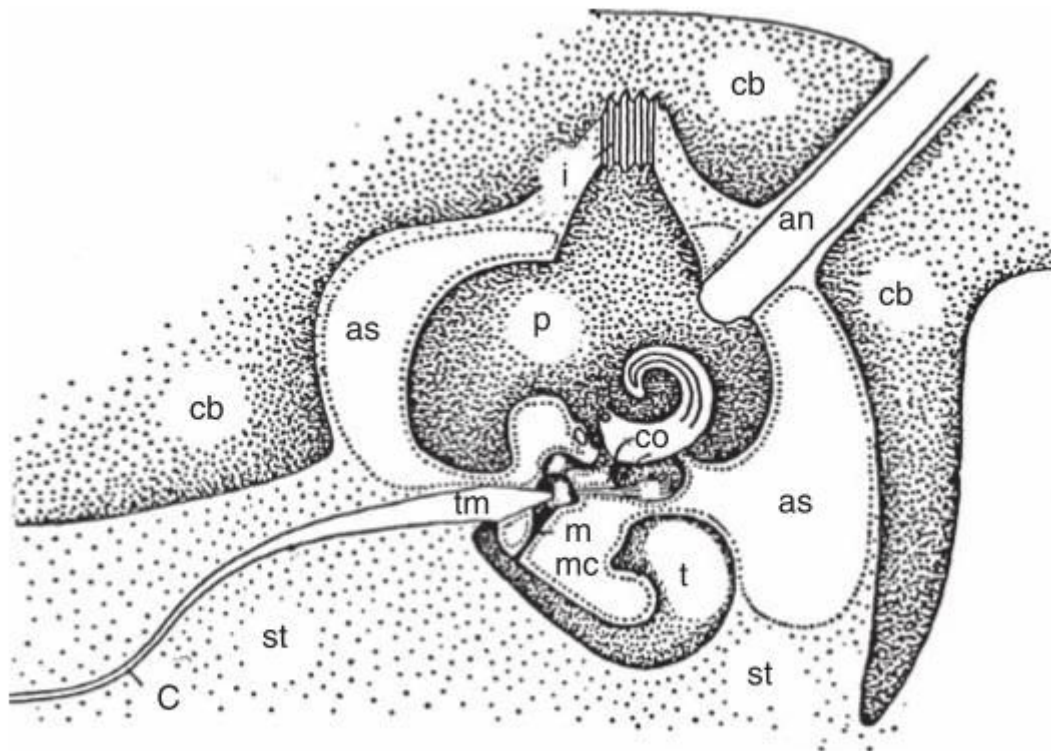
Pulsed and whistle-like sounds seem to be produced at the phonic lips (a structural complex previously known as monkey lips; Cranford et al., 1996). Paired nasal plugs muscles control the pressurized airflow from the nasal cavities past the phonic lips (Ridgway et al., 2015), and then sounds are focused through the skull, air spaces, connective tissue sheaths, and inside the melon (mass of adipose tissue on dolphin's forehead, composed of isovaleric acid, acting as an acoustic lens (Evans, 1973) before propagating to the environment (Soldevilla et al., 2005). Also, dolphins have a mechanism of air recycling within the nasal sacs, with a storage centre and energy supply for air used for phonation (Dormer, 1979). Other adaptations include



medial thickening of the tympanic bulla, functional replacement of the tympanic membrane by a bone plaque, and changes in the orientation and shape of the ossicles (Reidenberg, 2007) (Figure 1). Almost everything we know about dolphins' sensory perception is about hearing, given their well-developed vocal abilities (see review in Kremers et al., 2016). Therefore, to adapt for underwater hearing, odontocetes lost the outer ear pinna, giving place to the lower jaw as the primary sound perception pathway and the external auditory meatus became vestigial (Akhatov et al., 2007; Hemilä et al., 2010; Møhl et al., 1999). Sounds, then, reach the middle ear ossicles via the lower jaw and the tympanic plate, with a large effective area (Hemilä et al., 2010). In addition, the dolphin's middle ear has biomechanical adaptations to the aquatic environment, transmitting a large part of the vibration energy to the oval window, which have resulted in a highly effective peripheral auditory system and a noticeable increase in their perceptible frequency band (Hemilä et al., 2010; Solntseva and Rodionov, 2012). Experiments showed that the maximum sensitivity to sound is located slightly in front of the pan-bone area of the lower jaw (a thin area overlaid with an oval fatty area, Mooney et al., 2012), through where the sound enters (Akhatov et al., 2007). Behavioural hearing tests showed that high frequencies are better detected by the dolphin when sounds are presented near the lower jaw; however, lower frequencies seem to be better detected near the opening to the ear canal (see review in Mooney et al., 2012).



(A)



(B)

Figure 1. (A) Structures in the odontocete head. (B) Odontocete middle ear region. The nasal valve lips, the blowhole and the melon contribute to sound production and focusing. an, auditory nerve; as, air sinuses; at, attachment of the mandibular wave guide onto the tympanic bulla; b, blow hole; c, auditory canal; cb, cranial bones; co, cochlea; i, ligaments; m, malleus; mc, middle ear cavity; me, melon; nv, nasal valve with lips; p, periotic bone; t, tympanic bone; tm, tympanic membrane; st, soft tissues; w, mandibular wave guide. (From Perrin et al., 2008).

### **1.3. Vocal communication of dolphins**

The phylogenetic order Cetartiodactyla consists currently of more than 330 species (ancient order Cetacea: 12 families with 85 species; ancient order Artiodactyla: 10 families with 247 species) (Vislobokova, 2013). The parvorder Odontoceti (odontocetes, or toothed whales) comprises 11 families and at least 70 species of dolphins, porpoises, killer whales and sperm whales. Mysticeti, other parvorder, includes four families and at least 15 species of the so-called baleen whales. The main morphological difference between the two parvorders is that odontocetes present teeth and a single blowhole, while mysticetes have baleen (and no teeth) and two blowholes (Reeves, 2003). Here, we will focus on the acoustic communication of Delphinidae, the largest odontocete family, comprising the most known species of dolphins.

Of particular interest in the study of the evolution of complex communication we found the delphinids. They are a family of approximately 35 species of mammals adapted to marine life since about 65 million of years ago of a common ancestor close to the Artiodactyla (Janik, 2009). Delphinids are among the most social of cetaceans.

Research was able to show that different species in this family of cetaceans produce a variety of acoustic emissions used in different behavioural contexts, including feeding activities and group cohesion (Caldwell et al., 1990; Podos et al., 2002; Richardson et al., 1995). Aspects such as behaviour and physiology, as body size (May-Collado et al., 2007b) can influence tonal signals variation between species. However, most studies of delphinid vocalizations are concentrated on bottlenose dolphins, *Tursiops* sp. (e. g. Boisseau, 2005; Connor and Smolker, 1996; Díaz López, 2011; Hill and Sayigh, 1999; Lopez and Shirai, 2009; Smolker et al., 1993) and the acoustic repertoires of most species remain poorly studied (Corkeron and Parijs, 2001).

### 1.1.1. Diversity of signals

The vocal repertoire of dolphins have suffered nomenclature difficulties over the years (Herzing, 2000). Dolphin sounds can be divided into three main categories: whistles, clicks and burst pulse sounds (Herzing, 2013). Whistles are tonal, frequency- and amplitude-modulated sounds with most of the energy below 20 kHz (frequency range of 2-35 kHz, and up to 100 kHz for harmonic frequencies, Lammers et al., 2003; Ryabov, 2016), that appear to play a role in maintain contact among individuals (Acevedo-Gutiérrez and Stienessen, 2004; Lopez and Shirai, 2009; Watwood et al., 2004). Whistle duration vary from less than 1 second to several seconds (Herman and Tavolga, 1980). These are the most variable and most commonly studied signals in bottlenose dolphins because they can be recorded in high numbers with good signal-to-noise ratios (Díaz López, 2011). Clicks are short broadband signals up to more than 100 kHz in frequency, mostly used for echolocation during navigation and hunting (Herzing, 2013; Kremers et al., 2016a). Burst pulse sounds, in turn, are broadband, sometimes described as consisting of rapid click trains (Janik, 2009). They are primarily social sounds and have received many different sub-categories denominations by different authors, as *harsh metallic cries*, *screams*, *squawks*, *barks* and *pops* (Herzing, 2013; Rossi-Santos et al., 2008). This sound category is still poorly known and marginally explored in repertoire descriptions (Lammers et al., 2003; Rossi-Santos et al., 2008), but appears to be strongly involved in communication (Herzing, 2000; Lammers et al., 2003; Mccowan and Reiss, 1995). Other sounds that may be or not included in the above-mentioned categories, have been described, as chirps, squawks, yelps, brays and more (see for example Caldwell and Caldwell, 1967; Dos Santos et al., 1990; Herzing, 1996; Papale et al., 2016). However, most of the time these sounds are described only qualitatively following human listeners' perception and receive different nomenclatures by different authors.

Whistles, the most studied vocal category, may have varying numbers of harmonics, but many studies focus only on the fundamental frequency (Janik, 2009). They have been examined often by their contours (frequency modulation, e. g. Bazúa-durán, 2004) and by the extraction of their acoustic parameters (e. g. Petrella et al., 2012), allowing comparisons among groups and populations (e. g. Bazúa-Durán and Au, 2004; Ding et al., 1995; Rendell et al., 1999). Varying degrees of complexity have been described for different populations (Ding et al., 1995; May-Collado and Wartzok, 2008; Morisaka et al., 2005).

In 1965, Caldwell and Caldwell opened a new line of research when they proposed the hypothesis of “signature whistles” (reviewed in Janik and Sayigh, 2013). The term “signature” has often been applied to animal vocalizations described as having an individually distinctive pattern (Sayigh and Janik, 2010). In dolphins, the idea, first proposed in the 1960s was that each individual was only capable of producing one kind of stereotyped whistle, and any whistle other than a signature was considered “aberrant” (Miksis et al., 2002). Classification of signature whistles are often done visually by human observers, based on the general form of the spectrogram (Kriesell et al., 2014; Janik, 1999). Although first described and more studied in bottlenose dolphins, evidence for signature whistles also exists for common dolphins (*Delphinus delphis*; Caldwell and Caldwell, 1968), Atlantic spotted dolphins (*Stenella frontalis*, Caldwell et al., 1973), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*, Caldwell and Caldwell, 1971), Pacific humpback dolphins (*Sousa chinensis*, Van Parijs and Corkeron, 2001) and Guiana dolphins (*Sotalia guianensis*, Lima and Le Pendu, 2014).

The signatures whistle hypothesis has been at the centre of most of the studies on dolphin vocalizations since it was first proposed, and according to that, these signals would be used for individual recognition, as between mother and offspring (Sayigh et al., 1998) and in maintaining group cohesion (Perrin et al., 2008; Smolker et al., 1993). Further studies showed

that the signature whistle accounts for close to 100% of all whistles produced in isolated dolphins (reviewed in Sayigh et al., 2007), however in the spontaneous production of wild and captive groups they account only about 38-70% of whistles; the rest are other shared or unshared whistle types (Buckstaff, 2004; Cook et al., 2004; McCowan and Reiss, 1997; Watwood et al., 2005). Dolphins do not seem to use voice cues in signature whistle recognition, since they do not respond differently to non-signature whistles of close relatives (Sayigh et al., 2017). Other studies, though, have refuted signature call hypothesis, presenting evidence for a shared whistle type instead (McCowan and Reiss, 1995, 2001). These authors argued that the large proportion of stereotyped signature signals may be an artefact of the unusual recording circumstances (animal isolated, temporary restraint) (Akhatov et al., 2007).

#### **1.1.2. Auditory perception, discrimination and recognition**

Hearing can be evaluated through behavioural or electrophysiological audiograms. Audiograms were measured for a dozen of odontocetes species maintained in aquaria or laboratories (reviews in Akhatov et al., 2007; Mooney et al., 2012; Nachtigall et al., 2000). Globally, they tend to have a functional hearing range between 1 and 150 kHz with peak sensitivity between 40 and 80 kHz, with some variation between species (Janik, 2009; Richardson et al., 1995; Wartzok and Ketten, 1999). Differences interspecies are often matched with the frequencies of sounds produced, such as the frequencies of echolocation clicks (Mooney et al., 2012). Some hearing loss appear as individuals get older, and males have a greater incidence of high-frequency hearing loss compared to females (Mooney et al., 2012). Even considering the loss of the sound-focusing mechanism provided by the pinna and auditory meatus found in terrestrial mammals, cetaceans are still up to 100 times more sensitive than humans in hearing. Delphinids can distinguish tonal sounds differing by only 0.2% to 0.8% of the base frequency of the tone (Thompson and Herman, 1975).

As the echolocation and hearing systems of odontocetes are completely adapted for efficient perception of the underwater environment, one can ask if dolphins are also able to detect acoustic signals in air. While most studies of odontocete hearing have emphasized the reception of waterborne sounds, only two studies have been conducted on their perception of airborne sounds, reporting a range of perception from 1 to 110 kHz with the greatest sensitivity in the lowest frequencies (1-40 kHz) in the air (Babushina, 1979; Babushina and Polyakov, 2011). Even if the question is still source of debate, captive dolphins have been shown to be capable of spontaneous imitation of auditory airborne stimuli (i.e., whale vocalisations, Kremers et al., 2011).

Other studies on cognitive abilities related to hearing identified that dolphins can discriminate small differences in pitch (Thompson and Herman, 1975), mimic a wide variety of sounds preserving their frequency contour and showing octave-generalization (see review in Herman, 2010). Together, these studies suggest a considerable level of vocal flexibility as well as a high sensitivity to sound nuances that may be key components of vocal communication among dolphins, especially in recognizing the contours of individualized whistles of others in their group. Furthermore, studies of imitation of artificial signals (Reiss and McCowan, 1993; Richards et al., 1984) prove that they discriminate well between different frequency modulation patterns.

On the perception of social sounds, research has also shown that dolphins can discriminate vocal signals of a kin or associated individual from that of a non-relative (Sayigh et al., 1998), memorize for at least 20 years the signature whistles of familiar individuals (Bruck, 2013), and even mimic the signature whistle of others, possibly as a means of calling or referring to this dolphin (e. g. Janik, 2000; Janik et al., 2006; Tyack, 1986). These evidences support the idea that dolphin individuals have concepts of one another as individuals and can track the historic of their social relationships (Sayigh et al., 1998). As dolphins interact with many

different individuals over the time, individual recognition seems important to maintain some long-term associations (Connor, 2007; Sayigh et al., 1998).

#### **1.4. *Studies on captive dolphins***

Bottlenose dolphins are among the first cetacean species to be maintained in captivity in the early 1860s (Defran and Pryor, 1980) and currently it is the species most found in captivity. Hundreds, if not thousands, of large dolphins live in captivity in the world, although their exact number is difficult to determine (CetaBase). Since the beginning of the twentieth century, then, descriptions of behaviour in rare opportunities of observation, like pregnancy and birth, have been given. Captive research has so far provided important information about the intelligence and cognition of cetaceans (see, for example, Herman, 2010; Marino et al., 2007; Reiss and McCowan, 1993), offering a level of experimental control and validation that cannot be as easily achieved in the natural setting (Marino and Frohoff, 2011). However, some researchers, philosophers and many funding agencies are increasingly questioning research on captive animals, mainly for ethical or philosophical reasons (Perrin et al., 2008).

There are advantages and disadvantages in the study of dolphins and whales in captivity versus in the natural setting (Marino and Frohoff, 2011). It is notoriously difficult to conduct experiments and observation of cetaceans in a controlled way in the ocean. Most behavioural studies on wild dolphins are confined to surface follows (which represents only a small percentage of cetaceans' lives; Janik, 2009) or recording of more general behavioural activities (e. g. Würsig et al., 1980), with rare exceptions under privileged conditions, as clear water and resident populations (Dudzinski, 1996, 2010; Evans-Wilent and Dudzinski, 2013). Encounters with most species in the wild are scarce and it is difficult to collect recordings of their sound emissions (Herman and Tavolga, 1980; Janik, 2009). Techniques of passive acoustics have become popular to detect the presence or absence of a species in the field, although these methods do not address questions on cetacean's social behaviour or cognition



(Herzing, 2013). One of the techniques used in the field to monitor these animals are the temporary capture, but while this method allows clear identification of a caller, it is invasive and animal is not recorded in a spontaneous expression of its activities. Another tool is the D-TAG, developed by Johnson and Tyack (2003). This is a very powerful method containing different sensors and a hydrophone, designed to monitor individual's behaviours. However, these devices are still too expensive and inaccessible for many researchers, not adapted to study some populations where individuals do not approach boats, researchers cannot always determinate which is the phonating dolphin, and require capture animals and a time of habituation for them to carry it, inhibiting many research groups from adopting this technology (López-Rivas and Bazúa-Durán, 2010; McMahon et al., 2011). Another alternative, less invasive, used to identify individuals when studying dolphin communication, is triangulation of the signal through the use of hydrophone arrays (Freitag and Tyack, 1993). However, this is a technique complicated to apply in the field, animals must not be too close to each other to identification of callers, and also, unless the animals are constantly vocalizing, they cannot be continually tracked. Moreover, simultaneous visual information are not given unless the system is plugged with cameras, becoming even more difficult to use in field situations. As a result, most of the current knowledge is centred on vocal production, and even so, descriptions of their acoustic repertoires are not always complete. Conversely, data on aspects like foraging behaviours or travel patterns are only available on the field.

Captive studies may be considered limited in their findings for a variety of reasons linked to the isolation of individuals, small sampling and behavioural changes induced by captivity, as temporal patterns, stereotyped behaviour and high level of interactions with humans. However, exactly because of the more controlled conditions, captivity provides the opportunity to observe in privileged conditions and measure details often unavailable from field setting. For example, internal body states or test of cognitive tasks cannot readily (or

cannot at all) be measured from wild dolphins. Also, being exclusively aquatic animals, dolphins are most of their time underwater, and most of their behaviours are expressed there. Captivity gives the opportunity to look closer to patterns of interactions between individuals, test methods to apply in the wild (as acoustic TAGs, for example) and allows to build a more detailed background on dolphin's behaviour. Great discoveries on dolphin cognition were obtained through captivity, some examples being evidences of being able to acquire some of the properties of human language syntax (Herman et al., 1984), underwater frequency discrimination (Thompson and Herman, 1975), the ability of detecting differences among objects, understanding of representations of the real world, referential pointing and the concept of "creating" (see review in Herman, 2006) and mirror self-recognition (Reiss and Marino, 2001).

Overall, data from both settings (captive and wild) can be mutually valuable to research on dolphin behaviour, being complementary and allowing beneficial comparisons for both (Dudzinski, 2010). Data obtained in captivity can help to understand free-ranging populations and, in turn, data collected in the field are valuable to know how to provide a behavioural and socially stimulating environment to captive dolphins, ensuring a best welfare for these animals.

## **2. STUDY SPECIES AND OBJECTIVES**

The bottlenose dolphin (*Tursiops truncatus*) is the best known, most studied species of all cetaceans. The species belongs to the Delphinidae family, suborder Odontoceti (toothed whales), order Cetacea. Cetacea are included in Artiodactyla, or Cetartiodactyla by some taxonomists (Geisler and Uhen, 2005). It is a cosmopolitan species found through all the world's tropical and temperate oceans (Shane, 1990).

Life expectancy was estimated by tooth analysis for up to 50 years in females and up to 45 in males (Hohn et al., 1989). Females generally have their first calf by the age of 12. The

gestation period lasts about 12 months, with an inter-calf interval of 2 to 4 years, reflecting periods of dependency of 3 to 5 years and, rarely, even longer (Connor and Krützen, 2015; Tyack, 1986).

They are considered as top-level predators, feeding on a large variety of fishes and squid, especially noise producing fish, depending on the habitat (Gannon and Waples, 2004). Coastal animals tend to feed on fish and invertebrates that live on or near the bottom, while offshore animals eat pelagic or mesopelagic fish and squid (Reeves et al., 2002). Typical preys in shelf waters are croakers, sea trout, mackerel, and mullet. The striped mullet, *Mugil cephalus*, is considered the mainstay of the bottlenose dolphin diet in the Gulf of Mexico (Blair Irvine et al., 1981). Predation by shark is a significant cause of mortality of bottlenose dolphins in various areas around the world (e.g., Australia: Heithaus, 2001; South-eastern United States: Wells et al., 1987). Occasionally they are also predated by killer whales (Gowans et al., 2008).

As for other marine mammals, it is hard to study bottlenose dolphins' behaviour since they pass the majority of their lives underwater, and just a small portion of the animal is visible when surfacing. Most studies describe large categories of behaviours for the species, as foraging/feeding, socialising and travelling.

They appear to be active day and night in the wild, with periods of feeding, traveling, socializing and resting depending on environmental factors such as tides, season and time of day and factors such as reproductive seasonality (Shane et al., 1986). For many populations, some activities seem to be linked to the time of day, with feeding clearly peaking in the morning and in the early evening (Allen et al. 2001; Blair Irvine et al. 1981; Brager 1993; Goodwin 1985; Saayman et al. 1973; Shane et al. 1986) and social activities temporally distributed between feeding times, with clear peaks during the afternoon (Brager 1993; Miller et al. 2010; Saayman et al. 1973).

Bottlenose dolphins are typically found in groups of 2-15 individuals, although groups of more than 1000 have been reported (Leatherwood et al., 1988; Shane et al., 1986). Composition and stability of these groups also vary. This species has very fluid social groups (fission-fusion society; Würsig, 1989), and some males may keep strong social bonds for years (Connor et al. 2000). Alliance bonds appear to form between non-siblings during their sub adult age, and may remain for the lifetime of the adult males (Watwood et al., 2004). It is known that they use signature whistles for individual recognition, and male partners may produce similar whistles (Watwood et al., 2004). There are evidences of female defence strategy in bottlenose dolphins (males stay with a female and prevent other males from mate with her while she is receptive) (Connor et al., 2000). So one of the hypothesis to explain male bonds is that they work as a consortship to chase and herd females. Captive bottlenose dolphins may develop dominance relations in the group. When fighting, it often involves a gradually escalating series of threats (Overstrom, 1983), with emission of pulsed sounds and open-mouth threat display (looks like the first step in preparing to bite), head movements and jaw claps.

Early studies tried to describe the repertoire of bottlenose dolphin vocalizations (e. g. Lilly and Miller, 1961). Since the proposition of the signature whistle hypothesis on this species (Caldwell and Caldwell, 1965), most current studies on vocal communication of bottlenose dolphins is focused on their signature whistles. It is known, for example, that they develop signature whistles in their first months of live (Janik and Sayigh, 2013) and that they are able to copy signatures of conspecifics (Janik and Slater, 1998). Captive studies have shown that besides the ability to mimic signature whistles (Tyack, 1986), bottlenose dolphins can also use novel signals to label objects (Herman, 2006), and learning how to associate dolphin whistles to different response paddles (Harley, 2008). While signature whistles seem to be more highly recorded from isolated individuals, they correspond to only about 38-70% of whistles in the

wild (Buckstaff, 2004; Cook et al., 2004; Watwood et al., 2005), and all the non-signature whistles present in the repertoire have very unknown functions and contexts associated, clearly not being linked with individual recognition (Sayigh et al., 2017). In the same way, contextual use and functions of other vocal categories (described in Section 1.1.1) remain large unknown. Descriptions of behaviour and associated vocalizations have been first reported for captive (e.g. Caldwell and Caldwell, 1968) and after for free-ranging dolphins (Connor et al., 1992; Herzing, 1996; Smolker et al., 1993).

Up to now, only some fields in dolphin communication have been deeply explored, specially echolocation, signature whistle production and usage, and underwater hearing.. Though, even if some research has found valuable information on the potential functions of specific vocal categories in dolphin's repertoire, it is still necessary to go further to understand with which behavioural contexts these acoustic signals are associated. As pointed before, this require a considerable amount of behavioural sampling with good observation conditions, so many questions are still open in every topic: cognition, sociality, vocal repertoire, signature whistles, contextual use of vocal signals, sound perception and others. Research also need to explore more the social use of whistles and burst pulse sounds and the communicative potential of click trains. Also, the combinations of different sound categories are still almost not studied in a contextual perspective.

The aim of this thesis is to explore further the use and perception of acoustic signals in the bottlenose dolphin, in order to add on the current knowledge on the vocal behaviour of cetaceans. We chose to go further in the comprehension of context of production of the different acoustic categories (focusing on burst pulse sounds, chirps, click trains and whistles) and their link with daily activities of dolphins. We also aimed to test the sound perception of dolphins using artificial individual labels, testing, in addition, their aerial hearing.

We explored the contextual use of acoustic signals describing the daily life of the 7 captive dolphins studied, looking if there is an impact of the temporality of human-controlled activities on it. We also recorded and described the vocal repertoire of the group, and crossed these measures in order to link the different acoustic structures to the contexts. Our assumptions were that these associations could help to understand the potential functions of the different vocal categories. We conducted observations from the surface in the main pool of the aquatic complex, to know the behavioural budgets and temporal distribution of daily vocal and non-vocal activities (Chapter 3, Paper 1) and, to have more precise links between behaviours and vocal activity, we took advantage of good observation conditions offered by an underwater window to search for preferential associations between acoustic structures and behaviours of individuals present in a given time in a part of the pool complex (Chapter 3, Paper 2). Here we expected to clarify the relations of the different vocal categories and behavioural contexts through a more precise look, with underwater observations. A correspondence has often been observed between the productive and receptive capacities of a species (Ralston and Herman, 1989). To better understand the communication system of dolphins, we should study also the perceptual processing. For the perception issues, based on the already known concept of identity of dolphins, we tested their ability to respond to artificial acoustic signals individually related to them, when played underwater and especially in the air (Chapter 4). Rather than just explore the limits of discrimination, experiments here aimed to emphasize the recognition of sound patterns and dolphin ability to understand them as individual labels.

## **CHAPTER 2: METHODOLOGY**

## 1. STUDY SUBJECTS

All data collection was undertaken within the delphinarium of Planète Sauvage Animal Park (Port Saint-Père, France), from February 2015 to May 2016. The animal information and housing conditions are described in Table 1. Our observations included seven bottlenose dolphins: four adult males (aged 5, 6, 12 and 16 years old in the beginning of data collection) and three adult females (aged 7, 14 and 26 years old in the beginning of data collection), all born in captivity. One of the dolphins arrived from other facility over the course of the thesis (Lucille, the older female). All subjects were born in captivity and lived together in a social group, with access to four differently sized pools.

Table 1. Group composition of bottlenose dolphins that participated to our study. \*Birth date. †Death date.

<b>Individual</b>	<b>Sex</b>	<b>Date of birth/death</b>	<b>Place of birth</b>	<b>Relatedness</b>	<b>Arrival at “Planète Sauvage”</b>
<b>Aicko</b>	M	* 13 August 2010 † 06 November 2016	Parc Astérix (France)	<i>Galeo</i> 's half-brother  <i>Peos</i> 's nephew	February 2015
<b>Amtan</b>	F	*13 May 2001	Dolfinarium Harderwijk (Netherlands)	Unrelated	October 2008
<b>Galeo</b>	M	*10 August 2009	Parc Astérix (France)	<i>Aicko</i> 's half-brother  <i>Peos</i> 's nephew	February 2015



<b>Lucille</b>	F	*16 April 1989	Sea World Orlando (USA)	<i>Parel's</i> aunt	April 2015
<b>Ocean</b>	M	*13 August 2003	Boudewijn Seapark (Belgium)	Unrelated	April 2014
<b>Parel</b>	F	*08 June 2008	Dolfinarium Harderwijk (Netherlands)	<i>Lucille's</i> niece	March 2012
<b>Peos</b>	M	*23 June 1999	Parc Astérix (France)	<i>Aicko's</i> uncle  <i>Galeo's</i> uncle	December 2008

Individuals could be easily identified based on differences in physical characteristics, as size, by the shape of dorsal fin, difference on colour patterns, or differences in the face (Figure 2). Some dolphins were already more or less familiar with each other due to a common housing period prior to their arrival in "Planète Sauvage" (Figure 3).



*Figure 2. Photo illustrating physical differences between dolphins allowing individual recognition by observer. Photo modified. Credits: Yvonnick Le Pendu.*

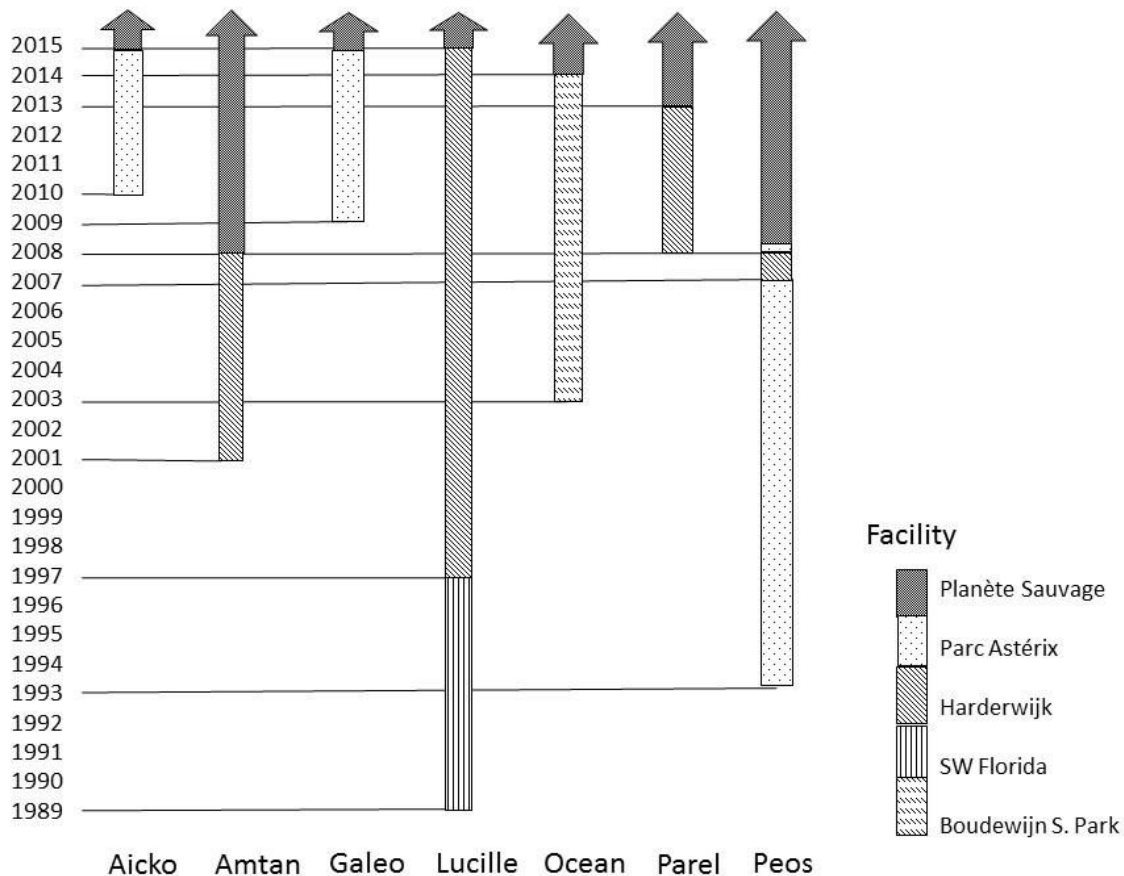


Figure 3. Historic of housing facilities of the six individuals of bottlenose dolphins (*Tursiops truncatus*) living in Planète Sauvage park during the study period.

## 2. STUDY SITE AND ANIMAL ROUTINE

The delphinarium comprises four pools totalling 8.5 million litres of salt (at 29 g/L) water. Dolphins had free access to four differently-sized and inter-connected pools (1: 4950 m<sup>3</sup>, 2: 1280 m<sup>3</sup>, 3: 220 m<sup>3</sup>, 4: 1040 m<sup>3</sup>) (Figure 4). The entire water is mechanically filtered in 4-5 hours and treated to prevent the development of algae, bacteria or fungi. Pool 1 is used for public presentation, with capacity for 1000 seats. Pool 4 is the pool used for care / nursery: all the bottom lifts in 1 min if intervention is needed (blood test, medical care, control of newborns). There is a 40m<sup>2</sup> room to accommodate the research team and their equipment in the basement in the middle of the pool complex. This laboratory has an underwater viewing window overlooking pool 4 and allowed centralize data collection.

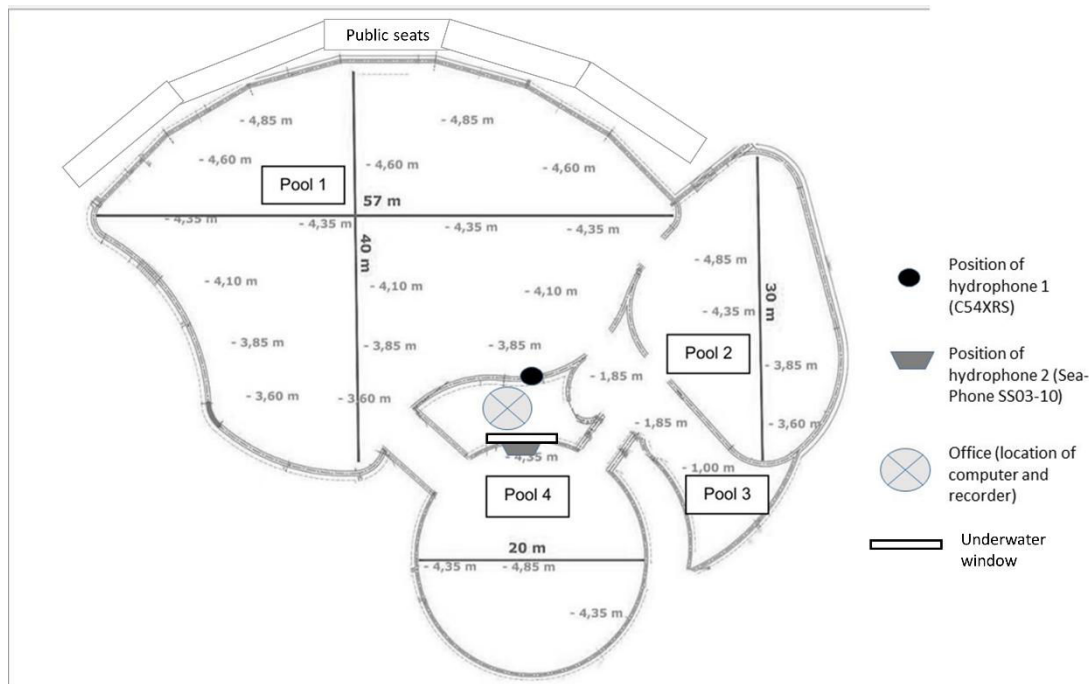


Figure 4. Outline and dimensions of the pools, showing locations of hydrophones and office with underwater view.

Human-related daily routine in the delphinarium lasts from 8:30 a.m. to 6:00 p.m. A day starts with the arrival of the first trainer, inspection of dolphins and preparation of fish in the morning. These dolphins are given 39kg of fish every day, i.e. herring, capelin, mackerel, sprat, whiting and squid; 4.5-8.5kg per dolphin; amount related to the size / age of individual) during two free (light) meals at 9:00 a.m. and 5:00 p.m., and in between, during five (two in the morning and three in the afternoon) training sessions per day (each one lasting between 15 and 30 min.; about every 1.5 h), during public shows (time depending on number of visitors, it can happen in the morning and/or in the afternoon) and training for shows and for medical treatments. Public presentations started from the end of February (lasting around 30 min. each), where the dolphins are trained with public presence or participate of public shows accompanied by a soundtrack), once each week in the beginning of park open season, and from April, two each day.

On average 5 to 6 types of enrichment (toys in the surface, toys in the pool bottom, alimentary or water jets, for example), are used per day, intending to trigger certain behaviours, as increase exploration or displacement of dolphins in the pool. Trainers manage to bring a maximum of diversity in the enrichment, making them available many times during a day, varying the time of distribution, duration and type.

### **2.1. Training**

Training consists in medical training (e. g. for desensitization of parts of the body to accept be touched, inspected by medical equipment and participate in medical procedures) and training of behaviours for public presentations. During these sessions, trainers communicate with dolphins by gestures, asking dolphins to realize a variety of behaviours, through standard operant conditioning procedures based on positive reinforcement (mainly food, but also gelatine, ice cubes and enrichment items, like toys) and a whistle sound signal to indicate that a behaviour was well executed. After training, trainers register the amount of food ingested, level of motivation and general observations about each dolphin.

Training with musical instruments was used for experimental tests on sound perception conducted during this thesis (CHAPTER 4). All the dolphins studied had been trained to respond to a sound signal produced by a different instrument for between one month and several years. At specific training sessions once a week, each dolphin was asked, one after another and in random order, to come to a trainer playing the corresponding instrument in exchange of a food reward. In order to carry out this exercise, the trainer working with the called dolphin would move into a "neutral" position at the time of the sound signal, thus allowing the dolphin to leave.

## **3. DATA COLLECTION**

Three studies have been conducted. With the exception, of the study on perception of individual artificial acoustic signals, all data were collected through direct behavioural

observations (methods detailed below) and acoustic recordings. For the third study, behavioural observations were made through video recordings.

### **1.5. Direct behavioural observations**

During four months (February to May 2015), behavioural data were collected using two methods: instantaneous scan sampling, where the activity of each individual was noted every 3-minutes (Altmann, 1974) from the surface of the main pool (Pool 1), near the Position of hydrophone 1 (see Figure 4) for study 1 (see Chapter 3, Paper 1), and *ad libitum* sampling from the pool 4, through an underwater window (193 cm by 92.5 cm, Figure 5), where all behaviours of individuals present in the pool were recorded for study 2 (see Chapter 3, Paper 2). During the whole study dolphins were free to move between pools. Observation sessions were conducted one to five times a day, between 0900h and 1700h, outside of training or show periods, and without the presence of trainers.

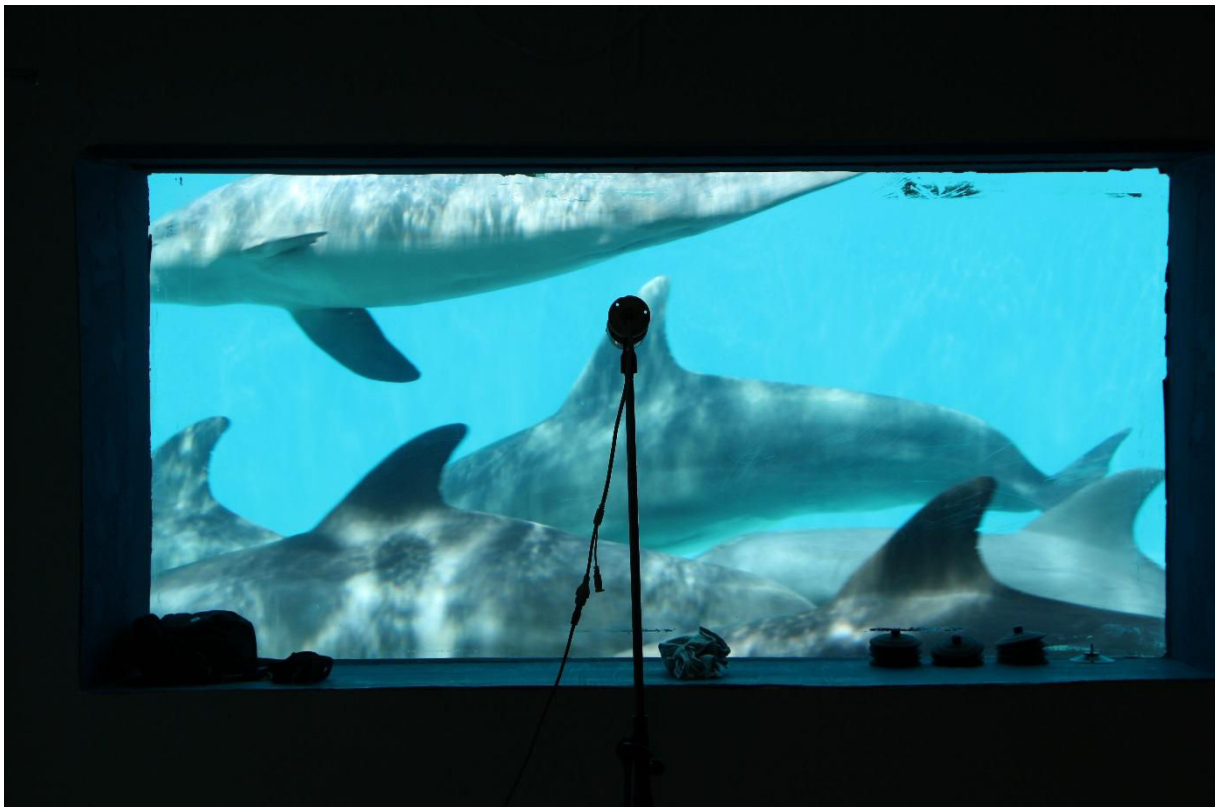


Figure 5. Photo illustrating underwater window, through where *ad libitum* sampling from pool 4 was done. Credits photo: Yvonnick Le Pendu.

Our definitions of behaviours were adapted from those commonly used in other studies (Dudzinski, 1996; Kyngdon et al., 2003; Lusseau, 2006; Mackey et al., 2014; Sakai et al., 2006; Scheer, 2010; Streit et al., 2011; Tamaki et al., 2006): social activities (play, socio-sexual behaviour, agonistic behaviour, positive or neutral social interaction), inactive (when animal is stationary, as rest), solitary play, body movements, spy-hopping and swimming (see Table 1, CHAPTER 3).

### **1.6. Acoustic recordings**

In addition to behavioural observations, we recorded continuously the group's vocal activity using all-occurrence (recordings from Pool 1, Hydrophone 1, Figure 4) and *ad libitum* (recordings from Pool 4, Hydrophone 2, Figure 4) sampling methods (Altmann, 1974). Vocalizations were recorded using a broadband system consisting of a Sea-Phone SS03-10 (-194 dB, re 1V/ $\mu$ Pa, 0.020 to 50 kHz) hydrophone in the beginning of data collection of Paper 2, and a C54XRS (-185 dB, re 1V/ $\mu$ Pa, 0.06 to 203 kHz) hydrophone in all data collection of Paper 1 and part of data collection of Paper 2, both connected to a TASCAM DR-680 recorder (sampling rate 192 kHz, 24 bit). The hydrophone was placed at a fixed location in each of the pools depending on where the behavioural observation was being performed. For *ad libitum* observations, there was an auditory feedback in the observation room and behavioural observations were recorded using a commentary channel in the same recorder, so we could cross more easily acoustical data and behavioural comments at time of data analysis.

### **1.7. Experimental approach for perception of artificial label sounds**

In April and May 2016, we tested the dolphins' responses to the sound signal in which they were trained in Pool 1. For this experiment, we used the same instruments to which individuals have been trained (for more details, see section above Training), and basically the same procedure, but more standardized, controlling position of trainers in the beginning of the



experiment, ensuring that they were blind to the chosen instrument, and removing all gestures directed to dolphins used in training. The seven instruments used were: castanets, claves, rattle, maracas, jingle sticks, Baoding balls and a triangle, one per individual. All trials were done in the same pool and same distance between dolphins and sound source (around 30m). We tested dolphins' responses first playing the instruments underwater, and then in the air. At the beginning of each session, some trainers (between 2 and 4 depending on the case) located on one edge of the pool 1, hit on the surface of the water to call to them the 7 individuals (Figure 6). The instrument (randomly chosen) was always played by a main trainer on the opposite edge of the pool. The sessions were filmed using 3 cameras: one underwater, below the sound source and the other two other (Sony HDR-XR155E) placed outside the water (for more details in these experiments see [CHAPTER 4](#)).

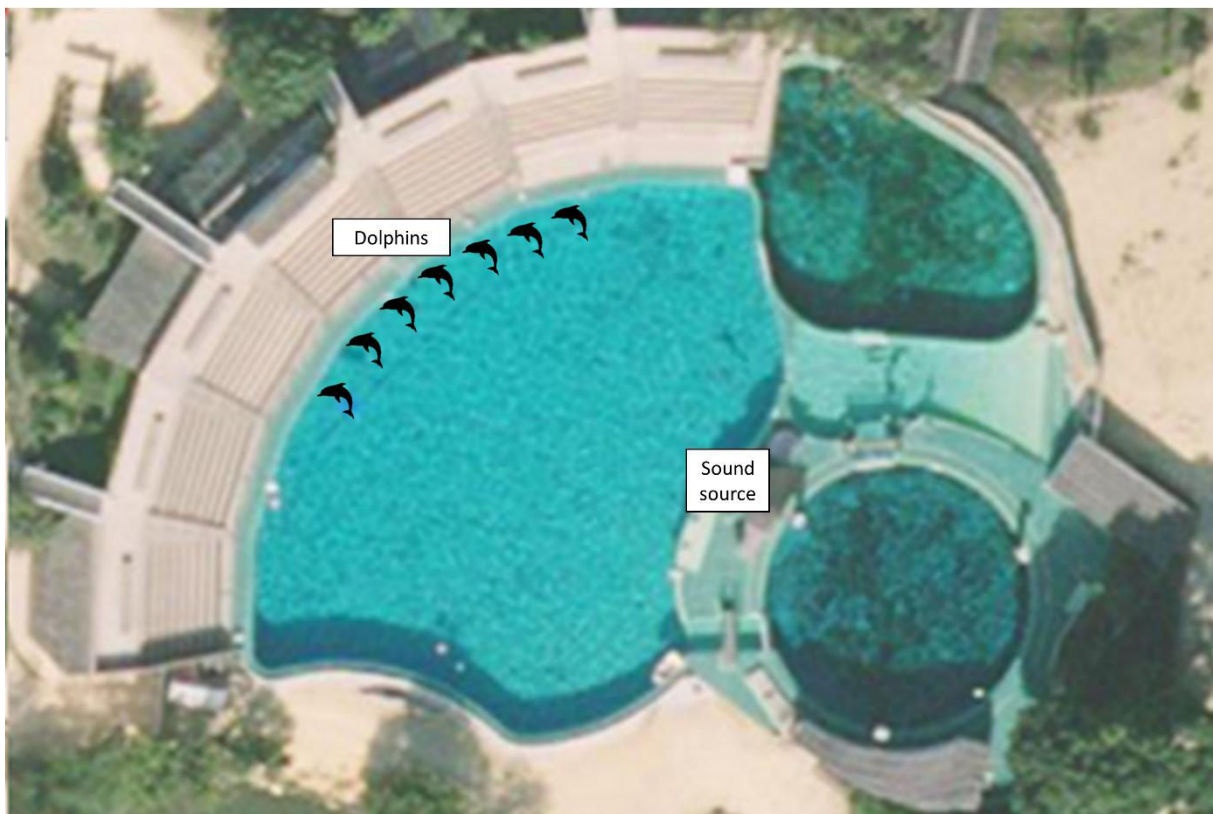


Figure 6. Schematic representation of the 4 pools at Planète Sauvage (adapted from [geoportail.gouv.fr](http://geoportail.gouv.fr)). The symbols represent the position of individuals at the beginning of each test ("Dolphin", random order of alignment) and the trainer operating the instrument ("Sound source").



#### **4. DATA ANALYSIS**

We performed statistical analyses (non-parametrical tests) with the softwares R 3.4.1. (R Core Team, 2014) and Statistica (TIBCO Software).

Non vocal behavioural data were analysed at the individual level, while for acoustical analyses, since the identity of vocalizing dolphin was not obtainable, data were analysed only at the group level. For time of day analyses, we divided the day by two time periods (i.e., morning: 09:00-12:00; afternoon: 12:00 to 17:00).

Vocalizations were classified by audio-visual inspections of spectrograms (FFT 1024 at 192 kHz sampling rate) drawn with Raven Pro 1.4 (Cornell Bioacoustics Research Program), and, for Paper 1, the frequency of occurrences of bottlenose dolphins' four most common vocal categories (Gridley et al., 2015) were scored: burst pulse sounds, whistles, chirps and click trains. The same call definitions were used in the call classification of Paper 2, but we did not consider chirps, which were too rare to be included in statistical tests. All analyses are detailed in the corresponding chapters.

## **CHAPTER 3**

# **CONTEXTS OF CALLING: DAILY TEMPORAL DISTRIBUTION AND ASSOCIATIONS BETWEEN BEHAVIOURS AND CALLS**

## SUMMARY OF PAPER 1

**Questions:** Time budgets of wild bottlenose dolphins vary slightly from one population to another. Nevertheless, a large number of studies reports peaks of feeding in early morning and late afternoon. When not feeding, dolphins socialize, and vocal activities seem related to these moments. In captivity, the temporal distribution of periods of socializing and the possible link with the temporal distribution of vocalizations have never been studied. Our first study aimed to describe diurnal time budgets in the routine of the zoological park and associated vocal behaviours.

**Methods:** We looked for differences on behaviours and vocalizations of the group between morning and afternoon, through surface observations each three minutes in the main pool. We then looked at the associations between number of behaviours and number of vocalizations over observation sessions.

**Results:** We found that dolphins engage more in social activities during the morning, while the only vocal category that showed a temporal pattern (chirps) was more emitted in the afternoon. However, the most remarkable result is that we found strong correlations between certain activities and vocal categories.

**Conclusions:** The pattern of social activities found in this zoological setting differs from what have been described in the wild and the vocal activity recorded can give a representation of the non-vocal activities. These observations should be taken in consideration in the management and organization of human-related dolphin activities in captivity.

This paper has been published in *Zoo Biology* in October 2017 and part of the results was presented at the 46<sup>th</sup> Conference of the French Association for the Study of Animal Behaviour (SFECA, 2016).

**Vocal activities reflect the temporal distribution of bottlenose dolphin  
social and non-social activity in a zoological park**

LIMA Alice<sup>1,2</sup>, LEMASSON Alban<sup>1</sup>, BOYE Martin<sup>2</sup>, HAUSBERGER Martine<sup>3</sup>

<sup>1</sup> Université de Rennes 1, Ethologie Animale et Humaine (UMR 6552) – CNRS, Université de Caen  
Normandie, Station Biologique, Paimpont, 35380, France

<sup>2</sup> Département Scientifique et Pédagogique, Planète Sauvage, Port-Saint-Père, 44710, France

<sup>3</sup> CNRS, Ethologie Animale et Humaine (UMR 6552) – Université de Rennes 1, Rennes Cedex,  
35042, Université de Caen Normandie, France

## Abstract

Under natural conditions bottlenose dolphins (*Tursiops truncatus*) spend their time mostly feeding and then travelling, socializing, or resting. These activities are not randomly distributed, with feeding being higher in early morning and late afternoon. Social activities and vocal behavior seem to be very important in dolphin daily activity. This study aimed to describe the activity time-budget and its relation to vocal behavior for dolphins in a zoological park. We recorded behaviors and vocalizations of six dolphins over two months. All subjects performed more non-agonistic social interactions and play in the morning than in the afternoon. The different categories of vocalizations were distributed non-randomly throughout the day, with more chirps in the afternoon, when the animals were “less social”. The most striking result was the strong correlation between activities and the categories of vocalizations produced. The results confirm the association between burst pulses and whistles with social activities, but also reveal that both are also associated with solitary play. More chirps were produced when dolphins were engaged in socio-sexual behaviours, emphasizing the need for further questioning about the function of this vocal category. This study reveals that 1) in a group kept in zoological management, social activities are mostly present in the morning; and 2) the acoustic signals produced by dolphins may give a reliable representation of their current activities. While more studies on the context of signal production are needed, our findings provide a useful tool for understanding free ranging dolphin behaviour when they are not visible.

Keywords: social activities; time-budget; behavior; meal times, dolphin, vocal activity



## 2. Introduction

Food availability is a major determinant of time budgets for animals living in natural environments (Beddia 2007). In many cases, access to resources, in particular to food, is relatively continuous and individuals can thus be the "actors" of the temporal distribution of their feeding activities (Spitz, Mourocq, Leauté, Quéro and Ridoux 2010; Spitz et al. 2012). Feeding strategies of bottlenose dolphins (*Tursiops truncatus*), for example, are flexible and adapted to the habitat and available food resources (Shane et al. 1986). Under natural conditions bottlenose dolphins spend at least 50% of day feeding or foraging for food (Beddia 2007; Steiner 2011), incorporating a large variety of fish and squid species in their diet year-round (Perrin, Würsig, Thewissen and Würsig 2008). The rest of the time is generally devoted to three main activities: travelling, social activities, and resting (Shane et al. 1986). These activities are not randomly distributed throughout the day and feeding activity is clearly higher in the early morning with a secondary smaller peak in the late afternoon (all year-round in Allen, Read, Gaudet and Sayigh 2001; Blair Irvine, Scott, Wells and Kaufmann 1981; Goodwin 1985; Saayman, Tayler and Bower 1973; from June to August in Brager 1993; see also review in Shane et al. 1982). Because of uncertainty concerning food availability, wild dolphins remain actively attentive to their food resources. Social activities are also very important in dolphin daily activities (Connor, Wells, Mann and Read 2000) and are temporally distributed between feeding times; beginning after the morning feeding period and continuing until the start of the evening feeding period (Brager 1993; Miller, Solangi and Kuczaj II 2010; Saayman et al. 1973). Because captivity puts temporal constraints on resource availability, and feeding time in particular, one question is whether this may have any effect on the animal's behavior (McPhee and Carlstead 1996; Charmoy, Sullivan and Miller 2015). Feeding can become, in captivity, the greatest significant event in an animal's routine (Bassett

and Buchanan-Smith 2007; Carlstead 1986). For example, feeding becomes a highly predictable event in captivity, contrary to the wild situation, and animals can learn the timing of events (e.g. Watters 2014). Whether feeding times should be predictable or unpredictable in captive/domestic animals remains a debated welfare issue with some authors arguing that temporal unpredictability, by providing more opportunities to seek and acquire food, can improve welfare (Bassett and Buchanan-Smith 2007), furthermore increasing the expression of species-specific behaviors (Gilbert-Norton, Leaver and Shivik 2009; Schneider, Nogge and Kolter 2014; Charmoy et al. 2015). In horses, for example, research has shown that the temporal feeding patterns have a major impact on reproductive success, welfare, and physiological state, that improves in conditions of semi-continuous access to food (Benhajali, Richard-Yris, Ezzaouia, Charfi and Hausberger 2009; Benhajali et al. 2013). In zoos, as bottlenose dolphins do not have to forage, the main behaviors observed seem to be low intensity or synchronous swimming, play and anticipatory behaviors (Clegg et al. 2017; Walker et al. 2017), however few studies have described time budgets (Ugaz et al. 2013; Walker et al. 2017). One further interesting and still poorly known aspect is the co-occurrence of vocalization types and activities, which could help understanding, in the long term, the potential relationships between the emitter's internal state, its current activity, and its vocal behavior.

Dolphins emit various types of vocalizations to convey information (Evans-Wilent and Dudzinski 2013) and two broad categories have been defined: frequency modulated narrow band sounds (whistles and chirps) and pulsed sounds (clicks and burst-pulsed sounds) (Tyack 1986). Although some are suggested to occur in particular contexts, their function and significance in terms of the emitter's internal state or current activity, are poorly known (Hawkins and Gartside 2010). Whistles are the most studied category and are often associated with social affiliative functions (Janik and Sayigh 2013; Mello and Amundin 2005; Tyack



1986), although there are controversies (e.g. Acevedo-Gutiérrez and Stienessen 2004). Chirps present strong acoustic similarities with whistles, but it is not clear whether chirps and whistles should be classified together or not (Gridley, Nastaki, Kriesell and Elwen 2015). In captivity, positively reinforced dolphins produce chirps more frequently than non-reinforced individuals (Caldwell, Caldwell and Tyack 1990). Pulsed sounds are traditionally associated with echolocation clicks (Au 2004), but they can be observed during foraging (Eskelinen et al. 2016), and sometimes in agonistic interactions (Vollmer, Hayek, Heithaus and Connor 2015). This category, less explored than whistles, could include several functional sub-categories (Gridley et al. 2015).

Thus, even though some work has been done on this topic (e.g. Dudzinski 1996; Papale et al. 2016), further research is needed to understand the potential functions of specific vocal categories in dolphin repertoire. This also could at some stage help determine whether vocal behavior could be a welfare indicator, as acoustic monitoring has been shown as a promising noninvasive method to assess the impact of stressful situations on bottlenose dolphins (Esch et al. 2009).

The aim of the present study, therefore, was to describe the diurnal time-budgets and associated vocal behavior of dolphins housed in a zoological park. This was done to provide information for dolphin management and welfare in a zoo setting, but also for the monitoring of dolphin activity elsewhere.

## 2. Materials and methods

### 2.1. 2.1. Dolphins

Our observations included six bottlenose dolphins housed at Planète Sauvage Animal Park (Port Saint-Père, France). The group included four males (aged 5, 6, 12 and 16 years old) and two females (aged 7 and 14 years old), all born in captivity. The group composition had been stable for one month when the observations started in March 2015. These dolphins had free access to four differently-sized and inter-connected pools (**Erro! Fonte de referência não encontrada.**; 1: 4950 m<sup>3</sup>, 2: 1280 m<sup>3</sup>, 3: 220 m<sup>3</sup>, 4: 1040 m<sup>3</sup>). These dolphins were given 39kg of fish each day, i.e. herring, capelin, mackerel, sprat, whiting and squid; 4.5-8.5kg per dolphin; amount related to the size / age of individual) during two free (light) meals at 0900 h and 1700 h, and in between, during five (two in the morning and three in the afternoon) training sessions per day (each one lasting 15-30 min.; about every 1.5 h), during public shows and training for shows, and for medical treatments.

### 2.2. 2.2. Data collection

Data were collected during two months (09:00–1700; March and April 2015, total 19 days), using instantaneous scan sampling, noting each dolphin's behavior every 3-minutes (Altmann 1974). Observation sessions lasted  $29 \pm 18$ min on average (mean  $\pm$  SD) recorded at random moments, one to three times a day, outside of training periods, and without the presence of trainers. There were 38 sessions: 18 (247 scans; 12h20min) in the morning (i.e. from 09:00 to noon) and 20 (147 scans; 7h20min) in the afternoon (from noon to 17:00). The activity of each individual (identified on the basis of physical differences, such as shape of dorsal fin, face, color patterns or natural marks) was recorded at each scan. Our definitions of activities were adapted from those commonly used in other studies: social activities (play, socio-sexual behavior, agonistic behavior, positive or neutral social interaction), inactive

(when animal is stationary, or as rest), solitary play, body movements, spy-hopping, and swimming (**Erro! Fonte de referência não encontrada.**), (Dudzinski 1996; Kyngdon, Minot and Stafford 2003; Lusseau 2006; Mackey, Makecha and Kuczaj 2014; Sakai, Hishii, Takeda and Kohshima 2006; Scheer 2010; Streit, Ganslosser and Fersen 2011; Tamaki, Morisaka and Taki 2006). The observer was positioned at a fixed point on the edge of Pool One (the largest) from where all the pools were visible. In addition to scan sampling, we recorded the group's vocal activity using the all-occurrence sampling method (Altmann 1974). For technical reasons, vocal recordings did not always totally overlap with the timing of the observation sessions. Therefore, for the analysis of the co-occurrence of activities and vocal production, we kept only the 17 sessions where both recordings had an equal duration: 9 in the morning and 8 in the afternoon). Vocalizations were recorded using a broadband system consisting of a C54XRS (-185 dB, re 1V/ $\mu$ Pa, 0.06-203 kHz) hydrophone connected to a TASCAM DR-680 recorder (sampling rate 192 kHz, 24 bit). The hydrophone was placed at a fixed location in Pool One.

### **2.3. 2.3. Data and statistical analyses**

#### **2.3.1. Acoustic Analyses**

To evaluate the group's vocal activities, the same person (A. Lima) first classified (by audio-visual inspections of spectrograms) the vocalizations recorded during the 17 observation sessions using Raven Pro 1.4 (Cornell Bioacoustics Research Program) software with resolutions of 256 bands, 1024 fast Fourier transformer size, and a Hamming window. The frequency of occurrences of bottlenose dolphins' four most common vocal categories (Gridley et al. 2015) according to the current classification were scored: i) burst-pulsed (BP) sounds (trains of closely spaced broadband clicks) including “squawks”, barks, and “pops” (Herzing 2013); ii) whistles (tonal and narrow-band signals, Acevedo-Gutiérrez and Stienessen, 2004); iii) chirps (short and stereotyped tonal upsweeps; Gridley et al. 2015), and

iv) click trains (series of narrow-band and high-frequency clicks, Au, 2004) (see **Erro! Fonte de referência não encontrada.** for example of spectrograms of each category). No sounds were found that did not fall into any of these four categories. Overlapping sounds were considered in the count of vocalizations as long as they fulfilled the above scoring criteria.

### **2.3.2. Statistical analyses**

Occurrences for each behavior were compared between mornings and afternoons, using Wilcoxon Signed-rank tests (Statistica software), with N being the total number of individuals. Since the number of scan samples could not be identical for each individual, statistical analyses were performed on the frequency of each activity divided by the total number of scans when the individual was visible (on average 66.5% of time).

Since dolphins produce sounds without any visible sign, vocal activity could only be considered at the group level. In order to assess nevertheless potential temporal changes in the distribution of the different sound categories and be able to relate those changes with the other activities, we chose to analyze the data at the level of sessions, each session being considered as the “unit” of measure. Therefore, we compared the production between morning and afternoon using a Mann-Whitney U test for each vocal category ( $n_1 = 9$  morning sessions,  $n_2 = 8$  afternoon sessions). The data are presented as percentages in the figures for more clarity but all statistical tests were performed on real data. We also tested the co-occurrence of vocal and non-vocal activities at this same level, by performing Spearman correlation tests comparing, for each vocal category, the number of events of this vocal category with that of each non-vocal activity and for each session.

## **3. Results**

Dolphin behavior differed significantly between morning and afternoon. All animals performed more non-agonistic social interactions (Wilcoxon tests:  $N = 6$ ,  $Z = 2.2$ ,  $p = 0.03$ ), in particular social play ( $N = 6$ ,  $Z = 2.2$ ,  $p = 0.03$ ) but also solitary play ( $N = 6$ ,  $Z = 2.2$ ,  $p =$

0.03) in the morning than in the afternoon (**Erro! Fonte de referência não encontrada.**). Conversely, we observed more solitary swimming in the afternoon than in the morning ( $N = 6$ ,  $Z = 2.2$ ,  $p = 0.03$ ). Frequencies of body movements ( $N = 6$ ,  $Z = 1.15$ ,  $p = 0.25$ ), socio-sexual behaviors ( $N = 6$ ,  $Z = 0.41$ ,  $p = 0.69$ ) and spy-hopping ( $N = 6$ ,  $Z = 1.57$ ,  $p = 0.12$ ), observed more rarely, did not differ significantly between mornings and afternoons. A total of 3449 (32.5%) burst-pulsed (BP) sounds, 331 (3.1%) chirps, 3350 (31.5%) click trains and 3497 (32.9%) whistles were identified from the 09h40min of vocal recordings (some examples are shown in **Erro! Fonte de referência não encontrada.**).

When looking if vocal categories were homogeneously distributed during the day, only chirps appeared to vary significantly with more of them in the afternoon (Mann-Whitney  $W = 14$ ,  $n_1 = 9$ ,  $n_2 = 8$ ,  $p = 0.036$ ). The most striking result was the strong correlations between the production of each vocal category and given non-vocal activities. The frequency of burst pulses was positively correlated with that of solitary play (Spearman correlation,  $r_s = 0.619$ ,  $p = 0.008$ ) and of positive or neutral social activities (Spearman correlation,  $r_s = 0.483$ ,  $p = 0.050$ ); whistles with solitary (Spearman correlation,  $r_s = 0.605$ ,  $p = 0.010$ ) and social play (Spearman correlation,  $r_s = 0.502$ ,  $p = 0.040$ ); Chirps with socio-sexual behaviours (Spearman correlation,  $r_s = 0.569$ ,  $p = 0.017$ ), and click trains with non-social swimming (Spearman correlation,  $r_s = 0.603$ ,  $p = 0.010$ ) (Figure 4).

#### 4. Discussion

Our data reveal that the temporal distribution of activities of dolphins in a zoological park differs strikingly from that described in the wild. There was more social activity in the morning than in the afternoon. More remarkable though is the strong correlation between the categories of vocalizations and social and non-social activities observed. Interestingly, although as proposed before in the literature, burst pulses and whistles are associated with some social activities, they were here also associated with solitary play. The association of

burst pulse sounds with affiliative social activities, differs from the predominant view about this vocal category, usually thought to correspond to agonistic contexts. Moreover, while some authors suggested that chirps and whistle should be pooled (Caldwell and Caldwell 1970; Bazúa-Durán and Au 2002), the finding that they do not present the same temporal pattern of production, nor were associated with the same activities, reveals that they probably have different functions. The co-occurrence found here between chirps and socio-sexual behaviours had not been reported until now.

In natural situations, bottlenose dolphin activity appears to be strongly influenced by prey availability, inducing variations among populations (Gregory and Rowden 2001; Mendes, Turrell, Lütkebohle and Thompson 2002). According to Beddia (2007) dolphin time budgets are centered on feeding and searching for food. However, the predominant pattern for many populations consists of significant increases of feeding activity early morning (07:00–10:00) and early evening (17:00–20:00; Saayman et al. 1973; Norris and Dohl 1980; Shane et al. 1986; Miller et al. 2010). Social activities generally occur when groups are not feeding, with increases of social interactions in the afternoon (Brager 1993; Miller et al. 2010; Saayman et al. 1973; Shane et al. 1982). Thus, it seems that feeding periods are followed by socializing periods in the wild. In captivity, it seems that these two activities are also linked, but here, as dolphins do not pass long time foraging in early morning, socializing comes earlier than in the wild, starting soon after the first feeding episodes in the morning. Miller, Mellen, Greer and Kuczaj II (2011) observed an increase in socializing and affiliative behavior after dolphin shows (with food as reinforcement; see also Clegg et al. 2017). It has also been suggested that the lack of predation risk and not having to forage to feed could also release more time to socialize in captivity (Levengood and Dudzinski 2016). Our results suggest further that dolphin circadian rhythms can be rescheduled in relation with the zoological park's management routines, in particular related to feeding temporal distribution.

Our results also contribute to the debate on the significance of this species' vocalizations as there are a lack of studies on daily acoustic behavior of wild dolphins (see Wiggins, Frasier, Henderson and Hildebrand 2013 for an exemple). Our finding that the distribution of chirps during the day is non-random is remarkable, since this vocal category has been associated with different contexts, like social activities (Dudzinski 1996) or milling and travelling (Papale et al. 2016). Here we found a significant correlation of this vocal category with socio-sexual behaviours, which suggests, together with the finding that it is less abundant when social behaviours are less frequent (the afternoon here), that it may rather reflect a certain level of excitement. This result also reveals that chirps and whistles should be studied separately (Gridley et al. 2015). While an increase in whistle rates during social play could be expected, the increase during solitary play was more surprising, as most studies consider whistles primarily as social signals (Caldwell et al. 1990; Janik and Slater 1998; Herzing 2000; dos Santos et al. 2005; King and Janik 2013; Gridley et al. 2015; Kuczaj II et al. 2015; Eskelinen et al. 2016). However, a few studies have found that whistles could be produced in more nonsocial contexts, such as feeding (Acevedo-Gutiérrez and Stienessen 2004; dos Santos et al. 2005). Whistles may then act as “contact calls” enabling widely spaced individuals to transfer information about their location or food availability (Lammers et al. 2006; Quick and Janik 2008; Hawkins and Gartside 2010). Both social and solitary play involve some excitement, and some authors proposed that the higher the level of excitation, highest are the richness and variability of whistle production (e.g. dos Santos et al. 2005). Burst pulses were associated with solitary play and positive or neutral social activities. This result confirms that burst pulse sounds are emitted in social contexts, but it does not match the agonistic nature often attributed to them (see for example Overstrom, 1983; Lopez and Shirai, 2009). If, as some authors suggest, burst pulses are a play-fight signal (Blomqvist et al., 2005), this could explain their high correlation with a play behaviour, even if solitary (see also Schwing et al., 2017 for a vocal play signal). Caldwell and Caldwell (1967) also found an

increase of burst pulse production during the introduction of novel objects, and this could be the case here. What was more surprising was the finding that these sounds were also associated with affiliative behaviours. Overall, our results confirm that context of burst pulse sounds are broader than expected. The possible acoustic subcategories of burst-pulsed sounds associated with observation of particular contexts need to be studied in detail to understand their potential functions. We recorded more clicks when the dolphins were swimming more actively at times when food was not available, possibly corroborating its exploration, navigation (Au 2004), and/or communication function (Kuczaj II et al. 2015). This last function is not yet clear and has been studied only in a context of calf retrieval by mothers. Following the idea that we could consider vocalizations as expressions of internal states (Boissy et al. 2007), passive recording of underwater sound production on a regular basis is a potential method for assessing patterns of activity and well-being of dolphins (Therrien et al. 2012), allowing care staff to identify any changes in the baseline pattern, which could then indicate the need for closer examination of animals.

Considering the hypothesis that feeding and socialization periods are connected in some way, the specificities of the zoological park (single feeding opportunities offered during narrow time windows, predictability, routine associated with daylight, and more food in the afternoon than in the morning) may be playing an important role in the observed timing of peak of this dolphin group's social activities. As captive dolphins cannot control feeding times, it could affect the timing of social activities, and social behavior could be replaced by anticipation behavior (as described by Jensen, Delfour and Carter (2013) and Clegg et al. (2017), with unclear consequences on welfare (e.g. Boissy et al. 2007). Studies of other taxa show that dolphins are not the only animals for which the distribution of non-feeding behaviors is significantly influenced by feeding times. For example, captive leopard *Panthera pardus* behavior is influenced by feeding times (Mallapur and Chellam 2002), and activity



levels are higher and levels of rest are reduced before feeding times, thus expressing food-anticipation activity. Finally, reports show that the predictable schedules adopted in many facilities can alter the behavior of different species. Making feeding times more unpredictable for primates seems to favor the increase of their natural behavior and reduce inactivity and abnormal behavior (Bloomsmith and Lambeth 1995; Waitt and Buchanan-Smith 2001). Similarly, Charmoy et al. (2015) have shown that enrichments based on temporal unpredictability increase the time spent feeding in gorillas, thus approaching the natural time budget for the species. Since unpredictability in feeding has shown positive benefits in other species, a similar study should be conducted on dolphins.

Dolphins are active day and night and, in the wild, their daily feeding starts much earlier than in captivity (Shane et al. 1986). Having a thorough understanding of the behavior and behavioral patterns of these animals can help with captive management of this species in respect of its needs. Results from the current study can help to better understand bottlenose dolphins' behavior in a zoo setting. Understanding behavioral patterns (e.g., socialization and vocal activity as a reflection on current dolphin state) should help define management that minimizes impacts on dolphin time budgets. This study also offers a promising way of monitoring dolphin activity using vocal production.

## **5. Conclusions**

5.1. This study showed that in a dolphin group kept in a zoological setting, social activities are mostly expressed in the morning, a pattern opposite to that found in wild conditions.

5.2. Dolphin acoustic signals may give a consistent representation of non-vocal activities, providing a useful tool for studies when dolphins are not visible.

5.3. These general observations on dolphin behavioral time-budgets may have important implications for the management and well-being of small cetaceans in zoological parks.

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**8. Table**

*Table 2 Behavioral repertoire for dolphins housed in Planète Sauvage (March – April 2015)*

<i>Behavior</i>	<i>Operational definition</i>
<i>Social behavior</i>	
<i>Social play</i>	Two or more dolphins interact playing. This behavior can be vigorous one dolphin chasing another or both spinning around each other quickly. Alternatively, play can be calmer with the dolphins circling gently around each other, or nudging one another. During chasing individuals took turns as a chaser and/or mouth-biting.
<i>Socio-sexual behavior</i>	Activities that involve erection, and potentially genital inspection, including two or more individuals within a distance of one body-length.
<i>Agonistic behavior</i>	One dolphin displays agonistically or attacks another dolphin, by chasing, without take turns between individuals, mouth-biting, hitting, threatening, or head butting another individual who is expresses avoidance or flight.

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#### *Positive or neutral social interaction*

Social behaviors not classified as agonistic or social play include many tactile behavioral events such as rubbing, swim contact, petting, and synchronous movements.

#### *Non-social behavior*

##### *Inactive*

Floating or lying on the bottom of pool, moving slowly, without significant displacement.

##### *Solitary play*

Playing alone, potentially with objects (such as a ball, buoy) or water. This can involve pushing, tossing, carrying, or biting an object, as well catching or manipulating water jets.

##### *Body movements*

Body movements not associated with regular swimming and not involved in playing with an object. This includes visual exploration (eye-out: a dolphin lifts its head above water until its eye is exposed).

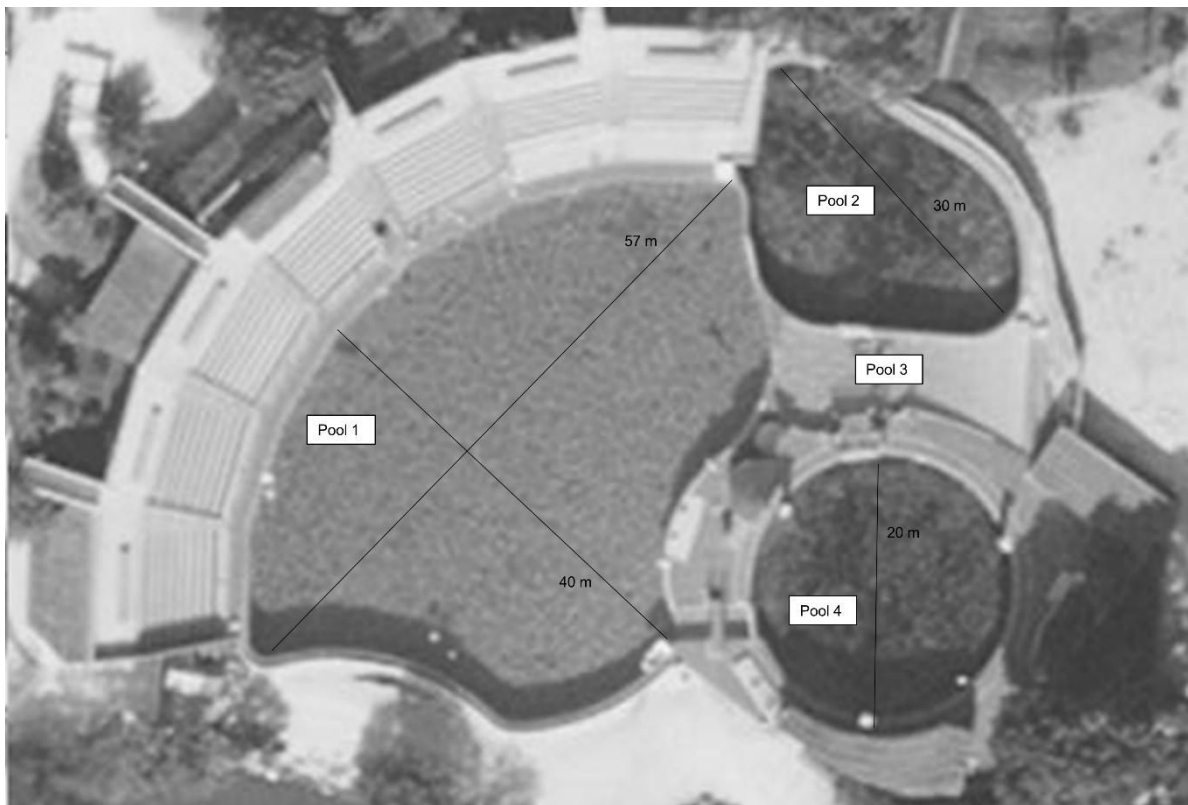
##### *Spy-hopping*

Sequence of spy-hops: the dolphin repeatedly extends its head vertically out of water.

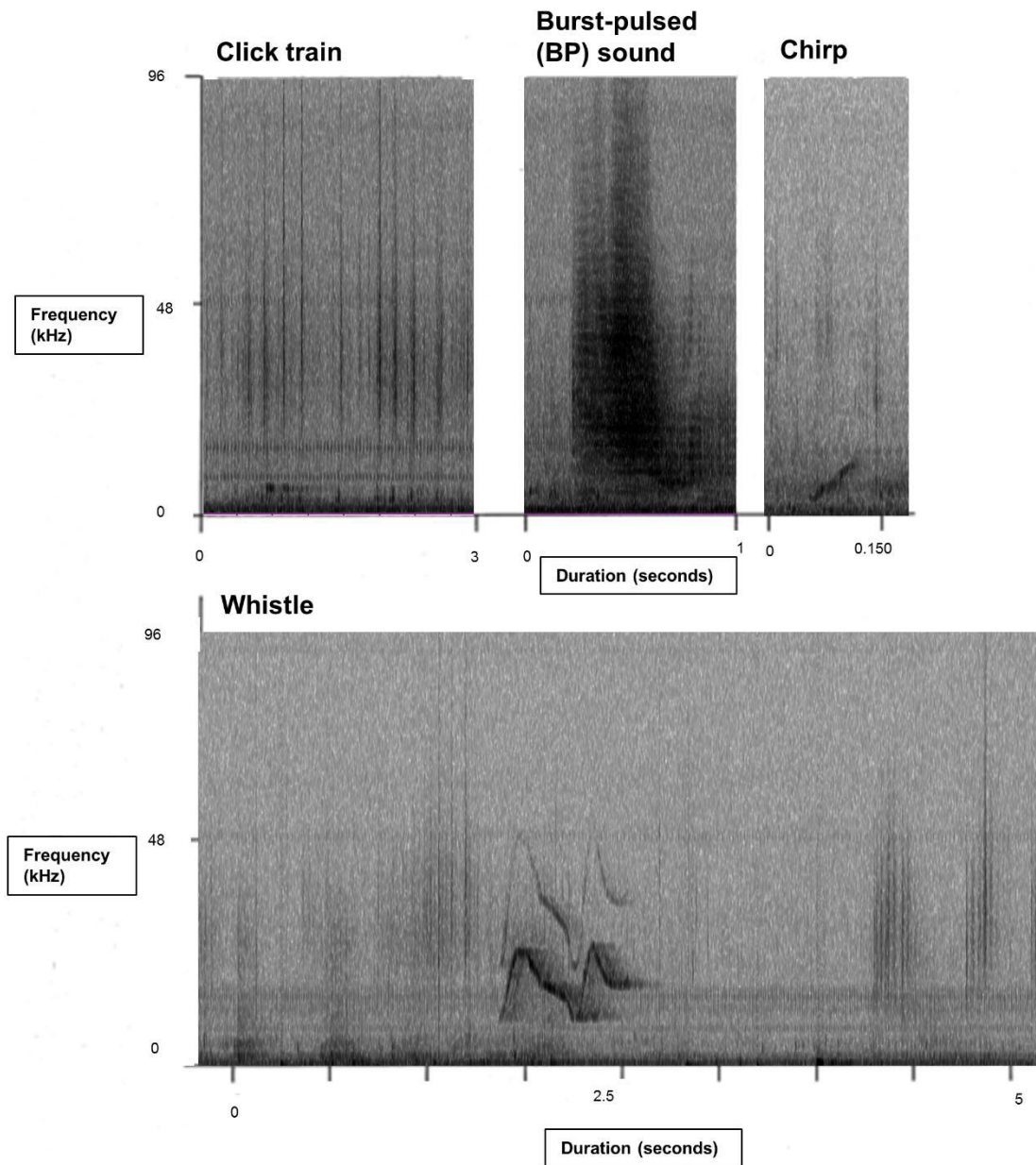
*Swimming*

Dolphin swims through the tank in any direction (swim around), in steady circles without changing direction or speed (steady swim) or swims at high speed (speed swim).

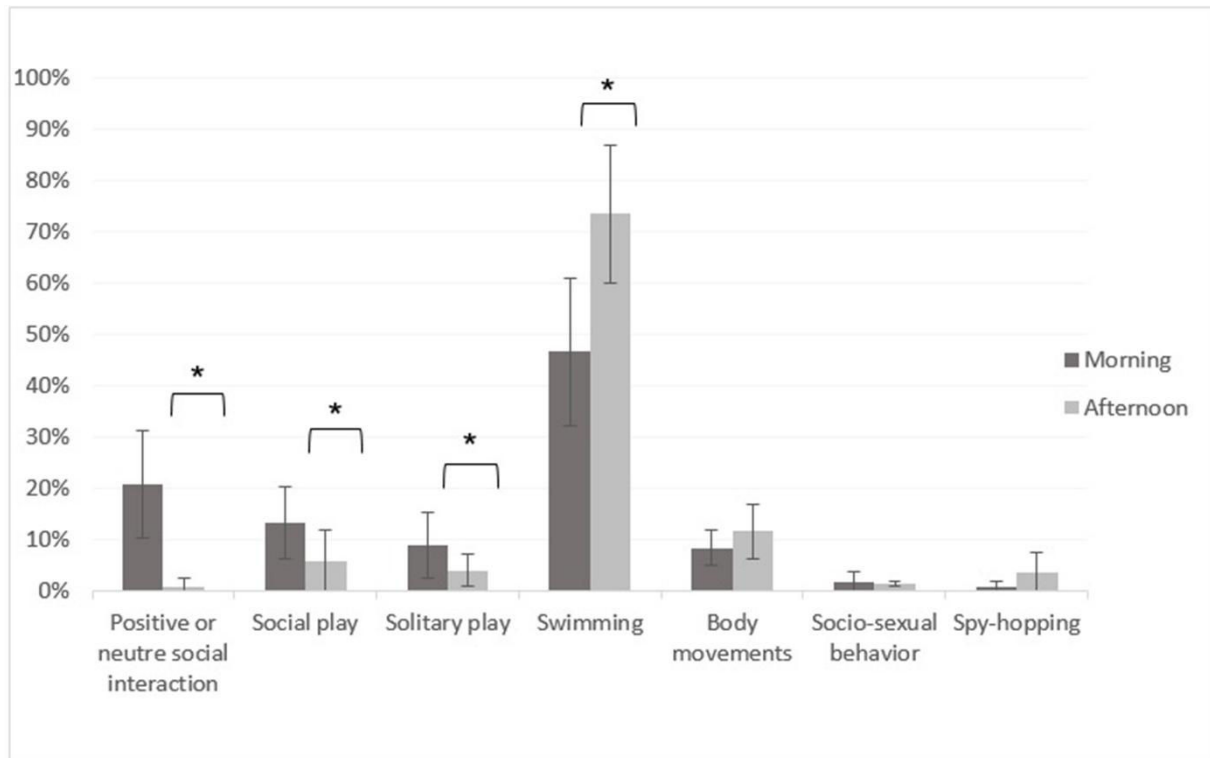
**Figures**



**Figure 7. The dolphin pools at Planète Sauvage, Port Saint Père, France. Maximum depths: 5m (Pool 1 and 2); 1.9m (Pool 3) and 2.8m (Pool 4). Adapted from © GEOPORTAIL.**



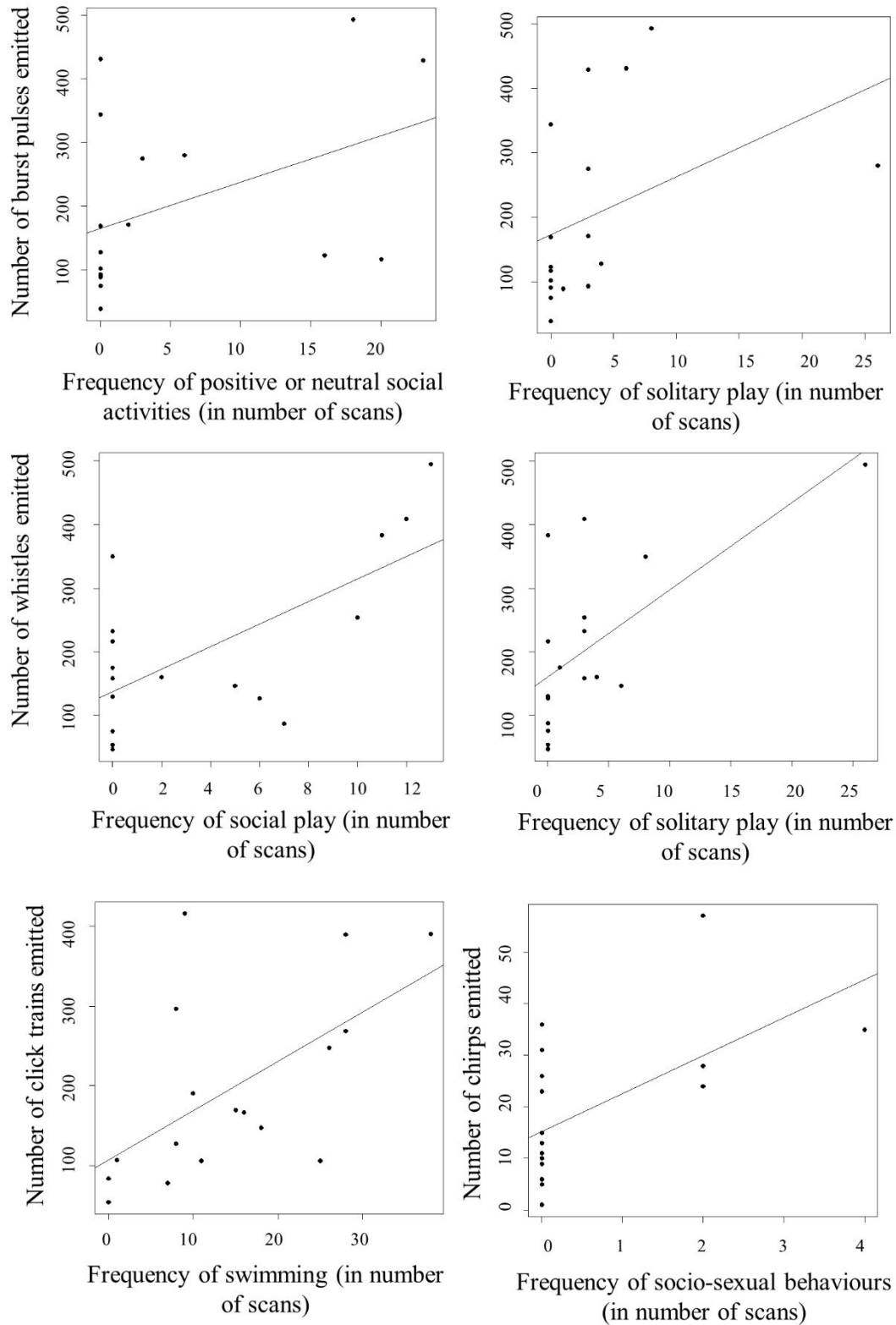
**Figure 8. Examples of four different categories of vocalizations analyzed.**



**Figure 9. Activities (mean %  $\pm$  standard deviation) of a group of six dolphins housed in a zoological park in the morning (12:00 and before) and in the afternoon (after 12:00).**

**\* Wilcoxon test,  $p < 0.05$ .**





**Figure 10. Significant correlations between emission rates of the different vocal categories in relation to activities (Spearman correlations, n = 17).**

## **SUMMARY OF PAPER 2**

**Questions:** Dolphin communication is known to be quite complex when focusing on acoustic structures, but the contextual usage of the different signals is still little known. Dolphin sounds are typically divided in burst pulse sounds, click trains and whistles. Here, we examined in a narrow scale the possible associations between vocal categories and behavioural contexts occurring simultaneously.

**Methods:** Acoustic recordings were made simultaneously to behavioural observations of all individuals present at a given time in one of the pools, through an underwater window. Calls were classified in whistles, click trains and burst pulse sounds. The latter were further subdivided in two types based on their duration.

**Results:** We found preferential associations between vocal categories and behavioural contexts, clarifying their contextual usage. We also showed the importance to consider types of burst pulses as functionally different calls. We also identified a broad range of context-dependent combinations between vocal categories. Some of them confirmed patterns found before in the literature, but others allowed to raise new hypothesis on functional use of vocalizations and combinations of vocalizations.

**Conclusions:** We confirm the contextual use for dolphin vocalizations and notably of combinations between different vocal categories. More studies should explore the functional use of these combinations and try to identify emitters to go further in the context-specificity of vocal production in dolphins.

Running head: dolphin calling contexts

**Contexts of calling in a captive group of bottlenose dolphins**

Alice Lima<sup>1,2</sup>, Martine Hausberger<sup>3</sup>, Alban Lemasson<sup>1</sup>

<sup>1</sup> Université de Rennes 1, Ethologie animale et humaine - EthoS, UMR 6552 - CNRS - Université Caen Normandie, Paimpont, France

<sup>2</sup> Planète sauvage, Port-Saint-Père, France

<sup>3</sup> CNRS, Ethologie animale et humaine - EthoS, UMR 6552 - Université de Rennes 1 - Université de Caen Normandie, Rennes, France

**Abstract**

Dolphin communication appears quite complex in terms of structural diversity and flexibility of acoustic signals. However, little is still known about the contextual usage of these signals, notably because of the difficulty to observe these animals in the wild. The literature agrees on the existence of different main vocal categories even if their social functions as well as the possibility to break them into several context-dependent types remains subject to controversies. Another constraint with dolphins is the difficulty to identify callers as they do not open the mouth while vocalizing. Here, we examined the potential existence of non-random relationships between bottlenose dolphins' vocalizations and behavioural contexts. We observed a captive group composed of seven dolphins in a four-pool setting. We recorded underwater sounds and concurrent spontaneous behaviours of all individuals simultaneously present at a given time and in a given pool equipped with an underwater window. We found the main categories mentioned in the literature (whistles, burst-pulses and clicks), with a preferential relationship between whistles and socio-sexual behaviours, and between clicks and socio-affiliative behaviours and solitary play. We also highlighted the interest to consider short and long burst-pulse sounds as two functionally different call types. At last, we identified a broad range of non-random and context-dependent patterns of association between vocalizations. Our results confirm the context-specific use of dolphin sound emissions. Furthermore, they open up avenues of research on less explored aspects, as the functional use of associations of different sounds.

## **1. Introduction**

The keys to understand a given animal species communication rely on the analysis of the contexts of emission of the different signals of their repertoire (Smith, 1965). The social function of a signal can hence be inferred from the contextual regularities found to be associated with the corresponding acoustic structure. Most studies on the contextual use of vocalizations have been done on birds and terrestrial mammals (e. g. Adret-Hausberger, 1982; Arnold and Zuberbühler, 2013). A species-specific vocal repertoire is typically composed of several call and/or song types. Some calls or songs of the repertoire are clearly associated with a specific social context of production, such as adopting a threat or submissive posture (e. g. Gouzoules et al., 1995), approaching a congener to interact positively (e. g. Balsby and Bradbury, 2009), discovering a food item (e. g. Slocombe and Zuberbühler, 2005), encountering a potential sexual partner (e. g. Gustison and Bergman, 2016), playing (e. g. Schwing et al., 2017) and spotting a danger in the environment (e. g. Ouattara et al., 2009). Other calls or songs of the repertoire are emitted in a broad range of contexts and rather function in signalling callers' identities and locations in order to maintain a socio-spatial cohesion all day long with other group members (e. g. Cortopassi and Bradbury, 2006). The latter signals are particularly crucial for animals living in habitats with a limited visibility, like forested areas (Candiotti et al., 2012). Also, the social-vocal coevolution hypothesis suggests that the more complex the social system, the more complex the vocal repertoire with diversified call types (Bouchet et al., 2013).

Cetaceans have attracted a lot of attention during the last decades, notably because they are highly social animals (Tyack, 1986) with high vocal rates and because they show a high degree of acoustic plasticity (Janik, 2009). Informing others about its individual and social

identities is particularly important in those species. For example, several cetacean species exhibit regional dialects (Weilgart and Whitehead, 1997), killer whales possess vocal clans based on matrilineal lineages (Yurk et al., 2002) and dolphins produce individually distinctive calls, named signature whistles (Janik & Sayigh, 2013). Also, vocal learning is widespread among cetacean species (Tyack & Sayigh, 1997). Dialects are culturally transmitted (Filatova and Miller, 2015; Garland et al., 2011), dolphins learn their individual signature during their first year of life (Caldwell et al., 1990) and cetaceans are even able to mimic heterospecific sounds from their environment (Kremers et al., 2011). However, contextual analyses of vocal emissions have remained scarce in cetaceans, notably because this requires a considerable amount of behavioural sampling with good observation quality, conditions rarely satisfied for odontocetes in the wild as they travel very fast, rarely stay at the surface and live sometimes in water with reduced visibility (Gridley et al., 2015).

Nevertheless, recent efforts have been made with different odontocete species (most of them with social delphinids), reporting possible associations between specific signals and behaviours (e. g. Herzing, 1996; dos Santos et al., 1995; Evans-Wilent & Dudzinski, 2013; Samarra, 2015; Janik, 2000; Nowacek, 1999; Herzing, 2015; Perazio & Kuczaj II, 2017; Rachinas-Lopes et al., 2017). One of the most studied acoustic repertoires is that of bottlenose dolphins (*Tursiops truncatus*), a species that lives in fluid fission-fusion societies (Connor et al., 2000). Their sounds are typically divided into three general categories: (1) narrow-band, frequency modulated whistles (Acevedo-Gutiérrez and Stienessen, 2004; Caldwell and Caldwell, 1965), (2) very short, broadband clicks (Herzing and dos Santos, 2004) and (3) wide-band burst pulse sounds (Herzing, 2000; Lopez and Shirai, 2009).

The first category of sounds (whistles) is historically the most studied dolphin vocalization, perhaps because of their ease in measurement (Díaz López, 2011; Herzing, 2013). This category has been documented frequently in social, more often non-agonistic, broad contexts

(e.g. Hernandez, Solangi, & Kuczaj, 2010; Quick & Janik, 2008) and would thus function in maintaining contact and advertise social bonds (Gridley et al., 2015; Herman and Tavorla, 1980; Tyack, 1986a), as well to address conspecifics through matching of signature whistles (Janik and Sayigh, 2013). In line with that, some studies found a positive correlation between whistle rates and group sizes (Cook et al., 2004), a result however subject to controversies (dos Santos et al., 2005; Quick and Janik, 2008). Also, Kremers, Jaramillo, Böye, & Lemasson (2014) found peaks of intense whistle activity that could function as pre-sleep choruses. Hawkins and Gartside (2010), found in a closely related dolphin species (*Tursiops aduncus*), that whistle acoustic diversity and repetition rate were higher in groups without calves, and that whistle acoustic structures may vary with behavioural states, with flat whistles more associated with socializing than feeding for example (Hawkins and Gartside, 2010). Some authors suggest that high levels of sociality in toothed whales influences tonal sounds complexity, with increased tonal sound modulation correlated with group size and social structure, for example (Herman and Tavorla, 1980; May-Collado et al., 2007). To explore the affiliative function hypothesis, some studies have tried to link these vocalizations with specific behaviours, showing that, at least in Atlantic spotted dolphins, differences in call characteristics may be indicative of behavioural activities (Papale et al., 2016). Other studies on the contrary suggest that whistles would rather be associated with feeding activity per se (Acevedo-Gutiérrez and Stienessen, 2004; dos Santos et al., 2005). The controversy may be due to the fact that some of these studies were done on few isolated individuals (less than five, e.g. Caldwell and Caldwell, 1968, see review in Caldwell et al., 1990). Also, broad correlations between activities and vocal emissions are made, although there are subtle differences within these behaviours that sometimes are not identified in surface observations (Hawkins and Gartside, 2010; Papale et al., 2016). Other studies use large temporal windows of analysis (not identifying specific concurrent behaviours, e.g. Herzing, 2000; Lima et al. in preparation). All these factors make the function of whistles unclear.

### *Chapter 3: Vocal production and use at the level of group*

The second category of sounds (clicks) was mainly studied for its echolocation function. Dolphins use it for detection, scanning, and discrimination of objects, by measuring the time interval between the instant of emission of the echolocation click and the instant of the echo signal arrival (Au, 2004; Dubrovsky, 2004). However, data on some dolphin species suggest that echolocation is not the only function for these sounds, and that they are likely to be used in communication as well (Dawson, 1991).

The third category of sounds (burst pulses) has received comparatively much less attention. Their function thus remains unclear, even if researchers agree that they are involved in social communication (Herzing, 2013). The existing literature is vague because authors do not use a standardized nomenclature and sometimes do not detail the acoustic structure (Gridley et al., 2015; Herman and Tavolga, 1980; Lopez and Shirai, 2009; Overstrom, 1983). Several studies show an association of burst pulses with agonistic contexts (Blomqvist et al., 2005; Blomqvist and Amundin, 2004; Herzing, 2015), such as withdrawal (Lopez and Shirai, 2009) or aggressive courtships (Connor and Smolker, 1996). However, its high rate in foraging contexts in some populations suggests also a possible association with prey manipulation (Gridley et al., 2015). Some dolphin species do not whistle and in that case would use burst-pulses instead for identity coding (Rankin et al., 2007). Recently, authors have suggested that they might in fact be associated with highly emotional but broad contexts, such as aggressive episodes (depending on burst pulse type, cf. Perazio and Kuczaj, 2017), before copulatory sequences, or even during the introduction of novel or unexpected objects or events (Caldwell and Caldwell, 1967; Lilly and Miller, 1961; Perazio and Kuczaj II, 2017; Ralston and Herman, 1989). Interestingly, Lopez & Shirai (2009) suggested to divide the burst pulsed sounds according to their duration, i.e. “short” and “long” burst pulses. Particularly, “long burst-pulses” could be used to solve hierarchical conflicts and avoid competition among



group members (Lopez and Shirai, 2009). Further studies, separating these two possible burst-pulse types are now needed.

Another important aspect of dolphin vocal behaviour is the regular occurrence of mixed vocal events, resulting in the association between different vocal categories (e.g. Herzing, 2015; Shapiro, 2006). Although we know that dolphins can produce tonal and pulsed signals simultaneously, there is just scarce descriptive information on the rhythmic aspect (dos Santos et al., 1995; Herzing, 2015) and no quantification of the rate of association between different categories. Sound combination has however attracted a lot of attention in other species (especially primates) recently with clear evidences of context-dependent combinatorial patterns (e.g. see Coye et al., in press, for a review). Dudzinski (1996) hypothesized that concurrent use of different vocal categories may enhance a communicative function in dolphins, but she did not analyse further the uses or functions of these associations.

Here, we examined the relationship of vocalizations with different behavioural contexts in bottlenose dolphins, taking advantage of good observation conditions offered by captivity to bring new quantitative elements on the production of the different categories of sounds (whistles, click trains and burst pulse sounds) and types (short and long burst pulse sounds) identified in the literature. A recurring difficulty when studying cetacean acoustics both in captive and wild conditions, is to identify the sound emitter. Therefore, we observed the activities of individuals present at a given time in a given space of reasonable size (a part of the pool complex), with good visibility conditions of all possible emitters. We searched for preferential associations between acoustic structures and behaviours of individuals present at the exact time of call emission. Our hypotheses were that different vocal categories should be related to different behavioural contexts that could be different when they are associated. As found predominantly in the literature, we expected more whistles in affiliative contexts, but

for the two other vocal categories (burst pulse sounds and click trains), we expected to clarify their controversial contextual usages.

## **2. Material and methods**

### ***2.1. Study site and animals***

Acoustic recordings were performed during 18 days between February and May 2015 on four male (aged 5, 6, 12 and 16 years old) and three captive female (aged 7, 14 and 26 years old) bottlenose dolphins (*Tursiops truncatus*) living in the facility of “Planète Sauvage” (Port-Saint-Père, France), all born in captivity. The group composition changed in April 2015, when the oldest female arrived in the facility. From our 18 days of observation, 14 days were done after her arrival. These dolphins had free access to four differently-sized and inter-connected pools (1: 4950 m<sup>3</sup>, 2: 1280 m<sup>3</sup>, 3: 220 m<sup>3</sup>, 4: 1040 m<sup>3</sup>). These dolphins were given 39kg of fish every day; i.e. herring, capelin, mackerel, sprat, whiting and squid; 4.5-8.5kg per dolphin (amount related to the size / age of individual).

At the start of data collection, the dolphins had no shows, but 5 trainings for shows and for medical treatments were conducted daily (2 in the morning and 3 in the afternoon, each one lasting between 15 and 30 min.; about every 1.5 h), and they received additionally a first meal at 9:00 and one last at 17:00. From the end of February, the dolphins started to have four public presentations lasting around 30 min each (training and feeding with public or public shows accompanied by a soundtrack) each week, and from April, two each day.

### ***2.2. Behavioral and acoustic recordings***

Behavioural observations were performed in animals visiting pool 4 (approximately 1040 m<sup>3</sup>, with a diameter of 30 m and depth that varied from 3.6 m at the shallowest point to 4.85 m at its deepest, with animals free to come and go). This pool is equipped with an underwater window of 193 cm by 92.5 cm allowing to see clearly its whole volume. Observation sessions

and continuous recording samples lasted  $30 \pm 16$ min on average (mean  $\pm$  SD) recorded at random moments, once or twice a day, between 09h30 and 16h00, out of training or show periods.

Emissions of vocal events were collected using ad libitum sampling (Altmann, 1974). A vocal event is defined here as a call or series of calls, overlapped or not, emitted in a short time frame with long silence gaps following and preceding of at least 500ms. We registered the concurrent behaviours (Table 1), displayed by all individuals in the pool.

**Table 1. Behavioural categories sampled**

*Context*

*Social behavior*

*Social play*

Two or more dolphins interact playing. This behavior can be vigorous with one dolphin chasing another or both spinning around each other quickly. Alternatively, play can be calmer with the dolphins circling gently around each other, or pushing one another. Individuals took turns as a chaser in chasing and/or mouth-biting.

*Socio-sexual behavior*

Activities that involve erection, and potentially genital inspection, including two or more individuals within a distance of one body-length.

*Agonistic behavior*

One dolphin displays agonistically or attacks another dolphin, by chasing, mouth-biting, hitting, threatening, or head butting another individual who is

*Social affiliative behavior*

expressing avoidance or flight.

Social behaviours not classified as agonistic or social play. Include many tactile behavioural events such as rubbing, swim contact, petting, and synchronous movements.

*Non-social behavior*

*Solitary play*

Playing alone, potentially with objects (such as a ball, pool float) or water. This can involve pushing, tossing, carrying or biting an object, as well as catching or manipulating water jets.

*Locomotion/Immobility*

Dolphin actively swims through the tank, or rather float (sometimes visually exploring above water) or even lie on the bottom of pool.

Dolphin signals were recorded continuously using a broadband system consisting of a Sea-Phone SS03-10 (-194 dB, re 1V/ $\mu$ Pa, 0.020 to 50 kHz) hydrophone in the beginning of data collection, and, from April, a C54XRS (-185 dB, re 1V/ $\mu$ Pa, 0.06 to 203 kHz) hydrophone connected to a TASCAM DR-680 recorder (sampling rate 192 kHz 24 bit). To preventing the analysis of sounds recorded from adjacent pools, only signals with high intensity and good ratio-to-noise were considered in sampling. Previous recording in two pools simultaneously and comparison between those recordings could give the observer more certainty to sample sounds from the same pool. There was an auditory feedback in the observation room and behavioural observations were recorded with a commentary channel using the same recorder, so acoustical and behavioural comments could be crossed at the time of data analysis.

### **2.3. Call classification**

Calls were classified using spectrograms (FFT 1024 at 192 kHz sampling rate) drawn with Raven Pro 1.4 (Cornell Bioacoustics Research Program). We called Clicks all relatively broadband, short signals (less than 1000 ms) that often reached far into the ultrasonic range (units of click trains were defined as bouts of clicks that were separated by a non-clicking period with a minimum duration of 200 ms); Burst pulse sounds, all rapid pulse trains (intervals of 0.5 to 10ms), calls that in the spectrogram display appear as horizontal band sounds in which pulses are visually and aurally indiscernible; and Whistles all narrowband, frequency-modulated signals of duration greater than 0.1s and with at least part of fundamental frequency higher than 3kHz (following previously published definitions of Acevedo-Gutiérrez and Stienessen, 2004 and Eskelinen et al., 2016). Burst pulses were further subdivided into two types on the basis of their duration: long burst pulse (>0.2 s) and short burst pulse (<0.2s) (as in Lopez and Shirai, 2009) (Figure 1).

The vocal events sampled above could be pure, i.e. composed of a single vocal category (unitary and multi-unit structure combined) or mixed, i.e. composed of more than one vocal category.

### **2.4. Statistical analysis**

After having described the diversity of acoustic and behavioural categories sampled, we analysed statistically the preferential relationships between behaviours and pure vocal events as well as between behaviours and mixed vocal events separately. We used chi-squared tests (when possible) or Binomial tests to evaluate vocal and behavioural category relationship in both ways (i.e. which vocal category is the most and the least expressed for each behaviour; and which behavioural category is the most and the least expressed for each vocalization). Some categories were more often expressed than others in general (for example whistles and

click trains were more frequent than burst pulses when summing all behavioural contexts, and affiliative interactions were more frequent than agonistic when summing all vocal events) so the expected frequencies in Chi-squared tests were weighted taking into account the general distribution of the categories. We then ran dyadic comparisons by comparing each given category to all the others. For Binomial tests, we applied the same principle, comparing the probability of occurrence of each category (P: occurrence of category tested, divided by total occurrences observed) with the sum of other behaviours' probability (Q, total occurrences minus occurrence of category tested, divided by total occurrences observed) using following formula:

$$p\text{-value} = \binom{N}{x} P^x Q^{N-x}$$

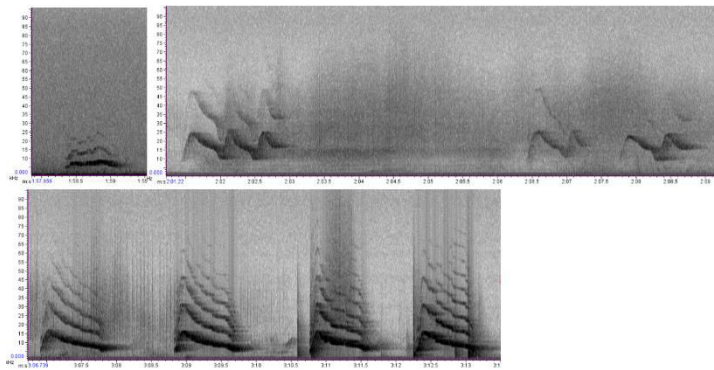
with N the total occurrences of all category in one behaviour or vocalization and x the number of occurrences of category tested. This test was applied for each vocal/behaviour pair.

### 3. Results

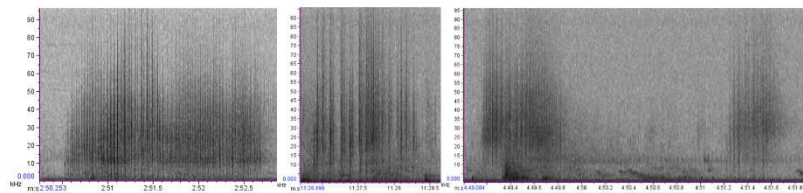
#### 3.1. Description of behavioural and acoustical datasets

The behavioural contexts observed while vocalizing were mainly non-agonistic interactions (i.e. social affiliative: 30%, social play: 27%, socio-sexual behaviour: 17%), and more rarely agonistic interactions (3 %) and non-social activities (solitary play: 17%, locomotion/immobility: 8%). The average number of dolphins present in the study pool during a sampled vocal event was five individuals (SD = 1). The 470 vocal events sampled consisted in 260 “pure” events (with only one category of vocalization) and 210 “mixed” events (with two or more categories of vocalizations). The average number of sound units was 1.7 (SD = 1.5) for “pure” vocal events (i.e.  $2.0 \pm 1.6$ ) for burst pulse sounds,  $1.6 \pm 1.3$  for click trains and  $1.7 \pm 1.5$  for whistles). In total, we collected 102 whistles, 103 click trains and 53 burst pulse sounds in these “pure” events.

### Whistles

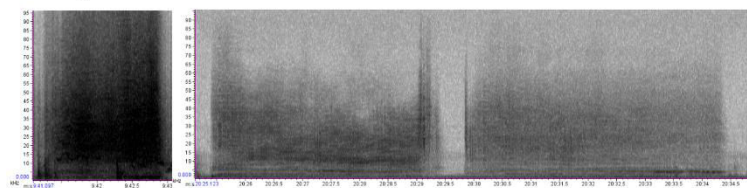


### Click trains

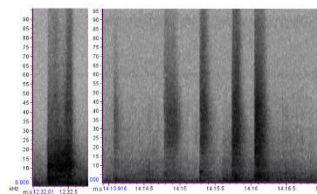


### Burst-pulsed sounds

#### Long BP



#### Short BP



### Mixed events

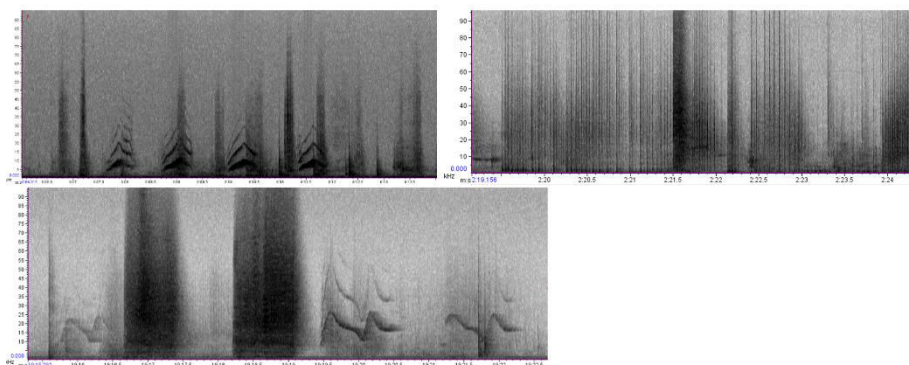


Figure 1.. Example of spectrograms of all vocal categories and call types sampled. Two first lines: three examples of whistle pure events (single- and multi-units); Third line: three examples of click trains pure events (single- and multi-units); Fourth line: two examples of Long burst-pulse pure events (single- and multi-units); Fifth line: two examples of Short burst-pulse pure events (single- and multi-units); Sixth and seventh line: Three examples of mixed vocal

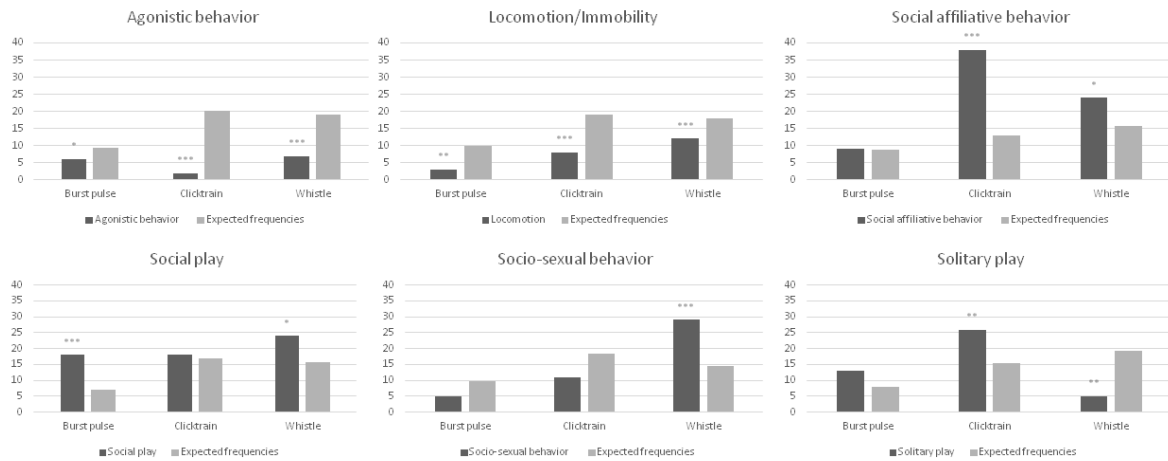
events: whistles superposed with short burst pulses, click trains superposed with short burst pulses, whistles alternating with long burst pulses .

### 3.2. Behavioural contexts of pure vocal events

When comparing the distribution of vocal categories per behavioural context, we found that:

- During social affiliative interactions, there were significantly more click trains (n = 38: test  $\chi^2=48.08$ , df=1,  $P<0.001$ ) and more whistles (n = 24: test  $\chi^2=4.52$ , df=1,  $P< 0.05$ ) than expected by chance.
- Social play, was significantly more related to burst pulses (n = 18: test  $\chi^2=17.29$ , df=10,  $P<0.001$ ) and whistles (n = 24: test  $\chi^2=4.52$ , df=1,  $P< 0.05$ ).
- Socio-sexual activities were more related to whistles (n = 30: test  $\chi^2=16.90$ , df=1,  $P< 0.001$ )
- Solitary play with more click trains (n = 26: test  $\chi^2=7.30$ , df=1,  $P<0.001$ ) and less whistles (n = 5: test  $\chi^2=10.69$ , df=1,  $P<0.01$ )
- Agonistic interactions were less related to burst pulses, click trains and whistles than expected during agonistic interactions ( $0.001<P<0.035$ ) and locomotion/immobility ( $0.001<P<0.002$ ) than expected by chance (Figure 11).

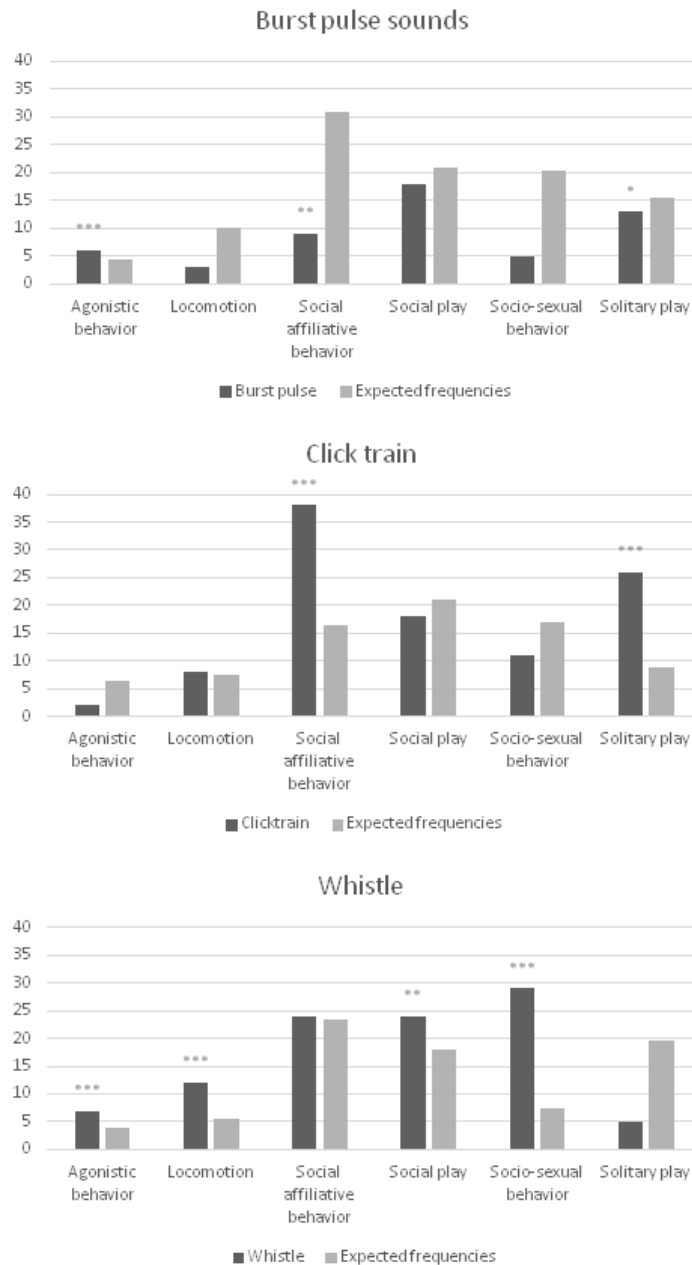




**Figure 11. Observed (black) and theoretical (grey) distributions of vocal categories per behavioural context ("pure" events only; N Agonistic behaviour = 15; N Locomotion/Immobility = 23; N Social affiliative behaviour = 71; N Social play = 60; N Socio-sexual behaviour = 45; N Solitary play = 44) (Binomial tests for Agonistic and Locomotion/Immobility; Chi-squared tests for other behaviours, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).**

When, on the other hand, comparing the distribution of behavioural contexts per vocal category, we found that

- Burst pulse sounds were more frequently emitted than expected during agonistic interactions (Binomial test:  $n = 6$ ,  $P < 0.001$ ) but less during social affiliative behaviour ( $n = 9$ ,  $P = 0.001$ ) and solitary play ( $n = 13$ ,  $P = 0.016$ ).
- Click trains were mostly produced during social affiliative behaviours ( $n = 38$ ,  $\chi^2 = 28.02$ ,  $df = 1$ ,  $P < 0.001$ ) and solitary play ( $n = 26$ ,  $\chi^2 = 32.11$ ,  $df = 1$ ,  $P < 0.001$ ).
- Whistles were more frequent than expected during agonistic behaviours (Binomial test:  $n = 7$ ,  $P < 0.001$ ), locomotion/immobility ( $n = 12$ ,  $P < 0.001$ ), social play ( $n = 24$ ,  $P = 0.002$ ) and socio-sexual behaviours ( $n = 30$ ,  $P < 0.001$ ) (Figure 3).



**Figure 12.** Observed (black) and theoretical (grey) distributions of behavioural contexts per vocal category ("pure" events only; N burst pulse sounds = 53; N Click train = 103; N Whistle = 102). (Binomial tests for BPS and Whistle, Chi-squared tests for Click train, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

A further examination of burst pulse sounds revealed some similarities and discrepancies in the context of production of both types. When comparing production of long and short burst pulses across contexts, long burst pulses occurred less than expected during social play (Binomial test:  $n = 7$ ,  $P = 0.047$ ), while the short burst pulses appeared more than expected during social play ( $n = 10$ : Binomial test,  $P = 0.023$ ) When comparing probabilities to record

one of both types in different behavioural contexts, their production differed only for social play (Binomial test:  $P=0.032$ ) (Figure 4).

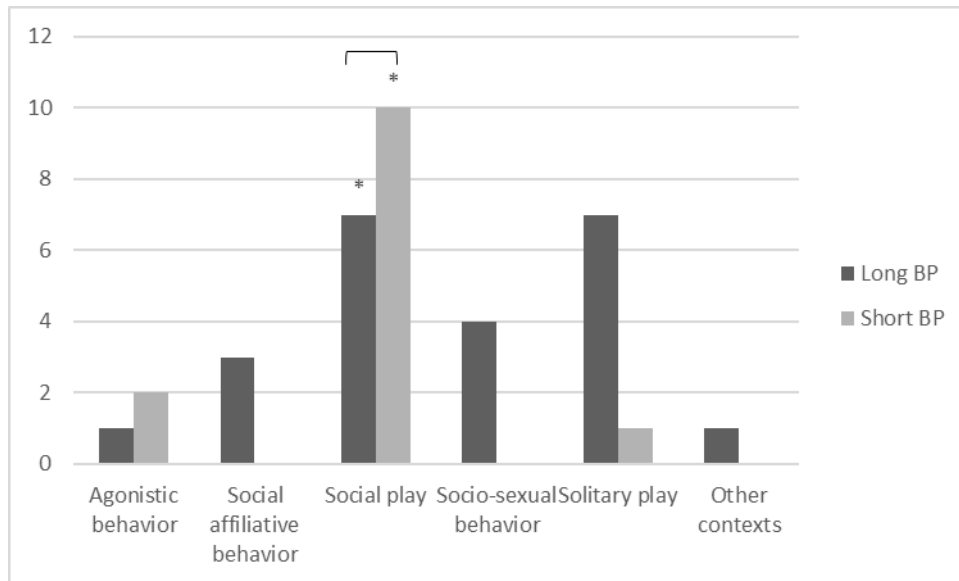


Figure 13. Frequency of types of burst pulse sounds associated with each behavioural context (only "pure" events,  $N=36$ ). BP = Burst pulse: Long ( $N=23$ ); and Short ( $N=13$ ). (Binomial tests ;  $*=p<0.05$ ).

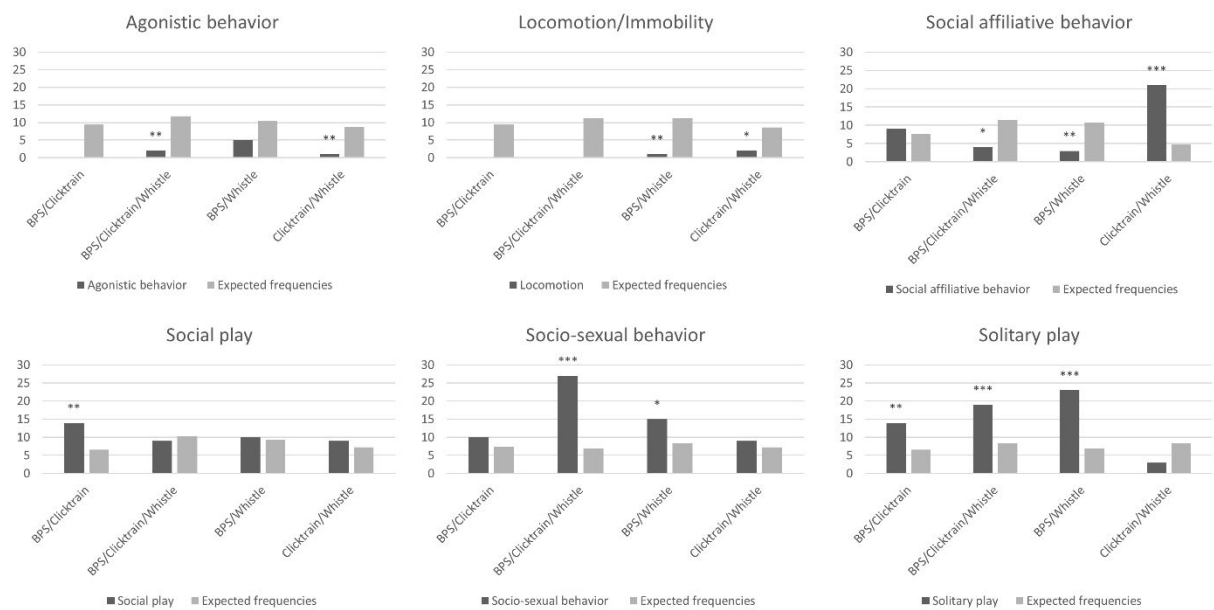
### 3.3. Behavioural contexts of mixed vocal events

All three vocal categories were found more often mixed than pure: burst-pulsed sounds ( $n = 190$ ,  $\chi^2=74.39$ ,  $DF=1$ ,  $P<0.001$ ), click trains ( $n = 170$ ,  $\chi^2=15.90$ ,  $DF=1$ ,  $P<0.001$ ) and whistles ( $n = 171$ ,  $\chi^2=14.22$ ,  $DF=1$ ,  $P<0.001$ ).

From the 210 mixed vocal events, 29.0% were composed of burst pulse sounds, click trains and whistles emitted altogether, 27.1% of burst pulse sounds and whistles, 22.4% of burst pulse sounds and click trains, 21.4% of click trains and whistles.

Agonistic interactions were not preferentially related to any particular mixed vocal event, but associations between burst pulses and whistles were significantly more rare than expected in this context ( $n=1$ ,  $\chi^2=6.91$   $DF=1$ ,  $P< 0.01$ ). Affiliation was positively related to click trains associated with whistles ( $n = 21$ , Binomial test,  $P< 0.001$ ), while most associations involving burst pulses were rare in this context (with clicks and whistles:  $n = 4$ , Binomial test,  $P= 0.006$ ; with whistles:  $n = 3$ , Binomial test,  $P= 0.03$ ). Conversely, during social play, burst pulses

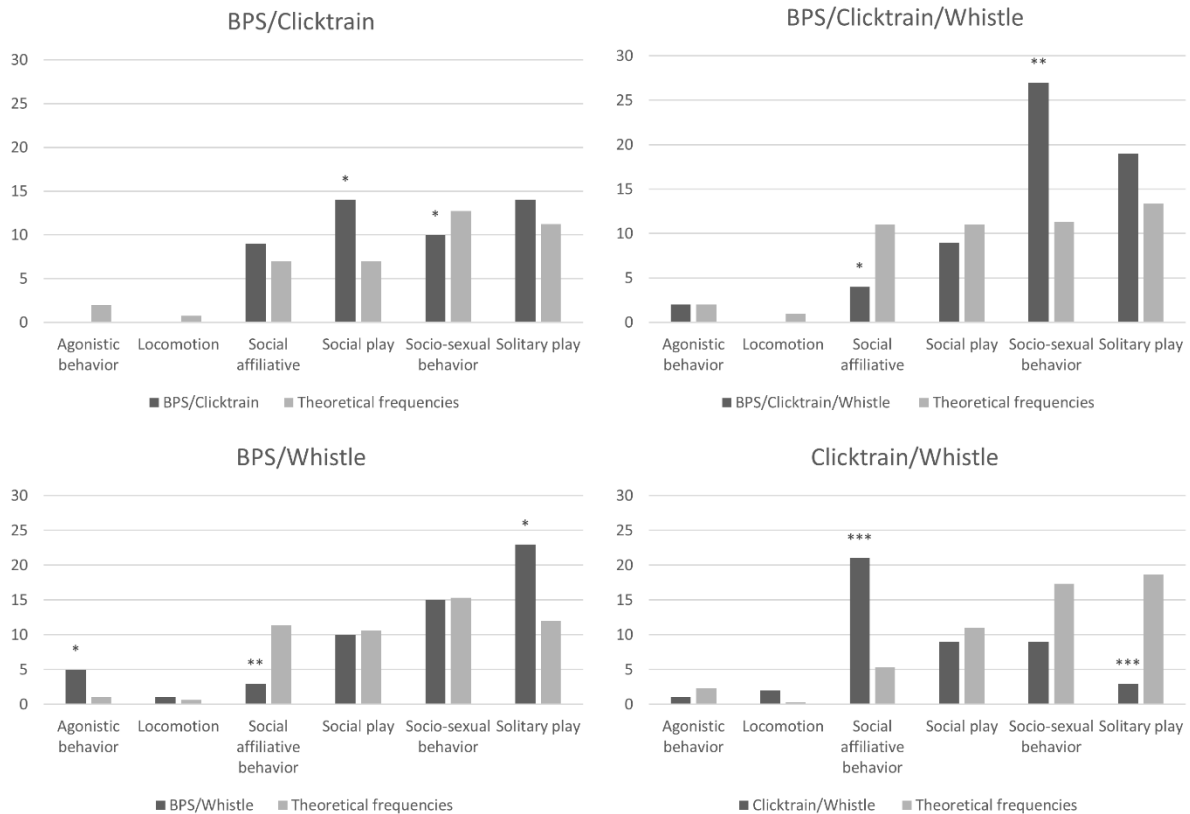
associated with click trains were found more often than expected ( $n = 14$ ,  $\chi^2=8.30$ ,  $DF=1$ ,  $P < 0.01$ ). During socio-sexual interactions burst pulses associated with whistles and click trains were found more often than expected (with whistles:  $n = 15$ ,  $\chi^2=5.19$ ,  $DF=1$ ,  $P < 0.05$ ; with both:  $n = 27$ ,  $\chi^2=60.01$ ,  $DF=1$ ,  $P < 0.001$ ). At last, solitary play was related to almost all types of mixed vocal event (burst pulse and click trains:  $n = 14$ ,  $\chi^2=8.30$ ,  $DF=1$ ,  $P < 0.01$ ; burst pulses, click trains and whistles:  $n = 19$ ,  $\chi^2=13.38$ ,  $DF=1$ ,  $P < 0.001$ ; burst pulses and whistles:  $n = 23$ ,  $\chi^2=38.59$ ,  $DF=1$ ,  $P < 0.001$ ) (Figure 5).



**Figure 14. Observed (black) and theoretical (grey) distributions of “mixed” vocal categories per behavioural context: N Agonistic behaviour = 8; N Locomotion/Immobility = 3; N Social affiliative behaviour = 37; N Social play = 42; N Socio-sexual behaviour = 61; N Solitary play = 59) (Binomial tests for Agonistic, Locomotion/Immobility and Social affiliative behaviour, Chi-squared tests for other behaviours, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).**

When comparing the distribution of behavioural contexts per mixed vocal category, we found that burst pulse sounds were more frequently emitted than expected during social play ( $n = 14$ , Binomial test,  $P = 0.017$ ) and less during socio-sexual interactions ( $n = 10$ , Binomial test,  $P = 0.01$ ) when associated with click trains, but more frequently emitted than expected during agonistic behaviour ( $n = 5$ , Binomial test,  $P = 0.032$ ) and solitary play ( $n = 23$ , Binomial test,  $P = 0.015$ ) when associated with whistles. Click trains associated with whistles were frequent during social affiliative behaviours ( $n = 21$ , Binomial test,  $P < 0.01$ ), but rare during solitary

play (n=3, Binomial test,  $P < 0.001$ ). At last, the pattern mixing all vocal categories were found more frequent than expected during socio-sexual behaviours (n=27, Binomial test,  $P = 0.004$ ) and less during social affiliative behaviours (n=4, Binomial test,  $P = 0.006$ ) (Figure 6).



**Figure 15.** Observed (black) and theoretical (grey) distributions of behavioural contexts per mixed category. BPS = burst pulse sounds (N BPS/Clicktrain = 47; N BPS/Clicktrain/Whistle = 61; N BPS/Whistle = 57; N Clicktrain/Whistle = 45; N total = 210). Asterisks indicate significant differences between observed behavioural contexts when a given mixed vocal category was recorded (Binomial tests, \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ).

#### 4. Discussion

The results of this study indicate that the three vocal categories (whistles, clicks and burst-pulses) were used in different contexts that corresponded partially to expectations. Also, the interest of subdividing burst pulse sounds into two types is supported, as they were here related to different contexts. We showed at last that preferred related contexts vary depending on if vocal categories are emitted pure or mixed.

We found whistles frequent in all social contexts but not just in affiliation as is often said (Herzing, 2015; Janik, 2014), but we rather found they also in play, socio-sexual and even agonistic sometimes. They were also a little related to a non-social context: locomotion/immobility. Whistles have been traditionally related to social contexts, however, contextual analyses often generalize social interactions without specifying the nature of these interactions (e.g. McCowan & Reiss, 1995) or while focusing only on signature whistles, that correspond to approximately 80-100% of the whistle individual repertoire when callers are socially isolated (Caldwell et al., 1990) and to approximately only 30-70% for free-swimming dolphins (Janik and Sayigh, 2013) (e.g. Janik & Slater, 1998). Whistle was the vocal category found in the most diverse contexts (socio-sexual, agonistic, locomotion/immobility, social play, affiliative, solitary play), alone or associated with other vocal categories. Therefore, we hypothesize as other authors (King and Janik, 2013; Quick and Janik, 2012) that this signal may have a very general function of contact call and then it is not related to a particular context, or that there are potentially several whistle types with different functions, but we did not test this hypothesis here. This idea is supported in particular by the mentioned idea that signature whistles are not the only type of whistle in the repertoire of an individual (Caldwell et al. 1990; Janik and Sayigh, 2013; McCowan and Reiss, 1995) and by some authors who find a link of this vocal category with other contexts, like sexual (Herzing, 1996). Our results on socio-sexual use of whistles brings the evidence that this vocalization may have in particular an important role in socio-sexual interactions. However, data presented here comes from a single group in a limited time frame. Also, we must acknowledge that we did not look at the reproductive status of individuals or the potential diversity of whistle types and that more studies need to be conducted, looking for whistle types and their possible different functions (as in dos Santos et al., 2005).

Burst pulses appeared mainly related to agonistic contexts and social play in our results. Other studies have already found a relationship between the production of burst pulses and agonistic behaviours (e.g. Lopez & Shirai, 2009; Overstrom, 1983). Blomqvist et al. (2005) also found that play-fighting dolphins typically emitted a short burst pulse combined with a whistle, acoustically different from aggressive burst pulses. The presence of burst pulses in both contexts may be explained taking in consideration that it is sometimes difficult to distinguish between agonistic behaviours and social play in dolphins (Janik, 2015) and a play context can sometimes turn in agonistic, so play can be interpreted as a pseudo-agonistic context. Many dolphin species engage in complex play behaviour in both wild and captive environments (Greene et al., 2011; Kuczaj et al., 2006), but little is known about acoustic communicative behaviours during such events (Eskelinen et al., 2016). Furthermore, acoustic behaviour can be expressed differently when comparing captive and wild dolphins, in part due to contexts that are present in both situations, making the interpretation of these signals still more complex. Here, more than 60% of “pure” long burst pulses were recorded during play behaviour (social and solitary) and almost 80% of “pure” short burst pulses in social play. It is widely studied in other mammals species how vocal structures reflect emotional states (see review in Briefer, 2012; e. g. Fichtel et al., 2001; Scherer, 2003) and bottlenose dolphins’ play is thought to be accompanied by high arousal (Held and Spinka, 2011). So, we can hypothesize that burst pulse duration could be related to the degree of arousal or emotion of these different play contexts. Burst pulse sounds had been suggested before as a reflection of emotion triggered by brain dopamine release in the context of prey capture (Ridgway et al., 2015). Since dolphins have remarkable temporal discrimination abilities, it is possible that the temporal characteristics of pulses may play a role in communication (Akhatov et al., 2007), and so the differences in duration of types of burst pulses could be signalling some relevant information, as the level of arousal. Alternatively, we can imagine that long and short burst pulses represent two distinct signals with different functions, short burst pulses being a social

play vocalization, and long burst pulses having a role on solitary play. Luís et al., (2016) already considered the possible existence of discrete pulsed vocal units with specific roles in the vocal repertoire of bottlenose dolphins. Short burst pulses have been associated with social functions in a delphinid species that do not whistle (Rankin et al., 2007). Some species present distinct play vocalizations, as Kea parrots, for example, that have a characteristic warble call which may sign the sender's playful state, associated both with solitary and social play (Schwing et al., 2017). The differences between solitary and social play still deserve further investigation to better understand the meaning of individual and group play behavior among social animals (Greene et al., 2011) and, consequently, the functions of burst pulse sounds in these contexts.

We found click trains pure related to affiliation and solitary play in our results. This is interesting compared to literature because is the first time to our knowledge that this vocal category is related to play. However, as solitary play was often composed of playing with an object, this result could be expected considering the echolocation function of click trains in detecting or discriminating objects (DeLong et al., 2006; Harder et al., 2016). The use of click trains when approaching an object has been described also in other dolphin species (e. g. Yoshida et al., 2014). The high emission rate of click trains related to social affiliative contexts is also surprisingly. In this case, click trains could be adding information and thus, playing a role in these social behaviours, as it has been proposed before as a communicative signal (Dawson, 1991; Gregg et al., 2007; Kuczaj II et al., 2015). The presence of click trains during mixed vocal events in other contexts, as socio-sexual and social play could add new possible functions for this signal, but it may be more simply explained by the presence of the other vocal categories.

The results of this study also showed that, according to the possible associations between categories of vocalizations, the most related context is expanded. For example, whistles are



produced more often during socio-sexual and agonistic contexts, burst pulses during social play and agonistic behaviours, and click trains during social affiliative and solitary play, regardless of whether they are alone or associated with other vocal category. However, if associated with other vocal categories, whistles are most emitted also in social affiliative and solitary play contexts. In the same way, burst pulses are also associated with socio-sexual behaviours and solitary play when mixed. Click trains, at their turn, when associated with other calls, can be found also in socio-sexual or social play contexts. If these associations are emitted by different individuals, as we can conceive, it is possible to conjecture some “conversational” importance on them. It is not clear if dolphins communicate by antiphonal exchanges as showed for other mammals (Carter et al., 2012; Owren et al., 1993) and even in odontocetes (Schulz et al., 2008; Vergara et al., 2010), but it was already proposed that dolphins could use antiphonal calling when producing other’s signature whistle (Harley, 2008). Also, in baboons, Cheney et al. (1995) showed that some associations of vocal categories elicit specific responses, varying with the caller's dominance rank through call sequences. In some of the recorded mixed events, however, we had just one individual present in the pool, corroborating the fact that dolphins can produce two vocal categories simultaneously, thanks to the nasal sac anatomy of delphinids (Cranford et al., 1996; Dormer, 1979; Ridgway et al., 2015), so it is possible to alternatively hypothesize a “combinatorial” ability and that such a combination between vocal categories could give a particular function to the call. For example, here and in Blomqvist et al., (2005), burst pulse sounds kept their associations with agonistic contexts when emitted with whistles, and those authors hypothesized the whistle presence in this association as a way to prevent play-fight from escalating into a real fight. However, concerning contextual use and vocal perception, rare studies addressed the role of sequences or simultaneous sound production in dolphins (Harley, 2008). This promises to be an important area for research and extending studies will help to determine the role of these mixed vocal events in communication behaviour.

To conclude, bottlenose dolphins seem to show a context-specific use of their different vocal categories and sound associations. We were unable to determine which dolphins produced which sound; however, the privileged conditions of observation through an underwater window and the use of a commentary channel to record the exact time that individuals exhibited each behaviour could assure in some level the reliability of relationships between vocal events and behaviours. To investigate better how the emission contexts affect the vocal production, it is still necessary to discriminate the whistler's identity in different contexts. Future research should also focus on functional use of associations between vocalizations.

## 5. Acknowledgments

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## **CHAPTER 4**

# **“AUDITORY UMWELT”: CONCEPT OF IDENTITY AND AERIAL PERCEPTION OF SOUNDS**

### SUMMARY OF PAPER 3

**Questions:** Bottlenose dolphins (*Tursiops truncatus*) use individual acoustic structures to signalling identity to group. However, to our knowledge, their ability to associate artificial sounds labels to themselves was never tested before. Also, their hearing system being very adapted to work underwater, there is still a debate if dolphins are able to listen to aerial sounds. Here, we asked 1) if dolphins are able to respond to human-made sound labels broadcast underwater; and 2) if yes, could they generalize this learning to the same sounds transmitted through the aerial medium?

**Methods:** Dolphins have been trained to respond to individual sounds played underwater, but training effectiveness have never been tested in a controlled context. We then investigated the response of the Planète Sauvage dolphins to individual learned sounds produced by music instruments. The same trainer first played the instruments underwater, and then the same experiment was repeated with instruments played in the air. All dolphins were tested at the same time with a random instrument every time.

**Results:** All the dolphins except one moved to their own sound when instruments were played underwater and did not move when the label was that of another individual. When experiment was done in the air, dolphins did not move, but they gazed more and longer to the sound source when their own individual instrument was played.

**Conclusions:** Bottlenose dolphins are able to associate sound labels produced by human to their own identity, even when sounds are transmitted in the air, giving new evidences about the range of their concept of identity.

This paper is published in *Frontiers in Psychology* in January 2018 and results were presented at the 35<sup>th</sup> International Ethological Conference (IEC, 2017).

Captive Bottlenose Dolphins Do Discriminate Human-Made Sounds Both Underwater and in the Air Alice Lima<sup>\*1,2</sup>, Mélissa Sébilleau<sup>1</sup>, Martin Boye<sup>2</sup>, Candice Durand<sup>3</sup>, Martine Hausberger<sup>4^</sup>, Alban Lemasson<sup>1^</sup>

<sup>1</sup> Université de Rennes, Ethologie Animale et Humaine, UMR 6552, CNRS, Université de Caen Normandie, Paimpont, France

<sup>2</sup> Département Scientifique et Pédagogique, Planète Sauvage, Port-Saint-Père, France

<sup>3</sup> Cité Marine, Planète Sauvage, Port-Saint-Père, France

<sup>4</sup> CNRS, Ethologie Animale et Humaine, UMR 6552, Université de Rennes, Université de Caen Normandie, Rennes, France<sup>^</sup> Same contribution

**Keywords: individual-specific sound cue, individual identity, cetacean, auditory perception, bottlenose dolphins**

### Abstract

Bottlenose dolphins (*Tursiops truncatus*) spontaneously emit individual acoustic signals that identify them to group members. We tested whether these cetaceans could learn artificial individual sound cues played underwater and whether they would generalize this learning to airborne sounds. Dolphins are thought to perceive only underwater sounds and their training depends largely on visual signals. We investigated the behavioral responses of seven dolphins in a group to learned human-made individual sound cues, played underwater and in the air. Dolphins recognized their own sound cue after hearing it underwater as they immediately moved toward the source, whereas when it was airborne they gazed more at the source of their own sound cue but did not approach it. We hypothesize that they perhaps detected modifications of the sound induced by air or were confused by the novelty of the situation, but nevertheless recognized they were being “targeted.” They did not respond when hearing another group member’s cue in either situation. This study provides further evidence that dolphins respond to individual- specific sounds and that these marine mammals possess some capacity for processing airborne acoustic signals.



## **1. Introduction**

Bottlenose dolphins are, with humans and a few species of birds, amongst the few species that have been shown to use learned individual-specific sound cues that use an individual's identity to signal affiliation to group members (e.g., Henry et al., 2015; birds' contact calls: Kondo and Watanabe, 2009 or songs: Hausberger et al., 1995; dolphins: Janik and Sayigh, 2013). Thus, they can copy the so-called signature whistles of others (Tyack, 1986) and these shared signature whistles constitute an affiliative signal that indicates strong social bonds (King et al., 2014). Other researchers have proposed that dolphins are able to "name" social partners by vocally copying one another and use this ability for spatial coordination (Janik and Sayigh, 2013; King et al., 2014). During evolution, the dolphin sensory world became primarily acoustic (Janik, 2013). In captivity, reports also show that they can learn to use acoustic signals consistently to report the presence or absence of particular objects, an ability shared with parrots (Pepperberg, 2007; King and Janik, 2013), and can label objects by copying artificial sounds (Richards et al., 1984). Miksis et al. (2002) found that dolphins can also incorporate features of artificial sounds made by humans into their own whistles. However, to our knowledge, the capacity of dolphins to learn artificial sound cues generated by humans has never been evaluated. The ability of animals to respond to individual sound cues (and not to respond to other group members' sound cues) has been successfully experimentally tested in a limited number of species (monkeys – Masataka, 1992; pigs – Puppe et al., 2007). Previous studies have however clearly shown that individually trained captive dolphins learn gestural signals (Herman et al., 1984; Kuczaj et al., 2008). This modality was typically chosen because cetaceans are thought to perceive acoustic signals only underwater (Ketten, 2000).

Research on evoked auditory potentials or behavioral audiograms certainly emphasizes the adaptation of the cetacean hearing system to waterborne sounds (Erbe et al., 2016). In

particular, their hearing system does not include an external auditory canal and their ossicular chain is stiff (Ridgway, 1988). Dolphins perceive sounds through their lower jaw, full of specialized fatty tissues that transmit sound directly to their middle and inner ears (Ketten, 2000). As a result, authors have questioned whether dolphins are able to perceive airborne sounds at normal intensity levels (Wartzok and Ketten, 1999; Erbe et al., 2016).

In two species of Delphinidae perception of airborne sounds has been tested (bottlenose dolphins: Babushina, 1979; a tucuxi: Liebschner et al., 2005). The results suggest that bottlenose dolphins and tucuxis are able to perceive certain airborne sounds, with hearing capacities in the air ranging from 1 to 110 kHz for the dolphin (Babushina, 1979; while different studies report hearing capacities underwater ranging from 0.075 to 180 kHz, review in Erbe et al., 2016) and from 2 to 31.5 kHz for the tucuxi (Liebschner et al., 2005; while underwater it ranges from 4 to 135 kHz; Sauerland and Dehnhardt, 1998). In these two studies, the animals were immobilized with the lower jaw out of water and a go/no go response paradigm was used to set the hearing thresholds. However sample sizes were small (two individuals in Babushina, 1979, and only one in Liebschner et al., 2005), while the subjects were restrained above water and not free to move or orient toward the sound source. Thus their ability to hear and to use airborne sounds remains unclear. Nevertheless, other indirect indications suggest that they may do so: captive bottlenose dolphins can mimic sounds broadcast in the air (Kremers et al., 2011), as do other odontocetes (e.g., belugas: Murayama et al., 2014). Moreover, training captive marine mammals by operant conditioning, with trainers using vocal signals, is common (Würsig, 2008). However, as trainers typically employ many different signals (e.g., gestural, postural, and vocal) simultaneously to give orders to the dolphins, it is difficult to know which signal is really effective.

In sum, it is known that (1) dolphins spontaneously use learned individual acoustic signals, (2) they are particularly sensitive to other sounds in captivity, (3) they can be conditioned

using a set of signals of different types, (4) they have adapted to detect sounds underwater but there is some evidence of airborne sound perception. We thus carried out experiments to answer two questions: (1) Can dolphins respond underwater to learned sound cues artificially generated by humans? And if so, (2) Can dolphins generalize this learning to the airborne situation? Our predictions were that dolphins, like pigs, monkeys and dogs, would be able to respond appropriately to their own sound cues and ignore the sound cues allocated to other group members, even in the absence of any visual cues. We also hypothesized that dolphins would behave differently when hearing their own sound cue compared to other sound cues, when the same signals were transmitted through the air medium, thus generalizing from underwater learning to other conditions.

## **2. Materials and methods**

### **6.1. Captive dolphins**

A group of seven (three females and four males, aged 6–27 years old) captive bottlenose dolphins (*Tursiops truncatus*) born in different delphinariums and now all living in the “Cité Marine de Planète Sauvage” (Port-Saint-Père, France) delphinarium was studied (Table 1). They were housed as a group in four interconnected pools, containing approximately 8 million liters of water. These dolphins were fed fish (herring, capelin, mackerel, sprat, whiting, and squid) according to their individual needs, seven times a day. Two “free” meals were distributed at 9:00 to 17:00 and five others were distributed as a reward during training sessions or public presentations spread over the day. The training sessions lasted approximately 20 min and allowed trainers to condition the dolphins to perform certain actions for public performances as well as actions that facilitate medical care (taking temperature, blood sampling...). All training, including habituation for medical or experimental procedures, was conducted by experienced caregivers using an operant

conditioning technique based on positive reinforcement (mainly food, but also gelatine, ice cubes and enrichment items, like toys). During a regular training session, several trainers operate at the same time, each one dealing with one or more dolphins. Thus, dolphins are all busy executing different exercises, unless they prefer not to participate. They know the gestures telling them to come, to stay, and to leave, and during all sessions they are asked by gesture to make particular movements in exchange for reward.

Prior to our study, all these dolphins had been individually trained for at least 1 year to respond to a sound signal produced using a musical instrument, different for each animal (seven instruments were used, i.e., one per individual and always the same: castanets, claves, rattle, maracas, jingle sticks, Baoding balls, and a triangle; see Table 1). During weekly training sessions, a single trainer played an instrument underwater to “call” each dolphin. The instrument was immersed in the water at the edge of the pool, from varying locations, and played live; no recordings were used. Each dolphin was called, one after the other in a random order. The goal was to have the subject coming to the main trainer when hearing its designated individual sound. In the early stages of training, dolphins were first taught to approach and touch the instruments, being rewarded only when approaching and physically contacting the object. As learning improved, the main trainer played the instrument progressively farther away from the dolphin. In this exercise, the instrument was always first played twice, then a third time when the animal is halfway and finally twice when the animal is in front of the main trainer. If another trainer was working with the dolphin at the time of the instrument trial, he/she would give a “go” hand signal to allow it to go toward the sound source. Once the dolphin arrived at the sound source, it was given a food reward. A trial was considered successful when a dolphin moved toward the main trainer playing its designated instrument, and not toward the instrument assigned to another group member.

## 6.2. *Experimental approach*

Our first goal was to test under standardized conditions, whether dolphins successfully learned to respond to their individual sound source without the help of any visual cues (trainer gaze and gesture, instrument shape), without being influenced by the possible responses of the other group members, and without the need to play the instrument repeatedly to motivate the animal. We then tested their ability to generalize the training to airborne instrument playing. Responses to the sound signal to which they had been trained were thus evaluated first by playing the instruments underwater (Experiment 1: seven trials between 28th April and 4th May 2016, 1 per sound signal). Then, we recorded reactions to the same sound signal, but this time with instruments played in air (Experiment 2: seven trials between 6th and 16th May 2016, 1 per sound). For a given trial, only one sound was played and we performed only one or two trials per day. The order of the instruments tested was randomized for both experiments and only the main trainer was aware of the sequence.

Initially dolphins were tested in a group. Trials were always conducted in the same pool and with the same distance between the dolphins and the sound source (about 30 m). Dolphins were positioned with their backs to the main trainer (avoiding the possible use of echolocation), in the same position for all trials, and the sound source was hidden behind a plastic screen (to ensure that sound was the only cue for dolphins but also that trainers could not guess which dolphin would be called). Other trainers were instructed not to gesticulate or look at the subjects when the test started. The usual “go” gestural sign was thus never given by trainers for these experimental trials. The other trainers were not aware of the sound tested during a given trial and those familiar with the instrument allocated to each subject wore earplugs. At the beginning of a trial, several trainers (between 2 and

4) stayed near one side of pool 1 and thrashed the water in order to call the seven dolphins (Figure 1). Trainers placed all the dolphins in a “neutral” position, staying in place

motionless, avoiding looking at the other dolphins, and allowing them to respond spontaneously (move or stay in place). When all the dolphins were in place with the right orientation, one of the seven instruments was played by the main trainer on the opposite side of the pool. The instrument was positioned approximately 30 cm under the surface of water (Experiment 1) or approximately 50 cm above the surface (Experiment 2).

All successful responses (a dolphin moves toward its designated sound, or it does not move when the sound is not its own specific sound cue) were rewarded when the dolphin arrived at the sound source or after 10 s when the dolphin did not move after hearing another sound cue. The behavior of the dolphins during the 10 s following playback was further analyzed: (1) we considered that a trial was successful when either the subject went toward the sound source when it was its own sound cue or when it did not move toward it when it was another dolphin sound cue; (2) we defined as a behavioral reaction any behavioral change; (3) we recorded temporal aspects such as latency of first reaction and duration of behaviors. Apart from locomotion, we also scored visual attention, estimated from head orientation as in Xitco et al. (2001).

Dolphin behavior was recorded during the trials with three cameras: one underwater [Sport digital compact camera PNJ Cam AEE S71 High Definition (HD)] below the sound source and two others (Sony HDR-XR155E) placed above the water, one filming the area where the main trainer played the instruments and the other focused on the dolphins' starting position. We also used a broadband system consisting of a C54XRS (-185 dB, re 1V/ $\mu$ Pa, 0.06 to 203 kHz) hydrophone connected to a TASCAM DR-680 recorder (sampling rate 192 kHz 24 bit) to confirm that instruments, when played in the air, could not be heard underwater by dolphins at the test position (30m away).

### **6.3. Ethicsstatement**

The experiments described in this paper were carried out in accordance with the current laws of the country in which they were performed. They complied with the current French laws (Centre National de la Recherche Scientifique) related to animal experimentation and were in accordance with the European directive 86/609/CEE. The research was approved by the “Direction Départementale de la Protection des Populations” committee of Loire-Atlantique prefecture. No further permit was needed as only behavioral observations were performed. Animal husbandry and veterinary care were under management of Planète Sauvage, from whom informed consent had been obtained, as this study involved animals from a private animal park (not laboratory animals) with whom informed consent has been granted.

### **6.4. Data and statistical analyses**

The behavioral data for the seven dolphins were analyzed using the focal sampling method (Altmann, 1974) during the 10 s of each test following the playing of an instrument. Movements and gazes as well as their targets were recorded (Table 2). Responses were classified as successful or failed (successful when the dolphin reached the sound source within 10 s after hearing its own sound cue or when not moving after hearing another dolphin’s sound cue; failed when it did not respond to its own sound cue or responded to another dolphin’s sound cue. We analyzed the first reaction (i.e., first change of behavior) and its occurrence, duration and latency. A binomial test compared movement toward source between

own and other sounds. Chi-square tests compared the numbers of dolphins performing each behavior in each situation. In order to compare changes of gaze direction, duration and latency in relation to the type of sound (i.e., own or other), we used Wilcoxon tests. Comparisons between reactions to own and other sound cues were computed using reactions

to the broadcast of own sound cue to the median of this subject's reactions to the six playbacks of the other individual sound cues. We performed all statistical analyses with the software R 3.2.2. (R Core Team, 2014).

### **6.5. Data availability**

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## **3. Results**

### **6.6. Experiment 1: Underwater Broadcast Conditions**

In the first experiment, dolphins were exposed to sounds emanating from one of seven instruments played underwater. Each dolphin was trained to respond to the sound of only one instrument. Responses to each instrument were recorded, as were latencies to approach. All the dolphins except one moved toward the main trainer located near the sound source when their individual instrument was played (six out of seven trials, binomial test,  $P < 0.05$ ) (Figure 2). They did not move in 90.5% of the trials when the individual sound cue of another dolphin was broadcast. Overall, the dolphins were successful, 89.8% responses were appropriate (Sign test,  $P < 0.01$ ). Failures included one (1/7) subject (Ocean, see Table 1) that did not react when its individual.

### **6.7. Experiment 2: aerial broadcast conditions (Figure 2)**

In the second experiment, dolphins were exposed to sounds emanating from the same seven instruments, but this time played in the air. Dolphins had only been trained to respond to these



sounds when played underwater. Responses to each instrument were recorded, as were duration and latencies of gazing at the sound source, at a trainer or at other objects of the environment. None of the dolphins moved toward the sound source during the tests (Figure 2). In 91% of the trials, dolphins had their heads (lower jaws) out of the water at the time of sound emission. Behavioral responses indicated that the dolphins not only heard the sounds but even discriminated between them: (1) latencies of first gaze toward the source were shorter when the sound broadcast was their own sound cue (Figure 2); (2) the type of the sound broadcast did not influence the number of gazes directed toward the source ( $V = 13.5$ ,  $P > 0.05$ ), but it influenced the total time spent looking at the source ( $V = 28$ ,  $P < 0.05$ ): time spent looking at the source was  $5.09 (\pm 0.3)$  seconds when the sound broadcast was the subject's own sound cue, but only  $2.40 (\pm 0.6)$  seconds when it was another dolphin's sound cue; (3) the dolphins' first reaction following the stimulus broadcast was generally to look at the sound source (chi-square test,  $n = 7$ ,  $DF=6$ ,  $P < 0.01$ ) (Figure 2). Number of gazes directed toward a conspecific ( $V = 133.5$ ,  $P=0.37$ ), a trainer ( $V = 130.5$ ,  $P=0.62$ ) or other features of the environment ( $V = 126$ ,  $P = 0.52$ ) did not differ significantly in relation to the sound broadcast.

#### **6.8. Comparison between underwater and aerial conditions**

Number and duration of gazes toward the sound source were significantly higher when the broadcast was aerial (Wilcoxon Tests:  $V = 354$ ,  $P < 0.01$ ;  $V = 343$ ,  $P < 0.01$ , respectively). As a consequence, duration of gazes toward conspecifics was significantly shorter in the aerial condition than in the underwater condition ( $0.46 \pm 0.1$  underwater and  $0.08 \pm 0.0$  s in the air,  $V = 1098$ ,  $P < 0.01$ ). Conversely, movements toward the sound source were restricted to the underwater condition (Figure 2). Number ( $V = 88.5$ ,  $P = 0.21$ ) and duration ( $V = 101$ ,  $P = 0.27$ ) of gazes toward other targets were not influenced by the type of broadcast.

#### **4. Discussion**

This study provides the first evidence that bottlenose dolphins can recognize a human-made sound cue played underwater, even when transposed to the aerial environment. Prior to these experiments, dolphins had been trained individually with the possible help of visual cues. Here, dolphins were tested while in a group with exclusively auditory stimuli, and we confirmed not only that the target subject responded to its specific human-made sound cue but also that it did not move when another group member was “called.”

In the first experiment, the dolphins performed the trained response (moved toward the source). Operant conditioning is widely used for the management and training of captive dolphins. Daily training and public performances are based on teaching the animals gestures associated with specific behaviors. Dolphins are able to associate a human movement with a specific action, or a specific part of their body, and can respond to orders combining these different elements thanks to their understanding of simple syntax rules (Herman, 2002; Herman et al., 1984). Furthermore, they can incorporate features of artificial sounds made by humans into their whistles (Miksis et al., 2002) or use novel sounds to refer to objects (Richards et al., 1984). They are also said to be self-aware, notably because they recognize their bodies in a mirror (Reiss and Marino, 2001). Their high-level cognitive abilities are further shown by imitation of computer-generated sounds, and of postural or motor behaviors of non-cetacean species and dolphin tank mates (Richards et al., 1984; Reiss and McCowan, 1993; Herman, 2002; King and Janik, 2013). They signal individual identity through signature whistles that they can share with other dolphins through affiliative copying (Harley, 2008; King et al., 2013), which implies labeling, a skill shared with humans and some bird species (Hausberger et al., 1995; Wanker et al., 2005; Pepperberg, 2007). Our findings suggest that dolphins can associate sound cues with individual identities and we believe that this contributes to the debate regarding the potential existence of a concept of self-identity in

dolphins. Responding to its own “label” and not to that of other group members is definitely not restricted to humans (Masataka, 1992; Puppe et al., 2007). Further experiments could test their ability to associate a given sound cue to the image of the appropriate group member, for example. In the second experiment, dolphins responded differently when the sounds were played in the air: they did not move toward the sound source, so did not generalize the training per se, but clearly discriminated between their own and other individual sound cues. Thus, they gazed more often and for longer toward the sound source and reacted faster when their own sound cue was being broadcast. The aerial hearing sensitivity of dolphins has been debated, and some authors doubt that cetaceans are really able to hear sounds emitted in the air (Ketten, 2000). Marine mammal ears are adapted to aquatic life (Breathnach et al., 1988). The absence of a functional ear canal similar to that of terrestrial mammals makes them less sensitive to sounds in the air and is probably one of the factors that accelerated the specialization of their inner and middle ear for perception of sounds underwater (Hemilä et al., 2010).

Nonetheless, most auditory studies have focused on reception of waterborne sounds (review in Erbe et al., 2016) and only three studies (bottlenose dolphins: Babushina, 1979; harbor porpoises: Kastelein et al., 1997 and tucuxis: Liebschner et al., 2005) investigated sensitivity to airborne sounds. These authors suggested that dolphins are able to perceive acoustic stimuli broadcast in air. Kremers et al. (2011) and Murayama et al. (2014) supported this by reporting imitation by odontocetes of aerial sounds from the environment (airborne playback of whale sounds or human speech). The fact that our dolphins reacted faster when the sound signal broadcast was their own sound cue than when it was that of a conspecific shows that the dolphins were able to perceive and recognize sound signals diffused in the air. The difference in reactions to underwater and airborne acoustic stimuli may be due to either poor hearing (Liebschner et al., 2005), inability to generalize the learned response, or more likely to a

“surprise” effect like that observed when unexpected sounds are heard (e.g., Lemasson et al., 2005) or in the context of an expectancy violation paradigm (e.g., Kastelein et al., 1997). They gazed more at the sound source when the instrument was played in the aerial condition, which could be an indication that they were trying to understand the demand, as shown in other studies when humans behaved unexpectedly or differently (Xitco et al., 2001). Thus, horses increased their monitoring behavior after hearing a familiar order given by an unknown person (Sankey et al., 2011). Dolphins look more at their trainer when their performance is inconsistent during a familiar task (Xitco et al., 2004). Dolphins could use cues based on human movements, as they are trained to be very attentive to gestures during training sessions (Tomonaga et al., 2015). The fact that dolphins possibly search for clues given by human postures could explain the multiple gazes toward the source.

## **5. Conclusion**

This study shows evidence that bottlenose dolphins are able to respond to individual sound cues produced by humans, even when sounds are emitted in the air. This evidence contributes to our knowledge of the cognitive capacities of this species and the extension of its hearing capabilities. Further studies could test if dolphins can associate these sound cues with individual identities.

## **6. Author Contributions**

ALi, MS, MB, MH, and ALe designed the research project; ALi, CD, and MS performed the experiments; ALi, MS, MH, and ALe contributed to data analyses; and ALi, MS, MH, and ALe wrote the paper.

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10. Figures

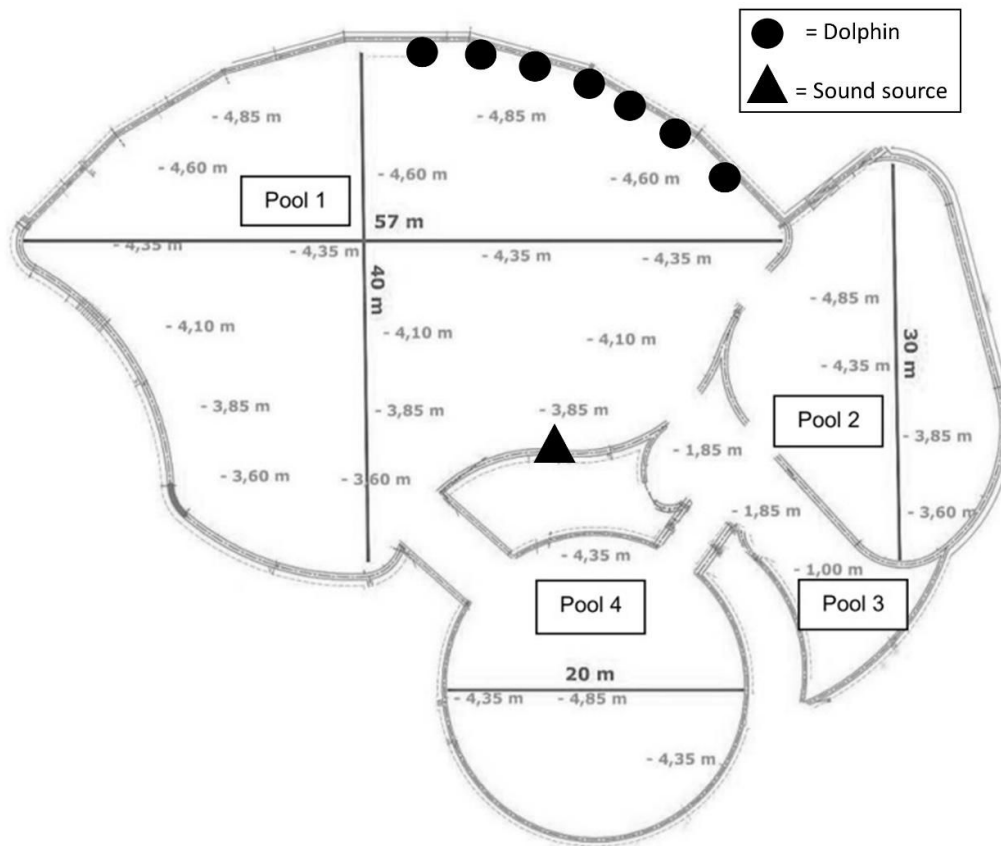


Figure 1. Schematic representation of the 4 pools at Planète Sauvage (adapted from Planète Sauvage ©). The symbols represent the position of individuals at the beginning of each test ("Dolphin", random order of alignment) and the trainer operating the instruments ("sound source").

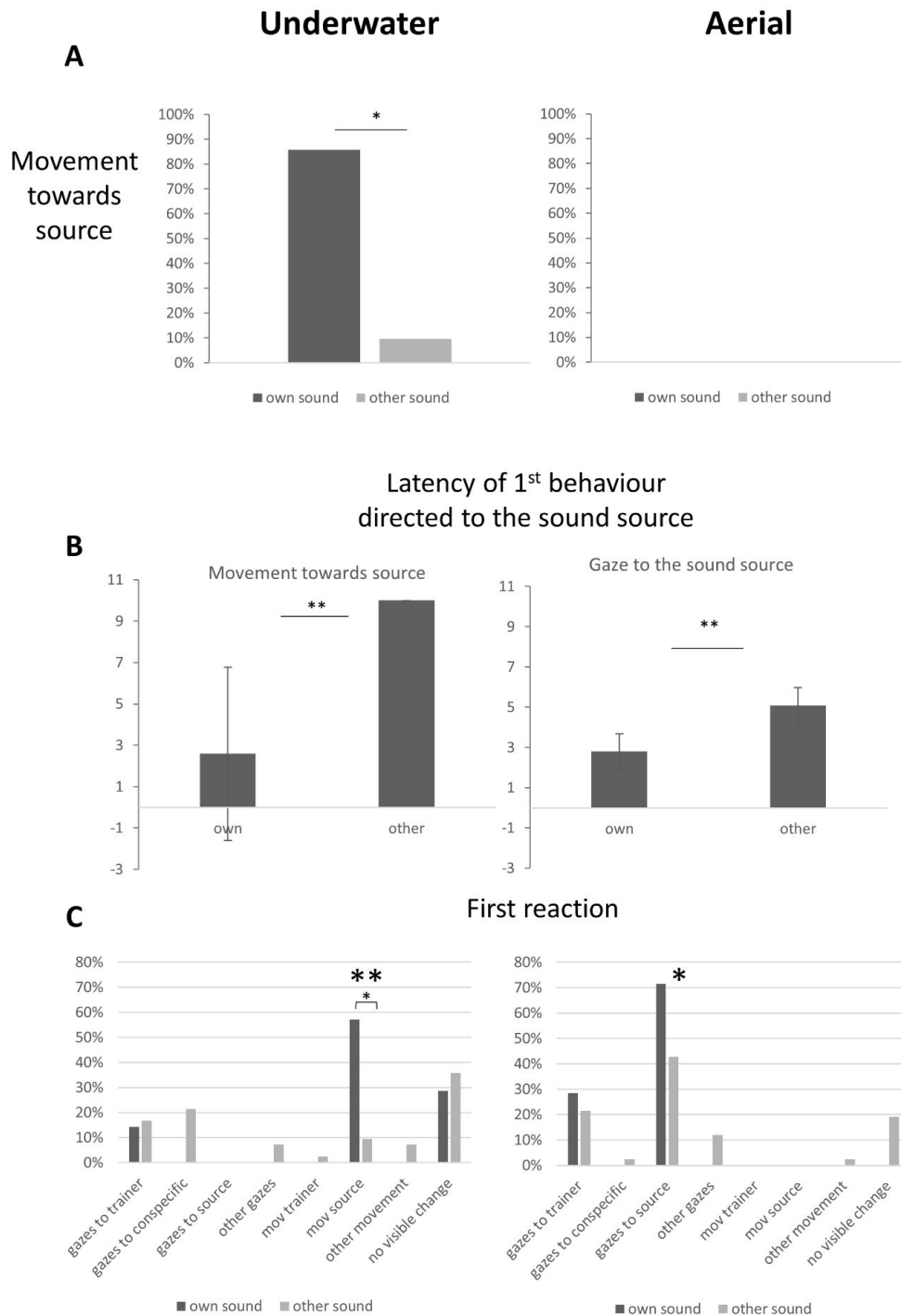






Figure 2. Dolphins' reactions to their own label and to other dolphins' sound labels broadcast underwater (left) and in the air (right). **(A)** Movements of dolphins towards the sound source (percentage of subjects; binomial test on real numbers, \*  $P < 0.05$ ). **(B)** Latencies of first reactions to the sound: movement when the sound was underwater and gaze when it was airborne; mean  $\pm$  standard error (Wilcoxon test, medians of latencies per subject for other labels versus own label, \*\*:  $P < 0.01$ ). **(C)** Dolphins' first reactions to a broadcast (percentage of subjects). One behaviour predominated in each situation: movement towards the source of the underwater sound, gaze towards the source of the airborne sound (chi-square test performed on real numbers, \*:  $P < 0.05$ , \*\*:  $P < 0.01$ ).

## 11. Tables

**Table 1. Instruments assigned to each individual and characteristics of the studied animals (M: male, F: female). Age in years. Photos: M. Sébilleau.**

Instrument	Name	Birth location	Sex	Age	Birth date
	Aïcko	Parc Astérix (France)	M	6	05/14/2010
Castanets					
	Galéo	Parc Astérix (France)	M	6	08/09/2009
Claves					
	Parel	Dolphinarium Harderwijk (Netherlands)	F	7	06/08/2008
Rattle					
	Ocean	Boudewijn Seapark (Belgium)	M	12	08/13/2003
Maracas					



Amtan Dolphinarium Harderwijk (Netherlands) F 14 05/13/2001

Jingle sticks



Peos Parc Astérix (France) M 16 06/23/1999

Baoding balls



Lucille SeaWorld Orlando (USA) F 27 04/16/1989

Triangle

**Table 2. Terminology of behaviors observed during the experiment**

<b>Behavior</b>	<b>Description</b>
<b>Movement</b>	<b>Source</b> Dolphin moves to the sound source.
	<b>Trainer</b> Dolphin moves to another trainer.
	<b>Other</b> Dolphin moves in a direction other than that of the sound source or a trainer.
<b>Gaze (Starting position - Dolphin on the edge of the pool)</b>	<b>Source</b> Dolphin looks in the direction of the sound source.
	<b>Trainer</b> Dolphin looks in the direction of one of the trainers.
	<b>Conspecific</b> Dolphin looks in the direction of a conspecific.
	<b>Other</b> Dolphin looks in a direction that does not correspond to trainers, sound source or conspecific.

## **CHAPTER 5: DISCUSSION**



## **1. WHAT THESE FINDINGS TELL US ABOUT DOLPHIN'S BEHAVIOUR**

If we consider social life as the driving force behind the evolution of communication (Snowdon and Hausberger, 1997), the study of vocal behavior provides a window into understanding nonhuman minds as well as the social complexity of other species (Perrin et al., 2008). Signalling behaviour facilitates the sharing of information between members of a group and is generally context-dependent (Smith, 1965).

It is in this context that we have studied the use and perception of acoustic signals in the bottlenose dolphin. We had access to a social captive group, with rare opportunities to conduct high quality observation and sound recordings.

The results of this thesis contribute to the understanding of the contexts and possible functions of dolphins' vocalizations, as well as their perception of sounds, bringing insights to understand their cognition and behavioural flexibility. With regard to the temporal distribution of social and vocal activities, we found that these dolphins socialized more in the morning, contrasting to what is found in wild populations. Concerning the relationship between vocal production and social and non-social activities, we identified preferential associations between some vocal categories and behaviours, expanding the knowledge on context-specific use of dolphin vocalizations. We also discuss the ability of dolphins to recognize individual sound labels and perceive these acoustic signals even when heard in the air.

### **1.1. Production and use of sound**

The aim here was to study the extent of communication ability of these animals and to update hypotheses on the social functions of vocal behaviour. We described time budget and social

life of the 7 captive dolphins studied in relation to the peculiarities of their routine in a zoological park, the vocal repertoire of the group and searched for associations between the different acoustic structures of their repertoire to emission contexts, formulating functional hypotheses for the different types of signals identified.

Understanding the mechanisms linked to social behaviour contributes to determine how the communicative behaviour contributes to the maintenance and management of interactions between individuals. For this thesis, understanding the rhythms of social activities was important to give clues about the temporal distribution and expression of vocal activity. This consisted first of all in a descriptive analysis of the acoustic structures recorded, taking into account both whistles and other types of vocalizations. Powel (1966) had searched for cyclic rhythms on vocal behaviour of captive bottlenose dolphins, already suggesting that their vocal activity may assume a pattern reflecting the captive routine. Here, even if we found more social activity in the morning than in the afternoon, among the vocal categories only chirps showed a temporal pattern, being more recorded in the afternoon (when there were less social activities), but more recorded with socio-sexual behaviours (Paper 1).

Our analyses of the vocalizations of the seven bottlenose dolphins showed a relatively complex vocal repertoire, as put in evidence before by many authors (e. g. Acevedo-Gutiérrez and Stienessen, 2004; Caldwell and Caldwell, 1965; Jensen et al., 2009; Lopez and Shirai, 2009; Luís et al., 2015; Mccowan and Reiss, 1995). In this thesis we only worked with the four main categories of dolphin vocalizations: burst pulse sounds, chirps, click trains and whistles. However, there are some other vocal categories described in the literature which were not addressed here. For example, brays are a two-part burst pulse sound (including a low-frequency narrow-band sound) first described during social behaviour by Dos Santos et al. (1990) in wild dolphins and after also detailed by dos Santos et al. (1995) and Janik (2000) as an indicative of aroused behaviours at the surface, or fast swimming, mainly detected in

feeding contexts. We did not find this vocal category in our sampled data, and we could hypothesize that this is a sound linked to foraging and, thus, not found in our captive dolphins (which, moreover, were not recorded in feeding contexts). Other vocal categories not explored in our sampled data are the buzzes. These are click trains that last more than 1 s up to minutes used both to foraging and social purposes, as competition or female pursuit, and that sometimes appear synchronized with brays (Herzing, 1996; Herzing, 2015). Since we did not find any click train lasting more than 1 s, we could hypothesize again that this category is mainly associated to contexts occurring in the wild and not recorded during this thesis on captive dolphins. Some other vocal categories appearing in the literature lack of a common nomenclature between authors, being based in part on the main reported vocalizations (tonal and pulsed sounds), and partly on novel interpretation (Lopez and Shirai, 2009) and then were not the target of this study. Some examples are: grunts (Rycyk, 2007), squawks (Herzing, 2013), pops (Connor and Smolker, 1996), moans (van der Woude, 2009) and creaks (Lilly and Miller, 1961). Looking closer for contextual and functional use of vocalizations that we could analyse, we found many associations that can help to understand functions of vocal signals and what they are expressing about dolphins.

Whistles did not show a temporal daily pattern, and were recorded in varied contexts (mainly social), but not only affiliative, as often reported (Janik and Sayigh, 2013; Mello and Amundin, 2005). Especially when our scale of analysis was narrowed, whistles appeared strongly associated to socio-sexual contexts. Their association with solitary play was noticeable. Other controversies about the supposed exclusive affiliative functions of whistles have been reported before, for example when the production of this category was associated with feeding activities (Acevedo-Gutiérrez and Stienessen, 2004; Luís et al., 2015). Therefore, our results raise the hypothesis that this signal may have a very general function of contact call (dos Santos et al., 2005; Gridley et al., 2015; Herman and Tavolga, 1980) and so

does not appear associated with a particular context. An alternative hypothesis is that there are several types of whistles with particular functions (since signature whistles seem to correspond to only part of the repertoire, Luís et al., 2015; Rachinas-Lopes et al., 2017), but we have not tested this hypothesis here. Dos Santos et al. (2005) found significant variation in the number of stereotyped contours regarding contexts of higher or lower arousal levels, which could corroborate this hypothesis of different types of whistles linked to different contexts. Our observations in a smaller scale of analysis, from the observations through the subaquatic window, allowed us to better discriminate social and non-social contexts during which this vocalization can be emitted.

The fact that burst pulse sounds were found mainly in social, but diverse contexts, without a daily temporal pattern, first confirms that this vocal category is associated with social interactions. Besides that, they were not exclusively associated with agonistic contexts, as often suggested (Lopez and Shirai, 2009; Overstrom, 1983). It is interesting to note, in addition, a high correlation of this category with play behaviours in both studies. This association highlights the potential emotional or excitatory aspect of these sounds, that have been proposed to be related to “highly emotional contexts” (Caldwell, 1967), such as aggressive episodes, play or prey capture associated with brain dopamine release (Ridgway et al., 2015). Also, play behaviours in dolphins are often difficult to distinguish from agonistic behaviours (Janik, 2015), and a play context may sometimes risks to escalate to agonistic (Palagi et al., 2016). Studies on primates emphasized the importance of play-fighting for social assessment and establish a position within the group’s social hierarchy (Palagi, 2006; Palagi et al., 2007). This vocal category remains the least understood in dolphin repertoire, notably because of different methods of classification used by different authors. Luís et al. (2016) highlighted the importance to improve the accuracy of categorizations for pulsed signals. Here, we chose to use a duration-based classification to analyse types of burst pulses

in the second study. This narrowed scale of analysis allowed us to find a difference between long and short burst pulse sounds, these last being more associated with social play than the first.

Click trains have been described before mainly as used in sonar-related tasks (dos Santos and Almada, 2004). In our results, they seemed to be a very flexible vocal category, being associated with diverse social and non-social contexts. We could hypothesize that these sounds are being used mainly in exploration (reviewed by Herzing and dos Santos, 2004; swimming or solitary play, in our study), or adding information to communication contexts (Kuczaj II et al., 2015), especially when in association with other vocal categories. In that point, our second study showed much more information on the production of click trains than the first one, especially when we looked for the associations between vocal categories.

Chirps were analysed just in the first study, because their emission rate was too low during the second study to participate in analysis. The association of this category with “less social” time of the day and at the same time with socio-sexual behaviours may seem contradictory, but examples of the other vocal categories showed that a further look in a narrow scale can bring new insights about contexts of call emissions. This vocal category was first and often described as a shortened whistle associated to arousal (Caldwell and Caldwell, 1970). In other studies, chirps were specifically recorded during foraging (Herzing, 1996) or non-aggressive contexts (Perazio and Kuczaj II, 2017), but often their production is too low for statistical tests that try to associate them with behaviours (e. g. Perazio and Kuczaj II, 2017). Unfortunately, we could not go further in contexts more related to chirp emission, but our results highlight the interest to treat them as an independent category from whistles and future research should focus on understanding their functions.

The results of this thesis discussed specific vocal signals and behavioural contexts in which dolphin calls occurred. However, vocal signals provide clues not only on the activity at the

time of the emissions, but also on the potential motivations and internal states of the individuals interacting (Smith, 1965). Thus, signals of an individual or group of individuals may provide valuable information on the meaning and responses involved in communication (Smith, 1965).

There is a growing consensus that well-being is associated with the presence of positive emotional states which have been proposed by some authors to be as important to animal welfare as the absence of negative emotions (Boissy et al., 2007; Moe et al., 2009). If vocalizations reflect positive or negative effects, they could help identifying the positive perception of experiences by captive animals (domestic, farm, laboratory or zoo). In rats, evidences shows that 50 kHz ultrasonic vocalizations reflect an acute positive emotional state of the animal emitting them, but also for animals exposed to a playback of these sounds (Burgdorf et al., 2011).

Kuczaj et al. (2012) discussed numerous methods and their relevance for studying dolphin emotion. They argued that it would be interesting to use physiological measures, but pointed out the fact that this kind of study can be very challenging with aquatic mammals. They suggest, instead, that vocalizations may represent a valuable indicator of emotional state on dolphins, taking into account their wide range of vocalizations produced in a variety of contexts (e. g. Hernandez et al., 2010; Herzing, 1996; Mccowan and Reiss, 1995). This kind of information could be useful to caregivers to understand more about the social functioning of the group of dolphins with which they work. Lilly (1963) found, for example, that a type of whistle is associated to physical distress, and Esch et al. (2009) proposed that whistles could serve as indicators of stress, with signature whistle rate appearing as directly related to disturbed conditions. Also, correlations have been found between whistling rates and stressful contexts, so dolphins accidentally captured in tuna seine nets or captive bottlenose dolphins newly introduced into a tank whistle more, nearly continuously (Perrin et al., 2008). Results

of other studies also suggest that dolphin vocalizations may convey information about the caller's emotional state (Caldwell and Caldwell, 1967, 1971; Dudzinski, 1996).

Affiliative behaviours may also reflect stable social bonds. Here we found some vocal categories (notably click trains) and associations (click trains and whistles) linked to social affiliative behaviours. This kind of association may help to know group activities by vocal recordings, since dolphins' underwater behaviours are not easy to observe. Such acoustic monitoring may give clues about the "atmosphere of the group", for example, giving valuable insights for caregivers in a captive context and improve researchers' efficacy trying to categorize dolphin behaviour by surface observations.

Our results about the use of burst pulse sounds during play raised hypotheses about this vocal category being an indicator of arousal or emotion. Herman (2010) argued that the high ability of dolphins to discriminate small differences in the durations of sound may be explained by a potential communicative value in this parameter. He hypothesizes that the sender's emotional state could be expressed by these duration differences. Although we have not analysed this parameter directly in this thesis, the differences that we found between types of burst pulses of different duration, and their most associated behavioural contexts, could be explained by Herman's hypothesis. Moreover, Overstrom (1983) described burst pulse vocalizations as being associated to aggressive displays, and accompanied by body postures and jaw claps, which may express different types of negative emotions such as annoyance, anger, or even fear. It would be necessary to understand better the relationship between particular behaviours and emotions if they were to be used as indicators.

We also explored a subject often neglected in studies of dolphin communication in our second study: the associations between vocal categories. Our results showed changes in most associated contexts following the presence of different mixed vocal categories. For example, in our results, burst pulses, when associated with click trains and whistles or only whistles

appeared in socio-sexual contexts; click trains associated with burst pulses are observed more with social play. The study of associations of vocalizations in dolphins is lacking, with just some studies bringing this point only for some specific contexts, as the association of burst pulses and whistles in whistle squawks, for example, common during aggression as well as sexual play (Herzing, 1996; Perazio and Kuczaj, 2017). Herzing (2015) recorded synchronized vocalization bouts (consisting of a whistle and a buzz, a kind of a click train of long duration) during aggressive interactions, but she was not able to know if it was one or two dolphins or more that were producing these bouts of sounds, which is also the case for the associations found here.

As dolphins can produce tonal and pulsed sounds simultaneously (Perrin et al., 2008), our data did not allow us to know if the associated vocalizations were been emitted by the same or different individuals. Anyway, results presented here are encouraging for further investigation of the role of associated vocalizations in dolphins. For example, if these associations are shown to be emitted by different individuals, as one might conceive, some "conversational" importance may be conjectured in them, as reported for other odontocetes (Schulz et al., 2008; Vergara et al., 2010). Harley (2008) already proposed that dolphins could use antiphonal calling when producing other's signature whistle. Alternatively, it is possible to imagine such associations between vocal categories as a factor giving a particular function to the calls, as the presence of whistles in associations between them and burst pulse sounds in agonistic contexts, as a way to prevent play-fight from escalating into a real fight (Blomqvist et al., 2005).

Ultimately, this study contributes to a better knowledge of the vocal repertoire of a cetacean species and encourage a larger debate on the functions of bottlenose dolphins' vocal communication.



## **1.2. Sound perception**

Another aim of this thesis was to study, in an experimental way, the extent of the communicative capacities of the dolphins on the perceptual aspect. The findings detailed in Chapter 4 puts in evidence for the first time the ability of bottlenose dolphins to recognize a human-made individual sound label played underwater and even when transposed to the aerial environment. This ability of generalization confirmed the sometimes controversial aerial audition of dolphins.

Cetacean hearing is extremely adapted to aquatic environment, but some authors showed that dolphins are able to perceive acoustic stimuli broadcast in the air (Babushina, 1979; Kastelein et al., 1997; Liebschner et al., 2005) and even to mimic them (Kremers et al., 2011). They also produce spontaneous aerial vocalizations sometimes (pers. observation) during training. Furthermore, there is still room for doubt that cetaceans keep some vestigial abilities on perception from their terrestrial evolutionary past. For example, looking to the other sensory modalities that were thought to be lost, there are evidences for chemoreception, including olfaction and gustation in dolphins (Kremers et al., 2016; Ridgway, 1988), while some authors have claimed that airborne odorants may be considered irrelevant to an aquatic lifestyle (Thewissen et al., 2011), although fish perceive the chemical solutions both by olfaction and taste (Kuznetsov, 1990). When considering hearing, it is worth remembering that the mammalian ear evolved for hearing in air. When the terrestrial quadrupeds ancestors of cetaceans entered the aquatic medium, they modified this aerial system, enhancing the characteristics that allowed for greater high-frequency hearing sensitivity and complex auditory processing (Ridgway, 1988). Studies on dolphin aerial hearing are rare, but one comparison of aerial and underwater audiograms of a bottlenose dolphin has shown that the sensitivity of the dolphin's ears to the sounds in the air deteriorates by 30-60 dB (depending on frequency; Babushina and Polyakov, 2011). Our results can confirm the ability of dolphins

to hear sounds transmitted in aerial medium based on their behavioural responses to known sounds transposed to the air.

### **1.3. Cognitive abilities**

Bottlenose dolphins have been a popular study species in animal cognition research since the 1950s, and many of their cognitive skills are compared to those of the great apes (Clark, 2013). Findings show that dolphins are able to perform imitative behaviour (Herman, 2002; Mercado et al., 1998), have a high-level cognitive ability, which presuppose these animals have a mental representation of others and themselves (Clark, 2013). Dolphins have the ability to imitate arbitrary computer-generated sounds, the postural or motor behaviours of non-cetacean species as seals, actions of human models, and the complex trained motor sequences of other dolphin tank mates (Herman, 2002; Reiss and McCowan, 1993; Richards et al., 1984). They also can use novel sounds to refer to objects (Richards et al., 1984) and understand syntactic rules of an artificial signalling system based on hand and acoustic signals (Herman et al., 1984). Miksis et al. (2002) studied the influence of trainers' whistles in the development of captive dolphin whistles, finding that in this case animals can incorporate features of acoustic artificial models made by humans into their own whistles. Also, captive dolphins have shown other great learning abilities, as associating different gestural symbols with different body parts, using the same body parts in different ways, as instructed (as in commands "shake your pectoral fin" versus "touch here with your pectoral fin"), and using different body parts in the same way (as in commands "touch the ball with your rostrum" versus "touch the ball with your tail") (Herman, 2012). Captive breeding facilities work since many decades with cetaceans (mainly bottlenose dolphins and killer whales) based on behavioural response techniques through operant conditioning with food reinforcement, and those species have been showing great performances and an impressive number of behaviours executed through command by gestural signals.

Our results from Chapter 4 have showed the ability of dolphins to associate human-made sound labels with individual identities (“names”), evidencing one more time their ability to learning through operant conditioning, but furthermore, as dolphins were tested in group, their correct responses to their own labels constitute further evidence that they have some concept of their own identity. They have shown to be able to understand which label correspond to each one of them and, further, to generalize this learning when labels are modified by the medium.

It is already known that dolphins use specific calls (signature whistles, Sayigh et al., 1998) for individual recognition, based on different frequency modulation patterns (see review in Janik and Sayigh, 2013). In addition, dolphins are able to remember the signature whistle of other individuals for at least 20 years (Bruck, 2013). The use of shared vocalizations as identity marker has also been reported in several other species, such as humans and some species of birds (e.g. Hausberger et al., 1995; Kondo and Watanabe, 2009; Wanker et al., 2005) and some studies in which artificial codes have been taught to other species also provide evidence of referential learning in primates (Savage-Rumbaugh, 1986) and parrots (Pepperberg, 2010).

There is a lot of speculation about how dolphins see themselves, and if they have a theory of mind. Studies of mirror self-recognition (Delfour and Marten, 2001; Reiss and Marino, 2001) support the hypothesis that dolphins, as great apes, elephants and magpies, may have at least a body self-awareness.

#### **1.4. Behavioural flexibility and life in captivity**

Cetaceans have been kept in captivity since the early 1860s (Defran and Pryor, 1980), and bottlenose dolphins have supposed to be one of the species that best adapt to the captivity among them. While comparative studies of individual associations, specific behaviours and social groups observed in both captive and free-ranging dolphins provide a better

understanding of how their activities relate to both environments (Dudzinski, 2010), some behavioural patterns differ between the two settings, while others are very similar.

Some characteristics from the wild, as predators, food shortages, and other environmental challenges are often absent in captive environments, and captive animals often have energy and time in abundance (Held and Spinka, 2011). Differences in routines between captivity and wild include single versus more continuous feeding opportunities; predictability versus unpredictability; more food in the afternoon versus peaks of feeding in the beginning and end of the day. Other natural characteristics may be absent in captivity and, in response, captive mammals adjust their behaviour to cope with their environment, potentially resulting in differences between wild and captive populations (McPhee and Carlstead, 1996).

Here, we first searched a better understanding of time budgets of the animals studied. Bottlenose dolphins maintained for public display are an interesting model to study how behavioural patterns are affected by human-controlled periods, since they have in general many of such periods in a day (training and shows with food as reinforcement). Concerning temporal patterns of behaviours, we found that in this group, housed in a zoological setting, social activities occur mostly in the morning. This pattern is not similar to that found in wild populations, where socialization occurs at low levels in the morning and increase in the early afternoon. We hypothesize that these differences are related to differences in feeding routines between the two conditions. Feeding is of great importance to the behavioural budgets of bottlenose dolphins (Beddia, 2007) and studies on many animal taxa show that the distribution of non-feeding behaviours is significantly influenced by feeding times. Feeding for captive dolphins differ from feeding in most other captive animals, as it is accompanied by interactions with humans, and requests to perform trained behaviours and learning new ones. Some of these occasions include presence of not so familiar people as veterinarians when being examined, or public presence, during shows. Other studies bring evidences on how the

context in which dolphins are fed may be considered key moments in their day. A recent study (Clegg et al., 2017), for example, showed that these animals exhibit anticipatory behavior before training sessions, corroborating the idea that they have the ability to anticipate the arrival of key moments.

Concerning the vocal repertoire, however, we did not find remarkable differences between our data and what is known in wild populations (Díaz López, 2011; Gridley et al., 2015; Lopez and Shirai, 2009), in the limits of what could be observed. Foraging contexts being not present in captive condition, we could not search for relations between vocal categories and this activity (as done by Acevedo-Gutiérrez and Stienessen, 2004; dos Santos et al., 2005, or studies describing feeding-related vocal categories, as dos Santos et al., 1995 and Janik, 2000). It is worth to mention also that, in captivity, we work on mixed groups, with individuals coming from different origins. This fact may have some implication regarding the result of ontogenetic effects or social learning on vocal behaviour, which we could not measure in our study. Anyway, we were able to observe behaviours performed during vocal emissions in a more fine scale than what is in general observable in the field, contributing with more detail to complete descriptions provided by studies on wild populations (e.g. Papale et al., 2016).

## **2. RESEARCH PERSPECTIVES**

To study communication between dolphins and go further in the understanding of production and use of sound, it is important to identify the various signals used by individuals as well as who the initiators and respondents are and their respective actions (Smith, 1991), so we should be able to determine which dolphin produces a sound to have more precise associations with contexts. Therefore there is a real need of new tools to explore vocal contexts at the individual level. Some studies are dedicated on this issue, developing telemetry devices to attach on the dolphin's head (Tyack, 1986), but besides the fact that this technique

is not easy applied in the wild, the attachment of the device may restrain the possibilities to get spontaneous behavioural observations of the equipped dolphin even in captivity (Tyack, 1985). Other techniques are developing, as the use of hydrophone arrays (López-Rivas and Bazúa-Durán, 2010) or video cameras equipped with hydrophones (Mcintosh et al., 2015; Nakahara and Miyazaki, 2011), but the efficacy of these methods depends on how often dolphins spend time next to each other and other logistical problems. During this thesis, an effort was made to develop a way to acoustic recording individual captive dolphins with a small device, attached on a dolphin with suction cups. The goal was to study dolphin acoustic signals at the individual level, describing repertoires and relating it to specific behavioural contexts. A simple individual recording device was developed, consisting of an EDIC-mini Tiny, a voice recorder with sampling rate of 22 kHz (4 bits). A plastic waterproof case housed the recorder and an 8.2cm (when relaxed; 9.0cm when sucking) suction cup for attachment. However, this project depending on training of dolphins, and technical adjustments of the acoustic device, to date we were able to collect data, but they are still in analysis. We got to have two male dolphins accepting to carry the device on, and we have promising results by associating observation of specific contexts and individual vocalizations.

Furthermore, our results on contextual use of vocalizations may give ideas to go further on understanding of the functions of the different vocal categories. Data on burst pulse sounds and chirps use revealed a broad range of contexts for these vocal categories, and raised hypothesis about their functions. Burst pulses showed to be a potential indicator of behaviours involving high levels of arousal, as play/agonistic contexts and chirps revealed an association with sexual contexts never reported before. Playback experiments could be valuable to test functions of the different vocal categories and behavioural responses of the animals. These experiments could associate for example video recordings of different behavioural contexts and dolphin recordings containing different vocal categories to test dolphin's reactions

associated to these matchings behaviour-call. To go further in the study of vocalizations as possible indicators of emotions, it should be essential to associate physiological indices to acoustic structures and vocal rates under varying levels of stress (as proposed by Esch et al., 2009 for whistles) or different emotional arousal and valence (Briefer, 2012).

Our results on associations between vocal categories are just preliminary. To better understand if these associations constitute conversational evidences or simultaneous emission of combined calls by the same individual, as well as their role in dolphins' vocal communication, it would be of great value first to identify individuals vocalizing to be sure if recorded associations are produced by one or more individual(s). Then, if characterized as acoustic sequences, many aspects could be more rigorously explored like the different paradigms characterized by repetition, diversity, combination, ordering, overlapping and timing, as proposed by Kershenbaum et al. (2016).

On the perception aspect, many other paradigms could be tested, such as the paradigm of violation of expectations based in particular on an intermodal approach (e. g. playback of vocalizations emitted by an individual A associated with the vision of the same individual or an individual B) (e.g. Proops et al., 2009). This would enable us to test the ability to decode information about the individual identity or gender of the emitter. Secondly, this same paradigm could be used to test the social function of a given type of vocalization proposed above (e. g. playback of a type of vocalization and broadcast a video showing appropriate or inappropriate associated behaviour).

## **RESUME EN FRANCAIS**

**Production et perception des signaux  
acoustiques chez les grands dauphins  
(*Tursiops truncatus*): Utilisation  
contextuelle des signaux sociaux et  
reconnaissance de « labels » artificiels**





## 1. INTRODUCTION

### **1.1. Communication animale, signaux acoustiques et utilisation contextuelle des vocalisations**

L'étude de la communication animale est fondamentale pour l'étude de leur comportement et pour la compréhension de la dynamique sociale d'une espèce. Les signaux doivent s'adapter à de nombreuses pressions sélectives, par exemple la qualité de l'habitat incluant la propagation du son (Marten *et al.*, 1977) et le bruit de fond (Mathevon, 1997); le risque de prédation (par exemple Elgar, 1986, Manser *et al.*, 2002) ; le mode de reproduction (par exemple, la relation entre la taille des voies vocales et la production de spermatozoïdes chez les singes hurleurs, Dunn *et al.*, 2015 et l'utilisation de fréquences graves par les paraitre plus gros face à leurs rivaux, Charlton *et al.*, 2013) et la socialité (Blumstein et Armitage, 1997, Freeberg *et al.*, 2012, McComb et Semple, 2005, Wilkinson, 2003) incluant la mobilité, la stabilité et la taille du groupe (Freeberg et Harvey, 2008). La complexité de la communication est le produit de processus évolutifs complexes et ne peut pas être expliquée par un facteur isolé (Ord et Garcia-Porta, 2012). Ceci participe ainsi à l'émergence de signaux vocaux multifonctionnels au sein du répertoire d'une espèce. Smith (1965) attire l'attention sur le fait que toute définition de la communication est limitée si les concepts de message (état du système nerveux central de l'émetteur, tel que l'état émotionnel) et de signification, ainsi que le contexte historique/immédiat (influences combinées des entrées sensorielles, du programme génétique et des souvenirs de l'individu) et la fonction ne sont pas pris en compte. De nombreuses études montrent que les signaux communicatifs peuvent transmettre diverses informations sur l'environnement externe (nourriture, danger, voir revue par Suzuki, 2016), l'identité de l'émetteur (taille, sexe, âge, espèce, identité individuelle et statut social ou sexuel, voir revue par Fernald, 2014), ou son état émotionnel et sa motivation (par exemple Jürgens,

1979 ; Morton, 1977). Des états émotionnels particuliers peuvent ainsi être accompagnés de comportements et/ou de signaux communicatifs spécifiques, et notamment de vocalisations (Manteuffel *et al.*, 2004). Il a été suggéré chez les porcs, par exemple, que la production vocale est fortement liée à leur niveau d'excitation (Kiley, 1972, Manteuffel *et al.*, 2004). Manteuffel *et al.* (2004) a proposé plus particulièrement qu'une simple vocalisation puisse être clairement associée à un état interne distinct (ou une classe d'états internes) renseignant ainsi sur l'état émotionnel de l'émetteur. Étant relativement faciles à enregistrer, les signaux acoustiques ont ainsi déjà pu être proposés comme indicateurs potentiels de bien-être par certains auteurs (Dawkins, 1998; Manteuffel *et al.*, 2004; Schön *et al.*, 2004).

Historiquement, l'étude de la communication acoustique a surtout porté sur les oiseaux chanteurs et les primates non humains (par exemple Adret-Hausberger et Jenkins, 1988, Bouchet *et al.*, 2013, Ouattara *et al.*, 2009), car ils présentent de grands niveaux de complexité: dialectes (Adret-Hausberger, 1986), périodes sensibles d'apprentissage (Bateson, 1979), sémantique (Bouchet *et al.*, 2010), syntaxe (Lemasson, 2008), règles conversationnelles (Lemasson *et al.*, 2011). Les cétacés représentent un modèle de choix pour l'étude de la communication de par leur grande plasticité vocale présente chez différentes espèces. Aussi, comme les mammifères marins sont des animaux très sociaux, l'étude de leur communication est cruciale pour comprendre leur comportement. La complexité de leurs interactions, la nécessité de négocier et de maintenir des relations sociales dans une grande société ont stimulé le développement de l'apprentissage vocal et d'autres compétences cognitives, notamment chez les odontocètes (Janik, 2014). La transition évolutive de la terre vers l'eau du groupe qui donnera la lignée des cétacés, amorcée il y a environ 50 millions d'années, a impliqué un grand nombre de changements morpho-anatomiques pour aboutir au plan corporel moderne des cétacés (Nummela *et al.*, 2007; Thewissen et Williams, 2002). Une des modifications les plus notables est le développement d'un système acoustique complexe

pour communiquer et explorer leur environnement (Janik, 2009) en raison de leur vie exclusivement aquatique et des contraintes spécifiques associées à ce milieu telles que la faible luminosité (spécialement pour les plongeurs profonds et les espèces vivant dans des rivières turbides).

Dans cette thèse, nous nous concentrerons sur la communication acoustique des *Delphinidae*, la plus grande famille d'odontocètes, comprenant la majorité des espèces de dauphins les plus connues. Cette famille est apparue il y a environ 65 millions d'années à partir d'un ancêtre commun proche de l'ordre des Artiodactyles et regroupe aujourd'hui environ 35 espèces (Janik, 2009). Les différentes espèces de cette famille de cétacés produisent des signaux acoustiques variés et utilisés dans différents contextes comportementaux, y compris les activités d'alimentation et la cohésion de groupe (Caldwell *et al.*, 1990, Podos *et al.*, 2002, Richardson *et al.*, 1995). Les vocalisations des dauphins peuvent être divisées en trois catégories principales: les sifflements, les clics et les sons pulsés (Herzing, 2013). Les sifflements, vocalisation la plus étudiée, peuvent avoir un nombre variable d'harmoniques, mais de nombreuses études se concentrent uniquement sur la fréquence fondamentale (Janik, 2009). En 1965, Caldwell et Caldwell ont ouvert une nouvelle ligne de recherche lorsqu'ils ont proposé l'hypothèse des «sifflements signature» (revue dans Janik et Sayigh, 2013). L'idée proposée était que chaque individu était seulement capable de produire un type de sifflement stéréotypé, et tout sifflement autre qu'un sifflement signature était considéré comme «aberrant» (Miksis *et al.*, 2002). Certaines études ont d'ailleurs montré que le sifflement signature représente près de 100% de tous les sifflements produits chez les dauphins isolés artificiellement de leur groupe (voir Sayigh *et al.*, 2007). Cependant, lors de production spontanée par des groupes sauvages et captifs, ils ne représentent environ que 38 à 70% des sifflements (Buckstaff, 2004, Cook *et al.*, 2004, McCowan et Reiss, 1997, Watwood *et al.*, 2005). Concernant la perception auditive, les dauphins ont globalement une gamme d'audition

fonctionnelle entre 1 et 150 kHz avec une sensibilité maximale entre 40 et 80 kHz, chiffres variant quelque peu selon l'espèce (Janik, 2009; Richardson *et al.*, 1995; Wartzok et Ketten, 1999). Malgré la perte du mécanisme de focalisation du son fourni par le pavillon et le méat auditif des mammifères terrestres, les cétacés ont une audition jusqu'à 100 fois plus sensible que celle des humains. Or les systèmes d'écholocation et d'audition des odontocètes sont complètement adaptés pour une perception efficace de l'environnement sous-marin, et l'on peut se demander si les dauphins sont également capables de détecter les signaux acoustiques dans l'air. Alors que la plupart des études sur leur audition ont mis l'accent sur la réception des sons dans l'eau. Seules deux études ont été réalisées sur leur perception des sons aériens, démontrant une sensibilité aérienne allant de 1 à 110 kHz (Babushina, 1979, Babushina et Polyakov, 2011). Même si la question est toujours source de débat, il a été démontré que les dauphins captifs étaient capables d'imiter spontanément des stimuli auditifs aériens (Kremers *et al.*, 2011).

D'autres études sur les capacités cognitives liées à l'audition ont permis d'identifier que les dauphins peuvent discriminer de faibles différences de fréquences (Thompson et Herman, 1975), et imiter une grande variété de sons préservant le contour de fréquence. Sur la perception des sons sociaux, il a également été montré que les dauphins peuvent distinguer les signaux vocaux d'un individu apparenté ou associé de celui d'un individu non familier (Sayigh *et al.*, 1998) ; mémoriser les sifflements d'individus familiers perdus de vue pendant au moins 20 ans (Bruck, 2013), et même imiter le sifflement signature d'autres dauphins , capacité pouvant peut-être être utilisée comme un moyen d'appeler le dauphin imité (Janik, 2000, Janik *et al.*, 2006). Ces informations soutiennent l'idée que les dauphins présentent la capacité de se reconnaître les uns des autres en tant qu'individus et peuvent mémoriser l'historique de leurs relations sociales (Sayigh *et al.*, 1998).

La recherche en captivité a jusqu'ici fourni des informations importantes sur l'intelligence et la cognition des cétacés (voir par exemple Herman, 2010; Marino *et al.*, 2007; Reiss et McCowan, 1993), offrant un niveau de contrôle et de validation expérimental qui ne peut être aussi facilement réalisable dans le cadre naturel (Marino et Frohoff, 2011). La plupart des études comportementales sur les dauphins sauvages se limitent à la surface (ce qui ne représente qu'un faible pourcentage de la vie des cétacés, Janik, 2009) ou à l'enregistrement d'activités comportementales plus générales (Würsig *et al.*, 1980), en eau claire et/ou sur des populations résidentes (Dudzinski, 1996, 2010; Evans-Wilent et Dudzinski, 2013). La portée des découvertes issues d'études en captivité peut être considérée comme limitée pour diverses raisons du fait de l'isolement des individus, du faible échantillonnage et des changements comportementaux induits par la captivité, mais aussi des spécificités temporelles, des possibles comportements stéréotypés et du niveau élevé d'interactions avec les humains. La captivité permet néanmoins, précisément grâce à des conditions plus contrôlées, d'observer les dauphins dans des conditions privilégiées et de mesurer des détails souvent impossibles à obtenir sur le terrain, de tester des méthodes à appliquer à des populations sauvages (comme des TAGs acoustiques par exemple) et de faire des observations plus détaillées sur leur comportement. Dans l'ensemble, les données provenant des deux milieux (captif et sauvage) peuvent être mutuellement utiles pour la recherche sur le comportement des dauphins, étant complémentaires et permettant des comparaisons bénéfiques pour les deux (Dudzinski, 2010).

### **1.2. Modèle d'étude et objectifs**

Le grand dauphin (*Tursiops truncatus*) est l'espèce la plus connue et la plus étudiée de tous les cétacés. L'espérance de vie a été estimée par analyse dentaire à 50 ans chez les femelles et à 45 ans chez les mâles (Hohn *et al.*, 1989). Ils sont considérés comme des prédateurs de haut niveau, se nourrissant d'une grande variété de calamars et de poissons, spécialement des poissons produisant du bruit, selon l'habitat (Gannon et Waples, 2004). La plupart des études

décrivent de grandes catégories de comportements pour l'espèce, comme la recherche de nourriture, la socialisation et les déplacements. Pour de nombreuses populations, certaines activités semblent être liées à l'heure de la journée, avec une alimentation culminant le matin et en début de soirée (Allen *et al.*, 2001, Blair Irvine *et al.*, 1981, Brager 1993, Goodwin 1985, Saayman et Shane *et al.*, 1986) et des activités sociales réparties entre les périodes d'alimentation, avec des pics clairs durant l'après-midi (Brager, 1993, Miller *et al.*, 2010). Cette espèce présente des groupes sociaux très fluides (société de fission-fusion, Würsig, 1989) et certains mâles peuvent garder des liens sociaux forts pendant des années (Connor *et al.*, 2000). Bien que le grand dauphin soit l'une des espèces de cétacés les plus étudiées, de nombreuses questions restent ouvertes au sujet de leur cognition, de leur socialité et de l'utilisation de leur répertoire vocal complexe. Même si certaines recherches ont apporté des informations précieuses sur les fonctions potentielles de catégories vocales spécifiques dans le répertoire des dauphins, il reste nécessaire d'aller plus loin pour comprendre avec quels contextes comportementaux ces signaux acoustiques sont associés. Le but de cette thèse est d'explorer davantage l'utilisation et la perception des signaux acoustiques chez le grand dauphin, afin d'ajouter des informations aux connaissances actuelles sur le comportement vocal des cétacés. Nous avons également cherché à tester la perception sonore des dauphins en utilisant des « labels » individuels artificiels, tout en testant leur audition aérienne. Nous avons effectué des observations à partir de la surface du bassin principal du complexe aquatique afin de décrire les budgets comportementaux et la répartition temporelle des activités vocales et non vocales quotidiennes, ainsi que de tester les liens entre les différents comportements et l'activité vocale (Chapitre 3, Article 1). Grâce aux bonnes conditions d'observation offertes par une fenêtre sous-marine, nous avons cherché à établir précisément les associations préférentielles entre les structures acoustiques utilisées par les dauphins et les comportements des individus (Chapitre 3, Article 2). Pour le volet de la perception, basée sur le concept déjà connu de la reconnaissance d'identité des dauphins, nous avons testé leur

capacité à répondre aux signaux acoustiques artificiels qui leur sont liés, lorsqu'ils sont émis sous l'eau et, surtout, dans l'air (Chapitre 4).

## **2. METHODOLOGIE**

### **2.1. Sujets d'étude**

Toute la collecte de données a été réalisée dans le delphinarium du parc animalier Planète Sauvage (Port Saint-Père, France), de Février 2014 à Mai 2016.

Sept grands dauphins ont été observés au total durant la thèse : quatre mâles adultes (âgés de 5, 6, 12 et 16 ans au début de la collecte de données) et trois femelles adultes (âgées de 7, 14 et 26 ans au début de la collecte de données). Un des dauphins est arrivé d'un autre delphinarium au cours de la thèse avant le début de la collecte de données (Lucille, la femelle la plus âgée). Tous les sujets sont nés en captivité. Lors de la thèse, ils ont vécu en groupe social au sein d'une structure marine de quatre bassins de tailles différentes.

Les individus pouvaient être facilement identifiés grâce à des différences morphologiques générales (taille, forme de la nageoire dorsale, couleur, cicatrices durables) et localisées (principalement au niveau de la tête : taille des yeux, forme de la mâchoire ...).

### **2.2. Site d'étude et maintenance des animaux**

Les dauphins avaient, pendant la thèse, un accès libre à quatre bassins de tailles différentes et interconnectés (1: 4950 m<sup>3</sup>, 2: 1280 m<sup>3</sup>, 3: 220 m<sup>3</sup>, 4: 1040 m<sup>3</sup>). Ces dauphins sont nourris de hareng, capelan, maquereau, sprat, merlan et calmar répartis en rations plus ou moins importantes selon la taille et l'âge de l'individu. Au total, chaque dauphin recevra 4,5 à 8,5 kg de nourriture par jour. Les rations sont distribuées lors de deux repas gratuits (légers) à 9 h et 17 h, et cinq séances d'entraînement par jour (pour les spectacles et les traitements médicaux - deux le matin et trois l'après-midi), chacune d'entre elles durant de 15 à 30 minutes et espacées d'environ 1,5 heure. La nourriture des dauphins leur est également distribuée lors de



spectacles en publics. En moyenne 5 à 6 types d'enrichissement (jouets en surface, jouets au fond du bassin, enrichissements alimentaires ou jets d'eau par exemple) sont utilisés par jour afin de déclencher certains comportements comme l'augmentation de l'exploration ou le déplacement des dauphins dans le bassin.

### 2.2.1. Training des dauphins

Au cours de cinq sessions d'entraînement par jour (*training*), les soigneurs animaliers communiquent avec les dauphins par des gestes, demandant aux dauphins de réaliser une variété de comportements, par des procédures de conditionnement opérant standard basées sur le renforcement positif (principalement de la nourriture, mais aussi de la gélatine, des glaçons et des objets d'enrichissement comme les jouets). Le *training* avec des instruments de musique a été utilisé pour des tests expérimentaux sur la perception du son menés durant cette thèse (CHAPITRE 4).

### 2.3. Collecte de données

À l'exception de l'étude sur la perception des signaux acoustiques artificiels individuels, toutes les données ont été recueillies par des observations comportementales directes et des enregistrements acoustiques. Durant quatre mois (de Février à Mai 2015), les données comportementales ont été recueillies à l'aide de deux méthodes: l'échantillonnage instantané par *scan sampling*, où l'activité de chaque individu a été relevée toutes les 3 minutes (bassin N°1, principale) pour la première étude (voir chapitre 3, article 1) ; et l'échantillonnage *ad libitum*, où l'activité des individus présents lors de l'observation a été relevée en continu (bassin N°4, médicale) à travers une fenêtre subaquatique de 193x92,5 cm, pour la seconde étude (voir chapitre 3, article 2). Nos définitions des comportements ont été adaptées de celles communément utilisées dans d'autres études (Dudzinski, 1996, Kyngdon *et al.*, 2003), Lusseau, 2006, Mackey *et al.*, 2014, Sakai *et al.*, 2006, Scheer, 2010) : activités sociales (jeu, comportement socio-sexuel, comportement agonistique, interaction sociale positive ou

neutre), inactif (lorsque l'animal est immobile), jeu solitaire, mouvements du corps, *spy-hopping* et nage (voir tableau 1, CHAPITRE 3). Les vocalisations ont été enregistrées à l'aide d'un système à bande large constitué d'un hydrophone Sea-Phone SS03-10 (-194 dB, re 1V /  $\mu\text{Pa}$ , 0,020 à 50 kHz) au début de la collecte de données du second article et d'un C54XRS (-185 dB, re 1V /  $\mu\text{Pa}$ , 0,06 à 203 kHz) dans toutes les collectes de données du premier article et une partie de la collecte de données du second article. Les hydrophones étaient tous deux connectés à un enregistreur DR-680 de TASCAM (fréquence d'échantillonnage 192 kHz, 24 bits). En avril et mai 2016, nous avons testé dans le bassin N°1 (principal) les réponses des dauphins au signal sonore auquel ils ont été associés lors d'entraînement préalable lors d'une émission sous l'eau puis dans l'air.

#### 2.4. Analyse des données

Nous avons effectué des analyses statistiques (tests non paramétriques) avec les logiciels R 3.4.1. (R Core Team, 2014) et Statistica (TIBCO Software). Les données comportementales non vocales ont été analysées au niveau individuel, tandis que pour les analyses acoustiques, l'identité du dauphin vocalisant n'étant pas disponible, les données n'ont été analysées qu'au niveau du groupe. Les vocalisations ont été classées par des inspections audiovisuelles de spectrogrammes (FFT 1024 au taux d'échantillonnage de 192 kHz) générés par Raven Pro 1.4 (Cornell Bioacoustics Research Program) et la fréquence des quatre catégories vocales les plus courantes des dauphins (Gridley *et al.*, 2015) a été mesurée: sons pulsés, sifflements, *chirps* et clics.

### 3. CONTEXTES D'ÉMISSIONS VOCALES: DISTRIBUTION TEMPORELLE AU COURS DE LA JOURNÉE ET ASSOCIATIONS ENTRE COMPORTEMENTS ET VOCALISATIONS

#### 3.1. *Résumé de l'article 1 : « Les activités vocales reflètent la distribution temporelle de l'activité (sociale et non sociale) des grands dauphins dans un parc zoologique »*

**Questions:** Les budgets temps des grands dauphins varient légèrement d'une population à l'autre. Néanmoins, un grand nombre d'études rapporte des pics d'alimentation tôt le matin et en fin d'après-midi. Lorsqu'ils ne s'alimentent pas, les dauphins socialisent et les activités vocales semblent liées à ces moments. En captivité, la distribution temporelle des périodes de socialisation et le lien possible avec la distribution temporelle des vocalisations n'ont jamais été étudiés. Notre première étude visait à décrire les budgets diurnes des dauphins dans les conditions d'un parc zoologique et les vocalisations associés.

**Méthodes:** Nous avons cherché des différences de comportements et de vocalisations du groupe entre le matin et l'après-midi, à travers des sessions d'observations en surface réalisées tout au long de la journée. Lors des sessions d'observation, le comportement de chaque individu est relevé toutes les trois minutes dans le bassin principal. Nous avons ensuite examiné les associations entre le nombre de comportements et le nombre de vocalisations à l'échelle de la session d'observation (fenêtres de 3 minutes).

**Résultats:** Nous avons constaté que les dauphins s'engageaient davantage dans les activités sociales pendant la matinée, tandis que la seule catégorie vocale affichant un schéma temporel (*chirps*) était plus émise l'après-midi. Cependant, le résultat le plus remarquable est que nous avons trouvé de fortes corrélations entre certaines activités et certaines catégories vocales.

**Conclusions:** Le profil des activités sociales trouvées dans ce parc zoologique diffère de ce qui a été décrit dans la nature et l'activité vocale enregistrée peut donner une représentation des activités non vocales. Ces observations devraient être prises en compte dans la gestion et l'organisation des activités liées aux dauphins sous les soins humains en captivité.

Cet article a été publié dans le journal *Zoo Biology* en Octobre 2017 et une partie des résultats a été présentée lors de la 46<sup>ème</sup> conférence de l'Association française pour l'étude du comportement animal (SFECA, 2016).

**3.2. Résumé de l'article 2 : « Les contextes d'émission des vocalisations chez un groupe de grands dauphins captifs »**

**Questions:** La communication des dauphins est connue pour être assez complexe lorsqu'on se concentre sur les structures acoustiques, mais l'utilisation contextuelle des différents signaux est encore peu connue. Les sons produits par les dauphins sont généralement divisés en sons pulsés, en séries de clics et en sifflements. Ici, nous avons examiné avec une échelle plus fine que dans l'étude précédente les associations possibles entre les catégories vocales et les contextes comportementaux se produisant simultanément.

**Méthodes:** Des enregistrements acoustiques ont été réalisés en même temps que les observations comportementales de tous les individus, à travers une fenêtre sous-marine. Les vocalisations ont été classées en sifflements, en séries de clics et en sons pulsés. Ces derniers ont été subdivisés en deux types en fonction de leur durée.

**Résultats:** Nous avons trouvé des associations préférentielles entre les catégories vocales et les contextes comportementaux, en clarifiant leur utilisation contextuelle. Nous avons également montré l'importance de considérer les types de sons pulsés comme des vocalisations fonctionnellement différentes. Nous avons également identifié un large éventail d'associations dépendantes du contexte entre les catégories vocales. Certaines d'entre elles ont confirmé des relations trouvées auparavant dans la littérature, mais d'autres ont permis de soulever de nouvelles hypothèses sur l'utilisation fonctionnelle des vocalisations et des associations entre vocalisations.

**Conclusions:** Nous confirmons l'utilisation contextuelle des vocalisations de dauphins et notamment des associations entre différentes catégories vocales. Plus d'études devraient explorer l'utilisation fonctionnelle de ces associations et essayer d'identifier les émetteurs pour aller plus loin dans la spécificité contextuelle de la production vocale chez les dauphins.

#### 4. "UMWELT" AUDITIF: CONCEPT D'IDENTITÉ ET PERCEPTION SONORE AÉRIENNE

##### 4.1. Résumé de l'article 3: "Les grands dauphins captifs discriminent les sons artificiels joués par l'homme sous l'eau et dans l'air"

**Questions:** Les grands dauphins (*Tursiops truncatus*) sont capables d'utiliser des structures acoustiques individuelles pour signaler leur identité au groupe. Les soigneurs des delphinariums utilisent ces capacités pour adresser les dauphins captifs individuellement via des signaux gestuels appris. De plus, leur système auditif étant très adapté pour fonctionner sous l'eau, il y a toujours un débat sur les capacités des dauphins à entendre des sons aériens. Ici, nous avons posé les questions suivantes: 1) si les dauphins sont capables d'apprendre des signaux sonores joués par l'homme sous l'eau; et 2) si oui, pourraient-ils généraliser cet apprentissage aux mêmes sons transmis par voie aérienne ?

**Méthodes:** Les dauphins ont été entraînés pour répondre aux sons individuels joués sous l'eau, mais l'efficacité de l'entraînement n'avait jamais été testée dans un contexte contrôlé. Nous avons alors étudié la réponse des dauphins de Planète Sauvage aux sons individuels préalablement appris, produits par les instruments de musique. Le même soigneur a d'abord joué les instruments sous l'eau, puis la même expérience a été répétée avec des instruments joués dans l'air. Tous les dauphins ont été testés en même temps avec un instrument aléatoire à chaque fois.

**Résultats:** Tous les dauphins, sauf un, se sont déplacés lors de l'émission de leur signal sonore lorsque les instruments ont été joués sous l'eau et ne se sont pas déplacés lorsque le signal était celui d'un autre individu. Quand l'expérience a été faite dans l'air, les dauphins ne

se sont pas déplacés, mais ils ont regardé de plus en plus la source sonore lorsque leur propre instrument a été joué.

**Conclusions:** Les grands dauphins sont capables de répondre à des signaux sonores individuels joués par l'homme, même lorsque les sons sont transmis dans l'air. D'autres études pourraient tester si les dauphins peuvent associer ces indices sonores avec des identités individuelles.

## 5. DISCUSSION

### 5.1. CE QUE CES CONSTATATIONS NOUS DISENT AU SUJET DU COMPORTEMENT DES DAUPHINS

La communication acoustique facilite le partage de l'information entre les membres d'un groupe et dépend généralement du contexte (Smith, 1965). Durant cette thèse nous avons étudié l'utilisation et la perception des signaux acoustiques chez le grand dauphin, contribuant ainsi à la compréhension des contextes et des fonctions possibles des vocalisations des dauphins, ainsi que de leur perception sonore. Ce travail apporte de nouvelles connaissances permettant de comprendre leur cognition et leur flexibilité comportementale.

#### 5.1.1. Production et utilisation du son

Nous avons décrit le budget-temps et la vie sociale de 7 dauphins captifs en relation avec les particularités de leur maintien en parc zoologique, et le répertoire vocal du groupe. Nous avons recherché des associations entre les différentes structures acoustiques de leur répertoire et les contextes d'émission, en créant des hypothèses pour les différents types de signaux identifiés. Ici, même si nous avons trouvé des variations de comportement avec plus d'activités sociales le matin que l'après-midi, seules les vocalisations de type *chirps* présentent un schéma temporel, étant plus enregistrées l'après-midi (quand il y avait moins d'activités sociales, article 1). En étudiant plus précisément l'utilisation contextuelle et fonctionnelle des vocalisations, nous avons trouvé de nombreuses associations pouvant aider à comprendre la communication acoustique des dauphins. Les sifflements n'ont pas présenté de pattern temporel quotidien et ont été enregistrés dans des contextes variés, principalement lors d'interactions sociales, mais pas toujours lors de comportement affiliatifs, contrairement à ce qui a souvent été décrit (Janik et Sayigh, 2013, Mello et Amundin, 2005). L'émission de sons pulsés a été observée principalement dans des contextes sociaux, mais divers, sans un pattern



temporel quotidien confirmant que cette catégorie vocale est associée aux interactions sociales. Cependant ils n'étaient pas exclusivement associés à des contextes agonistiques, comme cela a souvent été suggéré (Lopez et Shirai, 2009; Overstrom, 1983). Il est intéressant de noter, en outre, une forte corrélation de cette catégorie de vocalisation avec les comportements de jeu dans les deux études. Les séries de clics ont été décrites principalement comme utilisées dans les tâches liées au sonar (dos Santos et Almada, 2004). Nos résultats suggèrent que cette catégorie vocale serait très flexible et associée à divers contextes sociaux et non sociaux. Concernant les contextes liés aux émissions des *chirps*, nos résultats soulignent l'intérêt de les traiter comme une catégorie indépendante, à part des sifflements, et les futures recherches devraient se concentrer sur la compréhension de leurs fonctions.

Les résultats de cette thèse portent sur l'association entre des signaux vocaux spécifiques et les contextes comportementaux dans lesquels les dauphins ont émis leurs vocalisations. Cependant, les signaux vocaux fournissent à la fois des indices sur l'activité au moment des émissions, mais aussi sur les motivations potentielles et les états internes des individus interagissant (Smith, 1965). Il existe un consensus croissant sur le fait que le bien-être est associé à la présence d'états émotionnels positifs qui ont été proposés par certains auteurs comme étant aussi importants pour le bien-être des animaux que l'absence d'émotions négatives (Moiss *et al.*, 2009). Ce type d'information pourrait être utile aux soigneurs pour mieux comprendre le fonctionnement social du groupe de dauphins avec lequel ils travaillent. Lilly (1963) a montré qu'un type particulier de sifflement est associé à la détresse physique, et Esch *et al.* (2009) ont proposé que les sifflements puissent servir d'indicateurs de stress, le sifflement signature apparaissant comme étant directement lié aux conditions perturbées. Un tel suivi acoustique peut donner des indices sur «l'ambiance du groupe», par exemple, donner des informations précieuses aux soigneurs dans un contexte captif et améliorer l'efficacité des chercheurs en essayant de catégoriser le comportement des dauphins par des observations de

surface. Nos résultats sur l'utilisation des sons pulsés pendant le jeu ont soulevé des hypothèses sur cette catégorie vocale étant un indicateur d'excitation ou d'émotion.

Nous avons également exploré un sujet souvent négligé dans les études sur la communication des dauphins dans notre deuxième étude: les associations de plusieurs catégories vocales (vocalisations mixtes). Nos résultats ont montré des changements de contextes comportementaux associés aux différents types de vocalisations mixtes. Nos données ne nous ont pas permis de savoir si ces vocalisations mixtes ont été émises par le même individu ou par des individus différents, car les dauphins peuvent produire des sons tonals et pulsés simultanément (Perrin *et al.*, 2008). Quoi qu'il en soit, les résultats présentés ici sont encourageants pour approfondir l'étude du rôle des vocalisations mixtes chez les dauphins. En fin de compte, cette étude contribue à une meilleure connaissance du répertoire vocal d'une espèce de cétacés et encourage un débat plus large sur les fonctions de la communication vocale des grands dauphins.

### 5.1.2. Perception du son

Un autre objectif de cette thèse était d'étudier de manière expérimentale l'étendue des capacités de perception des signaux sonores chez les dauphins. Les résultats détaillés au chapitre 4 mettent en évidence pour la première fois la capacité des grands dauphins à reconnaître un « label » sonore individuelle joué par l'homme sous l'eau et même lorsqu'il est transposé dans l'environnement aérien. Cette capacité de généralisation confirme les capacités, parfois controversées, d'audition aérienne des dauphins.

L'audition des cétacés est extrêmement adaptée à l'environnement aquatique, mais certains auteurs ont montré que les dauphins sont capables de percevoir des stimuli acoustiques diffusés dans l'air (Babushina, 1979, Kastelein *et al.*, 1997, Liebschner *et al.*, 2005). Ils produisent aussi parfois des vocalisations aériennes spontanées (observation personnelle) pendant l'entraînement. Ainsi, il y a encore lieu de douter que les cétacés aient réellement

perdu toute capacité de perception auditive aérienne. Par exemple, en se focalisant sur d'autres modalités sensorielles que l'on croyait perdues, il existe aujourd'hui des preuves montrant des capacités de chemoréception, y compris l'olfaction et la gustation chez les dauphins (Kremers *et al.*, 2016, Ridgway, 1988), malgré l'idée que les odeurs transportées par l'air seraient non pertinentes pour un mode de vie aquatique (Thewissen *et al.*, 2011). Lorsque l'on considère l'audition, il convient de rappeler que l'oreille des mammifères a évolué pour entendre les signaux sonores émis dans l'air. Lorsque les ancêtres quadrupèdes terrestres des cétacés sont entrés dans le milieu aquatique, ils ont modifié ce système aérien, ce qui a amélioré la sensibilité auditive des hautes fréquences et a induit l'apparition d'un traitement auditif complexe (Ridgway, 1988). Les études sur l'audition aérienne des dauphins sont rares, mais une comparaison des audiogrammes aériens et sous-marins d'un grand dauphin a montré que la sensibilité des oreilles du dauphin aux sons de l'air se détériore de 30-60 dB (selon la fréquence, Babushina et Polyakov, 2011). Nos résultats permettent de confirmer la capacité des dauphins à entendre les sons transmis dans le milieu aérien en fonction de leurs réponses comportementales à des sons connus émis en dehors de l'eau.

### 5.1.3. Capacités cognitives

Plusieurs études montrent que les dauphins sont capables d'imiter des comportements (Herman, 2002; Mercado *et al.*, 1998) et ont une capacité cognitive de haut niveau, ce qui présuppose une représentation mentale des autres et d'eux-mêmes. Nos résultats du chapitre 4 ont montré la capacité des dauphins à associer des « labels » sonores émis par l'homme à des identités individuelles («noms»), mettant en évidence une fois de plus leur capacité à apprendre par le conditionnement opérant ainsi que leur capacité à discriminer les sons. Le fait de tester la réponse des dauphins en groupe et leurs capacités à répondre correctement à leurs propres « labels » constituent une preuve supplémentaire qu'ils ont un certain concept de leur propre identité ; résultat concordant avec l'utilisation de signaux acoustiques spécifiques (sifflements signature, Sayigh *et al.*, 1998) pour transmettre leur identité individuelle, sur la base de différents modèles de modulation de fréquence (voir Janik et Sayigh, 2013).

#### 5.1.4. Flexibilité comportementale et vie en captivité

Les cétacés sont maintenus en captivité depuis le début des années 1860 (Defran et Pryor, 1980), et le grand dauphin est l'une des espèces qui s'adaptent le mieux à la captivité. Des études comparatives d'associations individuelles, de comportements spécifiques et de groupes sociaux observés à la fois chez les dauphins captifs et en liberté offrent une meilleure compréhension de la relation entre leurs activités et ces deux environnements (Dudzinski, 2010).

Certaines caractéristiques de la nature, comme les prédateurs, les pénuries alimentaires et d'autres problèmes environnementaux sont souvent absentes dans les environnements captifs, et les animaux captifs ont souvent de l'énergie et du temps en abondance (Held et Spinka, 2011). Les différences entre la captivité et la vie sauvage comprennent également des modifications du rythme d'alimentation (ponctuelles *versus* plus continues), de la disponibilité alimentaire (prévisibilité *versus* imprévisibilité) et de la période d'abondance de nourriture (l'après-midi en captivité *versus* pics d'alimentation en début et fin de journée). D'autres caractéristiques naturelles peuvent être absentes en captivité et, en réponse, les mammifères captifs adaptent leur comportement pour faire face à leur environnement, ce qui peut entraîner des différences entre les populations sauvages et captives (McPhee et Carlstead, 1996).

Ici, nous avons d'abord cherché une meilleure compréhension des budgets temporels des animaux étudiés. Les grands dauphins maintenus pour être exposés au public sont un modèle d'étude intéressant, car les schémas comportementaux sont influencés par de nombreuses périodes contrôlées par l'homme au cours d'une journée. En ce qui concerne les schémas temporels des comportements, nous avons constaté que dans ce groupe, logé dans un parc zoologique, les activités sociales se produisent surtout le matin. Ce schéma n'est pas similaire à celui des populations sauvages, où la socialisation se produit à de faibles niveaux le matin et

augmente en début d'après-midi. Nous émettons l'hypothèse que ces différences sont liées aux différences dans les routines d'alimentation entre les deux conditions. L'alimentation est d'une grande importance pour les budgets comportementaux des grands dauphins (Beddia, 2007) et des études sur de nombreux taxons animaux montrent que la distribution des comportements non alimentaires est fortement influencée par les périodes d'alimentation. L'alimentation des dauphins captifs diffère de l'alimentation de la plupart des autres animaux maintenus en captivité, car elle s'accompagne d'interactions avec les humains (réalisation de comportements connus ou apprentissage de nouveaux). Certaines de ces interactions incluent la présence de personnes moins familières telles que les vétérinaires lors d'un examen, ou la présence du public, pendant les spectacles. D'autres études apportent des preuves sur la façon dont les moments de nourrissage peuvent être considérés comme des moments clés de leur journée. Une étude récente (Clegg *et al.*, 2017), a montré que ces animaux présentent un comportement d'anticipation avant les séances d'entraînement, corroborant l'idée qu'ils auraient une capacité d'anticipation de l'arrivée des moments clés.

En ce qui concerne le répertoire vocal, cependant, nous n'avons pas trouvé de différences notables entre nos données et ce que l'on connaît dans les populations sauvages (Díaz López, 2011, Gridley *et al.*, 2015, Lopez et Shirai, 2009) observées. Les contextes d'alimentation active n'étant pas présents en captivité, nous n'avons donc pas pu rechercher les relations entre les catégories vocales et cette activité (comme l'ont fait Acevedo-Gutiérrez et Stienessen, 2004; dos Santos *et al.*, 2005). Nous avons pu observer des comportements effectués au cours des émissions vocales à une échelle plus fine que ce qui est généralement réalisable sur le terrain, contribuant ainsi avec plus de détails aux descriptions fournies par les études sur les populations sauvages (Papale *et al.*, 2016).

## 5.2. PERSPECTIVES DE RECHERCHE

Pour étudier la communication entre les dauphins et aller plus loin dans la compréhension de la production et de l'utilisation du son, il est important de déterminer quel dauphin produit un son pour étudier plus précisément les associations entre vocalisation et contextes comportementaux. Il existe donc un réel besoin de nouveaux outils pour explorer les ces associations au niveau individuel. Au cours de cette thèse, un effort de développement a été fait dans le but de créer un système d'enregistrement acoustique individuel des dauphins captifs, en utilisant un dispositif fixé par ventouses. L'objectif était d'étudier les signaux acoustiques des dauphins au niveau individuel, en décrivant des répertoires et en les reliant à des contextes comportementaux spécifiques. À ce jour, nous avons pu collecter des données, mais elles sont encore en analyse.

Nos résultats sur l'utilisation contextuelle des vocalisations peuvent donner des idées pour aller plus loin dans la compréhension des fonctions des différentes catégories vocales. Les données sur les sons pulsés et l'utilisation des *chirps* ont révélé un large éventail de contextes pour ces catégories vocales et ont soulevé des hypothèses sur leurs fonctions. Des expériences pourraient associer par exemple des enregistrements vidéo de différents contextes comportementaux et des enregistrements de dauphins contenant différentes catégories vocales pour tester les réactions des dauphins face à ces appariements comportement-vocalisation. Pour aller plus loin dans l'étude des vocalisations en tant qu'indicateurs possibles des émotions, il devrait être essentiel d'associer les indices physiologiques aux structures acoustiques et aux taux vocaux sous différents niveaux de stress (comme proposé par Esch *et al.*, 2009 pour les sifflements).

Nos résultats sur les associations entre les catégories vocales ne sont que préliminaires. Pour mieux comprendre si ces associations constituent des évidences conversationnelles ou des émissions simultanées de vocalisations par un même individu, ainsi que leur rôle dans la

communication vocale des dauphins, il serait d'abord important d'identifier les individus vocalisant pour s'assurer que les associations enregistrées sont produites par un ou plusieurs individus.

En ce qui concerne la perception, de nombreux autres paradigmes pourraient être testés, comme le paradigme de la violation des attentes fondé notamment sur une approche intermodale (par exemple la lecture de vocalisations émises par un individu A associé à la vision d'un même individu ou d'un individu B) (Proops *et al.*, 2009). Cela nous permettrait de tester la capacité de décoder des informations sur l'identité individuelle ou le sexe de l'émetteur.

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## **ABSTRACT**

Studies on animal bioacoustics, traditionally relying on non-human primate and songbird models, converge towards the idea that social life appears as the main driving force behind the evolution of complex communication. Comparisons with cetaceans are also particularly interesting from an evolutionary point of view. They are indeed mammals forming complex social bonds, with abilities in acoustic plasticity, but that had to adapt to marine life, making habitat another determining selection force. Their natural habitat constrains sound production, usage and perception but, in the same way, constrains ethological observations making studies of captive cetaceans an important source of knowledge on these animals. Beyond the analysis of acoustic structures, the study of the social contexts in which the different vocalizations are used is essential to the understanding of vocal communication. Compared to primates and birds, the social function of dolphins' acoustic signals remains largely misunderstood. Moreover, the way cetaceans' vocal apparatus and auditory system adapted morphoanatomically to an underwater life is unique in the animal kingdom. But their ability to perceive sounds produced in the air remains controversial due to the lack of experimental demonstrations. The objectives of this thesis were, on the one hand, to explore the spontaneous contextual usage of acoustic signals in a captive group of bottlenose dolphins and, on the other hand, to test experimentally underwater and aerial abilities in auditory perception. All data collection was done from February 2015 to May 2016. Our first observational study describes the daily life of seven dolphins housed in a French facility, and shows that vocal signalling reflects, at a large scale, the temporal distribution of social and non-social activities in a facility under human control. Our second observational study focuses on the immediate context of emission of the three main acoustic categories previously identified in the dolphins' vocal repertoire, i.e. whistles, burst-pulses and click trains. We found preferential associations between each vocal category and specific types of social interactions and identified context-dependent patterns of sound combinations. Our third study experimentally tested, under standardized conditions, the response of dolphins to human-made individual sound labels broadcast under and above water. We found that dolphins were able to recognize and to react only to their own label, even when broadcast in the air. Apart from confirming aerial hearing, these findings go in line with studies supporting that dolphins possess a concept of identity. Overall, the results obtained during this thesis suggest that some social signals in the dolphin repertoire can be used to communicate specific information about the behavioural contexts of the individuals involved and that individuals are able to generalize their concept of identity for human-generated signals.

## **RESUME**

Les études de bioacoustique animale, qui reposent traditionnellement sur des modèles primates non humains et oiseaux chanteurs, convergent vers l'idée que la vie sociale serait la principale force motrice de l'évolution de la complexité de la communication. La comparaison avec les cétacés est également particulièrement intéressante d'un point de vue évolutif. Ce sont des mammifères qui forment des liens sociaux complexes, ont des capacités de plasticité acoustique, mais qui ont dû s'adapter à la vie marine, faisant de l'habitat une autre force de sélection déterminante. Leur habitat naturel impose des contraintes sur la production sonore, l'utilisation et la perception des signaux acoustiques, mais, de la même manière, limite les observations éthologiques. Étudier les cétacés captifs devient alors une source importante de connaissances sur ces animaux. Au-delà de l'analyse des structures acoustiques, l'étude des contextes sociaux dans lesquels les différentes vocalisations sont utilisées est essentielle à la compréhension de la communication vocale. Par rapport aux primates et aux oiseaux, la fonction sociale des signaux acoustiques des dauphins reste largement méconnue. En outre, les adaptations morpho-anatomiques de l'appareil vocal et auditif des cétacés à une vie sous-marine sont uniques dans le règne animal. Leur capacité à percevoir les sons produits dans l'air reste controversée en raison du manque de démonstrations expérimentales. Les objectifs de cette thèse étaient, d'une part, d'explorer l'utilisation contextuelle spontanée des signaux acoustiques dans un groupe captif de dauphins et, d'autre part, de tester expérimentalement les capacités à percevoir les sons sous l'eau comme dans l'air. Toutes les données ont été collectées entre Février 2015 et Mai 2016. Notre première étude observationnelle décrit la vie quotidienne de sept dauphins dans un delphinarium français et montre que les signaux vocaux reflètent, à grande échelle, la répartition temporelle des activités sociales et non sociales dans un établissement sous contrôle humain. Notre deuxième étude met l'accent sur le contexte d'émission des trois principales catégories acoustiques précédemment identifiées dans le répertoire vocal des dauphins, à savoir les sifflements, les sons pulsés et les séries de clics. Nous avons trouvé des associations préférentielles entre chaque catégorie vocale et certains types d'interactions sociales ainsi que des combinaisons sonores non aléatoires et également dépendantes du contexte. Notre troisième étude a testé expérimentalement, dans des conditions standardisées, la réponse des dauphins à des « labels » acoustiques individuels donnés par l'homme et diffusés dans l'eau et dans l'air. Nous avons constaté que les dauphins peuvent reconnaître et réagir uniquement à leur propre « label » sonore, même lorsqu'il est diffusé dans l'air. En plus de confirmer l'audition aérienne, ces résultats soutiennent l'idée que les dauphins possèdent une notion d'identité. Dans l'ensemble, les résultats obtenus au cours de cette thèse suggèrent que certains signaux sociaux dans le répertoire des dauphins peuvent être utilisés pour communiquer des informations spécifiques sur les contextes comportementaux des individus impliqués et que les individus sont capables de généraliser leur concept d'identité à des signaux générés par l'homme.