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1 **Study of repertoire use reveals unexpected context-dependent vocalizations in bottlenose dolphins**

2 (*Tursiops truncatus*)

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15 **Statements and Declarations**

16 **Competing interests:** Authors declare no competing interests

17

18 **Authors contributions:** ADML, AL, MB and MH contributed to the study conception and design. ADML
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20 drafted the manuscript, all authors contributed to the final version of the manuscript.

21

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24 Université de Rennes.

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Availability of data and material: Raw data supporting the conclusion of this study will be made available by the authors without undue reservation.

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4 **Abstract**
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38 Dolphins are known for their complex vocal communication, not least because of their capacity for
39 acoustic plasticity. Paradoxically, we know little about their capacity for flexible vocal use. The difficulty
40 in describing the behaviours performed underwater while vocalizing makes it difficult to analyse the
41 contexts of emissions. Dolphins' main vocal categories are typically considered to be used for scanning the
42 environment (Clicks), agonistic encounters (Burst Pulses) and socio-affiliative interactions (Whistles).
43 Dolphins can also combine these categories in mixed vocal emissions, whose use remains unclear. To better
44 understand how vocalizations are used, we simultaneously recorded vocal production and the associated
45 behaviours by conducting underwater observations (N=427 events) on a group of 7 bottlenose dolphins
46 under human care. Our results showed a non-random association between vocal categories and behavioural
47 contexts. Precisely, clicks were preferentially emitted during affiliative interactions and not during other
48 social/solitary contexts, supporting a possible complementary communicative function. Burst pulses were
49 associated to high arousal contexts (agonistic and social play), pinpointing on their use as an "emotionally
50 charged" signal. Whistles were related to solitary swimming and not preferentially produced in any social
51 context. This questions whistles' functions and supports their potential role as a distant contact call. Finally,
52 mixed vocalizations were especially found associated with sexual (Burst pulse-Whistle-Click), solitary play
53 (Burst Pulse-Whistle) and affiliative (Click-Whistle) behaviours. Depending on the case, their emission
54 seems to confirm, modify or refine the functions of their simple counterparts. These results open up new
55 avenues of research into the contextual use of dolphin acoustic signals.

56
57 **Keywords:** Bioacoustics; cetacean; social behaviour; communicative signals, repertoire use
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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 given signal can hence be inferred from the contextual regularities found to be associated with it (Tyack 1981; Manser 2010). Most studies on the contextual use of vocalizations have been done on birds and terrestrial mammals (e.g. Adret-Hausberger 1982; Faragó et al. 2010; Briseño-Jaramillo et al. 2017). 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 conspecific 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), or alerting about a danger in the environment (e.g. Ouattara et al. 2009). Other calls or songs of the repertoire are emitted in a broader 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; Balsby and Bradbury 2009; Thomsen et al. 2019). The latter signals are particularly crucial for animals living in habitats with a limited visibility, like forested areas (Candiotti et al. 2012).

Cetaceans have attracted a lot of research 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). 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 some dolphin species produce individually distinctive calls, named signature whistles (Janik and Sayigh 2013). Also, vocal learning is widespread among cetacean species (Tyack and Sayigh 1997, Janik 2014).

The contextual analyses of vocal emissions have however 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, Nowacek et al. 2016). Lammers and

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85 Oswald (2015) consider that “the primary area that must be improved is our ability to reliably match
86 behavioural and acoustic observations”.

87 Indeed, despite recent efforts in different odontocete species (most of them social delphinids),
88 reporting possible associations between specific signals and behaviours (e.g. dos Santos et al. 1995; Herzing
89 1996, 2015; Janik 2000; Evans-Wilent and Dudzinski 2013; Samarra 2015; Heiler et al, 2016; Perazio and
90 Kuczaj II 2017; Rachinas-Lopes et al. 2017), there are still numerous questions remaining about the
91 association between vocal and behavioural categories. Specifically, the difficulty to associate acoustic
92 signals to their emitter and record the behaviour performed while vocalizing underwater limits the
93 knowledge on how different vocalizations are contextually used (Tyack 2000; Thomas et al. 2002). Also,
94 correlations between broad activities and vocal emissions are made, but there are differences within
95 behavioural categories that are not always identified in surface observations (e.g. “socializing” involves
96 affiliative as well as agonistic behaviours and even sometimes sexual behaviours) (Díaz Lopez and Shirai
97 2009; Hawkins and Gartside 2010; Gridley et al. 2015; Papale et al.,2016). Other studies use large temporal
98 windows of analysis (not identifying specific concurrent behaviours, e.g. Herzing 2000; Lima et al. 2017)
99 and focal group sampling, noting what the majority of the group is doing at the time of the vocal event, thus
100 not identifying the synchronised behaviour (e.g. Grindley et al. 2015, Papale et al. 2016).

101 One of the most studied cetacean species is the bottlenose dolphin (*Tursiops truncatus*), a species
102 that lives in fluid fission-fusion societies (Connor et al. 2000). There is a general agreement that bottlenose
103 dolphins’ sounds are typically divided into two main structural types (tonal sounds: mainly whistles; pulsed
104 sounds: mainly burst-pulses and click trains) and two functional categories (communication and exploratory
105 echolocation) (Lilly 1962; Caldwell and Caldwell 1967; Herzing 2000; Boisseau 2005; Jones et al. 2020).
106 The vocal repertoire of bottlenose dolphins has not been completely described though (Boisseau 2005) and
107 additional sounds have also been described that seem to be limited to particular contexts (e.g. multi-unit
108 signals, like the bray series, observed when wild dolphins are in foraging grounds) (dos Santos et al. 1995;
109 Luís et al. 2019).

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4 110 The main three sound emissions can be described as follows (1) whistles are defined as narrow-
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6 111 band tonal sounds (Caldwell and Caldwell 1965; Acevedo-Gutiérrez and Stienessen 2004) used for social
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8 112 interactions, (2) burst pulses as wide-band sounds (Herzing 2000; Díaz Lopez and Shirai 2009) whose
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10 113 function remains unclear, and (3) click trains as signals formed by a series of short broadband clicks
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12 114 (Herzing and dos Santos 2004) used to scan the environment.

15 115 The first category of sounds (whistles) is historically the most studied dolphin vocalization, perhaps
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17 116 because of their ease in measurement especially in the field, in particular in terms of signal to noise ratio
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19 117 (Boisseau 2005; Díaz López 2011; Herzing 2013). However, maybe precisely because whistles have been
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21 118 largely studied, there have been large controversies about their significance and use. Thus, whereas they
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23 119 have been documented frequently in social, more often non-agonistic, broad contexts (e.g. Quick and Janik
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25 120 2008; Hernandez et al. 2010) and are believed to function in maintaining contact and advertising social
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27 121 bonds (Herman and Tavalga 1980; Tyack 1986; Gridley et al. 2015), other studies on the contrary suggest
28
29 122 that whistles would rather be associated with feeding activity per se (Acevedo-Gutiérrez and Stienessen
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31 123 2004; dos Santos et al. 2005) or may be indicative of high arousal (dos Santos et al. 2005), stress (e.g.
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33 124 capture, isolation) (Esch et al. 2009) or excitement, such as during food anticipation, presence of trainers or
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35 125 of swim-with-dolphin tour operations (Moore and Ridgway 1996; Scarpaci et al. 2000; Sekiguchi and
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37 126 Koshima 2003; Therrien et al. 2012; Probert et al. 2021). Moreover, some studies found a positive
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39 127 correlation between whistle rates and group sizes (Cook et al. 2004), whereas others found either a negative
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41 128 correlation between whistles' rates and group size or no correlation at all (dos Santos et al. 2005; Quick and
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43 129 Janik 2008). Finally, peaks of intense whistle activity could function as pre-sleep choruses (Kremers et al.
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45 130 2014). Therefore, despite intensive studies, more information is still needed on the significance of whistles.
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51 131 The second category of sounds (clicks) was mainly studied for its echolocation function and studies
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53 132 on behavioural context of vocalizations do not always record clicks (e.g. Díaz Lopez and Shirai 2009; Papale
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55 133 et al. 2016). Whereas dolphins do use clicks for detection, scanning, and discrimination of objects (Au 2004;
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57 134 Dubrovsky 2004), studies suggest that it is not the only function for these sounds, and that they are likely to
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59 135 be used in communication as well (Lang and Smith 1965; Watkins 1980; Dawson 1991; Connor and
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Smolker 1996; Herzing 1996; Ryabov 2016). As a matter of fact, click trains have been recorded during affiliative pectoral fin contacts (Evans-Wilent and Dudzinski 2013) and were recorded in 20% of the socializing bouts recorded by Martin et al. (2019). The presence of click trains has also been recorded during courtship, aggressive and play contexts (Herzing and dos Santos 2004). In sperm whales (*Physeter macrocephalus*) and odontocetes (e.g. harbor porpoises *Phocoena phocoena*), species that do not whistle, clicks occur in a social context (Watkins 1985; Weilgart and Whitehead 1988; Nakamura et al. 1998; Clausen et al. 2010). As a whole, assumptions on a potential communicative role, along with click trains documented in some social contexts, might lead in the direction of a proper communicative function.

The third category of sounds (burst pulses) has received comparatively much less attention, despite the fact that they constitute the majority of conspecific vocalizations (Herzing 2000), maybe because of its low amplitude levels (Boisseau 2005). There is growing evidence that they play a major role in communication (e.g. Lammers et al. 2003, Rankin et al. 2007). Burst pulse signals are graded with no clear separation of distinct types (Martin et al. 2019) which may explain that there is no standardized nomenclature of types of burst pulses in the existing literature (Herman and Tavorlga, 1980; Overstrom 1983; Lopez and Shirai 2009; Gridley et al. 2015; Jones et al. 2020). Burst pulses have been recorded during competitive contexts such as agonistic/sexual or play fighting (Connor and Smolker 1996; Blomqvist and Amudin 2004; Blomqvist et al. 2005; Díaz Lopez and Shirai 2009; Perazio and Kuczaj II 2017; Herzing 2015) but also socializing overall (Lima et al. 2017; Martin et al. 2019). Authors suggest that burst pulses are directional, short-range and socially (e.g. Gridley et al. 2015; Lammers and Oswald 2015) or non-socially (e.g. introduction of novel objects, Lilly and Miller 1961; Caldwell and Caldwell 1967; Ralston and Herman 1989; Perazio and Kuczaj II 2017) “emotively charged” signals. There are also some dolphin species that mostly relies upon burst pules for communication, such as the beluga (*Delphinapterus leucas*) with an acoustic repertoire composed of 80 % of pulsed calls (Sjare and Smith 1986) or the northern right whale dolphin which uses repeated and stereotyped burst pulses (*Lissodelphis borealis*; Rankin et al. 2007). For Lammers and Oswald (2015), “the greatest shortcoming in our understanding of dolphin signals is the role that burst pulse play in communication”.

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4 162 Another important aspect of dolphin vocal behaviour is the regular occurrence of mixed vocal
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6 163 events, resulting in the association between different vocal categories (e.g. Shapiro 2006; Herzing 2015).
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9 164 Thus, there have been regular observations of simultaneous production of whistles and burst pulses in
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11 165 different contexts, which seemed to enhance their significance in terms of excitement or distress (Caldwell
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13 166 and Caldwell 1967; Reiss 1988; Herzing 1996). Although we know that dolphins can produce tonal and
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15 167 pulsed signals simultaneously, there is just scarce descriptive information (dos Santos et al. 1995; Herzing
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17 168 2015) and no quantification of the rate of association between different categories. Possible associations
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20 169 between click trains and whistles for example may be overlooked in studies where clicks are not recorded.
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22 170 However, dos Santos et al. (1995) observed associations of clicks and whistles in high arousal contexts.
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24 171 Dudzinski (1996) hypothesized that concurrent use of different vocal categories may enhance a
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26 172 communicative function in dolphins, but she did not analyse further the uses or functions of these
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29 173 associations.

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31 174 There is a crucial need for more detailed analyses of the behavioural context of vocal production in
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33 175 dolphins, that includes underwater observations and finer behavioural categories (Dudzinski et al. 1995), if
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35 176 we are to go further in the understanding of dolphins' vocal communication (Boissereau 2005; Grindley et
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38 177 al. 2015; Lammers and Oswald 2015). Even though the captive situation may not totally reflect the free-
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40 178 living communication system (e.g. limitations in foraging), it does provide conditions for disentangling
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42 179 some of the current issues. In the present study, we analysed the behaviours performed in concomitance
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44 180 with the emission of whistles, bust-pulses, clicks as well as of mixed call categories in a captive group of
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46 181 bottlenose dolphins (*Tursiops truncatus*) for which we could conduct underwater observations of detailed
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49 182 behaviours, separating social contexts according to their valence or significance. We thus searched for
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51 183 preferential associations between acoustic structures and behaviours of individuals present at the exact time
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53 184 of call emission. We expected to find a non-random association between all vocal categories and behavioural
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55 185 contexts and by this way to better understand the flexibility of contextual use of vocalizations in this species.
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59 187 **Materials and methods**

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4 188 *Study site and data collection*

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6 189 Data collection was conducted for 18 days in February-May 2015 on a group of four male (aged 5,
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8 190 6, 12 and 16 years old) and three females (aged 7, 14 and 26 years old), all captive-born, bottlenose dolphins
9
10 191 (*Tursiops truncatus*) under human care (living in the facility of Planète Sauvage, Port-Saint-Père, France).
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12 192 In the wild, dolphins form fission-fusion groups (King et al. 2022). Here also, our group composition
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14 193 changed during our study (the third female arrived after 14 days of data collection). The study group had
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16 194 free access to four inter-connected pools of different sizes (P₁: 4950 m³, P₂: 1280 m³, P₃: 220 m³, P₄: 1040
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18 195 m³). The dolphins' diet was composed of 4.5-8.5kg fish per dolphin per day (i.e. herring, capelin, mackerel,
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20 196 sprat, whiting and squid) according to size and age. A first meal was distributed at 9:00 am, one last at 5:00
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22 197 pm and the rest during training/public presentation sessions. At the time of study, dolphins were involved
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24 198 in five daily training sessions for public presentations and medical surveys (2 in the morning and 3 in the
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26 199 afternoon, each one lasting between 15 and 30 min; about every 1.5 h).
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33 201 *Behavioural sampling*

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35 202 Data were collected in the pool P₄ (diameter: 30 m, depth: from 3.6 m to 4.9 m) which dolphins
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37 203 could access freely (Fig. S1). An underwater window of 193 cm x 93 cm allowed an entire underwater view
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39 204 on this pool, and thus behavioural observations when individuals were present. Observation sessions lasted
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41 205 30 ± 16min on average (mean ± SD) recorded at random moments between 09:30 am and 4:00 pm when
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43 206 dolphins were not involved in any training/public presentation sessions and there was no trainer around the
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45 207 pool. Emissions of vocal events were collected using all occurrences sampling (Altmann 1974). A vocal
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47 208 event is defined here as a call or series of calls, overlapped or not, emitted in a short time frame with long
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49 209 silence gaps (> 500 ms) before and after its production. The concurrent behaviours at the precise time of a
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51 210 vocal event were collected in order to obtain the behavioural context of vocal emissions. Behavioural
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53 211 categories were: Affiliative; Agonistic; Sexual; Social play; Solitary play and Other (the latter including
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55 212 behaviours where dolphins were swimming alone and resting). For a detail of each behavioural category see
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57 213 Table S1 (based on the behavioural repertoire of Clegg et al. 2017)
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Behavioural, acoustic recordings and sound categories

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Acoustic signals produced by dolphins were recorded continuously using a broadband system consisting of: a Sea-Phone SS03-10 (-194 dB, re 1V/ μ Pa, 0.020 to 50 kHz) hydrophone in the beginning of data collection, and, from April on, a C54XRS (-185 dB, re 1V/ μ Pa, 0.06 to 203 kHz) hydrophone connected to a TASCAM DR-680 recorder (sampling rate: 192 kHz - 24 bit). The two main pools were equipped with a hydrophone, which allowed the observer to distinguish the sounds produced in the sampling pool by applying two-channel recordings. To prevent the analysis of sounds recorded from adjacent pools, only signals heard exclusively in the P4 hydrophone as well as those captured with a higher intensity were considered for the analyses. There was an auditory feedback in the observation room and behavioural observations were recorded with a commentary channel using the same recorder by one single trained observer (ADML) (i.e. through headphones the observer listened live to the sounds recorded by the hydrophone while commenting on the behaviours observed simultaneously). We applied a clear-cut *criterion* to associate a vocalization to a context, analysing only simultaneous behaviour/vocalization events.

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Vocal events were classified using spectrograms (FFT 1024 at 192 kHz sampling rate) obtained through Raven Pro 1.4 (Cornell Bioacoustics Research Program). In accordance with the literature (Acevedo-Gutiérrez and Stienessen 2004; Eskelinen et al. 2016; Jones et al. 2020), click trains (Cl) were classified as high-frequencies signals emitted in a beam, reaching peak frequencies of 100-130 kHz, bandwidths of 30-55 kHz (Au 2004) and with inter-click interval between 0.007 and 1.0 s (Jones et al. 2020); Burst pulse sounds (BP) as broadband and short duration packets of clicks emitted with an inter-click interval typically 10 times shorter than the one of echolocation click trains (e.g. below 0.01 s; Lammers et al. 2003; Jones et al. 2020) and Whistles (Wh) as tonal narrowband signals sometimes with harmonic components (Smolker et al. 1993), frequency-modulation ranging between 1 and 40 kHz (Hiley et al. 2017) and a mean duration of 0.06 s (Kaplan and Reiss 2017) (Fig. 1).

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4 238 The vocal events sampled above were subsequently categorized as simple (i.e. composed of a single
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6 239 vocal category: BP; Cl; Wh) or mixed (i.e. composed by the association of more than one vocal category:
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8 240 BP-Cl; BP-Wh; Cl-Wh; BP-Cl-Wh).

11 241 12 13 242 *Statistical analyses*

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15 243 A first step consisted in exploring the whole set of data through a Chi-square test performed on the
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17 244 whole matrix context/vocal event in order to see whether the distribution was random or not (e.g. to assess
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19 245 potentially relevant relationships, see also Walker et al. 2017). In a second step, we used a Generalized
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21 246 Linear Model (GLM) in order to go further and examine more precisely how contexts and vocal events were
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23 247 related (the statistical unit of the GLM being a single sampled vocal-context event). We could not include
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25 248 caller identity as random factor in the model since it was not possible to identify who emitted the recorded
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27 249 calls when more than one dolphin was present in the sampling pool. Observation of the production of
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29 250 bubbles, as used by different authors for identifying emitters (e.g. Herzing et al. 1997), did not occur in a
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31 251 majority of cases. However, all dolphins came in that pool on a regular basis and thus all contributed to the
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33 252 data set (on average max 3 dolphins at the same moment in the study pool). Statistics were performed using
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35 253 R function *glm* (R studio version 1.4.11, R Core Team 2019) of R-package *lme4* (Bates et al. 2015) to model
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37 254 a binomial GLM where the response variable was “Emission” (i.e. coded as ‘presence’ or ‘absence’ of the
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39 255 emission of a certain vocal category in a given behavioural context) and the fixed variables were the
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41 256 interaction between the factor “Vocal category” (i.e. coded according to the seven possible vocal categories
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43 257 obtained in this study: Burst pulses; Click trains; Whistles; Burst pulse-Click trains; Burst pulse-Whistles;
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45 258 Click trains-Whistles; Burst pulse-Click trains-Whistles) and the factor “Context” (i.e. coded according to
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47 259 the six categories of behavioural contexts observed: Affiliative; Agonistic; Sexual; Social play; Solitary
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49 260 play; Other), as well as the single variables Context and Vocal category without interaction. Finally, with
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51 261 the R function “*emmeans*” of R-packages “*emmeans*” (Russell 2022) we conducted post hoc analyses (with
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53 262 Tukey method to compare the estimates) to assess the relative importance of the different contexts per vocal
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55 263 category, as well as the different vocal categories per context.
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Results

During the 64 hours of recordings (118 sessions), we recorded 479 vocal events with simultaneous behaviours. These events mostly occurred during social contexts (73%) (i.e. Affiliative: 23%, Social play: 23%, Sexual: 22%, Agonistic: 6%) and less often under non-social contexts (27%) (i.e. Solitary play: 21%, Others: 5%). Among the 479 vocal events collected, 258 consisted of simple vocalizations (14.33 ± 10.38 SD per session) and 221 of mixed vocal emissions (9.20 ± 7.95 SD per session).

In total, 104 click trains (Cl), 102 whistles (Wh), and 52 burst pulses (BP) were recorded as simple vocalizations. Mixed calls included BP-Cl-Wh (N= 67), BP-Wh (N=60), BP-Cl (N= 47) and Cl-Wh (N=47). Out of the 221 mixed vocal events, 89 were recorded when only one dolphin was in the study pool and 132 when at least two individuals were present. The average number of dolphins in the study pool during the acoustic recordings was 1.67 ± 0.89 SD per session, and this was similar whether the vocal events were simple (1.67 ± 0.83 SD) or mixed (1.69 ± 0.96 SD).

Behavioural contexts of vocal emission

The first data exploration using the Chi-square test revealed that different vocal categories occurred in different contexts ($\chi^2 = 121.60$, $df = 30$, $p < .0001$; Fig. 2). The GLM analysis confirmed the non-random association between contexts and vocal categories ($\chi^2 = 162.98$, $p < .0001$, for an overview of the GLM Output see Table S2), and post-hoc comparisons in both ways were made to further examine how each vocal category was distributed across contexts and which vocal categories were preferentially produced in a given context.

In the case of simple vocal events, all three categories were produced more in some behavioural contexts than others (Post-Hoc Tukey tests; Fig. 2). BP were produced more during social play (social play vs sexual: $p = .04$) and agonistic (agonistic vs sexual: $p = .03$) interactions than during sexual interactions, during which they were less emitted in particular than Wh (BP vs Wh: $p = .0009$) and BP-Cl-Wh (BP vs BP-Cl-Wh: $p = .001$). Cl were produced more during affiliative than sexual interactions ($p = .0006$) and

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4 290 social play ($p = .05$) as well as more in solitary play than in sexual ($p = .03$). They were more emitted than
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6 291 most other vocal categories in affiliative contexts (i.e. CI vs BP: $p = .0002$; CI vs BP-CI: $p = .0002$; CI vs
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8 292 BP-Wh: $p < .0001$; CI vs BP-CI-Wh: $p < .0001$), more than CI-Wh in solitary play ($p = .002$) and less than
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10 293 whistles in sexual interactions (Wh: $p = 0.03$). Wh were produced less during solitary play than in all other
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12 294 contexts (affiliative: $p = .01$; agonistic: $p = .02$; sexual: $p = .001$; other: $p < .0001$; social play: $p = .008$),
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14 295 which was further shown by whistles being less emitted than BP-Wh ($p = .009$) and CI ($p = .002$) during
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16 296 solitary play. Whistles were however more emitted than CI-Wh ($p = .01$) and BP-CI ($p = .02$) during sexual
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18 297 interactions.

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22 298 Concerning mixed vocal events, **BP-Wh** were more emitted in both **solitary play** ($p = .002$) and
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24 299 **sexual** ($p = .05$) contexts than in the affiliative context in which they were actually the least emitted sound
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26 300 category (i.e. BP-Wh vs CI: $p < .0001$; BP-Wh vs CI-Wh: $p = .01$; BP-Wh vs Wh: $p = .004$) whereas they
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28 301 were more emitted during solitary play than Wh ($p = .009$) and CI-Wh ($p = .005$). **CI-Wh** were more emitted
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30 302 in **affiliative** than in solitary play context ($p = .01$) during which they were less emitted than BP-Wh (see
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32 303 above), CI ($p = .002$) and BP-CI-Wh ($p = .02$). **BP-CI-Wh** were more emitted in **sexual** than in the affiliative
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34 304 ($p = .002$) and social play contexts ($p = .02$), in particular more than BP ($p = .001$), BP-CI ($p = .03$) and CI-
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36 305 Wh ($p = .01$).

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40 306 One mixed type, **Burst pulse-Click trains, BP-CI**, was not significantly associated with any of the
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42 307 behavioural contexts considered, but it was also a **combination rarely emitted in general**. All post-hoc
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44 308 comparisons not reported above were not statistically significant ($p > 0.05$).

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46 309 To sum up, our results showed that (Fig. 2): i) **BP** were mostly associated to **social play** and
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48 310 **agonistic interactions**; ii) **CI** were especially emitted in **affiliative contexts**, also when emitted with Wh
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50 311 (CI-Wh) iii) **Wh** were generally emitted in all contexts other than solitary play and preferentially while
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52 312 swimming/resting at some distance from others (i.e. outside social interactions) ; iv) contextual use of some
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54 313 of these categories changed when two or more of them were mixed: **BP-Wh** was associated with **solitary**
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56 314 **play, BP-CI-Wh** with **sexual interactions**.

Discussion

In this study we described the spontaneous behavioural contexts of vocal emission in a group of bottlenose dolphins under human care. Seven different vocal categories were recorded, corresponding to the classical structural categories (Burst-pulses - BP, Clicks - Cl and Whistles - Wh) but also mixed vocalizations associating these vocal categories (BP-Wh, BP-Cl, Cl-Wh or BP-Cl-Wh). As predicted, we found a non-random association between the categories of vocal emissions and the behavioural categories concomitantly observed. Precisely, we found that click trains were mainly associated with affiliative contexts, burst pulses with social play and agonistic interactions, and whistles with a broad range of contexts apart from solitary play, and were especially emitted when resting/milling at some distance from the group. Interestingly, some mixed vocal events were found in separate contexts such as BP-Wh occurring during solitary play and BP-Cl-Wh recorded mostly during sexual interactions.

Whistles accounted for half of the vocal production and were present in most contexts, but were significantly more numerous when dolphins were quietly staying on their own. Although this may seem contradictory with the general assumption of a socio-affiliative function (e.g. Quick and Janik 2008; Hernandez et al. 2010), this finding fits very well with evidences that whistles are also produced in non-affiliative contexts (e.g. Herzing 2015) and when at great distances from social partners than burst pulses (Lammers and Oswald 2015). Under this perspective, whistles can possibly function as contact calls useful to inform groupmates on respective locations (Quick and Janik 2012; Janik and Sayigh, 2013). Interestingly, Lopez-Marulanda et al. (2020) found that non-signature whistles were preferentially emitted by captive dolphins while swimming alone and that their rate decreased during socio-affiliative contacts. Regular information through contact calls have been reported in a broad range of group-living species (e.g. pied babblers, *Turdoides bicolor*, Radford and Ridley 2006, barnacle geese, Hausberger et al. 1991, zebra finches, *Taeniopygia guttata*, Vignal et al. 2008; Greater spear-nosed bats *Phyllostomus hastatus*, Bohn et al. 2007; African elephants, *Lexodonta Africana*, Leighty et al. 2008; white-faced capuchin monkeys, *Cebus capucinus*, Digweed et al. 2007; Japanese macaques, *Macaca fuscata*, Koda et al. 2008; vervet monkeys, *Chlorocebus pygerythrus*, Cheney et al. 1996; Ordóñez-Gómez et al. 2019). In non-human primates, contact

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4 342 calling has been suggested to play a function of “grooming-at-distance” (Dunbar 1996; Arlet et al. 2015;
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6 343 Pougnault et al. 2022), which is also a hypothesis proposed by Chereskin et al. (2022) to explain that
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8 344 bottlenose dolphins with the weakest social bonds and the least physical contacts presented the highest rate
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10 345 of signature whistles’ exchanges. The authors proposed the term “bonding at distance”, which is more
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12 346 appropriate in the dolphins’ case and for non-primate species in general such as songbirds (e.g. Hausberger
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14 347 et al. 1997). However, we did not investigate the contextual use of signature and non-signature whistles
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17 348 separately, so our findings are more general on the use of this vocal category. Other studies found that
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19 349 whistle rate is low overall when dolphins are undisturbed (Luís et al. 2014) and increases with arousal or
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21 350 stress (Cook et al. 2004; dos Santos et al. 2005; Esch 2009; Rachinas-Lopes et al. 2017). Our results are in
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23 351 accordance with these observations as while our observations were mostly performed in undisturbed
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25 352 contexts (outside feeding/training or trainers’ presence of trainer, Thierren et al. 2012), when the whistle
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27 353 rate was low, whistles were also recorded in negative (agonistic) or high arousal (sexual) contexts. There is
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29 354 obviously more to find in whistles’ significance, amongst which information on internal state.
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33 355 Click trains were clearly associated with affiliative behaviours, confirming their importance for
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35 356 social communication in bottlenose dolphins beyond their echolocation function (Lang and Smith 1965;
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37 357 Watkins 1980; Connor and Smolker 1996; Herzing 1996; Lammers and Oswald 2015). This first
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39 358 demonstration converges with observations in non-whistling odontocetes. Martin et al. (2019) also found
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41 359 that click trains were present in 20% of the socializing bouts in their observations of free-living Heaviside
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43 360 dolphins (*Cephalorhynchus heavisidii*), but the valence of the social interactions was not noted (see also
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45 361 Miller et al. 1995, 2004; Wisniewska et al. 2014). Dawson (1991) had noticed in Hector’s dolphins
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47 362 (*Cephalorhynchus hectori*) that click trains produced with a very low inter-click interval were not useful for
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49 363 echolocation and therefore had probably a communicative function. One hypothesis was that dolphins may
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51 364 gather information from the echoes of each other sonar pulses, suggesting “eavesdropping” (Gregg et al.
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53 365 2007). Another hypothesis has been that the emission of fast series of clicks during play, sexual or aggressive
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55 366 behaviours could function as a form of tactile stimulation (Herzing and dos Santos 2004). Although the
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57 367 tactile stimulation remains hypothetical, the preferential and delimited use in affiliation in our data set
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4 368 supports a potential function associated with positive social approaches. Informing others about the friendly
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6 369 nature of an approach exists in other mammals (e.g. squeaking vocalization of grey wolves, *Canis lupus*,
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8 370 Weir et al. 2021; grunts in chacma baboons, *Papio ursinus*, Silk et al. 2016). Hence, it is possible that
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10 371 dolphins use clicks to reduce the uncertainty associated to social approaches, which would make perfect
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12 372 sense given the fission-fusion nature of their social system (King et al. 2022). When considering other
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14 373 mammals capable of echolocation, communicative functions of clicks have also been demonstrated. In
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16 374 Mexican free-tailed bats (*Tadarida brasiliensis*), small variations in both spectral and temporal parameters
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18 375 of buzz punctuate the difference between echolocate and communicative buzzes (Schwartz et al. 2007).
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20 376 Although the discrimination between different types of click trains was not the purpose of this study, next
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22 377 steps would consist of investigating possible variations in click trains parameters and their relationship with
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24 378 context. Our result paves the way for further discoveries on the communicative function of clicks, whose
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26 379 multiple functions of clicks may be an illustration on how small repertoire size promotes the evolution of
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28 380 context-dependent communication in odontocetes (Boisseau 2005).

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31 381 The significance of burst pulses (BP) remains one of the primary unsolved issues in dolphins'
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33 382 communication (Janik 2009), despite of growing evidence showing their important role (e.g. Lammers et
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35 383 al. 2003; Gridley et al. 2015). This may be due to the fact that BP production has been largely overlooked
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37 384 (Herzing 1996) and that their classification differs greatly according to authors (e.g. Luis et al. 2016). Our
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39 385 finding that BP were associated with agonistic behaviours confirms the existing literature (e.g.; Connor and
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41 386 Smolker 1996; Blomqvist and Amudin 2004; Díaz Lopez and Shirai 2009) although many of these studies
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43 387 included aggressive/sexual interactions (Overstrom, 1983; Connor and Vollmer 2009). However, we also
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45 388 found frequent burst-pulses during social play. The presence of burst pulses in both contexts may be
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47 389 explained taking in consideration that is sometimes difficult to distinguish between agonistic behaviours
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49 390 and social play in dolphins as in other animals (Burghardt 2005; Janik 2015) and a play context can
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51 391 sometimes turn in agonistic. Some studies have also shown that dolphins can become more affiliative
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53 392 following agonistic situations (Weaver 2003). Many dolphin species engage in play behaviour in both wild
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55 393 and captive environments (Kuczaj and Yeater 2006; Greene et al. 2011; Weaver and Kuczaj 2016), but little

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4 394 is known about acoustic communicative behaviours during such events (Eskelinen et al. 2016). In any case,
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6 395 different authors agree that BP are close-distance communication signals as they are short-range and
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8 396 directional and that they are “emotively charged” (Gridley et al. 2015). For example, in free-living dolphins,
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10 397 the average distance between dolphins when interacting producing burst-pulses is 14 meters while for
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12 398 whistles it is 23 meters (Lammers et al. 2006). In spinner dolphins, BP emission induce an answer in
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14 399 individuals that are in close proximity (Watkins and Schevill 1974; Lammers and Oswald 2015). In free-
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16 400 living heaviside’s dolphins, burst pulses were mostly recorded during socializing bouts (Martin et al. 2019).
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18 401 Both agonistic and social play interactions are produced during excitation (Mendl et al. 2010), so BP may
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20 402 be indicative, like the other calls of the repertoire, of a certain level of arousal.
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24 403 This seems to be still more the case when BP are associated with whistles, as this mixed vocal
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26 404 category seems to be associated with high excitement or distress (Lilly 1962; Caldwell and Caldwell 1967;
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28 405 Reiss 1988, Herzing 1996). Blomqvist et al. (2005) found that play-fighting dolphins typically emitted a
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30 406 short burst pulse combined with a whistle, acoustically different from aggressive burst pulses. In the present
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32 407 study, BP-Wh were mostly found during solitary play which may be associated with some degree of
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34 408 excitement, but the association between BP reflecting arousal and whistles as possible distant contact calls
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36 409 could also be a way of trying to attract social partners to share the object play. Only further investigations
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38 410 could inform about the meaning of such mixed calls. In any case, most mixed calls were found in contexts
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40 411 that differed from those of their respective simple calls and it seems possible that the combination could
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42 412 confirm, refine or modify the message associated with the primary calls used. Clicks mixed with whistles
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44 413 and burst pulses (BP-Ct-Wh) were preferentially associated with sexual interactions, a context during which
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46 414 BP and Cl were rarely found emitted alone. The only exceptions are click trains emitted with whistles (Ct-
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48 415 Wh) which were preferentially used during affiliative behaviours as the simple clicks (but not the whistles).
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51 416 Whether or not such call combinations correspond to the semantic combinations observed in several
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53 417 mammal and bird species (Coye et al 2017) remains to be investigated. Specifically, we cannot totally
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55 418 exclude that mixed vocal sounds were actually single vocalizations simultaneously produced by more than
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57 419 one individual (also considering that same animals contributed multiple times to the dataset). We did record
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4 420 mixed events when only one individual was present in the pool, corroborating the fact that dolphins can
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6 421 produce two vocal categories simultaneously (thanks to their nasal sac anatomy, Dormer 1979; Cranford et
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8 422 al. 1996; Ridgway et al. 2015). However, this situation occurred rarely. Also, the number of dolphins present
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10 423 in the sampling pool did not differ on average between simple and mixed vocal events. These limitations
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12 424 caution against the generalization of our results on the contextual use of mixed vocal categories or possible
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14 425 semantic use of them by dolphins. Nevertheless, this could just be one of the starting points for further
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16 426 investigations in our understanding on the contextual use of mixed vocal emissions. It is noticeable though
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18 427 that earlier (scarce) studies mention also the occurrence of such mixed vocal events (Harley 2008). Despite
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20 428 the limitations associated with the difficulty of identifying callers and the difference in the diversity of
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22 429 situations that captive or wild dolphins may encounter, this study provides new and important insights on
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24 430 dolphins' vocal communication. Underwater sound recordings could be matched with the immediate
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26 431 underwater behaviours, allowing in particular the differentiation of different social behaviours. Our results
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28 432 support some previous assumptions found in the literature on cetaceans but also question others, and open
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30 433 up numerous research perspectives on this issue (communicative use of clicks, role of mixed calls,
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32 434 information on the internal state conveyed by the different signals). Further research conducted on both wild
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34 435 and captive populations by using new emergent technologies allowing to individually identify the emitters
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36 436 are now required in order to deeply investigate further the acoustic communication in dolphins (e.g. Lopez-
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38 437 Marulanda et al. 2019; Gallo et al. 2022).

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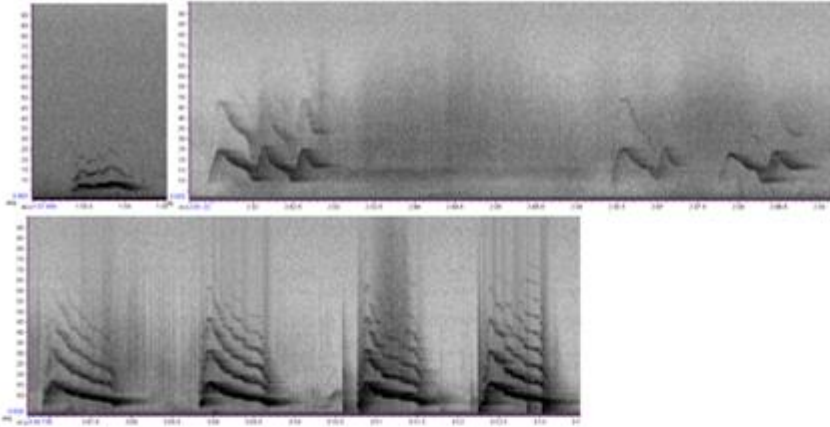
Figures captions

Fig.1 Three examples of recordings for each vocal category sampled. Starting from the top:
whistle simple events (single- and multi-units); click trains simple events (single- and multi-units);
burst-pulsed simple events (single- and multi-units); mixed vocal events (1st: whistles superposed

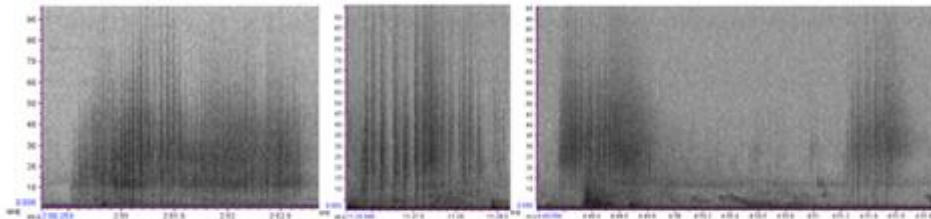
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803 with burst-pulses, 2nd: click trains superposed with burst pulses, 3rd: whistles alternating with burst
804 pulses)

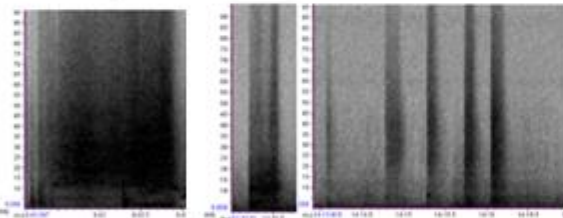
Whistles



Click trains



Burst-pulsed sounds



Mixed events

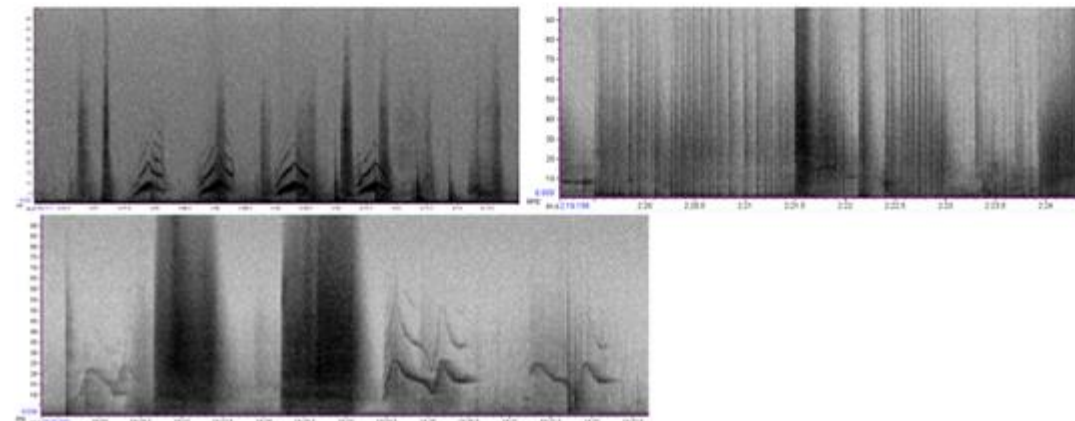
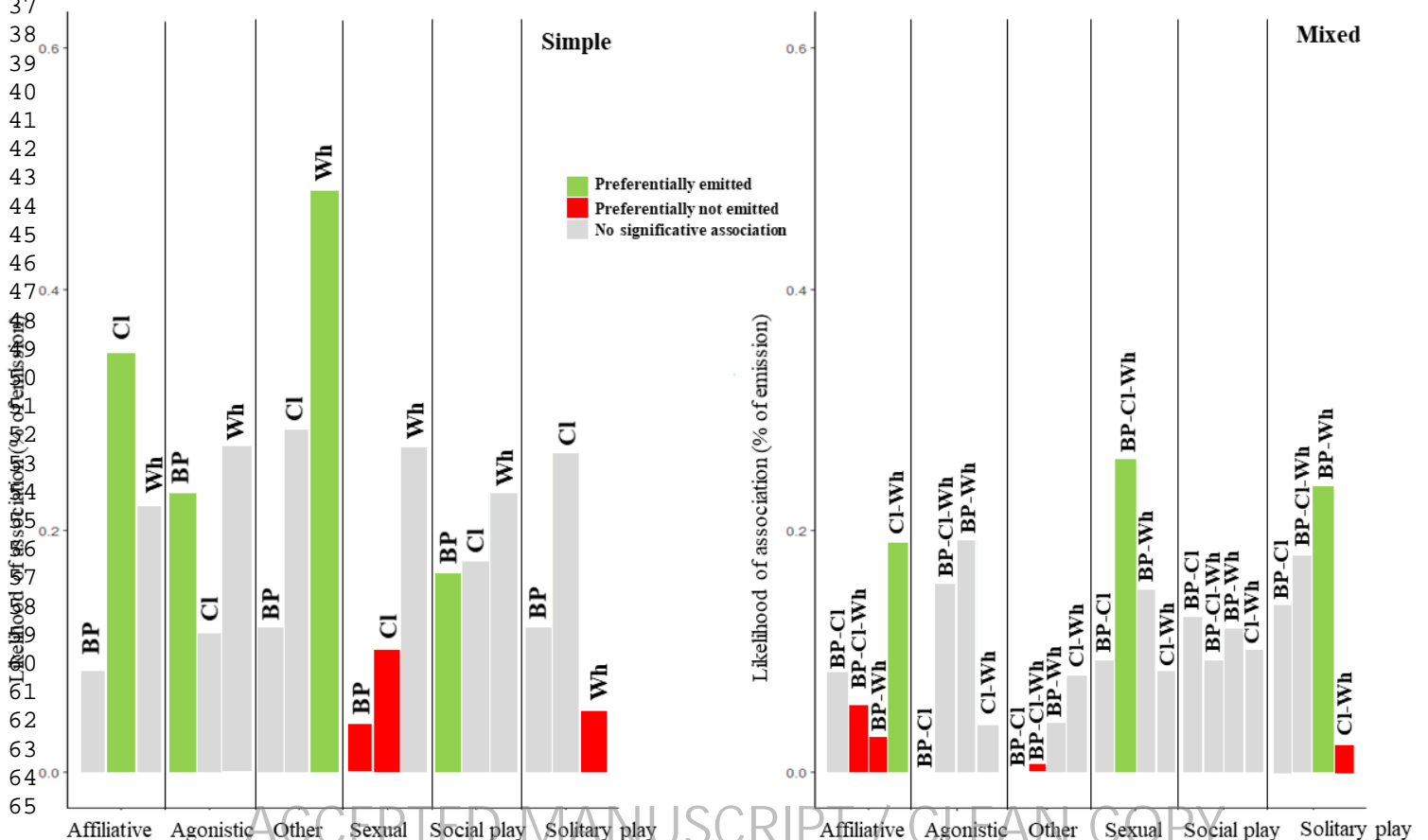
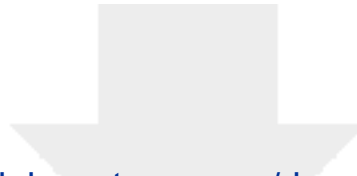


Fig.2 Bar plot showing the emission of each vocal category across the behavioural contexts considered. The vocal categories sampled were: Burst pulses (BP), Click trains (CI), Whistles (Wh) for simple vocal categories (bar plot on the left side); Burst pulses-Click trains (BP-CI), Burst pulses-Whistles (BP-Wh), Click trains-Whistles (CI-Wh), Burst pulses-Click trains-Whistles (BP-CI-Wh), for the mixed vocal categories (bar plot on the right side). The behavioural contexts considered were: Affiliative, Agonistic, Other, Sexual, Social play, Solitary play. For clarity, only the statistically significant results were highlighted on the graph. Specifically: green bars represent the vocal event for which a positive association with a given context was found (Adjusted residual > 2 in the Chi2 test); red bars represent a negative association in the emission of the given vocalization in a certain context (Adjusted residual < - 2 in the Chi2 test); grey bars represent the vocal events for which no significant association was found. **Although the single and mixed vocal events were statistically analysed together, they are presented here separately for ease of reading and discussion.**





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Supplementary Material

R1_Supplementary Material_Gallo_et_al.docx

