

Echolocation inter-click interval variation among specific behaviours in free-ranging bottlenose dolphins from the coast of Uruguay

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ABSTRACT

To assess whether behaviour can be inferred from echolocation trains (inter-click intervals) this study examines acoustic recordings of free-ranging bottlenose dolphins using Passive Acoustic Monitoring (PAM). Inter-click intervals from 17 groups of free-ranging bottlenose dolphins were monitored over a 36 day period in an area within the Cerro Verde (Marine Protected Area), Uruguay. Simultaneous visual observations were made from shore nearby. Results show that inter-click intervals in the echolocation trains had significant differences for three specific behaviours: feeding, socialising and travelling. The natural environment was quiet, with no disturbances in the immediate vicinity from boats, drones or other man-made noises.

KEYWORDS: ECHOLOCATION; BEHAVIOUR; BOTTLENOSE DOLPHIN; PASSIVE ACOUSTIC MONITORING

INTRODUCTION

Many studies of cetaceans rely purely on behavioural observations during surfacing, but details of behaviour can be difficult to identify accurately from visual observations conducted at the surface (Nuutila *et al.*, 2013). Cetaceans are only visible at the surface for between 1 to 10% of the time (Tyack and Miller, 2002), therefore studying the sounds emitted by cetaceans makes bioacoustics a very good tool to use to describe the activity of animals (Martin and Reeves, 2002).

Toothed whales have evolved biosonar systems to locate prey and acquire information about their surroundings (Au, 1993; Norris *et al.*, 1961; Surlykke and Nachtigall, 2014; Wood and Evans, 1980). The echoes returned from biosonar signals emitted by the animal are used to determine the direction and distance to potential prey items or obstacles in the water (Au, 1993; Madsen and Surlykke, 2013; Surlykke and Nachtigall, 2014). Odontocete echolocation has been extensively studied, a primary focus being the beam axis (Au, 1993; Kyhn *et al.*, 2009; Nachtigall and Moore, 1988; Thomas and Kastelein, 1990; Villadsgaard *et al.*, 2007). Like toothed whales, bottlenose dolphin (*Tursiops truncatus*) emit different types of vocalisations for different behaviours (Acevedo-Gutiérrez and Stienessen, 2004; Janik, 2009; Nowacek, 1999; Nowacek, 2005; Quick and Janik, 2008; Simard *et al.*, 2011; ECS, 1993) and they use biosonar for foraging (Au, 1993; Herzog, 1996; Nowacek, 2005) and orientation (Simard *et al.*, 2010). Bottlenose dolphin echolocation clicks are broadband pulses with high peak frequencies (up to 130kHz), high source levels (180–227B re 1 Pa peak-to-peak), short duration (individual pulses 8–70µs), and moderate to high directionality (3dB beamwidth 10°–40°, Au *et al.*, 1978; Au *et al.*, 1986; Au *et al.*, 1974; Moore *et al.*, 2008; Wahlberg *et al.*, 2011). Inter-click intervals (ICIs) vary with context (Au, 1993). Bottlenose dolphins steadily decrease their ICIs with decreasing distance to a target (e.g. Jensen *et al.*, 2009; Ridgway *et al.*, 2015). However, odontocete echolocation does not appear to be limited to this model. A study of a captive beluga whale (*Delphinapterus leucas*) found that

when the target was greater than 100m the whale emitted packets of clicks in which the intervals were less than the two-way transit time, but the intervals between the packets were greater than the two-way transit time (Turl and Penner, 1989).

The ability to process a series of echolocation clicks produced at a small ICI rate rather than the two-way travel time has also been demonstrated using a trained bottlenose dolphin in a natural environment (Finneran, 2013; Finneran, 2014; Ivanov, 2004). Penner (1988) found that when dolphins are in the presence of a target of unknown distance, captive bottlenose dolphins would begin acoustic searching behaviour by echolocating at pulse rates appropriate for the maximum distance they expect to encounter the target. Sperm whales (*Physeter macrocephalus*), Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales alter their ICIs from slow, relatively constant foraging clicks, to a rapid ICI (buzzing) during final approach to prey (Johnson *et al.*, 2008; Johnson *et al.*, 2004; Madsen *et al.*, 2002; Miller *et al.*, 2004). A similar pattern when approaching a target has also been observed in harbour porpoises (*Phocoena phocoena*; Verfuß *et al.*, 2009) and in a free-swimming bottlenose dolphin (Ridgway *et al.*, 2015). For bottlenose dolphins, studies have shown that echolocation ICI varies with different behaviours (Jones and Sayigh, 2002), and that during foraging, bottlenose dolphins produce shorter and faster ICIs (termed feeding buzzes) hence faster or slower click train emission, with the shortest ICIs reported between 3.0 and 7.1ms (Wahlberg *et al.*, 2011). In fact, the feeding activities for cetaceans typically involves fast echolocation click trains with a minimum ICI of < 10ms (Carlström, 2005; DeRuiter *et al.*, 2009; Dibble *et al.*, 2016; Miller, 2010; Ridgway *et al.*, 2015; Ridgway *et al.*, 2018; Ridgway *et al.*, 2014; Verfuß *et al.*, 2009; Wisniewska *et al.*, 2012), an extremely short ICI.

The odontocetes sonar system performance (directionality and sound pressure level, SPL) depends on the source parameters of the transmitted echolocation clicks, and analysis of click properties can therefore convey valuable information about the acoustic physiology and behavioural

ecology of recorded odontocetes species (Au, 1993; Madsen and Wahlberg, 2007).

Most echolocation studies involve captive specimens performing an echolocation task with man-made targets at relatively long and static ranges (Wisniewska *et al.*, 2014). Contemporaneously with these earlier captive studies, the development of new technology meant there were more results from animals in their natural habitat, which allowed new data to be obtained. (Aguilar Soto *et al.*, 2008; de Freitas *et al.*, 2015; DeRuiter *et al.*, 2009; Johnson *et al.*, 2004; Ladegaard *et al.*; Miller *et al.*, 2004; Ridgway *et al.*, 2015).

The aim of this study was to examine and describe the inter-click interval in the echolocation click trains among groups of free-ranging bottlenose dolphins in relation to different behaviours. Additionally, the occurrence (percentage) of potential feeding buzzes based in ICI criteria was examined for each behavioural category. This study will provide new and extensive data on whether click trains can relate to a specific behaviour and across several species.

METHODS

Study area

Data were collected on 36 non-consecutive days between March of 2017 to April 2018 in the Cerro Verde (Green hill – Marine Protected Area – 33° 38'S, 53° 24'W) of the Atlantic coast in Uruguay (Fig. 1). Visual observations were conducted by two to four observer teams with sea states ≤ 3 over a visible sea-surface area of approximately 500m radius around the passive acoustic monitoring (PAM) stations. The visual observation point was a 30m hill rounded by beaches. Two PAM underwater stations were deployed 100m from shore at a depth of 3m and these were placed the day before in the designated positions.

Bottlenose dolphins occur year-round in the Atlantic coastal waters of Uruguay, using the coastal zone mainly for feeding, socialising and reproduction (Fruet *et al.*, 2014; Laporta *et al.*, 2016; Menchaca *et al.*, 2019; Ott *et al.*, 2016; Tellechea *et al.*, 2014). Groups are variable in size and age composition, ranging from one to 30 individuals, with larger groups also including calves (Laporta *et al.*, 2016; Menchaca *et al.*, 2019; Tellechea *et al.*, 2014).

Data collection

During animal sightings, observers recorded behaviour, group size, travel direction, group composition and group cohesion. Binoculars with magnification 7x 50mm² were used to aid in the detection and tracking of animals. A group was described as a number of dolphins in close association, within approximately 100m of one another and often engaged in the same activity (Bearzi *et al.*, 1999; Shane, 1990). To ensure that the acoustic and visual data originated from the same group, all periods with multiple groups were excluded from the analysis.

The area was continuously monitored from dawn until dark. When a group of dolphins were sighted that were in the 500m range (distance at which the binoculars could distinguish the behaviour) this focus group was monitored. A 10 minute observation of the group was then carried out and the precise time this observation began was noted. The clock of the PAM station recording device was synchronised with the time of day; therefore it was possible to obtain the recording made by the PAM station at the exact moment of that of the dolphin observation group. The time observation was every 5 minutes and if the group was in the 500m recording range, it would be taken again for 10 minutes and so on describing the behaviour in each 10 minute tandem every 5 minutes (Piwetz, 2019; Quick and Janik, 2008).

Behaviour was recorded using the following categories: foraging/feeding (visible surface foraging and prey pursuit/capture where fish were seen fleeing, tossed about, or in the dolphin's mouth, fish shoals visible under the surface and demersal foraging consisting of repetitive, long feeding dives in the same location), socialising (physical contact, chasing each other, mating, synchronised movement, aggression and play), aerial behaviour, travelling, and milling (where dolphins are moving in varying directions with no observable surface behaviour) (Bearzi *et al.*, 1999; Shane, 1990). Because of the low number of observations in some of the behaviour categories (e.g. only 10 minutes of resting behaviour), only the foraging/feeding, socialising and travelling categories were used for analysis. Typically, the term foraging describes the search for food while feeding is the actual event of food intake.

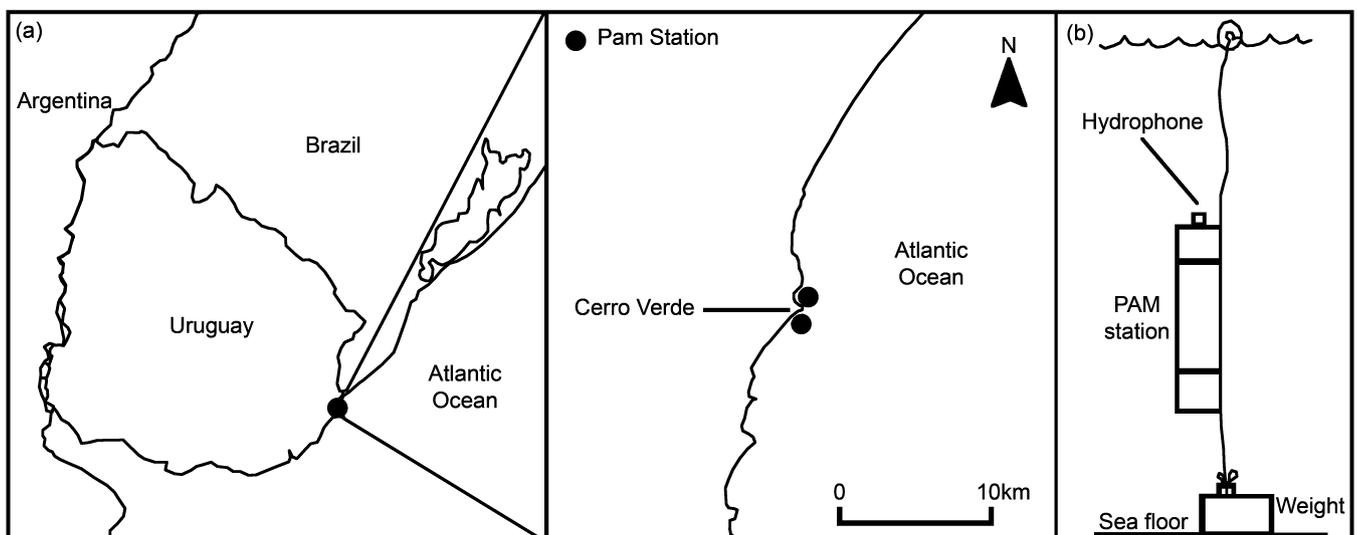


Fig. 1. Map of Uruguay and the Atlantic coast of Uruguay showing the position of the PAM buoys (A) and location of the PAM station underwater (B).

Because of other dolphin species in the area (Tellechea *et al.*, 2016) and the omnidirectional recording system it was important to ensure that only single-species groups of bottlenose dolphins were present during recording sessions. Therefore, only groups recorded under excellent weather conditions that allowed unambiguous confirmation were used for analysis.

Acoustic monitoring was conducted with a home-made PAM underwater station, an acoustic self-contained data logger, comprising a hydrophone, digital memory, and power source. These PAM stations are commonly used in acoustic monitoring of several marine mammals species in Uruguay (Tellechea *et al.*, 2014; Tellechea *et al.*, 2016) and were set to continuously record for 48h with a calibrated omnidirectional Aquarian hydrophone H1a (useful range: 1Hz to 100KHz, 100KHz = -220dB re: 1V/ μ Pa). This was connected to an amplifier with antialiasing filter and a TASCAM DR-100mkIII digital recorder with maximum resolution of 24 bits (96kHz, sample rate = 192kHz) stored data in SD card. A voltage regulator was built to keep the system working for 48hrs.

Recordings were analysed using custom-made scripts in MATLAB 7 (Natick, MA, USA) and Audacity free software, Version 1.2.3 (Mazzoni, 2006). Bottlenose dolphin click trains were analysed manually, and high quality click trains from single dolphins were chosen for the analysis. Files containing overlapping echolocation from more than one dolphin were omitted from the analysis. This was important in order to determine the ICI of individuals, since overlapping pulse trains would artificially increase the pulse rate.

Statistical analyses

Descriptive statistics were performed using PAST software (Hammer *et al.*, 2001) to provide mean, standard deviation, maximum and minimum values for ICIs for each train for

observed feeding, socialising and travelling behaviours. To test data normality assumptions and variance homogeneity Shapiro-Wilk and Levene test were used. As data did not meet the criteria Kruskal-Wallis and Mann-Whitney tests were used for non-parametric analysis (Zar, 2010).

The ICIs acoustic dataset was then inspected for underlying structure using multidimensional scaling (MDS), the number of dimensions used was two and used Bray-Curtis distance (Borg and Groenen, 2005). Patterns in the distribution of ICIs were used to identify distinct groups of behaviour. An analysis of similarity (ANOSIM) was also used to investigate the similarity within predefined groups of ICI characteristics for the behavioural categories. For all tests, the level of significance was $\alpha = 0.05$.

Several studies (Carlström, 2005; DeRuiter *et al.*, 2009; Dibble *et al.*, 2016; Miller, 2010; Ridgway *et al.*, 2015; Ridgway *et al.*, 2018; Ridgway *et al.*, 2014; Verfuß *et al.*, 2009; Wisniewska *et al.*, 2012) reported fast click trains with a minimum ICI of < 10ms which were found to be in relation to potential feeding activity. With this information, the percentage of ICI < 10ms was calculated for each behavioural category. This was to see if there were higher percentages of ICI < 10ms when feeding behaviour was observed.

To ensure that the acoustic and visual data originated from the same group of animals, all periods with multiple groups were excluded from the analysis.

RESULTS

Seventeen groups of bottlenose dolphins with acoustic recordings were sighted during the days of deployment and 625 high quality clicks trains (10,638 pulses) were selected for analysis. Clicks were recorded during feeding (333 clicks trains; 5,340 clicks), socialising (154 click trains, 2,800 clicks) and travelling (147 clicks trains, 2,498 clicks).

Table 1

Group identification, group size, pulses analysed, click trains and the corresponding behaviour data for 17 groups of bottlenose dolphins from the Atlantic coast of Uruguay.

Group id (date)	Group size	Ten minutes record number	Pulses	Click trains	Behaviour
23/04/2017	5	3	1,005	29	Feeding
11/05/2017	4	2	125	27	Socialising
15/06/2017	3	3	317	38	Socialising
13/08/2017	8	4	224	16	Socialising
26/09/2017	3	3	444	37	Travelling
25/11/2017	12	7	415	30	Feeding
25/11/2017	12	6	309	28	Feeding
25/11/2017	8	5	293	24	Feeding
25/11/2017	8	3	191	29	Feeding
14/12/2017	5	2	330	30	Travelling
27/12/2017	3	3	180	17	Travelling
27/01/2018	2	9	883	47	Feeding
28/01/2018	7	6	321	17	Feeding
28/01/2018	4	4	244	22	Feeding
28/01/2018	4	4	188	13	Feeding
28/01/2018	3	3	234	11	Feeding
04/02/2018	2	7	210	17	Travelling
04/02/2018	2	5	168	4	Travelling
22/02/2018	3	5	521	19	Socialising
27/03/2018	6	3	613	14	Socialising
28/03/2018	3	2	726	33	Socialising
04/10/2018	2	3	132	22	Travelling
02/11/2018	6	6	533	19	Feeding
02/11/2018	6	7	917	43	Feeding
23/11/2018	4	5	346	17	Feeding
23/11/2018	4	6	769	31	Feeding

The sightings are shown in Table 1. A total of 16 minutes of echolocation was obtained, divided into 174 recordings of 10 minutes (feeding: 74 ten minutes records; socialising: 19 ten minutes records; travelling: 34 ten minutes records) and included groups of 2 to 12 dolphins (mean = 4.5, SD = 2.6).

The mean, minimum and maximum ICI were calculated for each group (Table 2). The distribution of ICIs for each sighted group is showed in Fig. 2, and the box plot for the ICIs for each behaviour with the pooled data is shown in

Fig. 3. ICIs emitted by wild bottlenose dolphin were different in feeding, socialising and travelling behaviours: ICIs for feeding (23.05 + 35.09ms), socialising (117.8 + 72.9ms) and travelling (315.5 + 208.6ms).

There were peaks of click trains with very short ICIs, indicating possible foraging behaviour. This was particularly notable in the feeding behaviour data, with 54% of click trains classified as potential feeding buzzes with minimum ICIs of < 10ms only 5.10% and 3.4% of ICIs < 10ms were present in click trains of socialising and travelling behaviours.

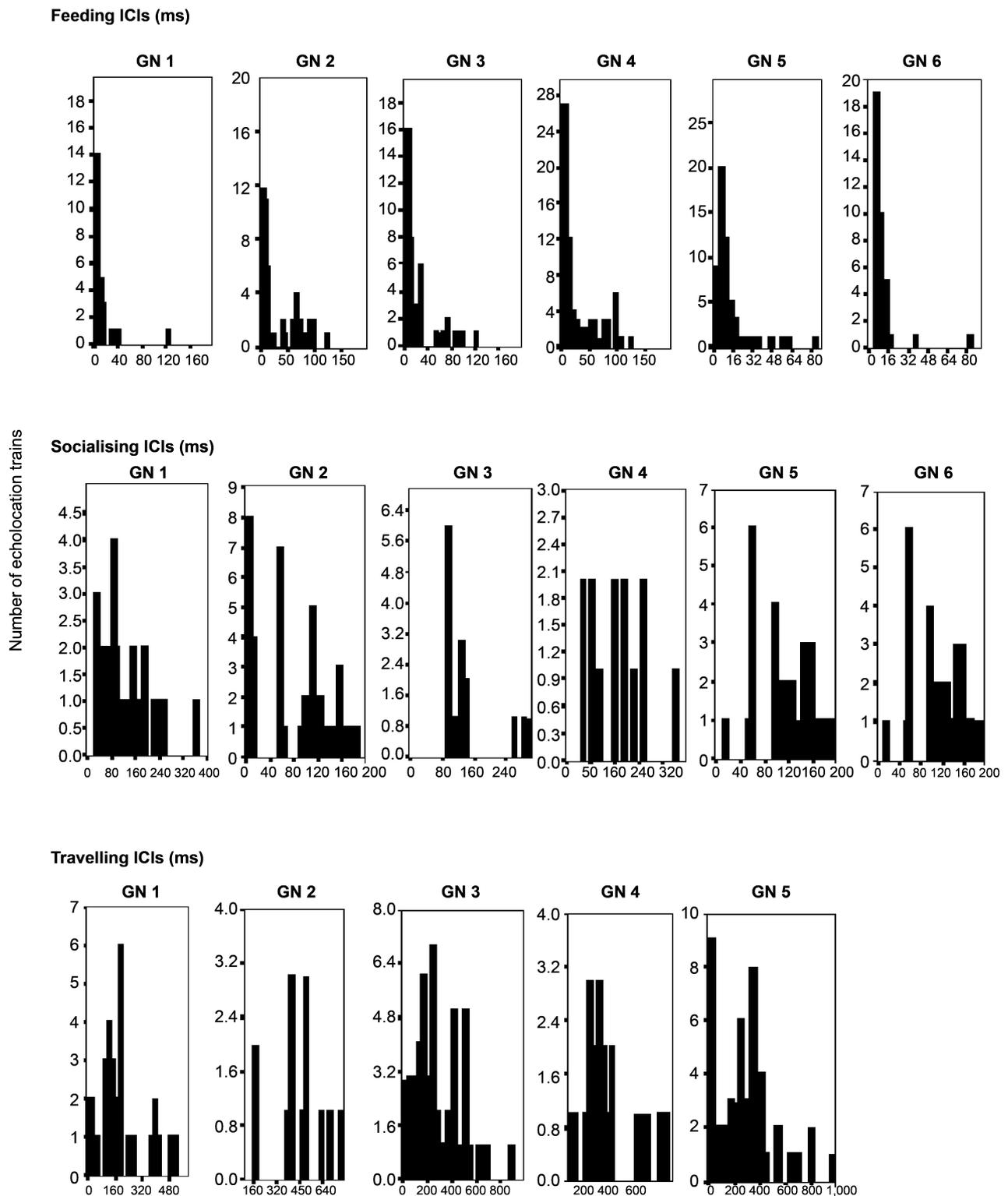


Fig. 2. Histograms of inter-click interval (ICIs) data from 17 groups of bottlenose dolphins. GN = group number identification (see Table 2).

Table 2

Behaviour identification, median, mean, maximum, minimum and standard deviation of ICI (inter-click interval) for each group and for the total data for each behaviour (GN: group number for each behaviour).

Group ID	Behaviour	GN	Median ICI (ms)	Mean ICI (ms)	Max ICI (ms)	Min ICI (ms)	± SD ICI
Apr-17	Feeding	1	9	44.3	126	1	75.6
Nov-18		2	11	81.4	127	3.9	96.7
Nov-18		3	9.8	23.2	124	1.2	29.3
Nov-17		4	12.7	38.9	128	1.4	38.7
Jan-18		5	8	11.01	84	5	13.1
Jan-18		6	9	13.9	85	2.9	15.1
Pooled data			35	23.05	444	1	35.9
May-17	Socializing	1	98	122	366	22	84.2
Jun-17		2	61	79.4	189	4	59.7
Aug-17		3	135	151.6	321	47	87.8
Feb-18		4	127.5	135.2	289	92	57.2
Mar-18		5	160	163.3	197	48	82.1
Mar-18		6	150	115.5	199	11	46.1
Pooled data			72	117.8	369	4	72.9
Sep-17	Travelling	1	132.5	198.1	529	15	90.1
Oct-18		2	177.2	475	781	159	177
Dec-17		3	190.6	329	789	44	191
Dec-17		4	206.1	421	832	120	207
Feb-18		5	221.4	285.6	841	3.9	221
Pooled data			271	315.5	841	3.9	209

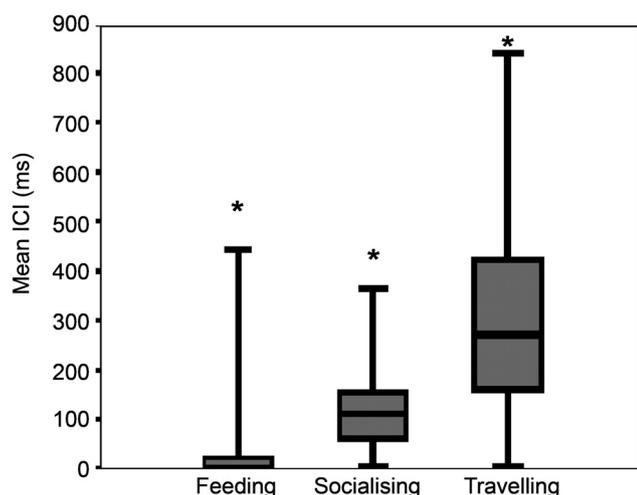


Fig. 3. Mean and standard deviation of ICIs of click trains emitted during feeding, socialising and travelling behaviour in free-ranging bottlenose dolphins.

According to a Kruskal-Wallis test, ICIs were significantly different among behaviours ($p = 3.39 \times 10^{-39}$), a Man-Whitney test showed significant differences among the three behaviours (feeding vs socialising $p = 1.69 \times 10^{-44}$; feeding vs travelling $p = 5.42 \times 10^{-55}$; socialising vs travelling $p = 2.21 \times 10^{-20}$).

ANOSIM revealed significant differences between ICIs of each category behaviour ($R = 0.621$, $p < 0.001$, 999 permutations). Also, a difference in ICIs was found from the MDS where the three groups are defined (Fig. 4).

DISCUSSION

There were insufficient visual observation data to assess the click characteristics potentially related to other behavioural categories such as milling or resting, which also form an important part of this species' behaviour (Mann *et al.*, 2000) and that could affect the content and rate of their vocal behaviour. Only the foraging/feeding, socialising and

travelling categories were used for analysis in this study, because they were the behaviours that could be successfully monitored at the time of the observations.

The ICIs in the echolocation trains were found to have significant differences in the three different behaviours (feeding, socialising and travelling) in wild bottlenose dolphins (Table 1). The data presented here is also consistent with the echolocation ICIs for foraging animals being larger than for travelling animals where the ICIs are smaller. This matches the findings of previous studies (Nowacek, 2005; Tyack, 2000). In fact, this study shows that for the feeding behaviour 54% of click trains were classified as potential feeding buzzes with minimum ICIs of < 10 ms. Only 5.10% and 3.4% of ICIs < 10 ms were present in click trains for socialising and travelling behaviours.

Dolphin echolocation trains have different inter-click intervals in different situations depending on many factors such as the distance of interest, difficulty in detecting a target, presence or absence of a target, and on the animal's expectation of finding a specific target (Au, 1993; Ridgway *et al.*, 2015; Wisniewska *et al.*, 2014). Several authors considered the percentage of ICIs < 10 ms (buzzing) indicative of foraging behaviour (Carlström, 2005; Johnson *et al.*, 2008; Verfuß *et al.*, 2009).

The relationship between target distance and pulse rate has been thoroughly investigated using trained captive dolphins under controlled conditions and dolphins in the wild. In most cases as a dolphin approaches a target, the inter-click interval decreases (Johnson *et al.*, 2004; Ridgway *et al.*, 2015; Wisniewska *et al.*, 2014). This is thought to be a function of the two-way travel time of the echolocation click, plus a lag time, both of which must occur before the next click is produced (Au *et al.*, 1974). This relationship was also found in other studies of free-ranging odontocetes (Akamatsu *et al.*, 2005; Jensen *et al.*, 2009) and suggests that the inter-click interval is affected by foraging patterns (Akamatsu *et al.*, 2005; Johnson *et al.*, 2008; Johnson *et al.*, 2004;

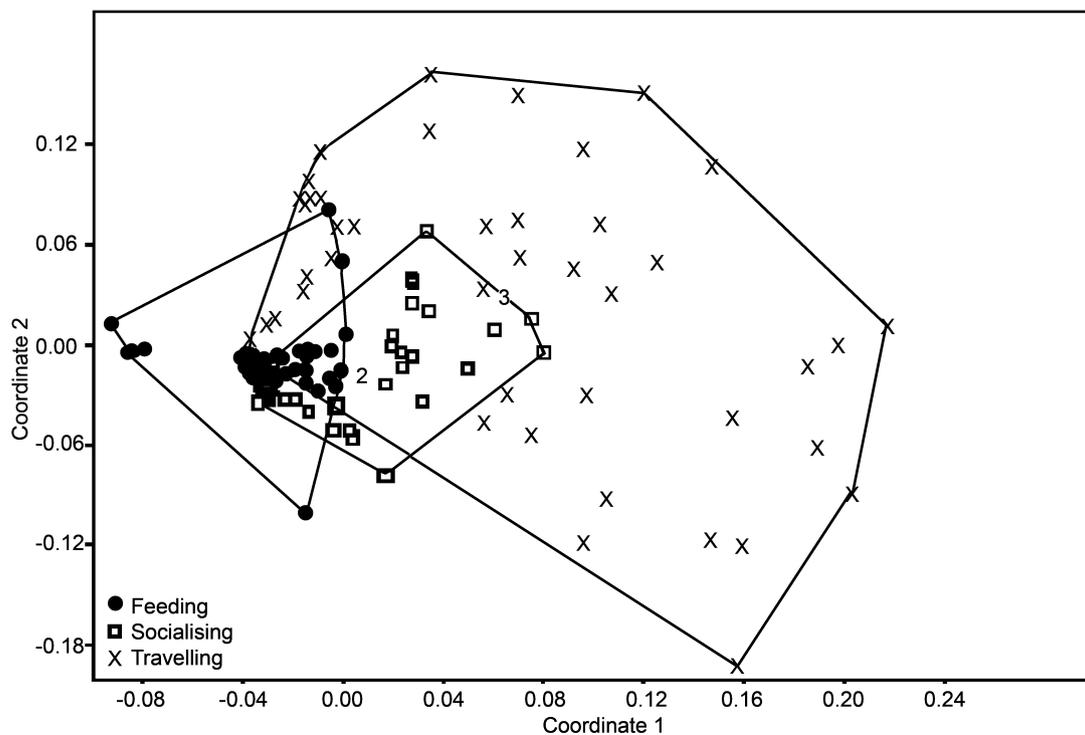


Fig. 4. MDS plot with mean ICIs pooled data for each behaviour.

Madsen *et al.*, 2002) and maybe navigation (Jaquet *et al.*, 2001; Ridgway *et al.*, 2015; Ridgway *et al.*, 2018; Simard *et al.*, 2010; Thode *et al.*, 2002). Therefore echolocation inter-click intervals vary with behaviour (Jones and Sayigh, 2002), and during foraging, bottlenose dolphins produce shorter and faster clicks (termed feeding buzzes) with the shortest ICIs reported between 3.0 and 7.1ms (Nuutila *et al.*, 2013; Ridgway *et al.*, 2015; Ridgway *et al.*, 2018; Ridgway *et al.*, 2014; Wahlberg *et al.*, 2011; Wisniewska *et al.*, 2012). Buzzing has been associated with feeding behaviour (Nowacek, 2005; Tyack, 2000).

In a novel experiment, free-swimming dolphins carried cameras on their heads to record video and sounds during search and capture of fish (see Ridgway *et al.*, 2015). The recordings found buzzes as they captured fish. There are three consistent acoustic phases in prey capture: sonar clicks locate the fish; about 0.4s before capture, the dolphin clicks become more rapid to form a second phase, the terminal buzz; at or just before capture, and the buzz turns to an emotional squeal (the victory squeal), which may last 0.2 to 20s after capture. The squeals are pulse bursts that vary in duration, peak frequency and amplitude.

Other studies have investigated free-ranging odontocete echolocation click rates in relation to assumed foraging patterns (e.g. searching, final approach) (Akamatsu *et al.*, 2005; Johnson *et al.*, 2008; Johnson *et al.*, 2004; Madsen *et al.*, 2002). These results are compatible with the data presented here in which buzzes occurred in a higher percentage in feeding click trains. There is not much information available about ICIs in the socialising behaviour of bottlenose dolphins. Herzing (1996) characterised the sounds recorded by Atlantic spotted dolphin (*Stenella frontalis*) and bottlenose dolphin in the wild. She describes a genital buzz and burst pulse vocalisation with click trains of very short ICIs. The social uses of click trains included

low-frequency buzzing during courtship, aggression, discipline, play, and exploration (Herzing, 2004). Click train source levels are used for tactile stimulation which has been measured in spotted dolphins (Au *et al.*, 1998) and for multiple delphinid species (Au, 1993). The use of click trains with ICIs < 10ms suggest that odontocetes use packets of clicks (burst pulse sounds) as a way to provide both social and prey information (Herzing, 2004). Therefore, the ICI data for socialising behaviour is relevant for bottlenose dolphins in the wild.

The data obtained from studies in free-ranging dolphins suggests that inter-click intervals overlap in a variety of behaviours and may indicate multiple purposes such as navigation, foraging on benthic or pelagic prey, and possibly communication, in several dolphin species (Akamatsu *et al.*, 1998; Herzing, 1996; Jensen *et al.*, 2009; Simard *et al.*, 2010; Tellechea *et al.*, 2016).

The ICIs in travelling behaviour in this study are similar to the results of other studies. The animals seem to be interested in interpreting the acoustic scene further ahead, thus requiring more intense clicks with longer ICIs to read echoes from distant targets (Nuutila *et al.*, 2013). There are several results in odontocetes that show that the variation of clicks (click duration, click interval) could be for navigation and orientation use (Jaquet *et al.*, 2001; Johnson and Tyack, 2003; Thode *et al.*, 2002; Zimmer *et al.*, 2003) and related to the variation of the depth at which the animals are moving which could presumably be an important factor in navigation (Simard *et al.*, 2010).

Past studies show overlapping ICIs with different characteristics in a variety of depths may indicate multiple purposes (Akamatsu *et al.*, 1998; Herzing, 1996; Jensen *et al.*, 2009; Nuutila *et al.*, 2013; Simard *et al.*, 2010).

Using PAM stations can help to record the ambient sounds of animals. Even though PAM stations cannot record the full

vocal repertoire produced by bottlenose dolphins, they can still reveal valuable behavioural information about the target species by detecting potential foraging events, or others behaviours. This makes the PAM station particularly useful for long-term monitoring studies and it was successfully used in Uruguay (Tellechea *et al.*, 2014). These devices can be used to identify important areas of cetacean behaviour, particularly, for example, in this region by the franciscana dolphin (*Pontoporia blainvillei*) (a dolphin species classified as Vulnerable (A3d) by the International Union for Conservation of Nature (IUCN, Reeves *et al.*, 2008)). Several acoustic studies have been carried out on this elusive dolphin (Cremer *et al.*, 2017; Melcon *et al.*, 2012; Tellechea *et al.*, 2014; Tellechea *et al.*, 2016) and it has been demonstrated that its presence can be determined with acoustic data.

This study, looking at free-ranging dolphins, suggests that specific inter-click intervals can be an indicator of the dolphin's underwater behaviour, something that until now has been studied very little in detail. Further studies to extract vocal repertoire and to further understand detailed behaviour (using the PAM station) are recommended. Behavioural observations using visual methods are limited to calm seas and daylight hours, typically during summer months. Acoustic monitoring is the only way to acquire detailed information on behaviour patterns for animals in all seasons and conditions.

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