

**Identification of potential signature whistles from free-ranging common dolphins
(*Delphinus delphis*) in South Africa**

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Abstract

Conveying identity is important for social animals to maintain individually based relationships. Communication of identity information relies on both signal encoding and perception. Several delphinid species use individually distinctive signature whistles to transmit identity information, best described for the common bottlenose dolphin (*Tursiops truncatus*). In this study, we investigate signature whistle use in wild common dolphins (*Delphinus delphis*). Acoustic recordings were analysed from 11 encounters from three locations in South Africa (Hout Bay, False Bay, and Plettenberg Bay) during 2009, 2016 and 2017. The frequency contours of whistles were visually categorised, with 29 signature whistle types (SWTs) identified through contour categorisation and a bout analysis approach developed specifically to identify signature whistles in bottlenose dolphins (SIGID). Categorisation verification was conducted using an unsupervised neural network (ARTwarp) at both a 91% and 96% vigilance parameter. For this, individual SWTs were analysed type by type and then in a 'global' analysis whereby all 497 whistle contours were categorised simultaneously. Overall the analysis demonstrated high stereotypy in the structure and temporal production of whistles, consistent with signature whistle use. We suggest that individual identity information may be encoded in these whistle contours. However, the large group sizes and high degree of vocal activity characteristic of this dolphin species generate a cluttered acoustic environment with high potential for masking from conspecific vocalisations. Therefore, further investigation into the mechanisms of identity perception in such acoustically cluttered environments is required to demonstrate the function of these stereotyped whistle types in common dolphins.

Key words: Acoustic, cetacean, communication, delphinid, individual identity, neural network

Introduction

Individually based relationships are fundamental to the success of social animals (Schülke *et al.* 2010; Silk *et al.* 2010). Such relationships can last years, or even decades. The most notable examples include long-lasting pair bonds (Bried *et al.* 2003; Huck *et al.* 2011), parent-offspring relationships (Weegman *et al.* 2016; King *et al.* 2017) and individual based relationships between allies (Mitani 2009; Cassidy & McIntyre 2016). In many terrestrial species, identity encoding can be achieved through visual (Leopold & Rhodes 2010; Perret *et al.* 2015) or olfactory (Stopfer *et al.* 2003; Ramm *et al.* 2008) cues as well as multi-modal displays (Rigaiil *et al.* 2013; Manica *et al.* 2016). Acoustic cues are effectively transmitted over long distances and play a vital role in identity encoding of many species (see review Kershenbaum *et al.* 2016), particularly when conspecifics are out of visual range. Cetaceans (whales, dolphins and porpoises) have evolved in the marine environment where visual, tactile, and olfactory senses are dampened, promoting the development and use of complex acoustic communication systems (Janik 2009; Ladich & Winkler 2017).

Identity encoding through acoustic signals most commonly results from morphological differences between individuals, whereby the unique traits of the sound production mechanism creates 'voice cues', otherwise known as 'by-product distinctiveness' (Boughman & Moss 2003). In these cases, individually distinctive features have been illustrated through statistical discrimination of call types (Podos 2010; Yajuvendra *et al.* 2013; Hick *et al.* 2016). Perceptual tests involving playback methodology have demonstrated individual discrimination through voice cues in a number of taxa, including bats (e.g. *Tadarida brasiliensis mexicana*, Balcombe & McCracken 1992), primates (e.g. *Papio cyncephalus ursinus*, Owren *et al.* 1997) and seals (e.g. *Arctocephalus tropicalis*, Charrier *et al.* 2003). Although evidence for voice cues can be detected in some cetaceans who share call types (Nousek *et al.* 2006), the variability in hydrostatic pressure on sound production mechanisms during diving can alter acoustic signals and affect signal stability, rendering voice cues less reliable for identity information transfer

(Jensen *et al.* 2011). In diving cetaceans, individually distinctive call types are more reliable for encoding identity information (Tyack 2000).

A small number of animal taxa demonstrate the capacity for vocal production learning, through which individuals are able to learn new sounds (Solis *et al.* 2000; Janik 2014a; Knörnschild, 2014). Vocal production learning of acoustic labels can result in call types containing unique temporal production or spectral characteristics which may be shared amongst group members or be individually distinctive (reviewed in Janik & Slater 1998; Tyack 2008). Examples of shared calls which are likely acquired through vocal production learning include social calls termed 'codas' used by sperm whales (*Physeter macrocephalus*, Weilgart & Whitehead 1997; Rendell & Whitehead 2003a) and the 'discrete' calls of killer whale pods (*Orcinus orca*, Ford 1989; Ford 1991; Strager 1995). In the natural world, examples of individually based 'designed acoustic labels' (Boughman & Moss 2003) are rare. However, signature whistles are well documented in bottlenose dolphins (Caldwell *et al.* 1990; Janik & Sayigh 2013; Gridley *et al.* 2014) and represent the best example of a designed individual acoustic label within the animal kingdom (Sayigh *et al.* 2007).

Bottlenose dolphins live in complex, fission-fusion societies that encourage individual based communication (Connor *et al.* 2001). Within dynamic social groups, conspecifics form long-lasting associations, including male-male foraging (Connor *et al.* 2000) and mating alliances (Connor & Smolker 1995; Connor *et al.* 2006) and extended maternal relationships with calves (Smolker *et al.* 1993; Grellier *et al.* 2003). Individually distinctive signature whistles help bottlenose dolphins maintain individual based relationships (Caldwell & Caldwell 1968; Fripp *et al.* 2005) by broadcasting individual identity over long distances (Janik & Sayigh 2013; Sayigh *et al.* 2017). Signature whistles are learnt within the first year of life (Sayigh *et al.* 1990; Fripp *et al.* 2005) and typically remain stable throughout life (Sayigh *et al.* 1990; Janik & Sayigh 2013). Nevertheless, there are exceptions to this, for example males may converge on

similar whistle contours during alliance formation (Smolker & Pepper 1999; Watwood *et al.* 2004), whilst retaining individual features in modulation pattern, akin to ‘voice cues’.

Although best studied in bottlenose dolphins, signature whistles have been reported from other odontocete species, including humpback dolphins (Van Parijs & Corkeron 2001; Cheng *et al.* 2017), narwhals (Shapiro 2006), short-finned pilot whales (Sayigh *et al.* 2013), and melon-headed whales (Kaplan *et al.* 2014). Because they are used as cohesion calls, the production of signature whistles is high under separation contexts (Janik & Slater 1998), when animals are stressed (Esch *et al.* 2009) and/or isolated in captivity (Caldwell *et al.* 1990). One of the first reports of signature whistle use in the Delphinidae family originates from a captive colony of four common dolphins (species historically referred to as *Delphinus delphis bairdi*, Caldwell & Caldwell, 1968) recorded in the period following capture. In this setting, five discrete stereotyped whistles were recorded, with one animal producing two stereotyped whistles. The term 'signature ' whistle was coined to describe these stereotyped, individually distinctive whistle types (Caldwell & Caldwell 1968). However, no studies have explicitly investigated signature whistle use in wild, free ranging common dolphins (*Delphinus* spp.).

Common dolphins predominantly inhabit continental shelf regions (Cockcroft & Peddemors 1990; Jefferson *et al.* 2009; Moura *et al.* 2011) and are common in South African coastal waters where they have been observed in group sizes ranging from 1 to 1000 (mean 267 ± 287 SD) animals (Findlay *et al.* 1992). Although the usual group sizes and ecology of common and bottlenose dolphins differ, behavioural and genetic studies of common dolphin associations and social organization demonstrate similarities to bottlenose dolphin social structure (Ball *et al.* 2017; Viricel *et al.* 2008). For example, common dolphins in the Mediterranean Sea also live in fission-fusion societies whereby individuals display non-random patterns of association (Bruno *et al.* 2004). In this population, long-term associations seemed to be weak, but there was strong evidence of preferred association and avoidance, suggesting that common dolphins develop short term relationships to increase fitness benefits, including predation

opportunities (Bruno *et al.* 2004). These similarities and indications from limited study in captivity (Caldwell & Caldwell 1968), indicate that common dolphins may also utilize stereotyped signature whistles to facilitate individual based acoustic communication in free-ranging settings.

In this study, we investigate the acoustic behaviour of common dolphins, using the methods of signature whistle identification developed for wild bottlenose dolphins (SIGID, Janik *et al.* 2013). Although common dolphins from South Africa were historically recognized as *D. capensis* (Samaai *et al.* 2005), there has been taxonomic uncertainty within the genus (Cunha *et al.* 2015). Following Cunha *et al.* (2015) and the Society of Marine Mammals (www.marinemammalscience.org), the species is currently accepted as *D. delphis*, but we will simply refer to the study species as 'common dolphins' throughout. We hypothesize that stereotyped whistles in common dolphins are used to communicate identity information and maintain group cohesion even within large group sizes. This is the first dedicated study of the vocalisations of wild common dolphins around southern Africa and provides insights into the communication behaviour of these oceanic dolphins.

Methods

Underwater acoustic recordings of free-ranging common dolphins were collected during three years (2009, 2016 and 2017) in the coastal waters of South Africa, between February and April. Data were collected from Hout Bay (34° 3'S, 18° 21'E), False Bay (34° 12'S, 18° 37'E) and Plettenberg Bay (34° 4'S, 23° 25'E). Recordings were made during focal follows (Altmann 1974) of groups during behavioural contexts likely to elicit whistles, i.e. during feeding and socialising. We used a single-element High-Tec HTI-96-MIN dipping hydrophone with a flat frequency response of 2 Hz to 30 kHz (± 1 dB) combined with digital acoustic recorders which sampled the data at 96 kHz (details summarized in Table 1).

Common dolphin whistles have a maximum frequency around 23 kHz (Ansmann *et al.* 2007; Petrella *et al.* 2012), well below the maximum recording frequency of the equipment used (48 kHz). Following Gridley *et al.* (2015), the hydrophone was bound to a 1 cm diameter steel chain and suspended ~3 m

below the surface of the water when dolphins were within recording range, i.e. less than 100 m from the hydrophone. This setup allowed for easy retrieval and redeployment of the hydrophone and ensured it got to and remained at full deployment depth throughout recording. Ideally, acoustic recordings were made from a stationary or idling vessel, but at times it was necessary to reposition the vessel to record the dolphins if they passed by, resulting in some recordings being stopped or interrupted by broadband engine noise.

Table 1. Details of acoustic data collection from free ranging populations of common dolphins (*Delphinus delphis*) in South Africa. Included in this table are the locations and dates of the encounters as well as the vessel and recording set-up used to collect the data.

Location	Period	Vessel Description	Recording Set up
Plettenberg Bay 34° 4' S 23° 25' E	2009/3/13	8 m ski-boat, 2 80hp 4 stroke engines	HTI with Edirol UA-25 sound card
False Bay 34° 12' S 18° 37' E	2016/02 - 2017/04	6 m RHIB, 2 50hp 2 stroke engines	HTI with Sony PCM D50 digital recorder
False Bay 34° 12' S 18° 37' E	2017/03/30 and 2017/04/18	6 m RHIB, 2 75hp 2 stroke engines	as above
Hout Bay 34° 3' S 18° 21' E	2016/05/11 and 2017/04/28	6 m RHIB, 2 75hp 2 stroke engines	as above

Many studies have demonstrated the reliability of visual categorisation or classification for acoustic signals (Jones *et al.* 2001), and bottlenose dolphin whistles in particular (Janik 1999; Sayigh *et al.* 2007). However, automated methods offer standardization of vigilance parameters (i.e. similarity thresholds) and

increased processing speed when dealing with large datasets (Ruau *et al.* 2011; Yannakoudakis *et al.* 2011). Combining visual and automated methods can offer the best all-around approach (Quick & Janik 2012).

Following Quick and Janik (2012), whistles were first identified and categorised visually. Visual categorisation was completed in the spectrogram display of Adobe Audition CC (version 6.0, Adobe Systems Inc., San Jose, CA, U.S.A.) created with an FFT of 1024 and a Hanning window. Acoustic recordings were visually scanned for repeating whistle contours that might collectively constitute a signature whistle type (SWT). Here we defined a ‘whistle’ as any narrow band tonal signal with a duration of more than 100 ms (Janik *et al.* 2013). Signature whistle types were defined as a collection of whistle contours, exhibiting highly similar frequency modulation patterns, and potentially constituting a stereotyped signature whistle (Janik *et al.* 2013). Repeating whistles were categorised into SWTs following the SIGnature IDentification (SIGID) approach of Janik *et al.* (2013), which has been applied in a number of studies of wild dolphins (Gridley *et al.* 2014; Kriesell *et al.* 2014; Luís *et al.* 2016). In essence, the SIGID method proposes that when multiple similar whistle contours are produced in sequence separated by inter-whistle-intervals (IWI) of 1 to 10 seconds, they are likely to be signature whistles. Janik *et al.* (2013) discuss two ways to approach this, either at the recording level: 1) by analysing the proportion of whistles produced within 1 to 10 seconds in a recording, or 2) at the sequence level, by analysing series of whistles which fulfil a bout temporal production criterion. We used the sequence approach (2), as this is not affected by recording duration. We therefore defined a SWT as those categories containing at least four repetitions of highly similar whistle contours, where on at least one occasion 3 out of 4 whistle repeats occurred within 1 to 10 seconds of each other (Janik *et al.* 2013; Kriesell *et al.* 2014). Because the temporal production of signature whistles has not been previously described for common dolphins, and might vary from bottlenose dolphins, we relaxed the lower limit of the IWI constraint imposed by the SIGID method. In this more relaxed analysis, we included whistle

types which contained whistle repeats produced at intervals of 0.2 to 10 seconds and discuss the results of both the stringent and relaxed version of this analysis.

Once the presence of a SWT was established within a recording, the recording was extensively scanned for any further whistles of that same SWT, whereby each whistle was assigned a unique identification code and added to a custom database. We took care to index all examples of a whistle type where we were confident of the contour form, as the inter-whistle-interval is an important component of the bout analysis approach applied in SIGID and we wanted to report on this. Therefore, some whistles with poor signal-to-noise ratio (SNR) and/or masked whistles were included in subsequent analysis if we were confident of a visual categorisation to a SWT.

Once identified and categorised, short individual recordings of each whistle were saved as separate ‘.wav’ files. The frequency trace of each contour was extracted using MATLAB based script files collectively termed 'Beluga' (<http://biology.st-andrews.ac.uk/SoundAnalysis/>). Beluga uses a peak extraction algorithm which can be manually edited to increase extraction accuracy. The frequency trace of each contour was extracted into a ‘.ctr’ file which is a digital representation of each visually extracted whistle saved as frequency points at standard 10 ms time intervals. Such down sampling of the contour reduces automated categorisation processing time whilst retaining key whistle contour features.

Visual categories were verified using the MATLAB based script, ARTwarp, developed for bioacoustic signals including dolphin whistles (Deecke & Janik 2005). ARTwarp incorporates an automated, unsupervised neural network to categorise contours based on frequency modulation patterns according to a set threshold of similarity, the vigilance parameter (VP). ARTwarp allows for temporal variation in whistle contours, through applying dynamic time warping which allows the contour to ‘stretch’ during comparison. This accounts for natural variation in a whistle duration and facilitates contour matching. To account for exponential frequency perception in vertebrates, whistle similarity in ARTwarp is expressed

as relative similarity in frequency (Deecke & Janik 2005). As thresholds for accurate signal discrimination are likely to vary between populations and species, we first conducted this analysis with a relatively lenient VP of 91% and then applied the more stringent VP of 96%. Previous studies have used the VP of 91% to support visual categorisation of sequences (Quick & Janik 2012) and for categorisation of whistle contours on a recording by recording basis (Gridley *et al.* 2014). The 96% VP has proven effective in identification of signature whistles from captive recordings of bottlenose dolphins, as well as categorisation of *Orcinus orca* discrete calls (Deecke & Janik 2005). However, the sample size of contours was relatively low in these studies (104 and 50 contours respectively). The following ARTwarp auxiliary settings were used throughout: bias = 0.000001, learning rate = 0.10, maximum no. iterations = 100.

Whistle types from the visual categorisations were first verified in a sequenced approach (following Quick & Janik 2012), where each visually identified SWT was run through ARTwarp separately, at a VP of both 91% and 96%. Additionally, we ran a global analysis of all extracted contours whereby all constituent whistle contours from the visually identified SWTs were included in a single categorisation task. This global categorisation approach, where several hundred whistles were included, is a more complex categorisation procedure than previously reported using ARTwarp. It was conducted to assess similarity in contours within and between encounters and locations which could help identify shared whistle types. The global analysis was conducted at both 91% and 96% vigilance, using the same auxiliary ARTwarp settings as above.

We assessed agreement between the visual and automated categorisation for the sequenced approach in the following way. We identified the dominant category for each automatically categorised grouping and generated an agreement level between this and the visually defined category which was expressed as a percentage. In some cases, visual and automated categorisation methods matched exactly, with all contours categorised together. Here agreement was 100%. In other cases, the automated categorisation

process split the visually identified SWT into two or more groups. In such cases, the ARTwarp generated category containing the largest number of contours was taken as the dominant group and ‘agreement’ between automated and visual categorisation outcomes was expressed as a percentage as follows: $\frac{\text{No contours in dominant grouping}}{\text{No in visually identified SWT}} \times 100$.

All extracted contours were re-categorised by ARTwarp during the global analysis using the two different vigilance parameters. Once complete, in order to satisfy the SIGID requirements, we identified those ARTwarp categories containing four or more whistles and discounted smaller groups from further analysis. Based on the SIGID criteria, which uses the sequential production of highly similar whistles to identify SWTs, we calculated the IWIs of whistles grouped together during contour categorization and defined SWTs for those groupings meeting the SIGID temporal production criteria. We then compared these SWT groupings to the visual categories. Here total agreement between automated and visual categorisation would result in all constituent contours from each visually categorised SWT being grouped as single, discrete categories in the global ARTwarp analysis. Disagreement between automated and visual categorisation would be apparent if during the global categorisation ARTwarp a) split the visually identified SWTs into several groups, b) combined multiple visually identified SWTs, c) simultaneously split and partially cross-grouped the visually identified SWTs. As this global analysis approach has not previously been conducted on such a large dataset or with the high 96% vigilance parameter, this analysis was exploratory in nature but worthwhile for investigating stereotypy in whistles necessary for identity encoding.

Results

Encounter Data

Data were analysed from eleven encounters with common dolphins in South African waters. Encounters took place over eight days with group sizes ranging from an estimated 18 to 1000 individuals ($n = 11$ groups, mean group size = 236 ± 251 SD). When estimated, average group area ranged between 50 m and

525 m ($n = 9$ groups). No estimates on group area were available for the largest group sampled or data collected in 2009 (details summarised in Table 2).

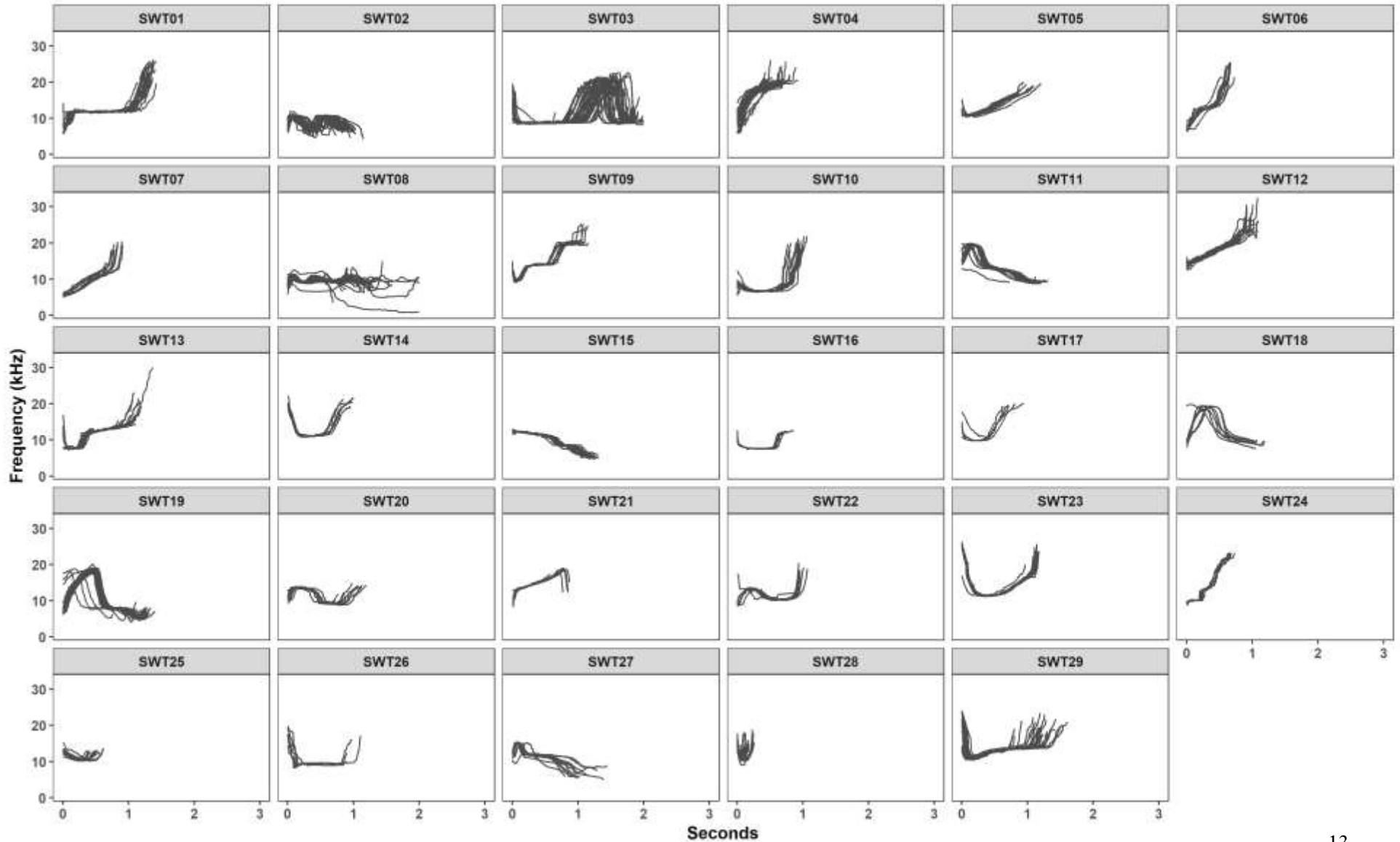
Table 2. Summary of acoustic data and encounter information used to identify signature whistle types (SWTs). Number of whistle contours and visually identified signature whistle types listed chronologically with corresponding group size and area (spread) of the group.

Encounter	Recording Length (h:mm:ss)	Group Size	Group Area (m)	No. of Whistles	No. of SWTs
1	0:53:15	200	n/a	69	4
2	1:01:59	19	100	147	4
3	0:19:00	30	475	14	1
4	0:53:25	1000	n/a	0	0
5	0:22:30	300	525	22	2
6	1:10:08	150	150	66	3
7	0:58:59	25	75	19	1
8	0:43:09	250	200	52	4
9	0:33:23	150	50	18	3
10	1:07:15	300	75	56	4
11	0:50:00	200	300	34	3
Total	8:53:03	-	-	497	29

Visual Categorisation

A total of 8 hours 52 min of recordings were scanned for stereotyped whistles (details summarised in Table 2). In total, 497 whistles were categorised into 29 different SWTs, of which 25 fulfilled the 1 to 10 second bout criteria specified by SIGID (Janik *et al.* 2013), and all 29 fulfilled the more relaxed 0.2 to 10 second bout criteria. However, high levels of whistle overlap, and resultant masking prevented many possible stereotyped whistle sequences, and potential SWTs, from being identified. In the most extreme case, the high masking rate prevented identification of any discrete whistle types from one entire

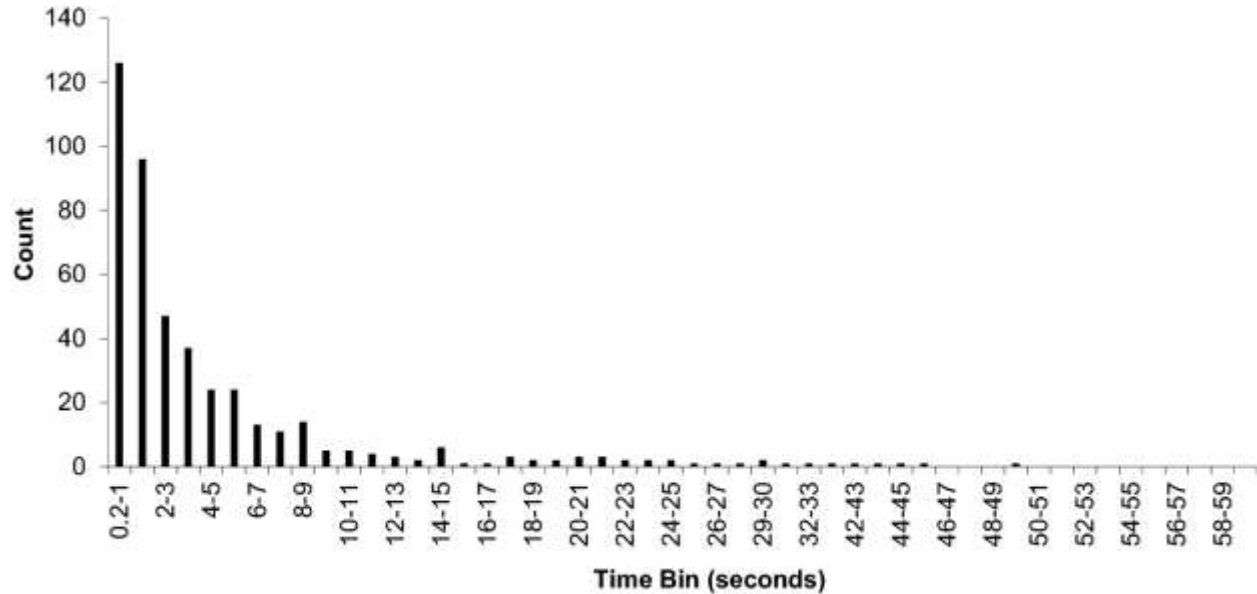
Figure 1- Visually identified signature whistle types from common dolphins (*Delphinus delphis*) recorded off South Africa in this study with extracted contours from each type overlaid. Frequency is on the y-axis (0 kHz – 35 kHz). Time (seconds) is on the x-axis. Sample sizes of extracted contours plotted for each type are shown in table 2.



recording session of the largest group, with approximately 1000 dolphins. The total number of signature whistle repeats in each SWT ranged from 5 to 45 (mean 17 ± 12 SD). The high degree of stereotypy of the frequency modulation pattern of these whistle contours can be observed in Figure 1, where the extracted contours from each group are overlaid without any time warping applied. Although similarities in the contour shapes of different SWTs were observed, visual categorisation indicated that each SWT was unique to a different recording encounter, suggesting that each individual was recorded only once.

In general, whistles of the same contour modulation pattern were often produced in bouts, adhering to the SIGID criteria. For seven SWTs, (SWT 01, 02, 03, 08, 10, 11, 29), there were appreciable breaks (i.e. 1 min to 33 min) in the temporal production of whistle repeats, which in some instances were attributed to engine noise during boat re-positioning. However, this accounted for only 16 (3%) data points. When considering only SWTs with an IWI of less than 1 min ($n = 451$), 28% were repeated at intervals between 0.2 and 1 second, 60% between 1 and 10 seconds and the remaining 12% were repeated at intervals between 10 seconds and 1 minute (Figure 2). From these values, the average IWI was calculated as 4.8 seconds (\pm SD 7.2 seconds). These results indicate that a significant number of IWIs were short, often shorter than the 1 second defined by the SIGID method. The results below are therefore based on SWTs identified with the more relaxed IWI criteria ($n = 29$ SWT) which included stereotyped contours occurring within 0.2 - 10 seconds when considered in the bout assessment criteria.

Figure 2. Summary of inter-whistle-interval (IWI) distribution in cases where IWIs were < 1 min ($n = 451$) showing. Data are highly skewed with most IWI under 5 seconds and the highest proportion under 1 second. Time (seconds) is on the x-axis. Whistle count is on the y-axis.



Automated Sequenced Categorisation

There was strong agreement between the visual and automated sequential categorisation. Under the more lenient 91% VP, 24 out of 29 SWTs (83%) showed complete agreement with the visual categorisation. For the remaining five whistle types, a predominant group, containing 78% or more of the categorised whistles was consistently apparent (Table 3). Based on the predominant groupings formed in ARTwarp at 91% VP, agreement between the methods was assessed as 98%.

The more stringent 96 % VP resulted in the complete agreement between the automated and visual categorisation for 12 out of the 29 SWTs (41%). As might be expected, categorisation at 96% VP generated more splits than at 91% VP. This resulted in both a greater total number of SWTs identified through the 96% VP, and in the number of splits within an SWT, but the whistles were again mainly grouped into a single predominant category. Five SWTs (01, 02, 03, 19, and 28) were principally split into only two groups. At 96% vigilance, overall agreement between the visual and automated

categorisation (assessed as detailed above) of SWTs dropped to 84%, with most SWTs containing a single predominant grouping (Table 3).

Table 3. Comparison between sequenced analysis of signature whistle types (SWT) through visual and automated methods of contour categorisation at 91% and 96% vigilance parameter (VP). Agreement between visual categorisation (VC) and automated categorisation is expressed as a percentage (%) calculated as $\frac{\text{No contours in dominant ARTwarp grouping}}{\text{No in visually categorized SWT}} \times 100$. The breakdown of groupings of the automated categories is shown in parenthesis after the agreement percentage.

SWT	Sample Size (No. of whistles)	Agreement (%) with VC at 91% VP	Agreement (%) with VC at 96% VP
01	23	100	52 (12/9/2)
02	40	100	58 (23/14/3)
03	45	78 (35/10)	44 (20/15/6/4)
04	39	100	67 (26/7/6)
05	14	100	93 (13/1)
06	12	100	83 (10/2)
07	10	100	100
08	38	95 (36/1/1)	79 (30/4/1/1/1/1)
09	10	100	100
10	18	100	94 (17/1)
11	19	95 (18/1)	95 (18/1)
12	18	100	100
13	10	100	70 (7/3)
14	6	100	100
15	18	100	100
16	6	100	100
17	5	100	80 (4/1)
18	7	100	86 (6/1)
19	33	91 (30/3)	52 (17/13/3)

20	8	100	100
21	6	100	100
22	9	100	89 (8/1)
23	12	100	100
24	6	100	100
25	16	100	100
26	6	100	67 (4/2)
27	11	100	91 (10/1)
28	23	91 (21/2)	39 (9/8/3/1/1/1)
29	29	100	100
Average	17	98.3	84.1

Automated Global Categorisation

At 91% VP, automated categorisation of all whistle contours resulted in 18 categories, which exhibited low levels of agreement with the 29 visually identified SWTs, both grouping and splitting whistle types. Four of these categories contained less than four whistles and were removed, following SIGID standards. Of the remaining 14 categories, five were in high agreement with the visual categorisation as they consisted only of whistles from one visually identified SWT. The remaining nine categories were amalgamations of between two and eight different visually identified SWTs, indicative of automated categorisation based on gross patterns of contour similarity, e.g. visually identified SWT with generally upsweeping frequency modulation patterns were grouped together in one amalgamated grouping in this analysis.

The global automated categorisation at 96% VP showed similarities to the automated sequenced categorisation at 96% VP, and both methods of automated categorisation differed from the visual categorisation in comparable ways. The global analysis at 96% VP resulted in the creation of 49 categories, 13 of which contained less than four whistles, or did not meet the (relaxed 0.2 - 10 seconds)

IWI standards to define a SWT. Of the effective 36 whistle categories, 26 contained whistles from only one visually identified SWT. The key difference being that at 96% VP some of the categorisation decisions were finer compared to the visual categorisation, so that some visually designated SWTs were further split at the 96% VP automated categorisation. This resulted in a greater number of resultant SWTs identified from the same sample of whistle contours. The remaining ten categories identified through the ARTwarp 96% global categorisation contained combinations of either two or three visually identified SWTs, indicating similarities in the frequency modulation patterns.

Analysis summary

In summary, the whistle contours of common dolphins were highly stereotyped (Figure 1) and mostly produced within 0.2 to 10 seconds. Agreement between visual and automated categorisation methods was greatest when whistles were categorised in a sequenced analysis in ARTwarp at 91% VP, assessing each SWT individually. However, our results indicate a common problem when attempting to identify signature whistles from wild populations in that the true number of SWTs produced by the animals encountered is unknown and the results of SWT identification are dependent on the categorisation method and stringency applied. Therefore, the different analysis approaches (sequential type-by-type versus global), categorisation tools (visual versus automated) and vigilance parameters (91% versus 96%) utilised resulted in between 14 and 36 SWTs being identified in the dataset of 497 whistle contours.

Discussion

This study has demonstrated evidence for production of stereotyped signature whistles in free ranging common dolphins in South Africa. Across the three sites, 29 signature whistle types were identified through visual categorisation and verified by an unsupervised neural network analysis. Signature whistle use has been studied in the common bottlenose dolphin (*Tursiops truncatus*) for more than 50 years (Janik & Sayigh 2013). More recently, evidence for signature whistles has been presented for several other odontocete species (Van Parijs & Corkeron 2001; Shapiro 2006; Kaplan *et al.* 2014; Cheng *et al.*

2017; reviewed in Janik & Sayigh 2013), suggesting that communication based on individually distinctive whistle types might be relatively common amongst delphinids in particular. If so, it might appear logical that the process of signal development i.e. vocal production learning, which has been well demonstrated in common bottlenose dolphins (Richards *et al.* 1984; Fripp *et al.*, 2005) and signal function, could be common amongst dolphin species. However, not all odontocetes produce whistles (see Morisaka (2012) for review) and even in those which do, some appear to have a communication system based on pulsed calls (e.g. dusky dolphins, Vaughn-Hirshorn *et al.* 2012), which may encode group level information rather than individual identity information (e.g. killer whales, Ford 1991; Miller & Bain 2000). Consequently, within each species, the development process and function of stereotyped calls cannot be assumed and needs to be clearly demonstrated. Although reported in a small captive population shortly after capture (Caldwell & Caldwell 1968), this is the first study to investigate the potential of signature whistle use by free-ranging common dolphins.

In the process of investigating signature whistle use in common dolphins, we applied several categorisation, vigilance and whistle analysis methods. We combined multiple methods in order to verify our data and to provide robust results in the identification of likely signature whistles. In all scenarios, stereotyped groupings of whistles fulfilling the SIGID criteria emerged. Visual categorisation of SWTs through SIGID provided baseline data, which was then validated in both a sequenced and global automated analysis, at multiple vigilance parameters. The greatest agreement in categorisation occurred when visually identified SWTs were validated during a type-by-type presentation of whistle contours to ARTwarp at 91% vigilance. Visual categorisation was conducted using the spectrogram representation prior to the contour extraction and down sampling procedures and also benefited from the additional contextual information associated with production such as amplitude and time series information. Consequently, although time consuming and open to subjectivity, we might expect higher accuracy in visual categorisation methods of signature whistle identification. This is supported by a wealth of studies

demonstrating high accuracy in visually classified signals (Tyack 1986; Caldwell *et al.* 1990; Sayigh *et al.* 1990, 1995).

The results of the automated global analysis at both 91% VP and 96% VP had a lower agreement with the visual categorisation, with SWTs often either being grouped together or split apart. During the global analysis all 497 contours were analysed simultaneously whereas in the sequenced presentation far fewer whistles (a maximum of 45) were categorised at any one time. Consequently, in sequenced presentation there was less space for overlap in the time-frequency domain, resulting in more stable categorisation outcomes. Further investigation revealed contour similarities in visually identified signature whistles which were combined under the ARTwarp global analysis. For example, SWT20 and SWT22 as well as and SWT11 and SWT27 were categorised together in global analyses at the 91% VP and 96% VP.

Comparison of the representative whistle traces in Figure 1 illustrates clear similarities in frequency modulation patterns between these pairs of SWTs, displaying a sinusoidal and down-sweep pattern, respectively. While it is possible that the same individual was recorded on multiple days, as is common in free ranging bottlenose dolphin populations (Cook *et al.* 2004; Kriesell *et al.* 2014), the ratio of identified SWTs to group sizes, combined with temporal and spatial distances between recording sites, makes this unlikely. Therefore, although in simple type-by-type scenarios, visual and automated categorisation tasks showed high levels of agreement, in more complex tasks it becomes apparent that these different categorisation modes may be discriminating based on different contour features, reducing categorisation agreement.

Our approach to signature whistle identification was based on the SIGID method, proposed by Janik *et al.* (2013) for the identification of signature whistles in common bottlenose dolphins. A key component to this analysis is the inter-whistle interval criteria, in which three of the required four whistles in a bout need to occur within 1 and 10 seconds of each other. Analysis of inter-whistle intervals from visually identified signature whistle types in our data revealed a peak at 0.2 to 1 second (Figure 2), indicative of

faster temporal production of signature whistles by common dolphins compared to bottlenose dolphins. We therefore adapted our SIGID inter-whistle interval criteria to 0.2 to 10 seconds. Our observation of a fast temporal production in likely signature whistles of common dolphins indicates the importance of developing signature whistle identification parameters to be species specific and where possible, having multiple validation methods to support the visual categorisation.

Such temporal differences in signal production between species might reflect emotional arousal, as dolphins, like many terrestrial species, are known to increase production rates of sounds under excited emotional states (Esch *et al.* 2009; Briefer 2012). The large group sizes of common dolphins encountered during this study were usually engaged in high energy activities such as socialising and feeding. Further, there may be greater need for redundancy in communication signals in the large groups typical of common dolphins, requiring faster signal production to facilitate inter-individual or group cohesion (Lengagne *et al.* 1999). Alternatively, morphological differences between species related to body size or features of their sound production mechanisms, the phonic lips, might account for differences in vocalisation behaviour between species (Podos 2001; May-Collado *et al.* 2007).

The large group sizes characteristic of common dolphin groups results in an acoustic communication challenge resulting from an acoustically cluttered environment. Common dolphins communicate within a highly complex and acoustically variable soundscape, with high degrees of biophony generated by conspecifics. In addition to whistle vocalisations, broadband echolocation and burst pulse sounds are produced simultaneously and at high rates in large social and feeding groups (Henderson *et al.* 2011). Surface generated wind noise (Urlick 1983) and anthropogenic acoustic pollution generated through vessels and seismic exploration further increase background noise levels, which can reduce communication distance (Jensen *et al.* 2009) and potentially influence whistle behaviour (Ansmann *et al.* 2007).

Under these conditions, how might common dolphins be communicating and perceiving identity information through signature whistles? One option, well studied in vertebrates (Busnel & Mebes 1975; Fishman *et al.* 2004; Nityananda & Bee 2011) and referred to as the ‘cocktail party effect’, describes the ability for individuals to differentiate a single auditory signal in the presence of a high amount of background noise (Cherry 1953). For example, Aubin and Jouventin (1998) describe the ability of king penguin chicks, living in large colonies, to perceive parental identity information amongst complex soundscapes. It is possible that common dolphin’s perception of identity cues is similarly acute, and that perception of the entire whistle contour might not be necessary for recognition, reducing the influence of masking. For example, Caldwell (1990) show that bottlenose dolphins can identify a signature whistle from a partial contour section lasting 0.5 seconds. In addition, it is likely that although large and dynamic, groups are somewhat structured, as in other group living animals (Acevedo & Würsig, 1991; Wiszniewski *et al.* 2009). For example, close proximity between mothers and calves or older offspring might be expected. The active space of signals produced within such sub-units, although restricted through masking noise generated by conspecifics, may still allow for propagation of identity information by signature whistles and play a pivotal role in maintaining this group structure. Communication is likely facilitated by repetitive signalling at regular, short intervals, as we have demonstrated. This signal repetition, in combination with directional information which may be encoded with the harmonic structure of whistles (Miller 2002; Lammers & Au 2003), can assist in acoustic localisation of individuals within fast moving groups. Additionally, in the sub-units, signature whistles may be used in combination with visual cues to help maintain contact between individuals (Herzing 2015).

In this study, identifying the acoustically active individual was impossible, but the presence of unique stereotyped whistles in all but one encounter (which could not be analysed due to the high level of masking), suggests that individuals were regularly advertising their identity, potentially to facilitate cohesion between specific individuals within the fluid and fast-moving groups typical of common dolphins. It is our understanding that signature whistles are used as a communication tool between

individuals. Beyond fine-scale associations, it is possible that in larger aggregations of delphinids, signature whistles might have multiple functions, and act as a tool for group cohesion as well. In these large, fast moving groups, the collective noise of the whistling pod might facilitate as an auditory beacon for wide ranging or lost individuals. The constant and large SWT production, as we observed in our data, could have more of a multi-functional role beyond that of individual conspecific communication.

Conclusion

In summary, we have provided evidence of signature whistles in free-ranging groups of common dolphins around South Africa. Signature whistle types were identified using SIGID (Janik *et al.* 2013), through visual categorisation, and verified in an automated neural network analysis, ARTwarp (Deecke & Janik 2006). Our study supports the existence of signature whistle types in this species; however, without the isolation of an individual animal to demonstrate that the whistle is being used to communicate identity, we cannot prove the use of signature whistles (Caldwell & Caldwell 1968). Highly stereotyped whistles were regularly present in all encounters, thereby supporting our claim for the existence of signature whistle types in common dolphins. To further understand the use, perception, and discrimination of stereotyped signature whistles in common dolphins, studies involving acoustic tags, captive individuals, or triangulation (in smaller groups) of individual whistle production are necessary. Further research into the social organisation, including individual relationships and patterns of affiliation would further benefit our understanding of the acoustic behaviour of common dolphins'.

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All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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