Sperm whale codas may encode individuality as well as clan identity

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Sperm whales produce codas for communication that can be grouped into different types according to their temporal patterns. Codas have led researchers to propose that sperm whales belong to distinct cultural clans, but it is presently unclear if they also convey individual information. Coda clicks comprise a series of pulses and the delay between pulses is a function of organ size, and therefore body size, and so is one potential source of individual information. Another potential individual-specific parameter could be the inter-click intervals within codas. To test whether these parameters provide reliable individual cues, stereo-hydrophone acoustic tags (Dtags) were attached to five sperm whales of the Azores, recording a total of 802 codas. A discriminant function analysis was used to distinguish 288 5 *Regular* codas from four of the sperm whales and 183 3 *Regular* codas from two sperm whales. The results suggest that codas have consistent individual features in their inter-click intervals and inter-pulse intervals which may contribute to individual identification. Additionally, two whales produced different coda types in distinct foraging dive phases. Codas may therefore be used by sperm whales to convey information of identity as well as activity within a social group to a larger extent than previously assumed. © 2016 Acoustical Society of America. [http://dx.doi.org/10.1121/1.4949478]

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I. INTRODUCTION

Many mammals have individual features in their communication calls which allow them to identify conspecifics. Whistles of bottlenose dolphins (*Tursiops truncatus*) (Caldwell and Caldwell, 1965; Sayigh *et al.*, 1990), social signals of little brown bats (*Myotis lucifugus*) (Melendez and

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Feng, 2010) and rumbles made by African elephants (*Loxodonta africana*) (McComb *et al.*, 2003) have all been shown to contain individually recognizable components. These species belong to different orders of mammals, but a common feature among them is strong reliance on acoustic signals for communication. Moreover, many of them, such as elephants and some delphinid species, live in long-term and complex social societies where it may be important to discern individual members of a group (Tibbetts and Dale, 2007).

Females, juveniles and calves of sperm whales (*Physeter macrocephalus*), the largest of the toothed whales, also live in stable family units (Weilgart *et al.*, 1996; Whitehead *et al.*, 2012; Gero *et al.*, 2008; Gero *et al.*, 2013). They produce clicks composed of a rapid series of pulses both for echolocation and communication. The pulses within individual clicks decrease in intensity and appear at intervals of 2–7 ms (Norris and Harvey, 1972; Gordon, 1991; Møhl *et al.*, 2003). These inter-pulse intervals (IPIs) are related to the length of the spermaceti organ (Møhl, 2001) and, there-fore, to the body length of the animal (Gordon, 1991), which changes gradually with the growth of the animal. Sperm whale clicks can be grouped into at least four types: usual clicks, buzzes (also called "creaks"), codas, and slow clicks (or clangs; Norris and Harvey, 1972; Weilgart and Whitehead, 1993; Madsen *et al.*, 2003; Møhl *et al.*, 2003; Zimmer *et al.*, 2005). Usual clicks and buzzes are used for long- and short-range echolocation, respectively (Jaquet *et al.*, 2001; Madsen *et al.*, 2002b; Madsen *et al.*, 2007; Møhl *et al.*, 2003; Miller *et al.*, 2004). Slow clicks are only produced by male sperm whales at low and high latitudes and appear to have a communication function (Mullins *et al.*, 1988; Weilgart and Whitehead, 1988; Madsen *et al.*, 2002b; Oliveira *et al.*, 2013). Codas are stereotyped patterns of 3–40 clicks and are mostly exchanged between individu-als within long-term, stable social units (females and their immature offspring) for communication purposes, presum-ably to maintain social cohesion while the animals are close to the surface (Watkins and Schevill, 1977; Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1993; Teloni, 2005).

Codas were initially thought to be unique for each sperm whale (Watkins and Schevill, 1977) but evidence of sharing of coda types by several individuals, did not support the hy-pothesis of individual specific coda types (Moore *et al.*, 1993; Weilgart and Whitehead, 1993). Codas are thought to function in reinforcing group cohesion via a shared vocal repertoire (Weilgart and Whitehead, 1993; Whitehead, 2003). Some coda types are geographically distinct (Moore *et al.*, 1993; Weilgart and Whitehead, 1997; Pavan *et al.*, 2000; Rendell and Whitehead, 2005; Antunes, 2009), and there are prominent unit-specific coda repertoire dialects among groups that share coda types (Weilgart and Whitehead, 1997). Large population subsets sharing coda types are called "vocal clans" and the clan signatures have been proposed to reflect and convey a cultural identity and be important for survival and reproduction (Rendell and Whitehead, 2003b). Besides geographical and unit-specific variations, the pattern of coda exchanges has a sequential

structure (Weilgart and Whitehead, 1993) and some coda "families" (groups of coda types, e.g., root, regular and pro-gressive coda groupings) seem to be related to different be-havioral contexts such as foraging and socializing (Frantzis and Alexiadou, 2008). Codas also seem to contain some individual characteristics in their temporal pattern of clicks, at least in 5 *Regular* (5Reg) codas from a social unit recorded in Dominica (Antunes *et al.*, 2011). As with other studies of codas, this study relied on IPIs to distinguish codas from dif-ferent individuals but this method is unreliable in groups where several individuals have similar lengths (and therefore similar IPIs) as is often the case for female nursery groups. Thus, the question of whether temporal patterns in codas carry individual-specific features in distinct coda types, within individuals with similar body lengths remains open.

Here the possibility of codas carrying information on individuality using onboard stereo-hydrophone tags (Dtags) was investigated. This is the first study to assign codas to distinct individual sperm whales using on-animal sound recordings. This study supports previous findings by show-ing that codas assigned to individuals have features that may allow for encoding of information beyond that of the coda type, suggesting that sperm whales use codas to radiate spe-cific information between individuals rather than just group or clan specific information.

II. MATERIALS AND METHODS

A. Study area

Sperm whales were studied during the summer of 2010 around the islands of Faial and Pico, in the Azores archipel-ago (38°N, 28°W), where they can be found year-round rela-tively close to the coast (Silva *et al.*, 2003; Silva *et al.*, 2014). Groups of females, juveniles and calves are com-monly observed in these waters and mature males are occa-sionally encountered (Matthews *et al.*, 2001; Silva *et al.*, 2014).

B. Tagging

Field work was carried out using two boats: a 6 m long rigid-hulled inflatable boat (RHIB, serving as tagging plat-form) and a 15 m long sailing boat. The observers on the RHIB located whales by visual observations and using a directional hydrophone (HTI-96-MIN, High Tech, Inc., with a custom-built baffle to add directionality). The sailing boat detected sperm whales using a towed-hydrophone array and Rainbow Click software (Gillespie, 1997), and was also used to recover the tags once they had detached from the whale. Visual observations of whales were further supported by local whale watching lookouts ("vigias") that monitor some areas around Faial and Pico almost continuously during summer daytime hours.

During the study period sperm whales were tagged with digital acoustic recording tags (Dtag) (Johnson and Tyack, 2003) that record 2-channel acoustic data (96 kHz sampling frequency, 16 bit resolution) while also sampling pressure, and three-axis accelerometers and magnetometers at 50 Hz (16 bit). Tags were attached with four suction cups and

J. Acoust. Soc. Am. **139** (5), May 2016

Oliveira *et al.* 2861

TABLE I. Deployment of Dtags on sperm whales producing codas.

Animal	Date (2010)	Duration (hours:minutes)[a]	Position of the Dtag
pm10_211b	30 July	14:44	about 2/3 distance between head tip and dorsal fin, slightly to the right side
pm10_222a	10 August	06:14	about half distance between head tip and dorsal fin, to the left side
pm10_222b	10 August	15:08	about 3/5 distance between head tip and dorsal fin, to the right side
pm10_226a	14 August	17:03	about half distance between head tip and dorsal fin, to the right side
pm10_228a	16 August	19:53	about half distance between head tip and dorsal fin, to the right side

[a]Duration of simultaneous recordings of audio and sensor data.

automatically released from the animal after a programmed maximum deployment period of 24 h.

Whales were tagged by carefully approaching them from behind at low speed (maximum 4 knots) and deploying the Dtag with an 11 m cantilevered pole. All Dtags were attached between the crest of the skull and the dorsal fin. Dtag attachment details for the coda producing sperm whales are found in Table I. Tag deployments were photographed with a Nikon D90 and a Nikkor AF 70-300 mm lens (Nikon Corporation, Tokyo, Japan) to collect information on the tag placement and photo-identify the tagged individual. Sperm whales responded mildly to the Dtag attachment typically performing a dorsal flex of the body [head lift according to Mate et al. (2007)], in some cases followed by defecation and a dive with or without fluking. Similarly as in Mate et al. (2007), all the responses were short-term. Tagged animals were tracked using the VHF beacon in the Dtag. The VHF transmissions were detected during the whales' surfacings using a four-element Yagi antenna, attached to a VHF receiver (R1000, Communication Specialists Inc., Orange, CA). The time and position of each surfacing were registered when possible, by moving the boat to the fluke print of the animal. After release, tags floating at the surface were recovered by radio tracking.

Sperm whale tagging procedures were allowed by the Regional Directorate for Sea Affairs, Autonomous Region of the Azores under research permit 49/2010/DRA. All procedures involving whales followed the guidelines of the American Society of Mammalogists (Gannon et al., 2007).

C. Data analysis

Data from the depth and movement sensors were decimated by sub-sampling to a rate of 5 Hz. To determine the orientation of the whale, accelerometer and magnetometer data were corrected from a coordinate system with the tag as a reference ("tag frame") to one with the whale as a reference ("whale frame"; Johnson and Tyack, 2003). The orientation corrections were re-evaluated at each surfacing from the accelerometer data by assuming that (1) sperm whales have a zero mean pitch and roll angle when at the surface, and (2) that whales maintain a zero roll in the initial seconds of a deep dive (Johnson and Tyack, 2003; Zimmer et al., 2003). Acoustic data were analyzed using MATLAB 7.0 (Mathworks, Inc., Natick, MA) with a custom spectrogram (512 sample FFT block size, 15 s segments with 2 s overlap) and dive depth display, to identify usual clicks, buzzes, codas, slow clicks, and other sound emissions.

Codas were distinguished from other click types by their distinctive temporal patterns and the castanet-like sounds of coda clicks (Weilgart and Whitehead, 1993). Codas produced by the tagged whales were distinguished from those of nearby whales by comparing the arrival angle of clicks at the tag, calculated from the time-of-arrival-difference between the two hydrophones of the tag (Johnson et al., 2006). If the angle-of-arrival of a coda was consistent with the angles-of-arrival from usual clicks emitted shortly before or after the coda by the tagged whale, the coda was assigned to the tagged whale (Fig. 1). Usual clicks were associated with the tagged whale mostly based on their much higher received level and temporal characteristics (Zimmer et al., 2005), depth context and their consistent angle-of-arrival. On this basis, coda clicks were ascribed either to the tagged whale, to another whale, or were marked as of uncertain origin. Only signals that were unequivocally attributed to the tagged whale were used in the analyses presented here.

Initially, codas were visually and aurally classified by an observer (C.O.). Later, codas with the same number of clicks were compared using principal component analysis (PCA) of ICIs and were then classified into different coda types with the PCA score for each coda. The observer classification was confirmed by the PCA classification, except for rare codas, where the PCA was not able to recognize their distinct ICIs. Therefore, a combination of the PCA classification with observer classification for the rare codas was used for the subsequent analysis. Coda types were named according to Weilgart and Whitehead (1997) based on their timing patterns and click number. For example, the 5Reg and *Four plus one* $(4 + 1)$ codas both have five clicks, but while the first one has regularly spaced clicks, the second one has a clearly longer gap between the last two clicks.

The time at the positive peak of each coda click waveform was measured to determine the start time and inter-click intervals (ICIs) of the coda (ICI1 is the time interval between the first and the second click, ICI2 is the time interval between the second and third click, and so on). The IPI parameter was measured only for the first click of each coda. It was calculated from the time difference between the positive peaks of the two first pulses (p1 and p2), since these have the highest signal-to-noise ratio (SNR) and the IPIs of the remaining pulses are identical to the first one (Madsen et al., 2002a). The measurement accuracy of these parameters depends on the SNR of the recorded clicks which was consistently high given the short distance between the sound
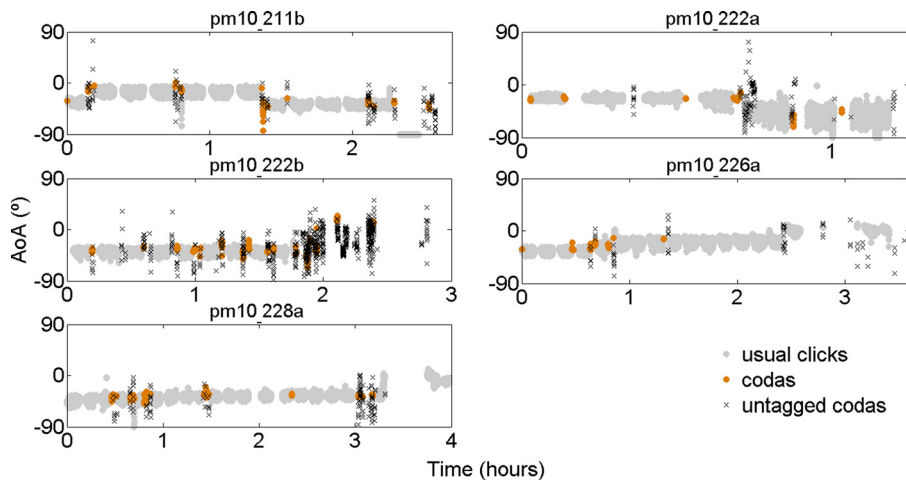
FIG. 1. (Color online) Angle-of-arrival (AoA) of usual clicks and codas (tagged and untagged) recorded on the two hydrophones of the Dtag. "Usual clicks" and "codas" are recorded from the tagged whale while "untagged codas" are assumed to come from neighboring whales. Note the step changes in the tag orientation in pm10_211b and pm10_222a due to movement of the tag on the whale.

source and the tag. Body lengths were calculated from IPIs using the equation in Gordon (1991).

Individual-specific coda differences were investigated in all 3 *Regular* (3Reg) and 5Reg codas (the most abundant shared coda types among tagged individuals) using discriminant function analysis (DFA) with the IPIs and 2 or 4 ICIs as parameters. In order to confirm the contribution of the ICIs to individual discrimination and to investigate if the IPIs are necessary for the discrimination of codas produced by different individuals, three scenarios involving different subsets of the parameters were investigated using DFA: (1) only ICIs; (2) only IPIs; and (3) ICIs and IPIs. The higher standardized coefficients from the DFA match the variables that contribute most to the discriminatory power of the function.

DFA classification error rates were calculated using a jackknife procedure by removing each coda at a time from the dataset and using the remaining codas to calculate linear discriminant functions that were then used to classify the removed coda. The individual discrimination error rate is the proportion of removed codas that were wrongly classified (Antunes *et al.*, 2011). The DFA and classification error rates were computed using custom-written MATLAB code, using a Discriminant Analysis Toolbox (Kiefte, 1999) and STATISTICA software. Posterior probabilities were also calculated to obtain the probability of each coda belonging to a particular individual. The value presented in the results section is the percentage of codas that had a high probability (>0.50) of being assigned to the correct individual.

III. RESULTS

Eleven sperm whales were tagged from 30 July to 18 August 2010. Multiple foraging dives were performed by seven of the tagged sperm whales, and five of these whales produced codas. Of the four whales excluded from analysis, three whales spent most of the time resting at or near the surface and did not produce codas, and the tag on the fourth individual detached 22 min after deployment.

A total of 802 codas were assigned to the five tagged whales. Fifty-one codas were classified as possible codas from the tagged individuals and were removed from the analysis to avoid potential errors in coda attribution. Codas were produced at depths from 0 to 650 m (Fig. 2), and most contained five (47%) or three (23%) clicks. The complete coda repertoire (found with PCA and observer classification) comprised 21 types of codas (Table II); however, the majority of these was produced by just a single whale (pm10_222b). Of the 377 codas with five clicks, the large majority was ascribed to two coda types: 5Reg (n = 290) and 2 + 3 (n = 83). The first two PCA components explained around 91% of the variance in the five-click codas, mainly separating these two major types [Fig. 3(a)]. Codas of type 5Reg were produced by all five sperm whales, although one whale (pm10_226a) only produced this type twice. This whale was therefore not included in the DFA described below. Type 3Reg was also produced by all five whales, but three whales only produced this coda once (Table II).
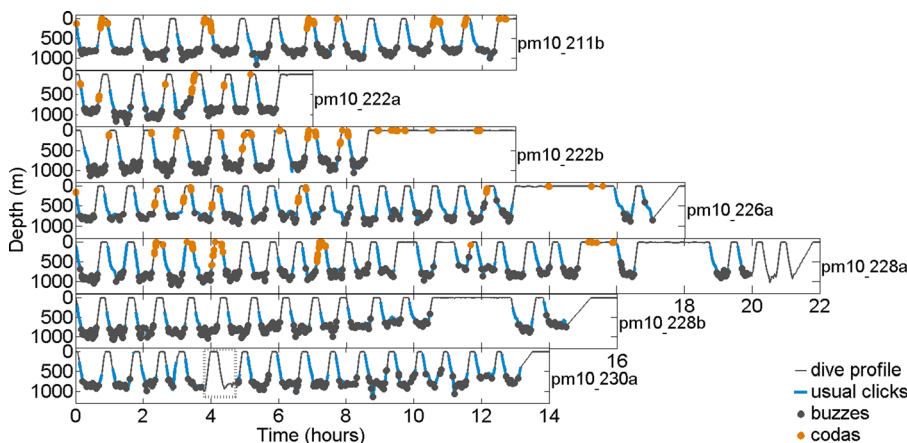

FIG. 2. (Color online) Depth profiles and acoustic signals (usual clicks, buzzes and codas) produced by tagged sperm whales. Usual click lines represent the interval between the first and last produced usual clicks within a foraging dive. Note: the acoustic data for pm10_228a ended after about 20 h of recordings and depth was logged for two more hours, and for pm10_230a there is a period (from 3:46 to 4:47, indicated with a dotted rectangle) without acoustic data due to an error in the audio file.

J. Acoust. Soc. Am. **139** (5), May 2016

Oliveira *et al.* 2863

TABLE II. Estimated body length from IPIs (inter-pulse intervals) and types of codas produced by five sperm whales tagged in the Azores.

Coda type	pm10_211b Mean body length, 9.6 m	pm10_222a Mean body length, 9.1 m	pm10_222b Mean body length, 9.3 m	pm10_226a Mean body length, 9.1 m	pm10_228a Mean body length, 9.4 m	Total
3Reg	1	1	1	81	103	187
4Reg	2	—	2	20	36	59
3 + 1	—	—	1	1	—	3
5Reg	37	57	164	2	30	290
2 + 3	80	—	3	—	—	83
3 + 2	—	—	2	—	—	2
4 + 1	1	—	1	—	—	2
6Reg	—	—	42	—	2	44
5 + 1	37	1	5	—	—	43
7Reg	—	1	23	—	—	24
4 + 3	12	—	—	—	—	12
6 + 1	—	—	4	—	—	4
8Reg	1	1	14	—	—	16
7 + 1	—	—	6	—	—	6
9Reg	—	—	10	—	—	10
8 + 1	—	—	4	—	—	4
10Reg	—	—	5	—	—	5
9 + 1	—	—	3	—	—	3
11Reg	—	—	3	—	—	3
10 + 1	—	—	1	—	—	1
13Reg	—	1	—	—	—	1
Total	171	62	294	104	171	802

Examination of the PCA results by individual [Fig. 3(b)] suggests that there are some differences in 5Reg coda type production between the whales.

Three different DFA scenarios were investigated with a total of 288 5Reg codas produced by four tagged sperm whales in order to test if the measured temporal parameters contributed to individuality in coda production. The number of possible discriminant functions in DFA is either the number of groups minus 1 or the number of predictors, whichever is the smallest. By visually inspecting the canonical function values for the three different scenarios (Fig. 4), it was possible to verify that, although there were overlapped areas with pm10_228a and pm10_222b distributions in both first and third scenarios, the general discriminatory power was improved in the third scenario (ICIs and IPIs). The decrease in the individual discrimination error rate (proportion of removed codas that were wrongly classified) and the increase of individual posterior probabilities (percentage of codas with a high probability of being assigned to the correct individual) between the first and the third DFA scenarios showed that for 5Reg codas ICIs and IPIs together have a higher discriminatory power than when compared one by one (Table III). Generally, in the first and third DFA scenarios, the best differentiation occurred between pm10_211b and the other individuals, but there was also a differentiation between sperm whales that were tagged on the same day (pm10_222a and pm10_222b) (blue and black dots, respectively, in Fig. 4). When performing a DFA with only these two individuals (from the same group) the results showed a good discriminatory power between them (Fig. 5 and Table III). The standardized canonical discriminant coefficients indicate the contribution of each of the individual predictor variables to the discriminant functions. For both first and third DFA scenarios with all the sperm whales that produced 5Reg codas, the discriminant functions were mostly determined by ICI1 and ICI2, with the highest standardized canonical discriminant coefficients (Table III). When comparing the whales from the same group that produced 5Reg codas, the discriminant functions were mainly determined by ICI3 and ICI1 in the first scenario and IPI and ICI1 in the third scenario (Table III).

For the DFA of the 3Reg coda type the dataset comprised 183 codas (one coda of pm10_228a was removed because it was not possible to determine ICI2 with precision due to noise masking of the third click). Similarly as for 5Reg codas, the canonical function values for the three DFA scenarios (Fig. 6) showed overlapped areas in the distributions of the two animals, but the general discriminatory power was slightly improved in the third scenario (ICIs and IPIs) with higher posterior probabilities (Table III). The discriminant function of the third DFA scenario was mostly determined by IPI and ICI1 (Table III).

Although the dataset is too limited for a rigorous analysis of coda behavioral context, two whales appeared to produce distinct codas linked to different dive phases (Fig. 7). For pm10_211b, 2 + 3 codas were mainly produced during ascents, 5 + 1 codas were mainly produced when reaching the surface, and 5Reg codas were mainly produced during descents. For pm10_228a, 3Reg codas were produced during the ascent phase while 5Reg codas were produced upon reaching the surface. The remaining tagged sperm whales did not show any clear connection between coda type production and diving behavior.

IV. DISCUSSION

A major limitation in studies of codas is the difficulty associated with allocating codas to individual sperm whales.
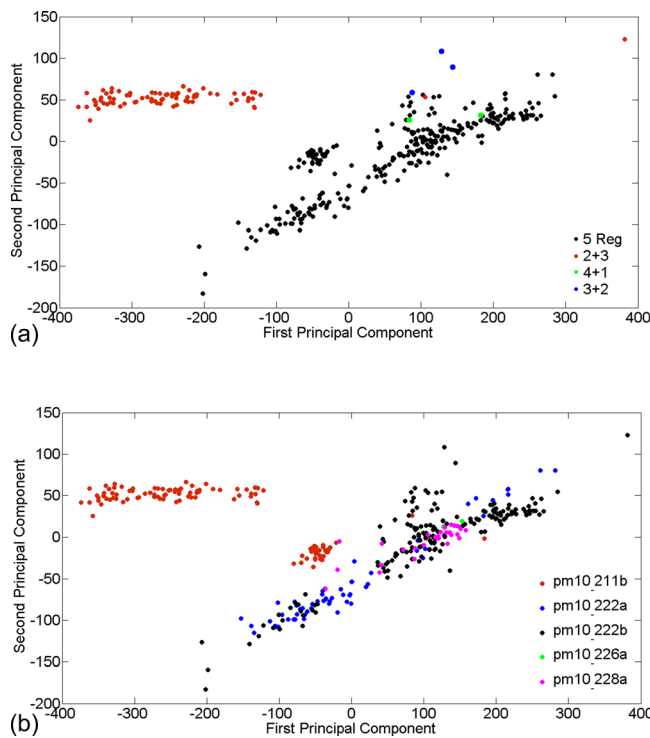
FIG. 3. (Color online) Two principal components of the PCA used to classify 5 click codas. Coda types 5Reg and $2+3$ are separated with a 91% explained variance; (a) distinction of coda types obtained from the PCA, and (b) distinction between individuals from the same PCA.

Previous studies have recorded codas with hydrophones far from the whales. They used several parameters (such as IPIs and signal direction together with surface observations) to assign codas to the producing individuals (Pavan *et al.*, 2000; Antunes *et al.*, 2011; Schulz *et al.*, 2011). The accuracy of these approaches will depend on the group structure and individual behavior which may have great consequences for the interpretation of the results. This problem was avoided by using on-animal stereo recordings that allow unequivocal assignments of codas to individual sperm whales throughout dives. The angle-of-arrival of coda clicks calculated from both hydrophones of the Dtag was used to assign the codas produced by the tagged individuals. All the clicks that were not clearly assigned were excluded from the analyses, which results in a very high confidence level of the coda assignment method. Because this method does not rely on click characteristics such as IPI, it is insensitive to the size of animals in the group. Moreover, because the multi-sensor tag remains attached to one whale for many hours, it obtains a complete record of the coda production of that animal concomitant with its movement and diving behavior.

Early research on codas has classified coda types with standardized ICIs (measurements of ICIs on codas normalized to a constant total duration) and k-means clustering (Weilgart and Whitehead, 1997; Rendell and Whitehead, 2003a, 2003b, 2004; Schulz et al., 2011). While k-means clustering using standardized ICIs appeared to work well to classify codas from the Pacific, where vocal clans exhibit strong differences, it did not perform as well in other cases, when using non-standardized ICIs and on large datasets
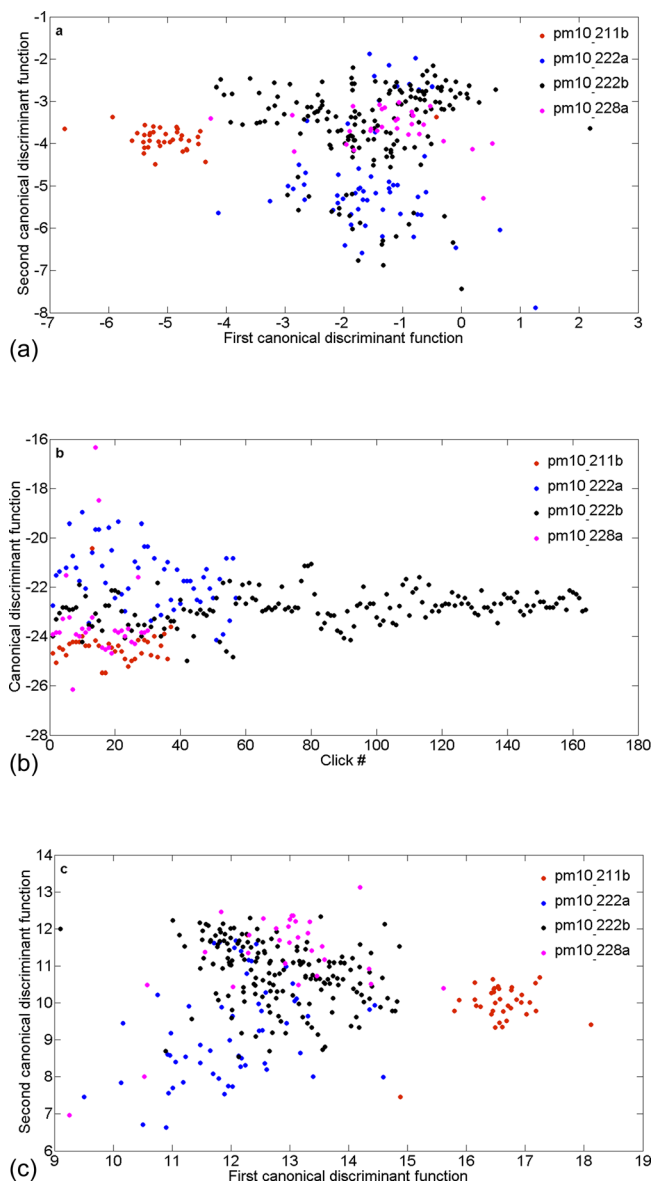

FIG. 4. (Color online) Canonical discriminant functions from DFA of 5Reg codas. Three DFA scenarios were performed for four sperm whales: (a) only ICIs, (b) only IPIs and (c) ICIs and IPIs.

where differentiation is not as strong (Antunes, 2009). K-means requires that the number of clusters is specified in advance, and while some methods exist to determine this (e.g., Rendell and Whitehead, 2003a), they do not always provide a clear solution. Also k-means partitions clusters into Voronoi cells, forming similarly sized clusters and there is no *a priori* reason to think that coda ICI data occur naturally like this. Another study used observer-based classification with absolute ICIs for sperm whale codas recorded in the Mediterranean Sea (Frantzis and Alexiadou, 2008) and Antune*s* et al. (2011) also concluded that the use of absolute ICIs is important to avoid discarding important coda information. In the current study, the classification of coda types used absolute ICIs and was based on PCA and observer classification (for the rare codas). There is confidence that the final classification was sufficiently robust and unbiased, as the first two principal components of the PCA explained 91% of the variance, and the only codas that were classified

TABLE III. Individual discrimination error rates (IDER, proportion of removed codas that were wrongly classified), posterior probabilities (PP, percentage of codas that had a high probability (> 0.50) of being assigned to the correct individual) and two variables with the highest standardized coefficients (SC, the variables that contributed most to the discriminatory power of the function) of the discriminant function analysis of 5Reg and 3Reg codas produced by five sperm whales tagged in the Azores (DFA with 5Reg codas of 4 sperm whales; DFA with 3Reg codas for 2 sperm whales; and DFA with 5Reg codas for 2 sperm whales of the same group).

	IDER (%)		PP (%)			SC
5Reg codas		pm10_211b	pm10_222a	pm10_222b	pm10_228a	
Only ICIs	30	97	40	82	3	ICI1 and ICI2
Only IPIs	31	32	42	96	0	
ICIs and IPIs	23	97	58	91	10	ICI1 and ICI2
3Reg codas		pm10_226a	pm10_228a			
Only ICIs	24	68	66			
Only IPIs	16	74	92			
ICIs and IPIs	16	79	93			IPI and ICI1
5Reg codas		pm10_222a	pm10_222b			
Only ICIs	57	33	89			ICI3 and ICI1
Only IPIs	34	47	98			
ICIs and IPIs	30	40	98			IPI and ICI1

differently from the observer classification in the PCA were the very rare ones. Therefore, the choice to combine the PCA and manual classification methods seems appropriate.

The coda types found in the sperm whales tagged around the Azores mainly comprised 5Reg, 3Reg, 2 + 3 and 4Reg, and the 5Reg was the coda type most frequently shared among all individuals. Previous studies reported that the 5Reg coda type was the most frequently found coda in the Azores archipelago and the majority of codas belonged to the *Regular* type (Antunes, 2000, 2009). This suggests that the current recordings albeit from a limited number of individuals represent the normal coda repertoire of sperm whales from this region.

When comparing the 5Reg and 3Reg codas as produced by different animals in the present data set, there was evidence for individuality in the coda signals in terms of both the IPI, which depends on body size (and therefore changes with the growth of the animal, in a long-term perspective), but also in the ICI which whales most likely have performance control over. In the 5Reg codas the IPI, the cue used widely in other studies to assign codas to individuals, has a slightly lower discriminatory power than ICIs, probably because the tagged whales had similar sizes (Table II). For studies with greater size differences between individuals, IPIs presumably

contribute more to individuality of codas (Antunes *et al.*, 2011; Schulz *et al.*, 2011; Gero *et al.*, 2016), although it is unknown if the whales in fact can detect detailed differences in the shortly spaced IPIs. For all the sperm whales producing 5Reg codas, the first two ICIs contributed most to the discriminatory power of the DFAs. Thus, these results provide additional support to the report of Antunes *et al.* (2011) that individual features are present in 5Reg codas in a different geographic region. However, individual differences in 3Reg codas were also detected (Fig. 6), indicating that there is potential in this coda type for encoding individual features which may extend the potential function of coda clicks. If sperm whales, like other toothed whales (Johnson *et al.*, 2008; Wisniewska *et al.*, 2012) are able to precisely control the ICI of usual clicks and buzzes and resolve the small delays between clicks and echoes when echolocating for prey (Teloni *et al.*, 2008), they should also be able to control and decode individual ICI differences within the same coda type from vocalizing conspecifics. Interestingly, even with the similar-sized whales in the current data, classification performance was improved by using both ICIs and IPIs (the third scenario of the analysis), indicating that the combination of voluntary and involuntary parameters resolves some ambiguity in individual performance of codas.
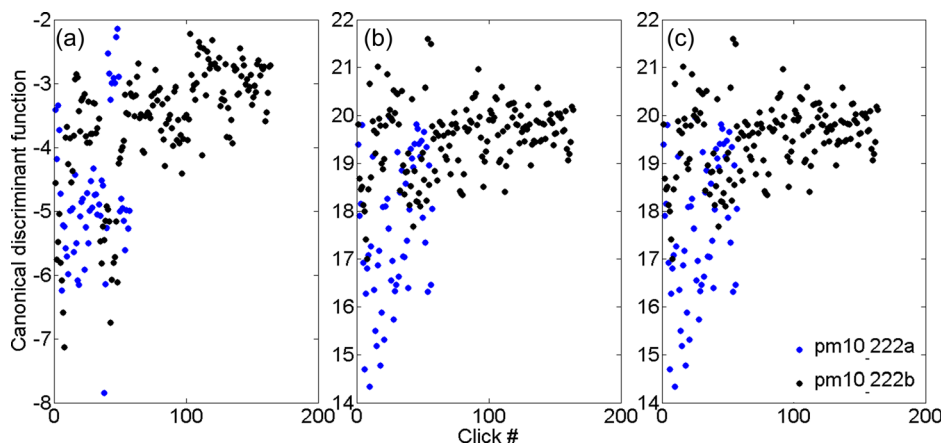

FIG. 5. (Color online) Canonical discriminant functions from DFA of 5Reg codas for two tagged sperm whales from the same group. Three DFA scenarios were performed for two sperm whales: (a) only ICIs, (b) only IPIs, and (c) ICIs and IPIs.
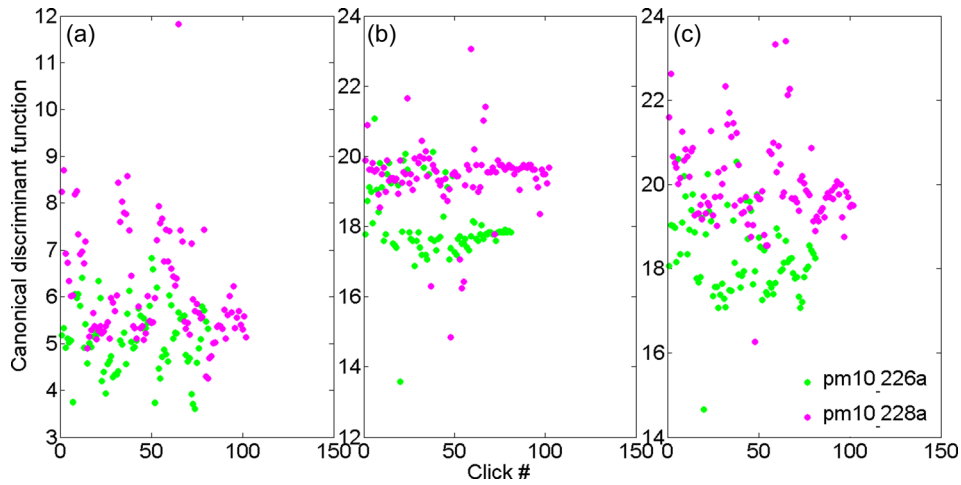
FIG. 6. (Color online) Canonical discriminant functions from DFA of 3Reg codas. Three DFA scenarios were performed for two sperm whales: (a) only ICIs, (b) only IPIs, and (c) ICIs and IPIs.

Besides temporal cues, frequency cues could also be used to encode individuality in the codas. Such frequency-specific individual traits are well-known from other mammals (Van Dommelen, 1990; Hammerschmidt and Todt, 1995; Fischer *et al.*, 2001). For example, in African elephants, frequency-related components contribute to the acoustic discrimination of individuals (McComb *et al.*, 2003; Soltis *et al.*, 2005). In the present recordings of sperm whales, the tagging technique necessitates that the signals will be recorded at an off-axis angle from the directional sound source (Møhl *et al.*, 2000), and this angle varies from individual to individual, depending on where on the whale the tag was attached. This will not modify ICI and IPI measurements (Madsen *et al.*, 2002a) but will strongly influence the spectral components, such as the centroid frequency and root-mean-square bandwidth (Johnson *et al.*, 2009). Thus, it is not possible to determine in the current data whether differences in click spectra are due to individual characteristics or small differences in the tag location on the animal and for this reason spectral parameters were not included in the DFA analysis. However, it is very likely that differences in the frequency content of signals emitted by different whales may contribute to the individual features of the codas as sperm whales are shown to be able to manipulate the spectra of their clicks (Madsen *et al.*, 2002a).

The individual differences found in this study could be a result of the distinct unit/group provenance of the tagged sperm whales analogous to the way that accents help to distinguish human individuals in a group. The whales tagged in this study do not necessarily belong to the same social unit or group. However, two whales tagged in the same day (pm10_222a and pm10_222b) were observed together in the area in 2010, 2011, and 2013 (Steiner, unpublished photo-id data) and, thus, very likely belong to the same social unit [if a pair of sperm whales is associated during at least 2 years they are considered to belong to the same social unit (Christal *et al.*, 1998; Gero *et al.*, 2013)]. Moreover, genetic studies carried out in the Azores suggest that sperm whales sighted together on the same day, as were these two whales, are highly related genetically and may be part of the same social group (Pinela *et al.*, 2009). The data clusters of these two whales are clearly distinguishable (Figs. 4 and 5),

indicating that the differences are caused by inter-individual rather than inter-unit/group variations. Although the clusters of points of these two animals are distinct, the closeness of the clusters (with DFA correct individual discrimination of 40%–58% for pm10_222a and 82%–96% for pm10_222b) hint that there may also be a unit effect such as described in previous studies of vocal clans and dialects (Weilgart and Whitehead, 1997; Rendell and Whitehead, 2003b, 2005; Gero *et al.*, 2016). More data on coda variations within and among groups are needed to better understand which acoustic differences may be individual vs group specific.

There is some evidence that certain codas are produced in specific behavioral contexts although these studies are limited in the range and precision of behavioral inferences
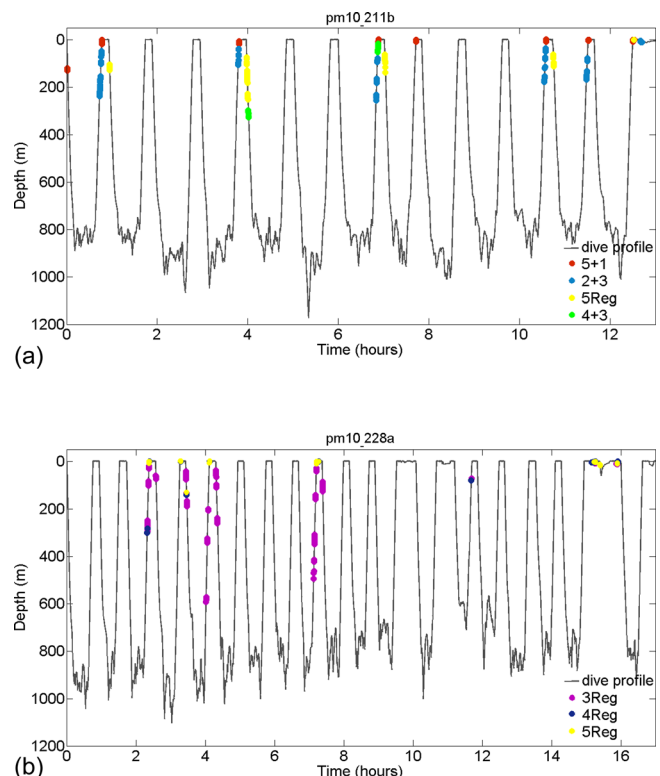

FIG. 7. (Color online) Distinct coda types in relation to depth for two tagged sperm whales. Production of different coda types as a function of depth for sperm whales pm10_211b (a) and pm10_228a (b). Coda types emitted less than four times were omitted for clarity.

J. Acoust. Soc. Am. **139** (5), May 2016

Oliveira *et al.* 2867

that can be drawn from remote sound recordings. For example, the 5Reg coda has been suggested to have the function of initiating coda exchanges (Weilgart and Whitehead, 1993). Moreover, the behavioral context of different coda groupings has been found to vary among male sperm whales (Frantzis and Alexiadou, 2008). Another study reported individual-specific information differences between coda types which seemed to point toward different functions of distinct coda types (Antunes et al., 2011). Patterns of coda type production were found in two individuals (Fig. 7) that support the notion of a specific behavioral context of coda types which may also be related with an individual function of coda clicks. Although only anecdotal given the small data size, these observations suggest that studies of variation in coda repertoire should take into consideration the context in which codas are produced. Thus, comparing sperm whale coda repertoires recorded in different contexts may highlight variation due to context instead of an actual difference of repertoire. Therefore, characterization of coda repertoire variability (e.g., geographic) should ideally include recordings in as many different contexts as possible, and care should be taken when comparing repertoires to ensure that a similar range of contexts are represented.

V. CONCLUSIONS

Until recently (Antunes et al., 2011), most studies on sperm whale codas emphasized their function in allowing different units and clans to distinguish each other on an acoustic basis (Weilgart and Whitehead, 1997; Rendell and Whitehead, 2003b). The current study provides data that reinforces the findings of Antunes et al. (2011), suggesting that individual information may also be encoded in codas in the form of subtle variations in the click pattern. Furthermore, the Dtag data presented here imply that individual differences in the types of codas produced may depend on the dive phase or behavioral context. Thus codas may encode individual information to a much larger extent than previously thought (Rendell and Whitehead, 2003b), which may have important consequences for the general understanding of the social system of sperm whales, where acoustic communication could convey much more than only group or clan identity.

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J. Acoust. Soc. Am. 139 (5), May 2016

Oliveira et al. 2869