ARTICLE

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Vocal repertoires and insights into social structure of sperm whales (*Physeter macrocephalus*) in Mauritius, southwestern Indian Ocean

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Abstract

Sperm whales communicate using codas (stereotyped click sequences). Females and juveniles live in long-term social units, and units with similar coda repertoires share vocal clan membership. Vocal clans exhibit culturally defined differences in their multilevel social structure. Here, we aimed to identify different social units among sperm whales in Mauritius in the southwestern Indian Ocean, and to describe and compare their coda repertoires to investigate the presence of different vocal clans. We conducted six boat-based surveys between 2008 and 2013, during which 101 different individuals were photo-identified. Analysis of associations between 22 resighted individuals divided them into four candidate social units, but a lack of resightings impedes solid delineation of social units. Based on number and rhythm of clicks, at least 24 discrete coda types were detected among 4,767 analyzed codas using two different classification methods. Comparison of coda repertoires recorded from seven sperm whale groupings revealed the possible existence of two sympatric vocal clans, but the size differences of recorded repertoires warrant caution of interpretation. To further evaluate social structuring and the presence of different vocal clans in this region, future

surveys should aim at obtaining long-term sighting and acoustic data, and cover a more extensive area.

1 | INTRODUCTION

The sperm whale (*Physeter macrocephalus* Linnaeus 1758) is a cosmopolitan, deep-water odontocete (Rice, 1989). It has a complex social structure, characterized by different levels of social groupings based on sex and age (see review by Whitehead, 2003). The most basic social grouping is the "social unit," consisting of on average 12 individuals (with an observed range of 3–24 individuals; Christal, 1998) and including only adult females, their calves, and juveniles (Whitehead, Waters, & Lyrholm, 1991). This social unit is long-lasting and generally stable, although splits, mergers, and transfers between units take place occasionally (Christal, Whitehead, & Lettevall, 1998). Males become more solitary with age and migrate between the polar waters and the equator when sexually mature, whereas the units of females and juveniles are largely philopatric and remain in low-latitude regions (Best, 1979; Rice, 1989).

In some regions, such as the Eastern Tropical Pacific, different social units may temporarily aggregate into larger groups, whereas in the North Atlantic, they do not or only rarely do so (Gero, Bøttcher, Whitehead, & Madsen, 2016b; Whitehead et al., 1991, 2012). Long-term studies have revealed significant differences in the characteristics of the multilevel social structuring among female sperm whales, both within and between ocean basins. For instance, differences were found in mean social unit and group sizes, the genetic relatedness between unit members, and group-specific behaviors such as movement patterns, habitat use, and diving synchrony (Cantor & Whitehead, 2015; Marcoux, Whitehead, & Rendell, 2007; Whitehead, 1999; Whitehead & Rendell, 2004). Furthermore, sperm whales have different vocal dialects which seem to play an important role in their social organization (Rendell & Whitehead, 2003a; Weilgart & Whitehead, 1997).

Sperm whales produce a range of clicking sounds on which they rely for orientation, prey detection, and communication (see review by Whitehead, 2003). When groupings of sperm whales are socializing at the water surface, stereotyped click sequences of 3–40 clicks can be heard (Watkins & Schevill, 1977). These click sequences were called "codas" by Watkins and Schevill (1977) and, given the manner and context in which they are produced, were inferred to be used for communication (Watkins & Schevill, 1977; Weilgart & Whitehead, 1993; Whitehead & Weilgart, 1991). Specific codas could not be linked to specific social behaviors (Weilgart, 1990; Weilgart & Whitehead, 1993, 1997), but Frantzis and Alexiadou (2008) were able to associate certain coda types with three behavioral contexts in subadult male sperm whales in the Mediterranean: socializing at the surface, ascending or descending during regular feeding dive cycles, and altering dive cycles due to disturbance. Furthermore, codas seem to contain information about the identity of the individual producing them, as well as about the social unit and vocal clan (see below) from which the individual originates (Antunes et al., 2011; Gero, Whitehead, & Rendell, 2016a; Oliveira et al., 2016; Schulz, Whitehead, Gero, & Rendell, 2011).

Each social unit has a specific repertoire of codas (i.e., vocal dialect). All sperm whales with similar vocal dialects are said to belong to the same "vocal clan," and different social units prefer to form groups only with units from within their own clan (Rendell & Whitehead, 2003a). In the Pacific, different vocal clans may occur sympatrically on a large geographic scale (Amano, Kourogi, Aoki, Yoshioka, & Mori, 2014; Rendell & Whitehead, 2003a; Weilgart & Whitehead, 1997; Whitehead, Dillon, Dufault, Weilgart, & Wright, 1998), but in the Atlantic, vocal dialects become less similar with increasing geographic distance and vocal clans are usually allopatric (Antunes, 2009; Whitehead et al., 2012), although a recent study revealed two socially segregated sympatric vocal clans in the Eastern Caribbean (Gero et al., 2016b).

Observed differences between groups of sperm whales (for instance, in group size or in feeding or social behaviors) were found to be linked to vocal clan membership (Cantor & Whitehead, 2015; Marcoux et al., 2007; Rendell & Whitehead, 2003a; Whitehead & Rendell, 2004). It has been suggested that the differences between vocal clans are a product of cultural transmission rather than genetic inheritance (Cantor et al., 2015; Gero et al., 2016b; Rendell, Mesnick, Dalebout, Burtenshaw, & Whitehead, 2012; Rendell & Whitehead, 2003a; Whitehead et al., 2012), with culture defined here as shared, socially learned behavioral patterns (Laland, Kendal, & Kendal, 2009; Whitehead, 2010). Differentiation in the biparentally inherited nuclear DNA was found to be low both between oceans (Alexander et al., 2016; Lyrholm, Leimar, Johanneson, & Gyllentsen, 1999) and within oceans (Alexander et al., 2016). Rendell et al. (2012) investigated variation in the maternally inherited mitochondrial DNA (mtDNA) among sympatric vocal clans in the Pacific Ocean and found that matrilineal population genetic structure was more defined by vocal clan membership than by geographic region. In addition, Alexander et al. (2016) found that the levels of within-ocean regional differentiation in mtDNA were much higher in the Atlantic and Indian oceans than in the Pacific, even when accounting for social unit/group (and thus vocal clan) membership. In other words, the influence of geographic philopatry vs. social philopatry on matrilineal population genetic structure differs per ocean basin (Alexander et al., 2016), correlating with the observation of vocal clans usually occurring allopatrically in the Atlantic (Antunes, 2009; Gero et al., 2016b; Whitehead et al., 2012) or sympatrically in the Pacific (Amano et al., 2014; Rendell & Whitehead, 2003a; Weilgart & Whitehead, 1997; Whitehead et al., 1998).

Without an evident geographic and/or genetic population structure, culture should be considered when designating management units for conservation. After all, socially learned vocal dialects and behavior reflect more recent changes in a population structure than genes do (Antunes, 2009). Even though global population numbers are estimated to be in the 100,000 s (Whitehead, 2002), current population trends are unknown (Taylor et al., 2019). However, the effect of current anthropogenic threats has become visible with multiple strandings in the last decade of sperm whales that had ingested large amounts of plastic and other marine litter (e.g., de Stephanis, Giménez, Carpinelli, Gutierrez-Exposito, & Cañadas, 2013; Jacobsen, Massey, & Gulland, 2010), highlighting the need for effective conservation measures.

To achieve effective regional management and conservation based on the cultural traits of sperm whales, knowledge of the different levels of social structure (i.e., from social unit to vocal clan) are needed for the sperm whales in that particular region. Here we present the results of the first assessment of social structure and vocal repertoires of sperm whales in Mauritius, a volcanic island located in the southwestern Indian Ocean, using photo-identification and acoustic data collected between 2008 and 2013. Given that sperm whales in the Indian Ocean show high regional mtDNA differentiation, similar to sperm whales in the Atlantic Ocean (Alexander et al., 2016), we expected to find a social structure similar to the one found in the Atlantic Ocean as well, i.e., possible absence of a pronounced group-level (Whitehead et al., 2012), and presence of allopatric vocal clans (although sympatric vocal clans are also possible; Gero et al., 2016b).

2 | MATERIALS AND METHODS

2.1 | Data collection

Six surveys were conducted on board a 14-m catamaran in the southwestern Indian Ocean between 2008 and 2013. Each survey, departing from and returning to Reunion, was about one week in duration and mainly covered the southwest coast of Mauritius (Figure 1). In total, 268.2 hr were spent searching for sperm whales.

Sperm whale vocalizations were detected and recorded using an array of two medium-frequency hydrophone elements (Benthos AQ4) and a matched pair of two broadband preamplifiers (Magrec HP/01) with noise filters set to −3 dB at 100 kHz, an amplifier (Magrec HP/27ST) providing additional gain of 10–50 dB and high-pass filtering between 0–3 kHz, a sound card (Fast Track Pro; M-audio), and a regular PC laptop equipped with the software
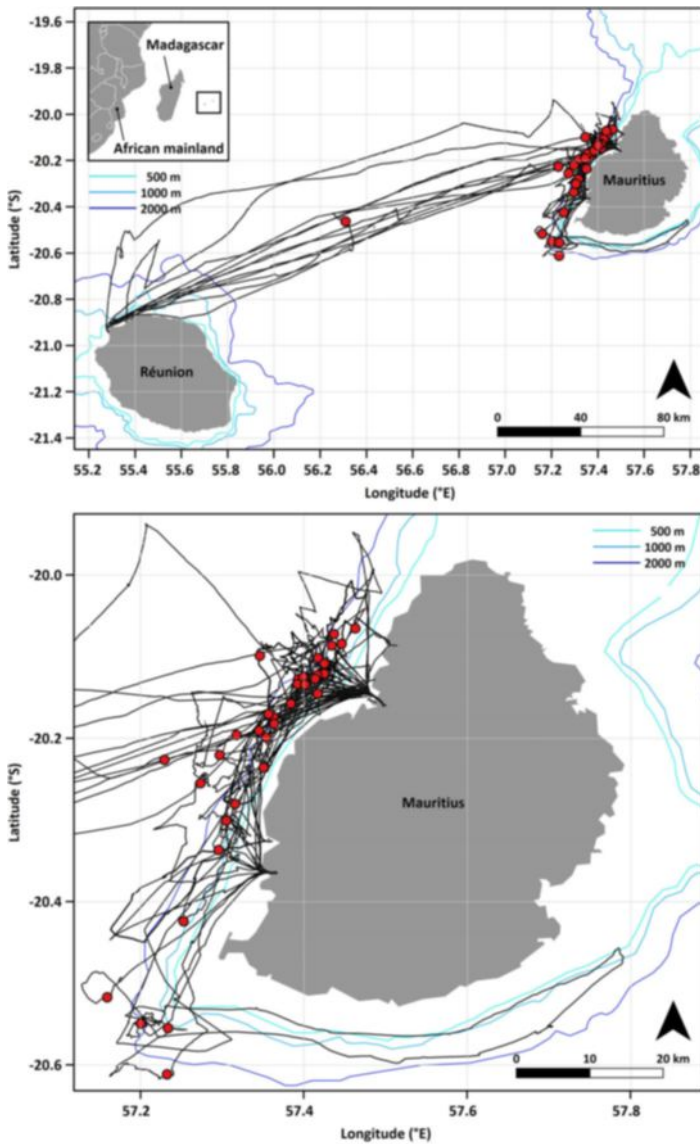
FIGURE 1 Maps showing crossing tracks between Reunion and Mauritius and overall survey effort around Mauritius (black lines) and sighting locations (red dots). The lower panel zooms in on Mauritius and does not show the sighting made during the 2011 crossing (see upper panel). Blue colored lines indicate bathymetric contours at 500 m, 1,000 m, and 2,000 m.

RainbowClick (v. 6.0; International Fund for Animal Welfare; see Gillespie, 1997; Gillespie & Leaper, 1996; Leaper, Gillespie, & Papastavrou, 2000). The hydrophone elements and preamplifiers were housed in a polyurethane tube filled with an inert oil and towed by the boat on a 100-m-long cable. The hydrophone was deployed in sufficiently deep water (i.e., >100 m) at the start of each surveying day.

Every 30 min, a 1-min audio recording (48-kHz WAV file; 16-bit stereo) was made to check for sperm whale vocalizations. Disturbing sound sources such as the boat engines and some electrical devices were turned off during sound recordings. When sperm whale clicks were heard, the real-time click-detecting program RainbowClick was used to estimate the direction and distance of the clicks with respect to the boat.

On arrival near a grouping of sperm whales, sounds were recorded continuously until the sperm whales stopped vocalizing or until the boat engines were turned on to follow them. Generally, the sperm whales were followed until fluke pictures for photo-identification (photo-ID; Arnbom, 1987) were obtained for as many individuals as possible, provided that the whales did not seem to be disturbed by our presence.

During sightings, multiple individuals near each other (<40 m), exhibiting similar behavior and if traveling, heading in the same direction, were termed a "cluster" following Whitehead (2003). Encountered clusters that consisted of individuals not previously sighted were given a name. If a cluster contained one or more resighted individuals, it was given the same name as the cluster which the resighted individuals were previously seen in. In this case, the "named grouping" did not necessarily correspond to any defined social grouping. No overlap of named groupings occurred (i.e., no individuals were observed in more than one named grouping).

As sperm whales make foraging dives that may last well over 30 min (Irvine, Palacios, Urbán, & Mate, 2017; Watkins, Daher, Fristrup, & Howald, 1993; Watwood, Miller, Johnson, Madsen, & Tyack, 2006), different sightings were temporally separated by at least 1 hr and/or spatially separated by at least 2 km distance.

2.2 | Data analysis

2.2.1 | Analysis of social structure

The photo-ID fluke pictures taken during each survey were manually cataloged and compared by different observers. Only photographs of sufficient quality (i.e., $Q \geq 3$ on a scale from zero to five; Arnbom, 1987) were used in the photo-ID catalog and for matching purposes. Calves were excluded, as their flukes were not marked yet and therefore difficult to identify. Adult males (recognized by their larger size, >12 m, compared to adult females and juveniles) were included in the photo-ID catalog, but excluded from analyses, as they associate with social units only for short periods of time and are not actually part of them (see review by Whitehead, 2003).

The social structure of photo-identified sperm whales was investigated using the software package SOCPROG (v. 2.4; Whitehead, 2009). For each pair of individuals that were sighted on at least three different days in all surveys combined, an association index was calculated, i.e., an estimate of the proportion of time that two individuals spend together. The half-weight association index (HWI) was calculated using the following formula (see Cairns & Schwager, 1987; Ginsberg & Young, 1992; Whitehead, 2008):

$$\text{HWI} = \frac{x}{x + y_{AB} + 0.5(y_A + y_B)} \tag{1}$$

where x is the number of sampling periods in which two individuals (A and B) were associated (i.e., sighted together); y_{AB} is the number of sampling periods in which A and B were identified, but not associated; y_A and y_B are the number of sampling periods in which only A or only B was identified, respectively. Values for the HWI calculated using Equation 1 can range from zero (i.e., never associated) to one (i.e., always associated).

The HWI was calculated because it is the least biased association index when not all associates are identified during each sighting (Whitehead, 2008), which was sometimes the case during the surveys. "Association" was defined in SOCPROG as being grouped during the sampling period, with "group" defined as sighting number (we never encountered more than one cluster during a sighting), and "sampling period" defined as day.

SOCPROG was then used to perform a hierarchical cluster analysis of the HWI association data, producing an average-linkage dendrogram (Milligan & Cooper, 1987). The cophenetic correlation coefficient (CCC; Sokal & Rohlf, 1962), an indicator of the correlation between the actual HWI values and the clustering levels in the dendrogram, was calculated to check the effectiveness of the hierarchical clustering (with a CCC of at least 0.8 being considered effective; Bridge, 1993). Subsequently, a cut-off value was defined for the dendrogram, such that clusters formed at association indices above the cut-off value were considered social units. The maximum modularity method was applied to identify the most appropriate cut-off value (Newman, 2004).

2.2.2 | Acoustic analysis

All recorded sound files were played through Windows Media Player (Microsoft) to evaluate their quality and check for the presence of codas. Recordings in which coda clicks were barely audible due to background noise were discarded. The retained recordings were cut into fragments of between 10 and 20 s using either Raven Pro (v. 1.4; Bioacoustics Research Program, Cornell Lab of Ornithology) or Cool Edit Pro (v. 2.0; Syntrillium Software) to remove long intervals without codas.

The short fragments were analyzed using RainbowClick, which automatically detects clicks and displays them as dots in a plot of bearing vs. time, with dot sizes corresponding to the relative loudness of the clicks. Dots that were recognized as being part of the same coda (i.e., that had the same intensity and bearing) were manually selected and labeled in the same color. When clicks were difficult to assign to a coda because of their short interclick interval (ICI; i.e., the time between two subsequent clicks) or overlap by surface reflections (at shallow hydrophone depths; Rhinelander & Dawson, 2004), echolocation clicks, or other codas, the 48-kHz sound fragments were played back at 8 kHz and click waveforms were investigated. Ambiguous codas were discarded. For each labeled coda, click-specific information such as timing and absolute ICIs were exported for further analysis.

The exported codas were sorted by their number of clicks (N) and classified into types based on the temporal pattern of their clicks. Codas were visualized as dots (i.e., clicks) connected by lines (i.e., ICIs) using a custom-written script (Lionel Morgado, email: lionelmorgado@gmail.com) in R (v. 3.2.5; R Development Core Team, 2016) and checked by a human observer. Based on these graphic coda representations, the observer first sorted N-click codas into visually similar "types" and then manually removed codas that did not fit into any such type from the data set altogether, as these were considered to be outliers.

All retained codas were run through a series of custom-written MATLAB (v. 9.4.0.8 [R2018a]; MathWorks, Inc.) scripts for automatic coda classification (Rendell & Whitehead, 2003a, b). These scripts contain an iterative algorithm for K-means clustering, a method which divides data (here: each N-click coda set) into a K number of clusters, so as to minimize the pooled within-cluster sum of squares (Ding & He, 2004). The "stopping rule" for objectively deciding on a proper K that was implemented in the scripts was based on the variance ratio criterion (VRC; Caliński & Harabasz, 1974). Initially, the K-means clustering ($2 \leq K \leq 10$) was run 20 times for each N-click coda set. However, the VRC suggested different optimal Ks in different attempts at running the iterative algorithm, or it did not show local maxima with increasing K at all (see Rendell & Whitehead, 2003a, b; Schreer, O'Hara Hines, & Kovacs, 1998). Final choice of K was therefore based on the minimum number of clusters identified by the observer using the graphic coda representations produced in R. If the VRC-identified clusters corresponded to the observed clusters, the analysis was run again with $K + 1$. If this resulted in addition of an observable cluster, $K + 2$ was used, etc., until no new clusters were found. If the VRC-identified clusters did not correspond to the observed clusters, the analysis was re-run with an adjusted K until they did. Clusters were automatically numbered by the MATLAB scripts; naming protocols based on coda rhythm (e.g., Van der Schaar & André, 2006; Weilgart & Whitehead, 1993, 1997) were not adopted.

In addition to K-means clustering, a density-based clustering method was adopted for comparison of classifications. The hierarchical clustering algorithm OPTICSxi (Ankerst, Breunig, Kriegel, & Sander, 1999) was run on each set of N-click codas following Gero et al. (2016a, b) and Cantor, Whitehead, Gero, and Rendell (2016). One of the advantages of OPTICSxi over K-means is that there is no preset number of clusters (i.e., K) and codas located in low-density areas between dense clusters may be labeled as "noise" instead of being forced into clusters. A priori sensitivity analysis to define initial parameter values (see Cantor et al., 2016) indicated that no fixed values for the parameters ξ (xi; contrast parameter, establishing the relative decrease in density) and MinPts (the minimum number of points a cluster should contain) could be used across all separate N-click coda analyses. Therefore, the reachability distance parameter ε (epsilon) was set at around 0.1 for each N-click coda set, but ξ was set at 0.015 for 8- and 9-click codas, at 0.03 for 10-click codas, at 0.04 for 6- and 7-click codas, and at 0.05 for 3-, 4-, 5-, 11-, and 12-click codas. MinPts was set at 3% of the sample size of each N-click coda set, but with a minimum value of 15. The

OPTICSxi algorithm was run using the software ELKI (v. 0.7.5; Schubert & Zimek, 2019; available at https://elki-project.github.io/).

All codas recorded from each named grouping of sperm whales, across different sightings and surveys, were pooled into a repertoire. Repertoires did not necessarily represent the entirety of different coda types produced by named groupings. To investigate the presence of different, sympatric vocal clans, coda repertoires consisting of a minimum of 50 codas were compared between named groupings using a function for multivariate similarity (S_{AB}) implemented in a series of custom-written MATLAB scripts (Rendell & Whitehead, 2003b):

$$S_{AB} = \frac{\sum_{i=1}^{n_A}\sum_{j=1}^{n_B} 1 \frac{b}{b + d_{ij}}}{n_A n_B}_{l_j = l_i} \qquad (2)$$

where n_A and n_B are the number of codas in repertoire A and B, respectively; $b/(b + d_{ij})$ is a measure of similarity, with d_{ij} being the Euclidean distance measure and "resolution measure" b set at 0.001; l_i is the number of clicks in coda i of repertoire A; l_j is the number of clicks in coda j of repertoire B (Rendell & Whitehead, 2003b). Note that Equation 2 does not produce one when a repertoire is compared with itself; instead, it produces a "self-similarity," an approximate indication of the within-repertoire coda diversity, such that relatively nondiverse repertoires will have relatively high self-similarities (Rendell & Whitehead, 2003b).

The resulting pairwise repertoire similarities were visualized in an average-linkage dendrogram using SOCPROG. Although SOCPROG was originally developed to investigate social structure, the software was used to create this dendrogram from acoustic data using matrices of similarity values instead of association indices. The CCC was calculated to check the effectiveness of the hierarchical clustering. Bootstrap support (1,000 iterations) was provided for each branching node.

3 | RESULTS

3.1 | Sightings and photo-identification

The six surveys in Mauritian waters resulted in 36 sperm whale sightings during which whales were photo-identified. (Figure 1, Table 1). Sizes of sperm whale clusters ranged from 3 to 34 individuals, with a mean cluster size of 8.9. Solitary individuals were encountered on two occasions; one of these was an adult male and the other was

TABLE 1 General and sighting information per survey.

Survey	Survey period	Survey hours	No. of sightings	New IDs	Total IDs	Total recorded duration[a]	Analyzed codas
2008	7–16 May	37.4	6	15	23	16:41:38	757
2009	17–25 October	37.2	7	21	27	09:18:14	612
2011	30 June–7 July	38.2	9	28	45	08:49:03	391
2012a	25 April–2 May	39.1	6	3	59	05:49:49	217
2012b	8–16 December	76.8[b]	5	22	27	06:00:52	462
2013	26 May–2 June	39.5	3	12	54	11:19:02	2,328
Total		268.2	36	101	235	57:58:38	4,767

[a]Hours:minutes:seconds.
[b]In this survey, one night between prospecting days was spent at sea. Continuous acoustic monitoring took place, but no photo-ID data were collected.
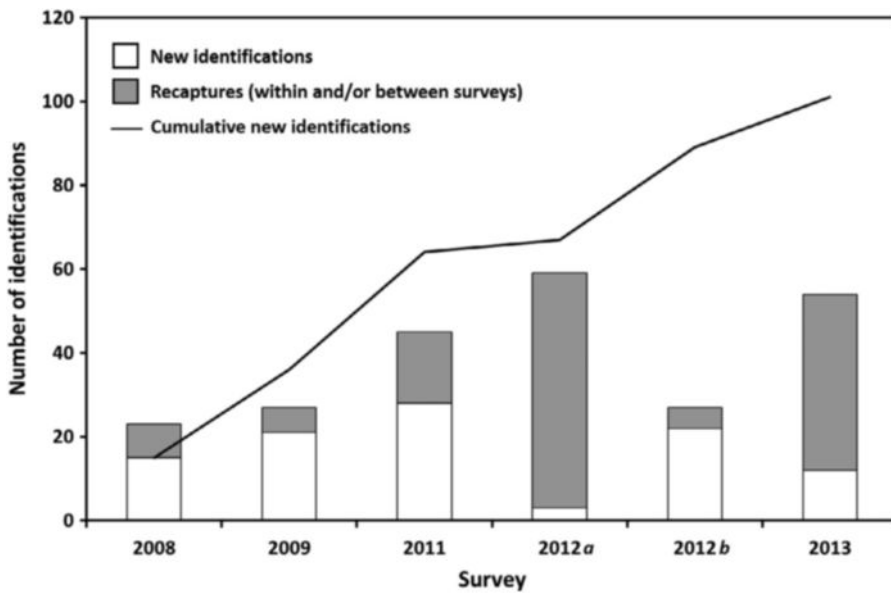
FIGURE 2 Sperm whale photographic identifications made during each survey.

not (inferred by its size), but its sex was unconfirmed. Only two adult males were encountered in all surveys combined. The total number of photo-identified flukes was 235; 134 of which were recaptures. After six surveys, the photo-ID catalogue thus consisted of 101 individuals (Table 1, Figure 2), 69 of which were only sighted once. On average, 16.8 new individuals were added to the photo-ID catalog after each survey. Of the 134 recaptures, 110 individuals were resighted between surveys and 85 within surveys (note that being sighted within- or between-survey is not mutually exclusive; Figure 2). Flukes were generally well-marked; some of the individuals that were resighted between surveys had significantly altered fluke markings, but could be identified correctly by eye.

3.2 | Social structure

The 99 photo-identified adult females and juveniles were divided over 11 named groupings (Table 2). Members of CAP were sighted most often and were resighted consistently between surveys; except during the 2012*b* survey when the south of the island was surveyed more than the west (see also Figure 1). During the 2012*a* survey, only members of CAP were sighted. Clusters including CAP members ranged in size from four to 34 individuals and were encountered during 18 of the 36 sightings. No members of the other named groupings were resighted between surveys (Table 2).

Of the 99 adult females and juveniles included in the photo-ID catalogue, 22 individuals (three ARO members and 19 CAP members) were sighted on at least three different days in all surveys combined and were thus included in the SOCPROG analysis. The hierarchical clustering dendrogram (Figure 3) based on the HWI calculated for each pair of individuals in SOCPROG (Table S1) had a CCC of 9.55×10^{-1}, indicating meaningful representations of clusters. The cut-off value as defined by maximum modularity corresponded to an association index of 5.96×10^{-1}, subdividing the 22 individuals into four clusters that represent social unit candidates (Figure 3). However, limited resighting data between years prevents solid delineation of actual social units.

TABLE 2 Information on 11 named groupings of sperm whales.

Named grouping name	Name abbreviation	Identified no. of members	No. of sightings	Survey(s) sighted	Recording duration	Analyzed codas
Arobase's group	ARO	8	4	2008	06:35:44	202
Capsule's group	CAP	33	18	2008–2012*a*, 2013	18:48:47	3,944
Dentelle's group	DEN	5	2	2009	00:18:26	2
Brisure's group	BRI	2	1	2009	00:33:01	103
Calypso's group	CAL	1	1	2011[a]	00:55:31	5
Lili's group	LIL	9	1	2011	00:24:37	55
Escarpe's group	ESC	8	1	2011	00:28:50	8
Socrate's group	SOC	5	1	2011	00:36:08	81
Baboo's group	BAB	1	1	2012*b*	00:09:45	0
Malik's group	MAL	8	2	2012*b*	01:03:24	75
Chouchou's group	CHO	13	2	2012*b*	00:44:28	393

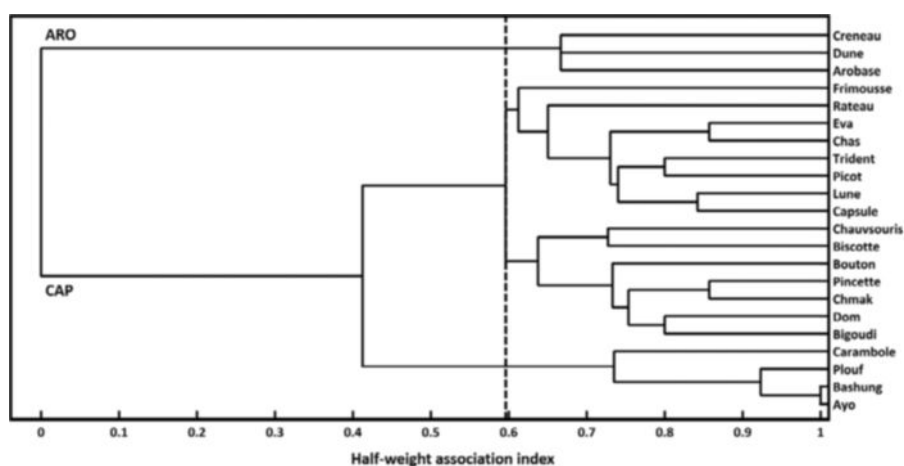[a]CAL was sighted during the crossing between Reunion and Mauritius.

FIGURE 3 Average-linkage dendrogram showing hierarchical clustering based on pairwise half-weight association indices between members of named groupings ARO and CAP calculated using equation (1). The dotted vertical line indicates the cut-off value for social units based on maximum modularity.

3.3 | Vocal repertoires

3.3.1 | Coda types

In total, over 58 hr of sound recordings were made during sperm whale sightings. About 5 hr of these recordings contained codas and were cut into 1,095 fragments of 10–20 s for analysis in RainbowClick. In total, 5,379 codas were extracted from the audio fragments, with a mean of 3.1 codas per 10 s. The number of detected codas per 10 s in the fragments ranged from one to 24.7.

Most of the labelled codas ranged in length from two to 14 clicks, with eight-click codas being the most common (32.3% of all codas; Figure 4). However, the 13- and 14-click codas and coda-like click sequences consisting of ≥15
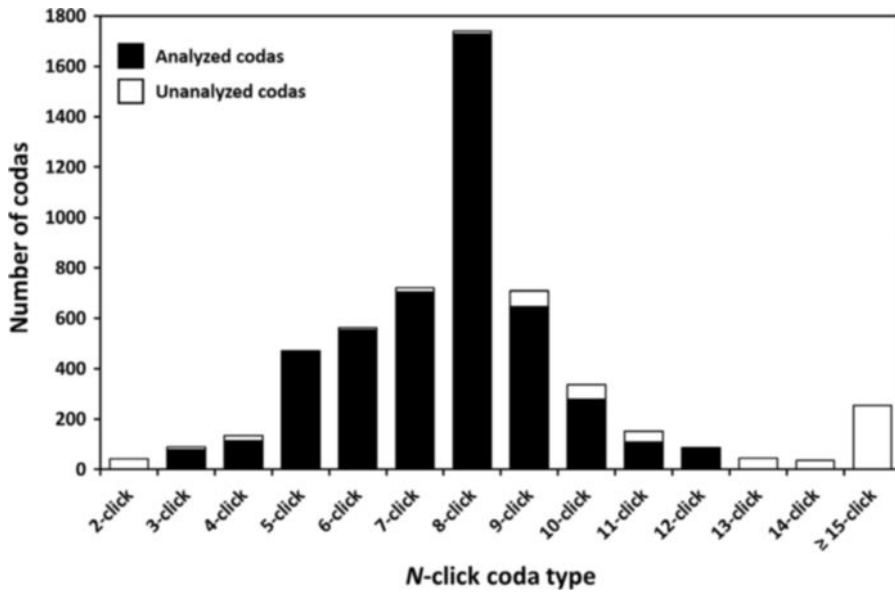
FIGURE 4 Frequency distribution of labelled and analyzed codas per *N*-click coda type.

clicks were not included in subsequent analyses, as they were rare and too variable to be divided into distinct types by the observer. The 2-click codas were excluded from the analyses as well, since two-click codas cannot be classified according to rhythm—they consist of only one ICI.

Of the 5,379 codas that were originally labeled and extracted with RainbowClick, 4,767 were retained for analysis (Figure 4). Following the *K*-means/observer clustering method, 37 different clusters, or coda types, were found in total (Figure 5; Table 3). Following the OPTICSxi method, 30 coda types were detected (Figure 5, Table 4). Among both the *K*-means/observer clusters and the OPTICSxi clusters, regular-type codas (i.e., codas with evenly spaced clicks; Weilgart & Whitehead, 1993) occurred among three-, four-, five-, six-, and seven-click codas (Figure 5). The minimum number of *K*-means/observer clusters found within an *N*-click coda type was three and the minimum number of OPTICSxi clusters found within an *N*-click coda type was one. The maximum number of *K*-means/observer clusters found within an *N*-click coda type was four and the maximum number of OPTICSxi clusters found within an *N*-click coda type was five. The mean numbers of *K*-means/observer clusters and OPTICSxi clusters per *N*-click coda type were 3.1 and 2.5, respectively. Comparing graphical representations of average codas from each type (Figure 5), 24 coda types were detected using both clustering methods. The most commonly heard coda type was among those; an eight-click coda, consisting of two rapidly succeeding clicks followed by six slower clicks (clusters K8.3 and O8.1 in Figure 5). The portion of each *N*-click type in the total number of codas differed per named grouping (Tables 3 and 4).

3.3.2 | Vocal clans

Coda repertoires were compared between seven of the 11 named groupings of sperm whales. DEN, CAL, and ESC were excluded from the analysis, as their recorded repertoires contained only two, five, and eight codas, respectively. For BAB, no coda recordings were available.

The level of similarity between pairs of repertoires was low (Table S2). Unsurprisingly, self-similarity was lowest for CAP, as CAP had the largest recorded repertoire. For the same reason, similarity values resulting from pairwise
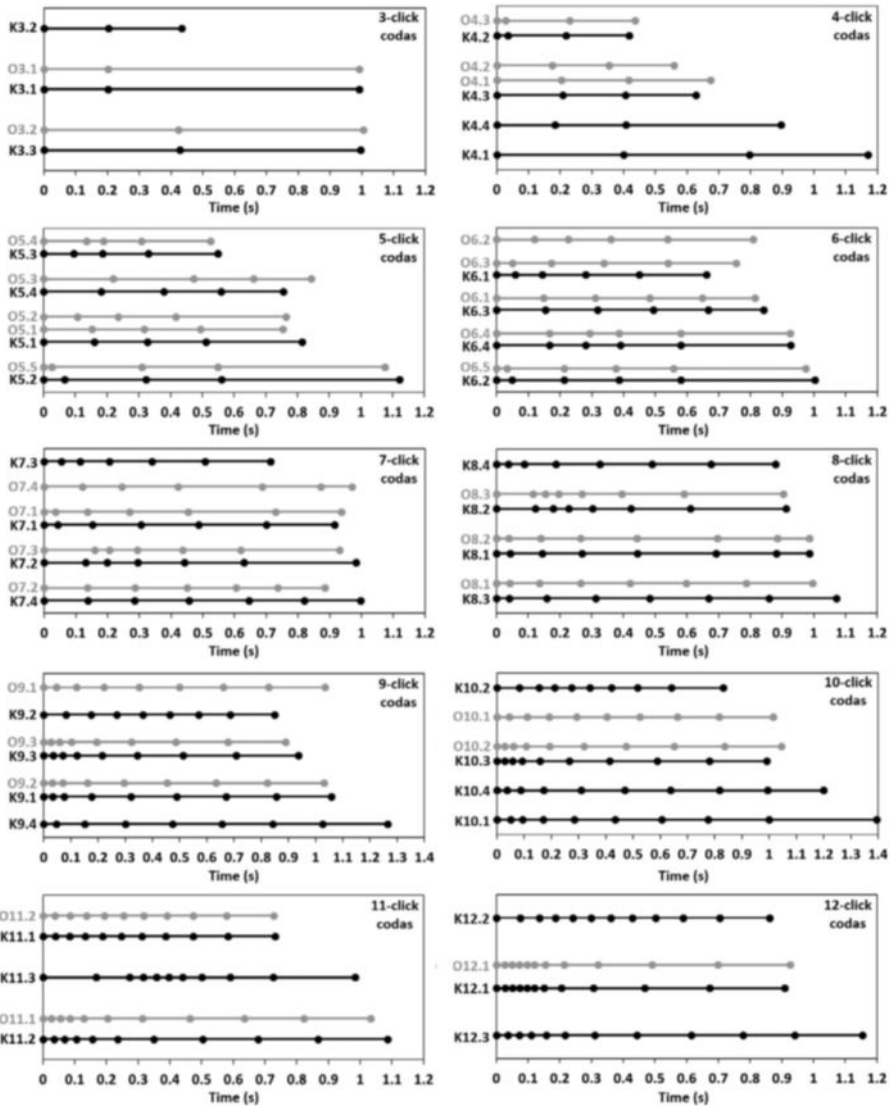
FIGURE 5 Graphical representations of coda types (i.e., cluster averages) defined using *K*-means cluster analysis in combination with observer classification (black) and using the OPTICSxi algorithm (gray). Dots represent clicks and the connecting lines represent absolute interclick intervals. *K*-means coda types are sorted by duration, with the shortest at the top and the longest at the bottom of each panel, and OPTICSxi types are placed above them; directly when corresponding to a *K*-means cluster and indirectly when different. *K*-means and OPTICSxi clusters are labeled on the *y*-axis as K and O, respectively, followed by *N* clicks dot cluster number. Sample sizes for each coda type can be found in Tables 3 and 4.

comparisons of CAP's repertoire with the other repertoires must be interpreted with caution. The average-linkage dendrogram (Figure 6) of the Euclidean-distance-based similarity values (Table S2) had a CCC of 9.72×10^{-1}, indicating effective hierarchical clustering. Bootstrap support was provided for the dendrograms' branches; 1,000 runs resulted in high bootstrap values for each branching node, except for the placement of the CHO repertoire (Figure 6).

TABLE 3 Number of codas per *K*-means cluster type in the repertoire of each named grouping.

	Number of codas per *K*-means cluster type per named grouping											
K-means cluster	ARO	BAB	BRI	CAL	CAP	CHO	DEN	ESC	LIL	MAL	SOC	Total
3.1	0	0	0	0	41	0	0	0	0	0	0	41
3.2	1	0	0	0	7	1	0	0	0	0	0	9
3.3	0	0	0	0	25	0	0	3	0	0	0	28
4.1	0	0	0	0	14	0	0	5	0	0	0	19
4.2	0	0	8	0	21	0	0	0	0	0	0	29
4.3	14	0	0	0	38	0	0	0	0	0	0	52
4.4	1	0	0	0	8	2	0	0	0	0	3	14
5.1	13	0	0	0	135	16	0	0	0	45	17	226
5.2	3	0	9	0	29	0	0	0	0	0	0	41
5.3	2	0	18	0	41	5	0	0	0	10	0	76
5.4	19	0	0	0	97	0	1	0	0	2	5	124
6.1	2	0	4	1	116	4	0	0	0	3	2	132
6.2	3	0	10	0	33	1	0	0	0	1	1	49
6.3	18	0	1	0	162	3	0	0	2	14	20	220
6.4	1	0	0	0	21	101	1	0	0	24	6	154
7.1	12	0	3	0	238	9	0	0	2	1	1	266
7.2	3	0	1	0	58	45	0	0	1	0	0	108
7.3	2	0	1	1	121	6	0	0	2	2	2	137
7.4	13	0	6	0	155	3	0	0	5	4	8	194
8.1	1	0	10	238	0	0	0	4	1	0	0	254
8.2	6	0	4	0	86	117	0	0	6	5	3	227
8.3	9	0	9	0	753	2	0	0	11	3	5	792
8.4	12	0	5	1	427	3	0	0	5	0	3	456
9.1	13	0	3	0	305	0	0	0	7	0	0	328
9.2	2	0	3	1	50	2	0	0	1	2	2	63
9.3	6	0	0	0	165	2	0	0	1	0	0	174
9.4	6	0	1	0	72	0	0	0	1	0	1	81
10.1	0	0	0	0	8	0	0	0	1	1	0	10
10.2	0	0	2	0	32	5	0	0	0	3	1	43
10.3	5	0	0	0	131	0	0	0	0	0	0	136
10.4	6	0	0	0	83	0	0	0	0	0	0	89
11.1	1	0	1	0	30	0	0	0	0	0	0	32
11.2	4	0	0	0	61	0	0	0	2	0	0	67
11.3	0	0	0	0	1	7	0	0	0	1	0	9
12.1	0	0	0	0	29	1	0	0	0	0	0	30
12.2	2	0	0	1	19	4	0	0	0	1	0	27
12.3	4	0	1	0	25	0	0	0	0	0	0	30
Total	184	0	100	5	3,875	339	2	8	51	123	80	4,767

TABLE 4 Number of codas per OPTICSxi cluster type in the repertoire of each named grouping.

| OPTICSxi cluster | Number of codas per OPTICSxi cluster type per named grouping | | | | | | | | | | | |
	ARO	BAB	BRI	CAL	CAP	CHO	DEN	ESC	LIL	MAL	SOC	Total
3.1	1	0	0	0	40	0	0	0	0	0	0	41
3.2	0	0	0	0	21	2	0	3	0	0	0	25
Noise	0	0	0	0	12	0	0	0	0	0	0	12
4.1	3	0	1	0	6	2	0	4	0	0	1	17
4.2	0	0	0	0	38	0	0	0	0	0	1	39
4.3	3	0	7	0	13	0	0	0	0	0	0	23
Noise	9	0	0	0	24	0	0	1	0	0	1	35
5.1	21	0	21	0	242	11	1	0	0	41	21	358
5.2	2	0	4	0	12	0	0	0	0	0	0	18
5.3	10	0	2	0	13	0	0	0	0	0	0	25
5.4	0	0	0	0	7	10	0	0	0	6	0	23
5.5	0	0	0	0	22	0	0	0	0	9	0	31
Noise	4	0	0	0	6	0	0	0	0	1	1	12
6.1	8	0	1	0	58	57	1	0	0	23	10	158
6.2	14	0	5	1	196	36	0	0	1	12	17	282
6.3	0	0	1	0	10	12	0	0	0	0	0	23
6.4	0	0	0	0	29	2	0	0	1	5	0	37
6.5	1	0	8	0	25	0	0	0	0	1	0	35
Noise	1	0	0	0	14	2	0	0	0	1	2	20
7.1	1	0	1	0	42	10	0	0	0	0	1	55
7.2	0	0	2	0	16	2	0	0	0	0	1	21
7.3	1	0	0	0	41	13	0	0	1	0	0	56
7.4	1	0	0	0	17	5	0	0	0	0	0	23
Noise	27	0	8	1	456	33	0	0	9	7	9	550
8.1	23	0	21	1	1149	99	0	0	14	8	3	1318
8.2	3	0	6	0	176	16	0	0	10	0	0	211
8.3	0	0	0	0	142	6	0	0	0	1	6	155
Noise	2	0	1	0	37	1	0	0	2	0	2	45
9.1	9	0	2	1	185	1	0	0	3	0	0	201
9.2	18	0	4	0	340	3	0	0	6	2	3	376
9.3	0	0	0	0	39	0	0	0	1	0	0	40
Noise	0	0	1	0	28	0	0	0	0	0	0	29
10.1	5	0	1	0	48	3	0	0	0	1	1	59
10.2	6	0	1	0	183	2	0	0	1	2	0	195
Noise	0	0	0	0	23	0	0	0	0	1	0	24
11.1	0	0	1	0	50	4	0	0	1	0	0	56
11.2	1	0	0	0	22	2	0	0	1	0	0	26
Noise	4	0	0	0	20	1	0	0	0	1	0	26

(Continues)

TABLE 4 (Continued)

| OPTICSxi cluster | Number of codas per OPTICSxi cluster type per named grouping | | | | | | | | | | | |
	ARO	BAB	BRI	CAL	CAP	CHO	DEN	ESC	LIL	MAL	SOC	Total
12.1	3	0	0	0	23	0	0	0	0	0	0	26
Noise	3	0	1	1	50	5	0	0	0	1	0	61
Total	184	0	100	5	3,875	339	2	8	51	123	80	4,767
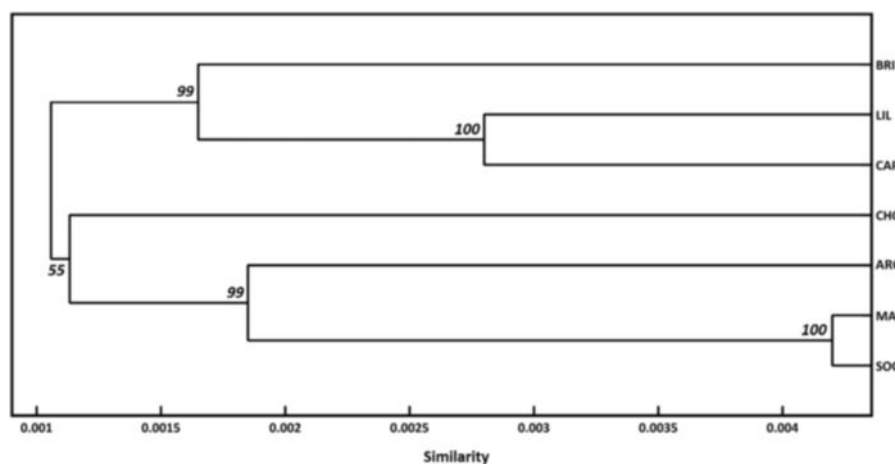
FIGURE 6 Average-linkage dendrogram showing hierarchical clustering based on pairwise similarity values between repertoires of named groupings BRI, LIL, CAP, CHO, ARO, MAL and SOC calculated using equation (2). The percentage of bootstrap replicates producing each branch are shown in italics.

Even though the large differences in analyzed repertoire sizes between CAP and the other named groupings may somewhat bias similarity values, the cluster that included CAP, LIL, and BRI (Figure 6) does appear to be separate vocal clan from the other repertoires. This putative vocal clan mainly used eight-click codas, whereas the cluster containing ARO, SOC, and MAL (Figure 6) was characterized by the use of shorter, mainly five-click, codas (Figure 5, Tables 3 and 4). As bootstrap support for the branch containing CHO was low (Figure 6), its placement in the dendrogram and thus clan status remains uncertain. However, this repertoire did seem to contain relatively more coda types with "fast middle clicks" (i.e., clicks separated by relatively short ICIs in the middle of the coda) among all N-click codas (Figure 5, Tables 3 and 4).

4 | DISCUSSION

4.1 | Social structure of sperm whales in Mauritius

We encountered 101 photo-identified individuals which were each assigned to a "named grouping" based on their visible associations. Only members of the named grouping CAP were resighted both within and between surveys. As the surveys in which CAP members were identified were conducted in different months, spanning the beginning of May until the end of October, these sperm whales are possibly resident in the area year-round. However, additional, continuous data are needed to confirm residency. Furthermore, with the current data (i.e., from surveys mainly

covering the west side of the island), it cannot be established whether other named grouping members are possibly resident to Mauritius, or have a larger home range in which they travel around—for instance, between Mauritius and neighboring island Reunion (Vély, Fossette, Vitry, & Heide-Jørgensen, 2015). With the sighting of CAL in oceanic waters, at mid-distance between the two islands (Figure 1), this is a possible scenario.

Analysis of association between 22 resighted individuals revealed four social unit candidates. One comprised the three analyzed members of ARO, the other three the 19 analyzed members of CAP. A split between a cluster of four CAP members from the rest seems evident, but the bifurcation of the clusters representing the two other putative social units (containing seven and eight CAP members, respectively) was very close to the cut-off value (Figure 3). As the amount of resighting data was generally low, even for CAP, solid delineation of social units among its members is impossible with the current data. More sightings are needed of named grouping members, with a high certainty that all individuals are identified during each sighting, to reliably identify long-term associates and thus social units.

Sizes of CAP's three social unit candidates, of ARO, and of the unanalyzed named clusters and groupings ranged from four to 14 individuals, which are realistic sizes for single social units. Social units have been observed ranging in size from three to 24 individuals (Christal, 1998; Christal & Whitehead, 2001). In the Pacific, mean unit size is 11 and mean group size is almost 30 (Coakes & Whitehead, 2004; Jaquet & Gendron, 2009; Whitehead & Kahn, 1992), which indicates that groups are made up of two to three social units. In the Atlantic, social units are slightly smaller and group size is about the same as unit size (Antunes, 2009; Gero et al., 2014, 2016b; Jaquet & Gendron 2009; Richter, Gordon, Jaquet, & Würsig, 2008), meaning that social units in the Atlantic rarely form groups together. Whitehead et al. (2012) investigated different possible explanations for this contrast between the two oceans and found that predation by killer whales (*Orcinus orca*) is the most likely driver for the formation of large groups in the Pacific; larger groups offer increased protection.

For the Indian Ocean, little is known about social unit and group sizes of sperm whales. Gordon (1987) reported on a group of 18 individuals off Sri Lanka that was always seen in subsets of no more than nine whales, and Whitehead and Kahn (1992) found a mean group size of 18 off the Seychelles, but without enough sighting information to infer mean social unit size. However, groups off the Seychelles were found to aggregate with other groups only very rarely (Whitehead & Kahn, 1992). Despite our inability to reliably detect social units, our observations of CAP's members and other associates in seemingly random subsets (clusters) of 4–34 individuals suggest similarity to the grouping behavior observed in the Pacific Ocean rather than the Atlantic. Alexander et al. (2016) found that stronger female philopatry at the geographic level in the Indian and Atlantic oceans may explain the differences in levels of regional mtDNA differentiation between these oceans and the Pacific. Predation pressure may be the explanation for the grouping differences between the Indian and Atlantic oceans, as it also likely explains the grouping differences between the Pacific and Atlantic (Whitehead et al., 2012). Little information is available on killer whale diet

FIGURE 7 Tailslapping photo-identified sperm whale *Cassecroute*, a member of named grouping CAP that was only sighted on 13 May 2008. Note the fresh bite wounds on the fluke tips and the rake marks along the entire trailing edge of the flukes.

preferences in the Indian Ocean, but at least one account exists of about six killer whales attacking an equally large grouping of sperm whales off Sri Lanka (Gemmell, McInnes, Heinrichs, & de Silva Wijeyeratne, 2015). On an anecdotal note, during the 2008 survey of this study, one sperm whale was observed lobtailing repeatedly, with fresh, bleeding bite wounds and rake marks clearly visible on the fluke edges (Figure 7). However, neither killer whales nor other odontocetes were observed at that time and the sperm whales had not assumed the defensive "marguerite formation" (Nishiwaki, 1962; Palacios & Mate, 1996; Weller et al., 1996). Large shark species such as the great white shark (*Carcharodon carcharias*), bull shark (*Carcharhinus leucas*) and tiger shark (*Galeocerdo cuvier*) occur in Mauritian waters (MMCS, unpublished data), but none of them are known to attack live adult sperm whales (Whitehead, 2003). The lack of a reliable body size estimate for the affected sperm whale prevents estimation of the fluke width and thus interteeth distance of the rake marks on the fluke, making inference of the species that inflicted these marks impossible.

4.2 | Coda repertoires and sympatric vocal clans

We detected 37 different coda types among our recordings of Mauritian sperm whale vocalizations based on *K*-means/observer clustering and 30 based on OPTICSxi clustering. Of these, 24 coda types were supported by both methods, which corresponds to the coda diversity reported elsewhere (e.g., Galápagos Islands, tropical southeastern Pacific: 32 types; Rendell & Whitehead, 2004; Dominica, eastern Caribbean Sea: 22 types; Gero et al., 2016a, b). However, neither of the applied clustering methods seemed optimal for identifying different coda types. Observer clustering is both subjective and time-consuming, thus not suitable for identifying discrete coda types among large data sets (Rendell & Whitehead, 2003b); rather, it is useful as a means to inspect coda diversity before subsequent (semi-)automated analyses. The *K*-means clustering method was found to be better at recognizing naturally occurring groupings (here: coda types) within data sets (Rendell & Whitehead, 2003b), but the VRC (Caliński & Harabasz, 1974) did not seem suitable as a stopping rule to decide on *K* as it did not provide consistent, unambiguous results (see also Rendell & Whitehead 2003a, b; Schreer et al., 1998). We therefore used a combination of observer and *K*-means clustering. In addition, we used the hierarchical clustering algorithm OPTICSxi (Ankerst et al., 1999) as previously applied to codas by Gero et al. (2016a, b) and Cantor et al. (2016). OPTICSxi had been shown to be more successful as well as more accurate at defining naturally occurring groupings in large datasets than *K*-means (Ankerst et al., 1999; Gero et al., 2016a). Coda classification using OPTICSxi is highly conservative, with ambiguous codas being removed from the analysis as "noise" rather than being forced into a defined cluster, resulting in objective delineation of discrete coda types (Gero et al., 2016a). However, this may result in a large part of a data set being labeled as noise (e.g., Cantor et al., 2016) and potential coda types remaining undetected. Furthermore, optimal values for the algorithm's input parameters have to be determined a priori, which introduces a similar problem as defining an optimal value for *K* in *K*-means clustering. We followed a similar sensitivity test scheme for parametrization as Cantor et al. (2016) did, but this did not result in parameter values that could be applied to all *N*-click coda type sets. Overall, OPTICSxi may outcompete *K*-means in terms of accuracy of detected clusters, but these clusters potentially underrepresent the entire coda repertoire, and finding optimal values for input parameters is not straightforward.

In the majority of previous studies, ICIs of codas were standardized for total coda duration, as it was generally believed that rhythm rather than duration is the functionally most important feature of codas (e.g., Moore, Watkins, & Tyack, 1993). However, more recent studies have classified codas based on their absolute ICIs (e.g., Cantor et al., 2016; Gero et al., 2016a, b), thereby retaining potential information encoded in duration. Codas are generally described as stereotyped click sequences of 3–40 clicks (Watkins & Schevill, 1977), but codas consisting of less than two or more than 12 or 13 clicks were often discarded in previous studies as they were usually rare, too variable to classify, or too difficult to distinguish from usual, echolocation click series (e.g., Antunes, 2009; Weilgart & Whitehead, 1993, 1997). In addition, two-click codas cannot be standardized as they consist of only one ICI. In this study, we detected but discarded coda-like click sequences of two and ≥ 13 clicks for the same reasons. Two-click codas

were almost never mentioned in previous literature; their existence mostly suggested by authors stating to have discarded codas consisting of less than three clicks (e.g., Weilgart & Whitehead, 1993, 1997). One exception is the study by Amano et al. (2014), who detected some two-click codas but did not analyze them.

Amano et al. (2014) studied coda repertoires of sperm whales in two areas off Japan and detected at least two different vocal clans, the repertoires of which not only differed by relative usage and rhythmicity of coda types, but also by absolute duration of codas which had the same rhythm. Whether absolute duration of codas plays a role in the communicative function of codas, it does seem to be a distinguishing factor between vocal clans (Amano et al., 2014). Given that coda repertoires are socially transmitted between members of the same vocal clan (Rendell & Whitehead, 2003a), it is possible that subtle differences in coda durations of the same coda types arise between clans with each generation, even with rhythmic properties of these codas being conserved, perhaps even giving rise to new coda types after enough generations have passed. However, no studies spanning an entire sperm whale generation length (i.e., ~60 years; Rice, 1989) have been conducted so far, and the few published studies spanning at least a decade (e.g., 1985–1999, Rendell & Whitehead, 2003a; 2005–2015, Gero et al., 2016b) did not report on temporal differences in (duration of codas in) the studied coda repertoires.

We compared repertoires of seven named groupings of sperm whales, and a separation between two main clusters was found (Figure 6); a putative "eight-click clan" and "five-click clan." Bootstrap support for the branch containing the seventh repertoire (CHOs) was low, leaving its sister position to the five-click clan and thus separate potential clan status rather uncertain. Because of the sighting bias towards CAP, the vocalizations of this group make up most of our acoustic data set (3,875 of 4,767 analyzed codas; Table 2). The other analyzed repertoires are much smaller, requiring careful interpretation of pairwise comparisons with CAP. However, the difference in usage frequency of certain coda types (Tables 3 and 4) as well as the social separation between CAP and ARO (Figure 3) do advocate for separate clan status. To further elucidate the presence of potential sympatric vocal clans in Mauritius, future surveys should aim at obtaining more acoustic data to ensure adequate sampling of different vocal clan repertoires.

4.3 | Concluding remarks

Despite the limitations of both our photo-ID and acoustic data sets, our results hint at the presence of social units that may aggregate into larger groups as well as of sympatric vocal clans in Mauritius, which suggests that sperm whale social structure in this area is more similar to that in the Pacific than that in the Atlantic. In turn, this suggests a similar predation risk in these oceans. As ecotourism continues to grow in Mauritius, adequate management and conservation of the Mauritian sperm whales are urgently needed. Future studies should aim at obtaining more sighting and acoustic data on larger regional and temporal scales to further elucidate sperm whale social structure and vocal clan occurrence in the southwestern Indian Ocean. With sperm whales lacking a clear genetic and/or geographic population structure, such data can be used to designate appropriate units for management and conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.