Matching signature whistles with photo-identification of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Fremantle Inner Harbour, Western Australia

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Abstract

The Swan-Canning River System is home to an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) community of currently 17 adult and juvenile individuals. While a complete photo-identification catalogue exists, visual monitoring requires repeated boat-based surveys and is thus laborious and expensive. Bottlenose dolphins are known to emit individually distinctive signature whistles, and therefore passive acoustic monitoring could be a reliable and more efficient tool. Archived acoustic and photographic data from the Fremantle Inner Harbour were reviewed for instances when dolphin whistles and individual identifying images were simultaneously available. As dolphin whistles are commonly used in social encounters, dolphins producing whistles in this study were always in groups. Consequently, to assess whether distinctive whistles could be attributed to individual dolphins, conditional probabilities for recording a specific whistle in the presence of certain individuals, as well as Bayesian posterior probabilities for encountering a specific individual at times of certain whistles were computed. While a larger sample size is needed to capture all individuals in diverse groupings, this study provides the first step in developing a passive acoustic program for monitoring this small dolphin community, in order to ultimately inform its conservation management.

Keywords:

bottlenose dolphin, Tursiops aduncus, signature whistle, photo identification

1 Introduction

A basic requirement of successful wildlife conservation management is regular abundance monitoring. It is imperative to know whether a population is growing, stable, or in decline. In the case of cetaceans, this information is commonly derived from visual surveys from aircrafts, boats, or land. Photo-identification (photo-ID) of individuals within a population is a valuable tool for conservation management, as it allows the number of individuals and population demographics to be monitored [1]. For example, photo-ID was key to determining the decline of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand [2] and for demonstrating improvement in the demography of endangered Hector's dolphin (*Cephalorhynchus hectori*) within a marine protected area in New Zealand [3].

However, photo-ID can be labour-intensive and expensive, requiring people in the field to survey animals and take photographs, as well as people in the lab to sort, quality-control, and catalogue those photographs. Additionally, visual surveys and photo-ID are limited to daylight hours and good weather conditions. Other cues by which individuals could be identified over extended periods with less effort would be an attractive alternative. Passive acoustic monitoring has this potential for species that produce individual-specific vocalisations. Such species include bottlenose dolphins (*Tursiops* spp.); and their individual-distinctive vocalisations are whistles [4,5].

In general, whistles are narrow-band tonal sounds used for conspecific communication (e.g., [6]). In bottlenose dolphins, whistles can range from a few hundred Hz to 40 kHz in fundamental frequency and from 0.1 s to up to 10 s in duration (see summary in [7]). Dolphin calves may develop their own unique 'signature whistle' within a few months after birth [8,9]. There is evidence of vocal learning as dolphins mould their own signature whistle after sounds from their environment, including from conspecifics, but not necessarily their mothers [5,10]. Female signature whistles appear more stable over time than male signature whistles [11]. Identity is encoded in the frequency modulation pattern. Dolphins appear to use signature whistles to broadcast their own identity when in isolation, during mother-calf reunions, when joining a group, and to maintain group cohesion [5]. In wild bottlenose dolphins, about half of the whistles recorded may be signature whistles [12]. The percentage of signature whistle emission increases to 100% when an animal is isolated [13]. Signature whistles are emitted repeatedly in bouts, with 1-10 s between the signature whistles in a bout, and this temporal patterning has been applied in several studies to identify signature whistles in wild dolphin populations (signature identification (SIGID) method [14]).

The Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of the Swan-Canning River System, Western Australia, also produce signature whistles based on the SIGID criterion [15]. This dolphin community is currently comprised of approximately 17 adult and juvenile individuals, plus calves (recorded as 21 in [16], but at time of writing, recently reduced due to a combination of disease and entanglements). Association patterns have been identified whereby some individuals spend significantly more time in specific groups than with other individuals [16,17]. The community is considered 'resident' as it uses the entire urbanised Swan-Canning River System year-round, including the Fremantle Inner Harbour, which is an important foraging area for these dolphins [18]. Since 2001, photo-ID data have been collected identifying all adult and juvenile dolphins based on unique dorsal fin shapes and markings [16,17,19]. Consequently, the aim of this study was to test whether signature whistles could be uniquely matched with sightings of individuals. If signature whistles can be assigned to individuals, or at least stable groups of dolphins, then passive acoustic monitoring programs can be developed using long-term, autonomous recorders and automatic whistle detection tools (e.g., [20,21]). These programs would provide information on dolphin distribution, demographics, and abundance throughout the Swan-Canning River System, for effective conservation management.

2 Materials & Methods

2.1 Study Site

All observations and recordings were undertaken within the eastern part of the Fremantle Inner Harbour, Western Australia (32°02'31.23" S, 114°45'10.21" E; Fig. 1). At this location, the Swan River is channelled and thus narrow, making it ideal for visual observations from land. The maximum water depth is ~13 m. Dolphins use this site predominantly for foraging, spending an hour or more at a time, repeatedly corralling fish towards the small craft jetty and port wharf walls [18,22]. This behaviour provides a unique opportunity to collect close-range photo-ID from the end of a small craft jetty within the Inner Harbour. Data were specifically collected between April and September in 2013, 2014, and 2017, as these months had previously been documented to show high occupancy by dolphins [23].

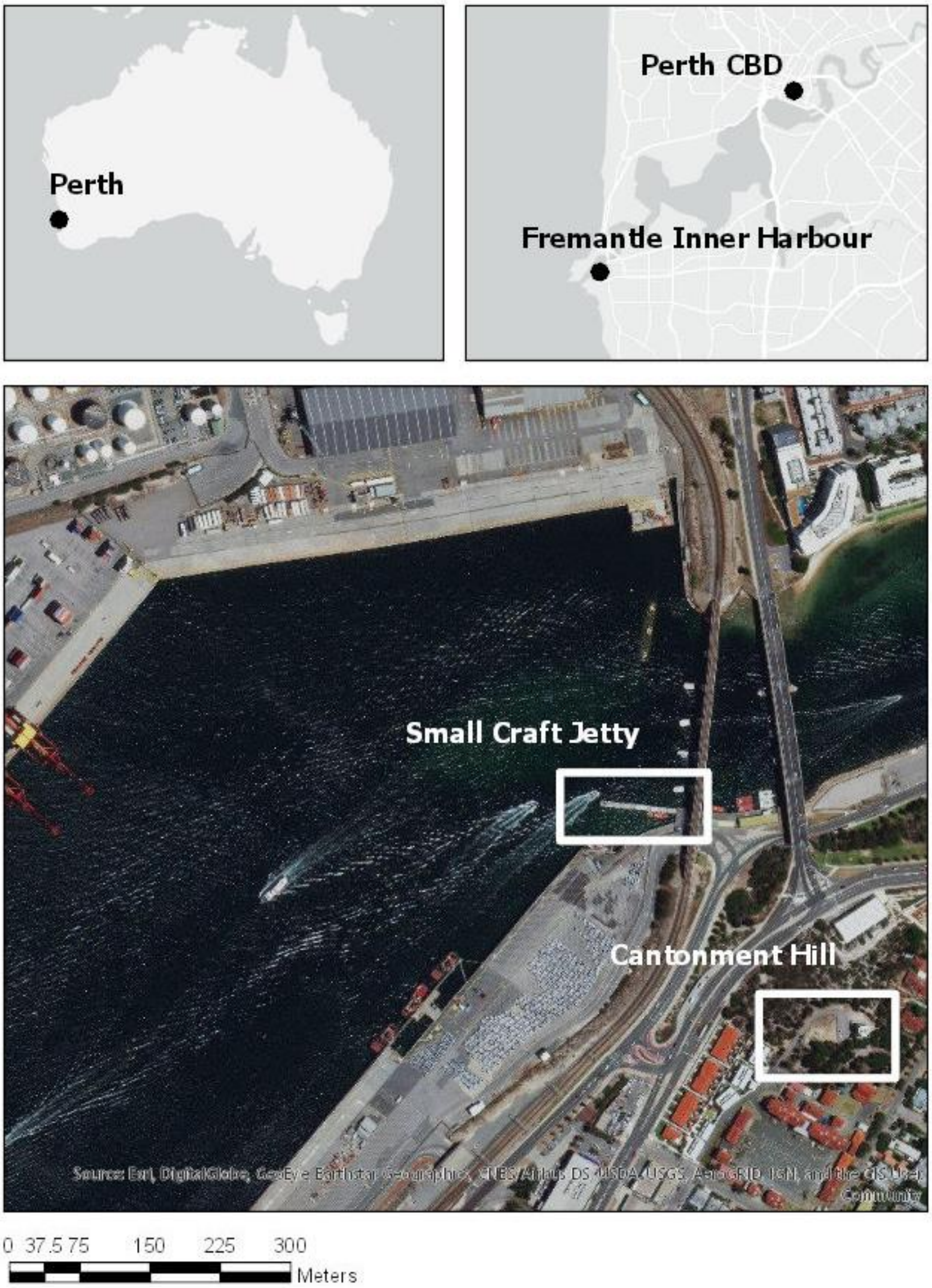


Fig. 1: Map of the Fremantle Inner Harbour (lower panel), where simultaneous photo-ID and underwater acoustic recordings were collected

2.2 Data Collection

Visual observations were undertaken systematically by one or two observers from the small craft jetty, with occasional support from a team of three observers from Cantonment Hill at 32 m elevation (Fig. 1), following a protocol to reduce potential biases (see [24]). A survey was a continuous observation period that usually had a duration of several hours. The following information was recorded: survey start time, observer names, dolphin sighting start times, dolphin sighting end times, and survey end time. In addition, environmental conditions were recorded at the start of a survey, every hour of the survey, and when conditions changed. These environmental conditions included: cloud cover (recorded in eighths), glare (0 to 3; 0 indicating 'no glare' and 3 'severe glare'), sea state (using the Beaufort scale), and wind direction. Observations were conducted in Beaufort conditions of 3 or less.

Once a survey commenced, the study area was scanned continuously by observers with the naked eye and with 7×50mm Bushnell binoculars. An encounter commenced whenever a new group of dolphins entered the study area. A group of dolphins was defined as a single dolphin or multiple dolphins in association and engaged in the same activity ('group' definition modified from [25]). When a dolphin group was sighted, the number of dolphins was counted every 5 minutes, and the estimated minimum and maximum numbers were recorded. Each group in the study area was given a unique name (from A to Z, in chronological order).

For each group, the following information was collected: group composition (number of adults and calves in the group; noting that juveniles can be hard to identify from a distance and would have been counted as adults), group spatial cohesion (low-high, as defined by [26]), predominant behavioural state (i.e., foraging, milling, resting, socialising, or travelling; as in [18]), and any active instantaneous behaviour (e.g., porpoising, leaping, tail-out diving, tail-slapping, fish tossing, petting, etc.). The predominant behavioural states were mutually exclusive and similar to those used in other studies at this site [18,27,28].

Group spatial cohesion was recorded when the group was first sighted and if it changed. Spatial cohesion was a qualitative index with three levels modified from [26]: low cohesion (i.e., the group was scattered through the study area, more than 100 m apart), intermediate cohesion (i.e., the majority occupied an area between ~30 and 100 m wide), and high cohesion (i.e., the majority were highly aggregated occupying a small area <30 m). Smaller social units were also recorded and were called sub-groups.

Photo-identification was obtained of as many individuals of a group as possible using a digital SLR camera (Canon 7D Mark II with a Canon EF70-200mm f/2.8L IS III USM telephoto lens, or Nikon D800 with a Nikon AF-S DX NIKKOR 28-300mm f/3.5-5.6G ED zoom lens). All observations from the small craft jetty were recorded on a dictaphone and transcribed later. Observations from Cantonment Hill utilised a theodolite to measure dolphin positions (TopCon GTS-603 AF Electronic Total Station), which were recorded in Vadar (version 2.00.01b; E. Kniest, University of Newcastle, Australia) on a laptop computer (for further details, see [22,28]).

Acoustic recordings were obtained with hand-held hydrophones deployed over the north side of the small craft jetty, with the exception of 23 May 2013, when the hydrophone was deployed over the west side of the jetty due to a strong current which could have resulted in flow noise. On all occasions, the hydrophone was lowered to a depth of approximately 1.5 m below the surface of the water. Acoustic recordings commenced upon sighting of dolphins. The equipment consisted of either a Jammin Pro HR-5 recorder and High Tech Inc. HTI-96-MIN hydrophone, or a Sound Devices 744T recorder, external Reson VP1000 pre-amplifier, and Reson TC4033-1 hydrophone. Both recorders had built-in preamplifiers. The Reson VP1000 pre-amplifier gain was set to 0 dB and had a high-pass filter cut-off at 10 Hz. The HTI hydrophone had a frequency response of 2 Hz – 30 kHz (±3 dB) and a sensitivity of -163.9 dB re 1 V/μPa, while the Reson hydrophone had a frequency response of 1 Hz – 140 kHz and a sensitivity of -202.3 dB re 1 V/μPa. All recording systems were calibrated with white noise at a known level.

During observations from Cantonment Hill in 2015, an autonomous, bottom-mounted recorder, developed by the Centre for Marine Science and Technology [20], fitted with a High Tech Inc. HTI-90-U hydrophone, was deployed off the west side of the small craft jetty on the sea floor at approximately 4 m depth. However, there were unfortunately no instances of simultaneous photo-ID, which is why these recordings were not used in this study.

All camera, computer, GPS, and acoustic recorder clocks were synchronised at the beginning of each survey. Table 1 summarises the equipment that provided the data for the current study.

Table 1: Metadata table; fs: sampling frequency.

Year	Acoustic Equipment	Photographic Equipment	Visual Observation Point	Number of Surveys
2013	Jammin Pro HR-5 recorder, HTI-96-MIN hydrophone, fs = 96 kHz	SLR Nikon D800 with a Nikon AF-S DX NIKKOR 28-300mm f/3.5-5.6G ED zoom lens	Small craft jetty	9 surveys between 13 May and 21 June
2014	Jammin Pro HR-5 recorder, HTI-96-MIN hydrophone, fs = 192 kHz	Canon 7D Mark II with a Canon EF70-200mm f/2.8L IS III USM telephoto lens	Small craft jetty (supported by Cantonment Hill)	6 surveys between 29 May and 11 September
2017	Sound Devices 744T, external Reson VP1000 pre-amplifier, Reson hydrophone TC4033-1, fs = 48 kHz	Canon 7D Mark II with a Canon EF70-200mm f/2.8L IS III USM telephoto lens	Small craft jetty (supported by Cantonment Hill)	19 surveys between 4 April and 15 August

2.3 Data Analysis

Following fieldwork, photos were reviewed in the office. Images of poor quality (e.g., not in focus, poor lighting, too distant, or at an angle other than perpendicular to the animal) were excluded from the study, leaving only high-quality images of dolphins to optimise accurate identification of individuals (see example photo in Fig. 2).

Fig. 2: Example of a high-quality photo-ID image showing prominent and unique markings on the dorsal fin

Dictaphone recordings and Vadar logs were transcribed and all information (including date and time stamps when dolphins were sighted) was compiled in a single spreadsheet. A second spreadsheet was created with the date and time stamps and image file names exported from the digital photographs.

The underwater acoustic recordings were analysed in Adobe Audition CS6 (Adobe Systems Inc., San Jose, CA, USA, 2013). The whistles were graded in increasing quality from 1 to 3 based on the signal-to-noise ratio and clarity in both the spectrogram and sound [27]. Only whistles of grade 2 or 3 were considered of sufficient quality and hence used in analyses. The following features were measured off each fundamental whistle contour in Raven Lite (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY, USA, 2017): duration, start frequency, end frequency, minimum frequency, maximum frequency, and numbers of extrema (i.e., local minima and maxima in the contour), inflection points (i.e., points along a contour where the curvature changes from clock-wise to counter-clock-wise or vice versa), and steps (i.e., discontinuities or jumps in frequency without any gap in time) [27]. Gaps in time identified the end of one whistle and the start of a new whistle. Some whistles had harmonically related overtones; these overtones were not measured.

A third spreadsheet was created listing all the whistles, the date and time when each was recorded, the measured features, and the contour type. Whistles were grouped into distinct types based on similarity in measured features and overall shape of the fundamental contour. Visual classification based on whistle spectrograms has previously been found reliable across different observers [11] and when compared to automated classification algorithms [29,30]. Grouping of whistles was done independently by three of the coauthors. In the absence of *a-priori* information on how many groups there should be (i.e., how many signature whistles might have been recorded), it was expected that observers produced different numbers of whistle types. Referring to observers who lump whistles into few categories as 'lumpers' and those who split whistles into many categories as 'splitters', good agreement was defined as the case where each of the whistle types determined by the splitter translated into no more than one whistle type of the lumper. Poor agreement was defined as the case where the whistles in any one of the splitter's groups were sorted into more than one of the lumper's groups. Inter-observer reliability was computed as the percentage of whistles that were uniquely matched from the splitter's into the lumper's groups. A confusion matrix was computed showing the numbers of whistles in the splitter's groups versus the lumper's groups. For each splitter's group, the lumper's group with the highest number of common whistles was considered the matched group. Any whistles that were sorted into other lumper's groups were counted as not uniquely matched. The greater the number (and percentage) of uniquely matched whistles, the greater the inter-observer reliability.

Analysis progressed by comparing the three spreadsheets. Commencing with the first spreadsheet, the dates and times of all dolphin encounters were looked up; the coinciding photographs were located based on the second spreadsheet; and any simultaneously recorded whistles were identified in the third spreadsheet. For each encounter, individual dolphins were identified in the photos based on the regularly updated photo-ID catalogue, using the edition most appropriate for that study period [16]. Similarly, for each encounter, the whistle types were extracted from the spreadsheet of all whistles. A matrix was created that listed the individuals photographed and the whistles recorded for each dolphin encounter.

All statistical analysis was done in MATLAB (version R2018b; The MathsWorks Inc., Natick, MA, USA). First, the probability $p(a)$ of encountering any specific animal a was computed, as was the probability $p(w)$ of recording a specific whistle w. Next, for each animal photographed, the conditional probability $p(w|a)$ that each of the whistle types was recorded was computed. Then, using Bayes' Theorem [31], the posterior probability $p(a|w)$ that a specific animal was present when a specific whistle was recorded was computed as:

$$p(a|w) = p(w|a) * p(a)/p(w)$$

Finally, given that no whistles were recorded in isolation, but instead, whistles were always recorded in the presence of groups of dolphins, we investigated whether specific dolphins were frequently seen together. Based on the photographs taken during each encounter, an agglomerative hierarchical binary cluster tree was computed using the *linkage* function in MATLAB. The distances between clusters were calculated as unweighted averages. A dendrogram was created with the *dendrogram* function in MATLAB showing which animals were frequently seen together. Similarly, a second dendrogram was created showing which whistle types were frequently recorded together.

3 Results

While there have been many studies on photo-ID and many studies on underwater acoustics in the Swan-Canning River System, only three field studies (in 2013, 2014, and 2017) were identified that combined the two yielding simultaneous and co-located photographs and whistle recordings. The cumulative period of simultaneous photographs and whistle recordings was 4 hours, 48 minutes, and 14 seconds. During this time, 15 encounters with dolphins occurred and 437 photographs of dolphins were taken. Table 2 lists the individual dolphins identified in the various encounters.

Table 2: Number of encounters in which each of the dolphins was identified from photographs.

Dolphin Name	Number of encounters in which each dolphin was identified
Akuna	8
Arrow	3
Blackwall	1
Bottomslice	2
Cruze	2
Daniele	5
Dunnedoo	6
Extreme	3
Garden	1
Gizmo	3
Highnitch	8
Hii	3
Kwillena Lookalike (LL)	4
Moon	1
Night	2
Panuni	6
Pebbles	3
Pirulli	1
Print	3
Product	3
Resource	3
Soul	2
Tupac	3
Two-Rakes	3
Zari	4

3.1 Whistle Types

In total, 513 whistles of good quality were matched to dolphin photos. Histograms of the whistle features are shown in Fig. 3 with means, standard deviations, range, and percentiles given in Table 3. Note that duration was not Gaussian, but rather log-norm distributed. The numbers of extrema, inflections, and steps were Poisson distributed. Whistles ranged from 0.05 to 2.29 s in duration and from 670 to 19 000 Hz in frequency. Whistles had up 9 local extrema and inflection points, and up to 12 steps.

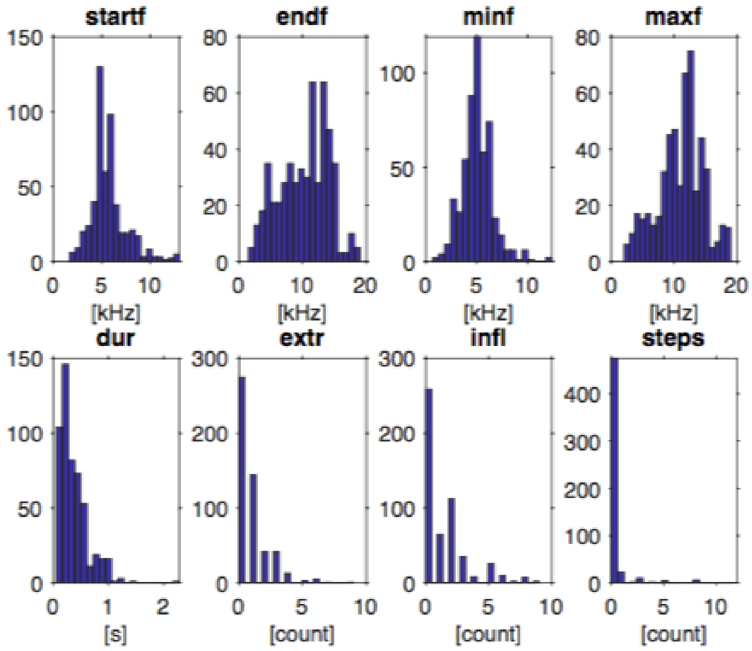
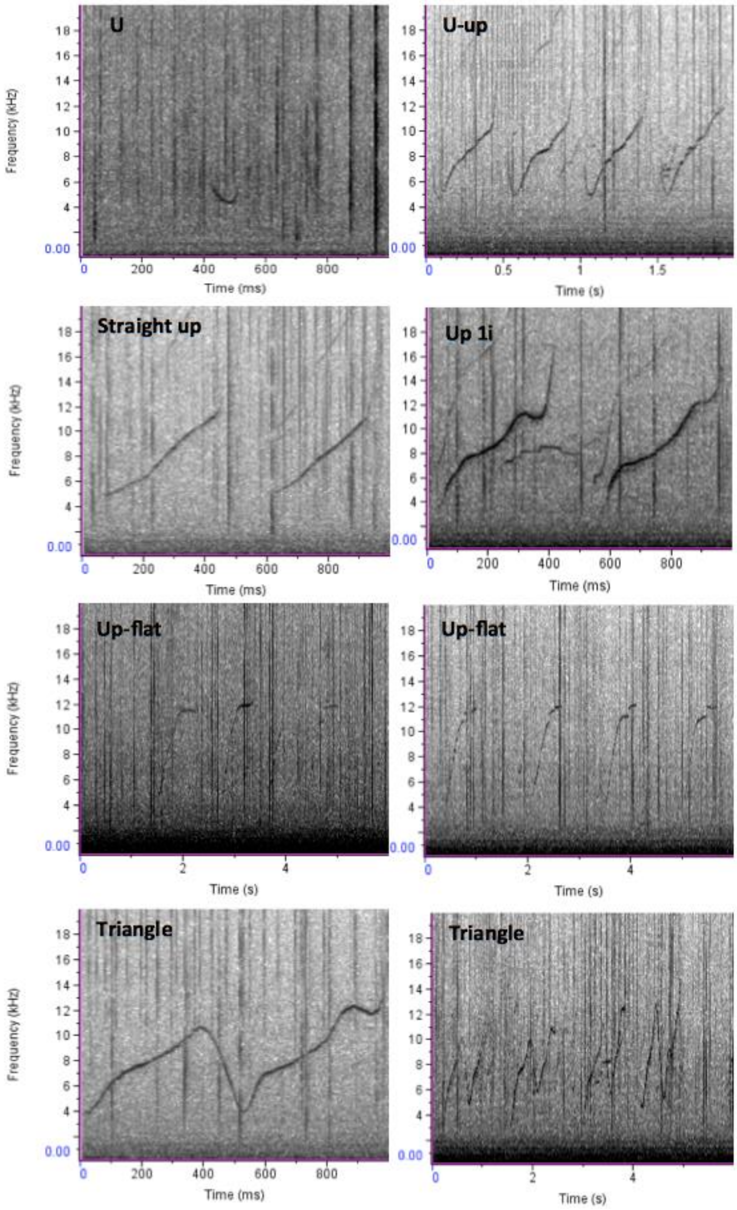


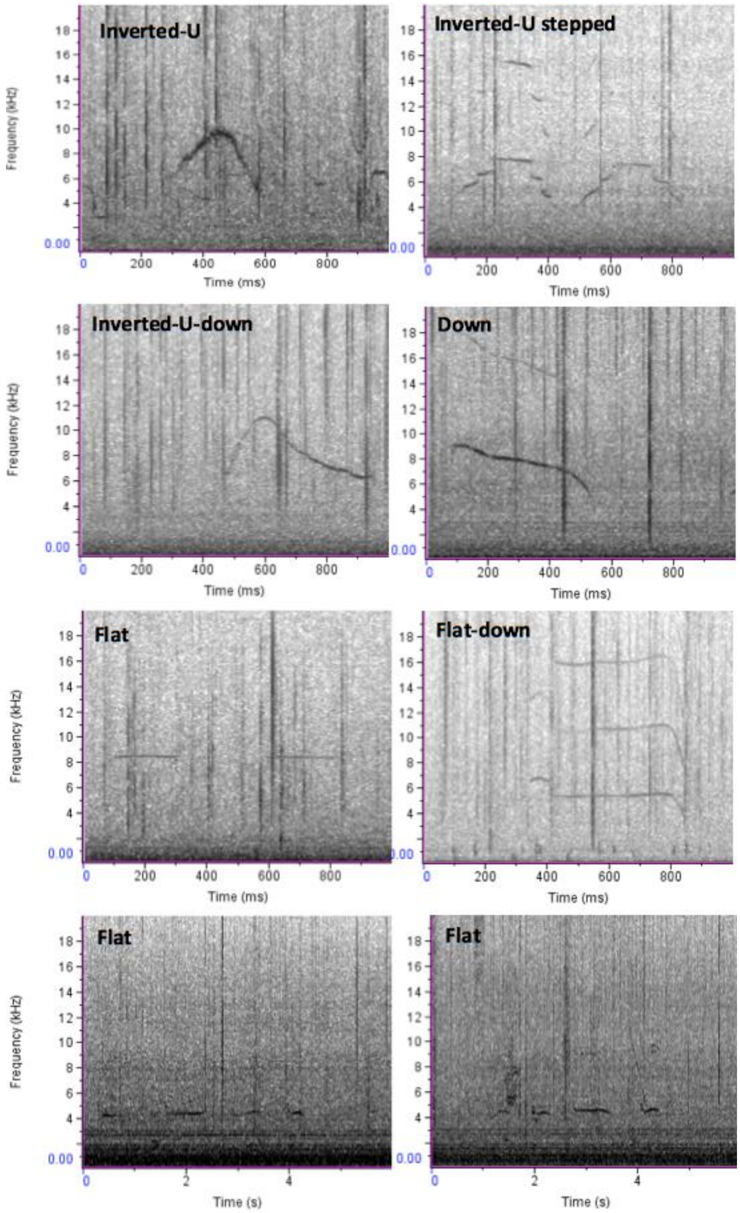
Fig. 3: Histograms for start, end, minimum and maximum frequency, duration, and numbers of extrema, inflection points, and steps of all fundamental whistle contours

Table 3: Statistics of whistle features showing the mean and standard deviation, range, and percentiles for duration, start frequency, end frequency, minimum frequency, maximum frequency, and numbers of extrema, inflection points, and steps.

	dur [s]	start f [kHz]	end f [kHz]	min f [kHz]	max f [kHz]	extr	infl	steps
mean	0.36	5.69	10.30	5.04	11.06	0.89	1.34	0.32
std	0.26	1.83	3.87	1.49	3.60	1.28	1.81	1.31
min	0.05	1.66	1.27	0.67	2.00	0.00	0.00	0.00
10th%	0.11	3.59	4.67	3.33	5.59	0.00	0.00	0.00
25th%	0.19	4.50	7.32	4.20	9.00	0.00	0.00	0.00
median	0.30	5.50	11.00	5.00	11.83	0.00	1.00	0.00
75th%	0.46	6.45	13.39	6.00	13.50	1.00	2.00	0.00
90th%	0.74	8.06	15.00	6.66	15.00	3.00	4.00	0.00
max	2.29	13.00	19.00	12.38	19.00	9.00	9.00	12.00

These whistles were grouped into 16 types based on their contours: U-shaped (U), U-to-upsweep (U-up), Downsweep (Down), Flat, Flat-to-downsweep (Flat-down), Inverted-U (Inv-U), Inverted-U-to-downsweep (Inv-U-down), m-shaped (m), Sine-shaped (Sine), Straight up, Triangle, Upsweep with at least one inflection (Up 1i), Up-to-flat (Up-flat), and stepped versions of Inv-U, Sine, and Up (Fig. 4).


U
U-up
Straight up
Up 1i
Up-flat
Up-flat
Triangle
Triangle
Frequency (kHz)
Time (ms)
Time (s)


Inverted-U
Inverted-U stepped
Inverted-U-down
Down
Flat
Flat-down
Flat
Flat
Frequency (kHz)
Time (ms)
Time (s)

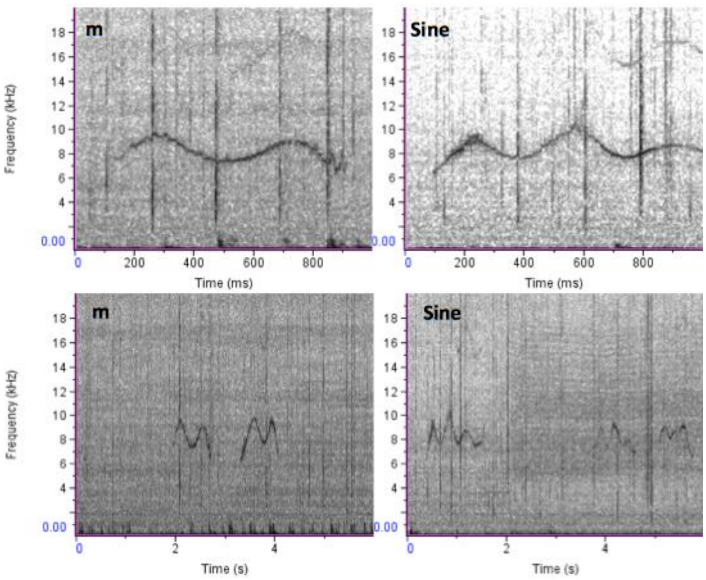


Fig. 4: Examples of whistle types and trains (bouts) of whistles. All y-axes are in kHz. The x-axes change from ms to s as samples extend beyond 1 s

The majority of whistles were of an overall upsweeping shape (Straight up, U-up, Up 1i, Up stepped, Up-flat, and Triangle; 69%), followed by those that were flat (11%), parabolic (U, Inv-U, and Inv-U stepped; 9%), downsweeping (Down, Flat-down, Inv-U-down; 6%), or sinusoidal (m, Sine, and Sine stepped; 6%)--as can be gleaned from Fig. 5. This scatter plot of end frequency versus start frequency shows overall upsweeping contours (in red and blue) lying above the diagonal, while overall downsweeping contours (green) lie below the diagonal, with flat contours (black) along the diagonal.

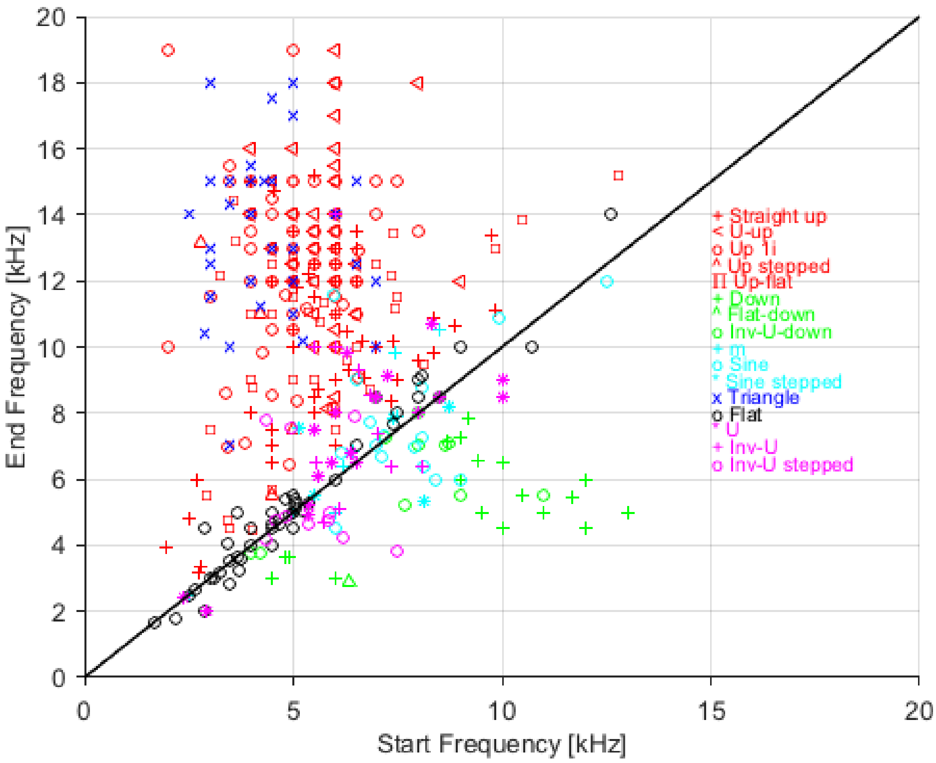
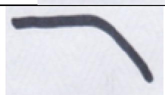
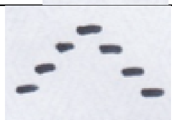
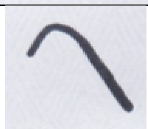
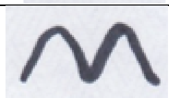
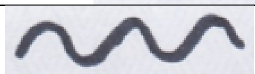
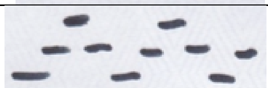
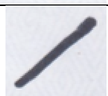
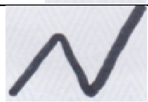
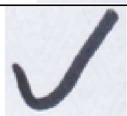
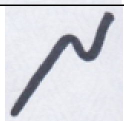


Fig. 5: End frequency versus start frequency of all whistles, marker-coded by type. Red markers belong to overall upsweeping contours. While the Triangle is also upsweeping overall, due to its frequent occurrence, this type was plotted in blue, for clarity. Overall downsweeping contours are shown in green, sinusoidal contours in cyan, flat contours in black, and parabolic contours in magenta.

All 16 whistle types were heard in bouts satisfying the SIGID criterion, and hence all qualified as potential signature whistles. Example bouts are also shown in Fig. 4. The number of dolphin encounters during which each whistle type was recorded is shown in Table 4.

Table 4: Number of dolphin encounters during which each whistle type was recorded over the three seasons.

Whistle Type	Contour Cartoon	Number of dolphin encounters during which this type was recorded
Down		8
Flat		10
Flat-down		1
Inv-U		5
Inv-U stepped		2
Inv-U-down		4
m		5
Sine		5
Sine stepped		4
Straight up		11
Triangle		3
U		6
U-up		5
Up 1i		9
Up stepped		2
Up-flat		10

3.2 Inter-Observer Reliability

Observers A and B grouped all 513 whistles, while Observer C grouped a subset of 408 whistles. These observers produced 16, 15, and 4 groups, respectively. All three observers named their groups after the shape of the fundamental whistle contour, although specific names varied. Of all the whistles that A and B grouped, 81% were uniquely matched from A's groups into exactly one of B's groups, with 19% sorted into other groups of B. For example, all of the whistles that A grouped as Downsweeps were also grouped as Downsweeps by B and C. While all of the whistles that A grouped as Flat were also grouped as Flat by C, a few were grouped as Upsweeps by B, though the majority were grouped as Constant (another name for Flat) by B. The whistles that A sorted into separate groups of U-up, Up 1i, Up-flat and Straight-up were lumped by C into Upsweeps. Comparing the groupings done by A and C, 93% of whistles were uniquely matched from A's groups into exactly one of C's groups, with only 7% sorted into other groups of C (Fig. 6).

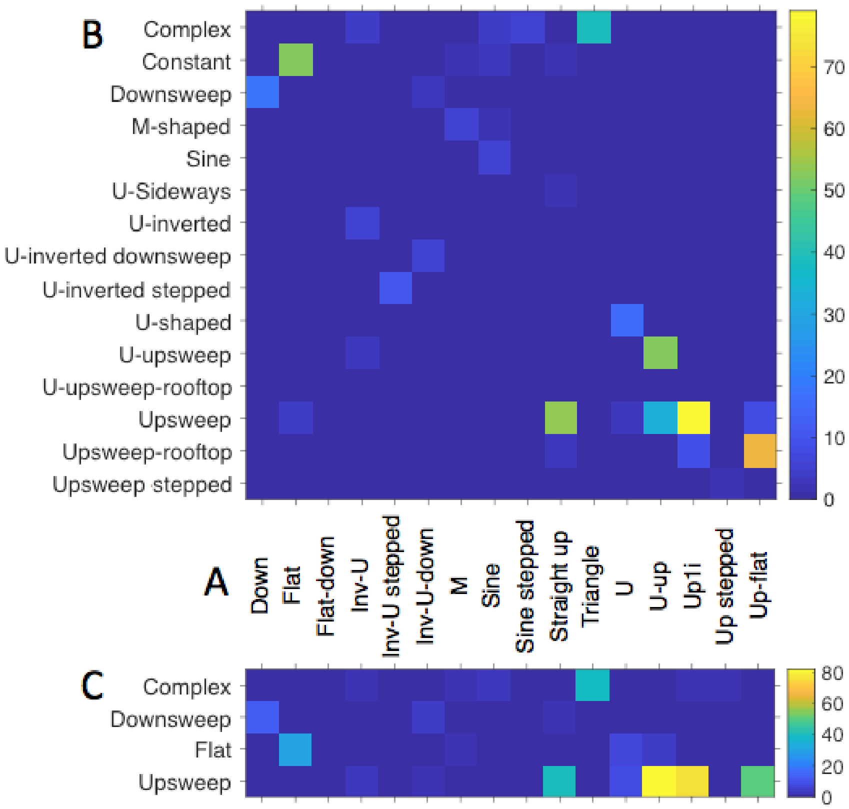


Fig. 6: Numbers of whistles (represented by colours) per group by Observer A versus B and A versus C. The lighter the colour, the more whistles were uniquely matched from one of A's groups into one of B's or C's groups

3.3 Whistle Type versus Photo-ID

The conditional probabilities that each of the whistle types were recorded when any specific individual of the Swan-Canning River System dolphin community was present are visualised in Fig. 7. Arrow and Hii were present together during three encounters, and each time, Straight up was recorded. Blackwall, Garden, Moon, and Pirulli were photographed during only one encounter each, in the presence of 3, 8, 7, and 8 whistle types, respectively; with Garden and Pirulli being in the same encounter. Bottomslice was part of two encounters and Sine and Straight up were recorded in both encounters, with additional whistle types recorded in just one of the two encounters. Cruze and Soul shared in the same two encounters that involved Straight up. Print was present both times as well, and in one additional encounter. Straight up was also the most likely whistle for Kwillena Lookalike. Every time that Danielle, Dunnedoo, Product, and Resource, while not all part of the same encounters, were photographed, Up 1i and Up-flat were recorded; Product and Resource were in the same three encounters. Gizmo and Tupac were in three encounters together hence show identical probabilities with Flat having been recorded during each of these three encounters. Flat, U-up and Up 1i were the most likely whistles of Pebbles and the only whistles recorded during the encounter that included Blackwall.

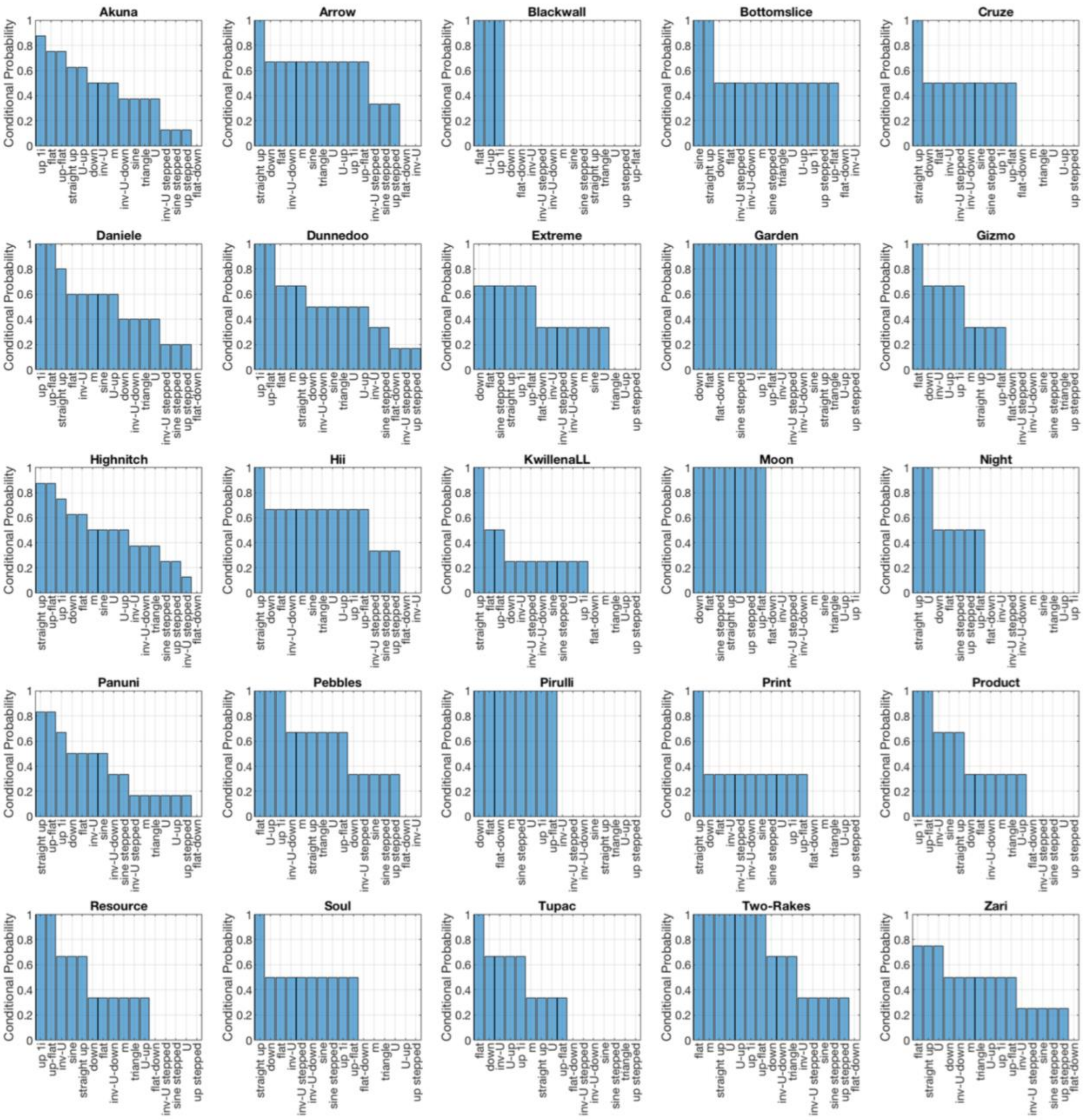


Fig. 7: Conditional probability that each whistle type was recorded when a specific individual was present (ordered according to decreasing probability)

Based on presence and absence of dolphins when whistles were recorded, most whistle types were narrowed down to a range of possible dolphins that could have produced it. The posterior probabilities for each animal to be present when a specific whistle was recorded are visualised in Fig. 8. Dunnedoo, Extreme, Garden, and Pirulli were present during the one encounter when Flat-down was recorded. Akuna, Dunnedoo, and Highnitch were always present when Triangle was recorded (3 encounters). Akuna was also always present when U-up was recorded (5 encounters); in fact, Akuna was the only dolphin always present when U-up was recorded. Finally, Highnitch was the only dolphin present in both encounters when Up stepped was recorded. The posterior probability of individual dolphins being present varied from less than 1 to 0 for all other whistle types.

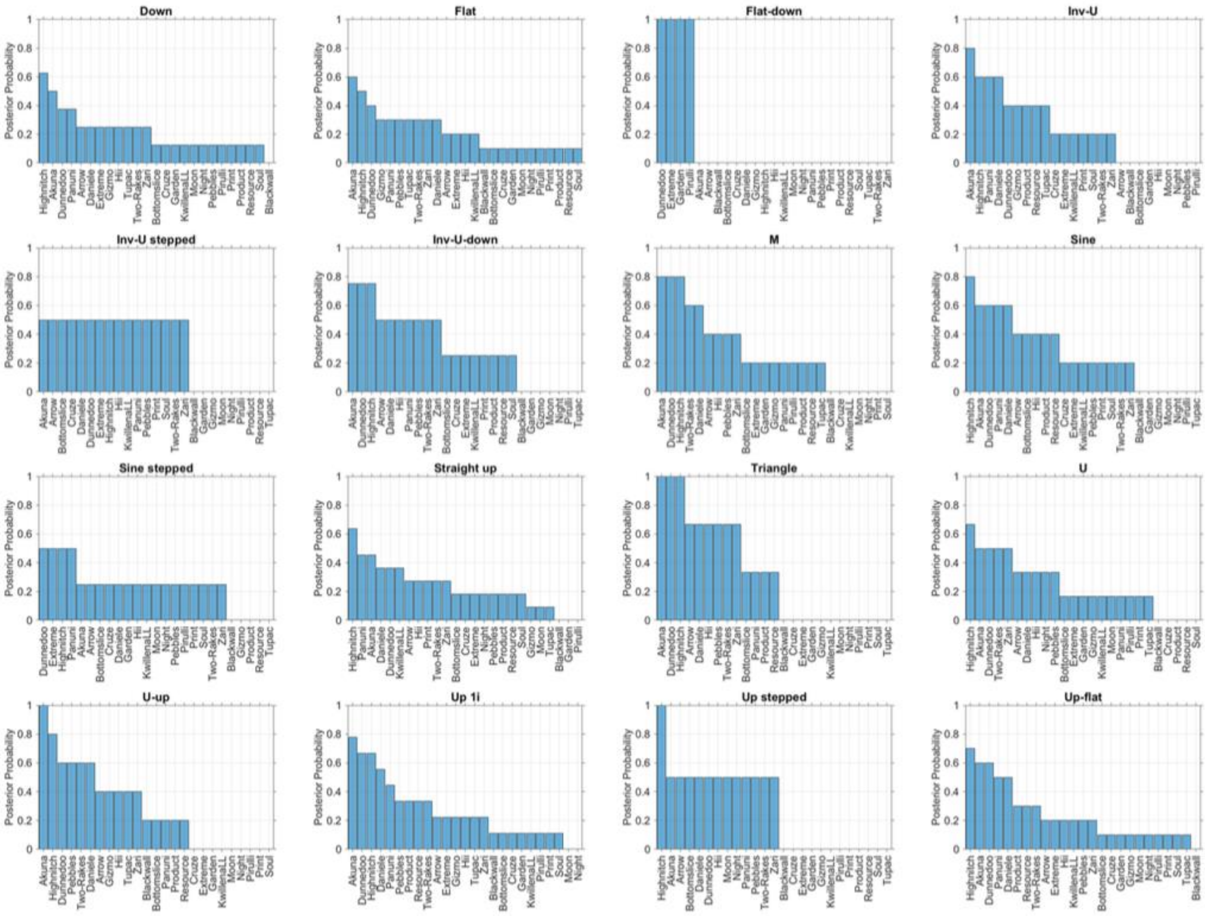


Fig. 8: Posterior probability that each animal was present when a specific whistle was recorded

3.5 Whistle Type and Individual Clusters

Given the previous sections failed to produce a unique match between whistle type and individual (and in fact, more individuals were photographed than whistle types recorded), cluster analysis was performed and confirmed that the distribution of individuals versus whistle types was not random. On the contrary, certain clusters emerged. Fig. 9 (top) gives a dendrogram (i.e., cluster tree) based on the frequencies that animals were photographed together). Fig. 9 (bottom) aligns the dendrogram leaves with the posterior probabilities that individual dolphins were present when each whistle type was recorded. Product and Resource, Arrow and Hii, Gizmo and Tupac, Garden and Pirulli, as well as Cruze and Soul were in the same encounters and thus show identical probabilities. The highest probabilities link Product, Resource, Daniele, and Dunnedoo with Up 1i and Up-flat; Arrow and Hii with Straight up; Bottomslice with Straight up and Sine; Gizmo and Tupac with Flat; Night with Straight up and U; Cruze, Soul, and Print with Straight up; and Kwillena Lookalike with Straight up.

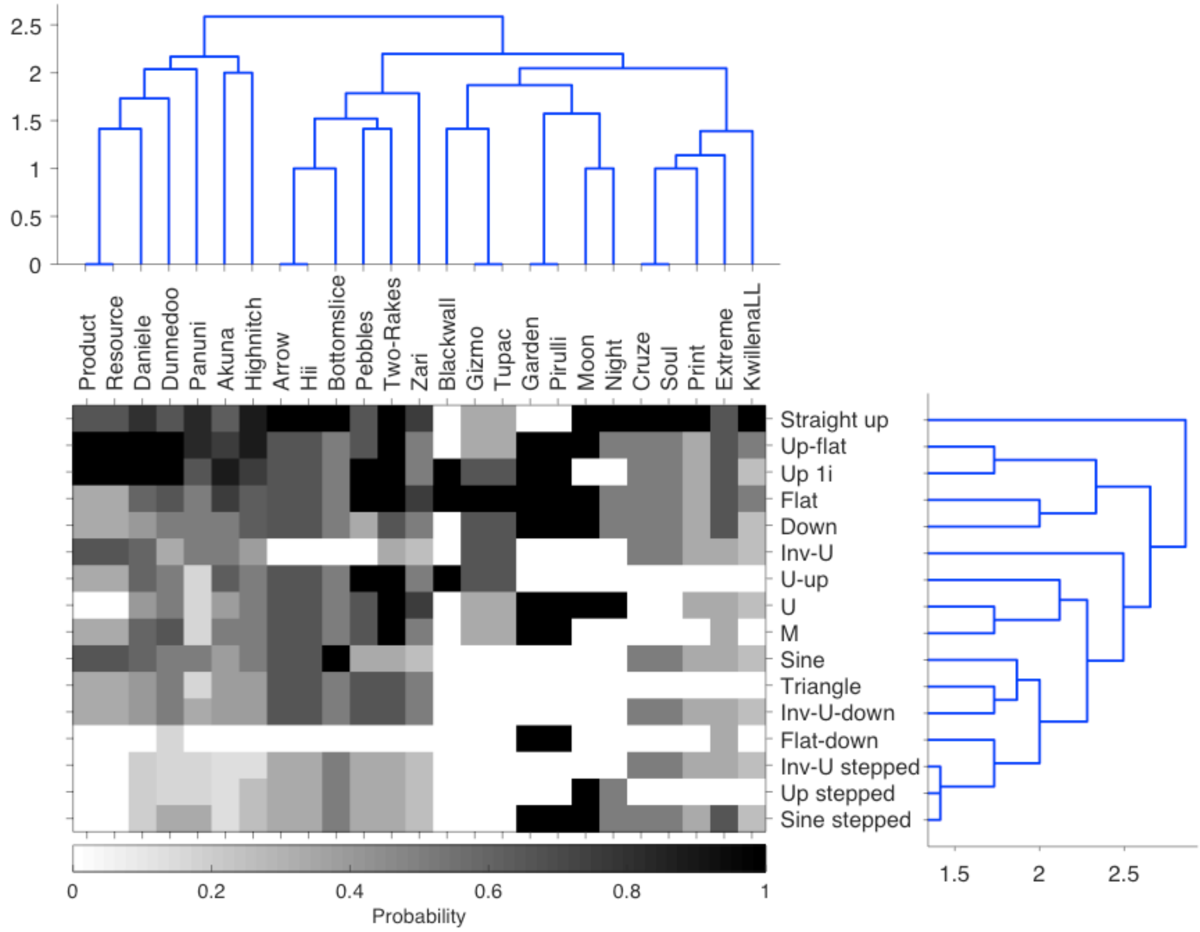


Fig. 9: Summary of posterior probabilities of individual dolphins present, given the whistle type was present. The matrix of probabilities was aligned (top) with the dendrogram of the frequencies that any individuals were observed together and (right) with the dendrogram of the frequencies that specific whistles types were recorded together.

4 Discussion

This study aimed to match photographs identifying individual dolphins of the Swan-Canning River System community with simultaneous underwater acoustic recordings in order to assign signature whistles to individual animals. In the approximately 5 h of concurrent recordings and photo-ID data (collected over 3 years), dolphins were never encountered singly but always in groups. Similarly, the acoustic recordings never showed only one whistle type per encounter, but rather multiple whistle types at the same time. Therefore, no individual dolphin was photographed and recorded in isolation. Both the visual and the acoustic data sets contained multiple animals at all times. As a result, assigning signature whistles to photographs became a matter of computing probabilities that certain individuals were photographed at the time of recording certain whistle types.

All of the whistle types recorded occurred in bouts and fulfilled the SIGID criterion [14], and were thus potential signature whistles. Whistle features covered almost two orders of magnitude in duration and frequency, and one order of magnitude in the numbers of local extrema, inflection points, and steps. Some of this variation might be due to ambient noise. Fremantle Port is the fourth largest harbour of Australia and the most important one for the state of Western Australia, resulting in high levels of vessel traffic and associated noise. Noise has been shown to affect the features of bottlenose dolphin whistles, including duration, frequency, and measures of modulation such as the numbers of local extrema and inflection points [28,32-38]. We did not consider the effects of ambient noise on specific whistle features, but instead assumed that the overall contours of signature whistles were stable, and we therefore tried to match contours to photo-ID rather than specific whistle measures. In doing so, it is possible that some variations in contour types that were classed as the same contour may have in fact been different signature whistles.

The vast majority of whistles were of an overall upsweeping contour. These included straight upsweeps, but also those that had a brief U at the beginning or slight frequency-modulations (identified as the number of inflection points) along the upsweep. On many occasions, these whistles ended with a very brief undulation in the contour (characterised by a local maximum and minimum) at the high-frequency end (see, e.g., Fig. 4 Up 1i). Such modifications have been described as embellishments, and could convey emotional state [39]. Indeed, the upsweeps with such embellishments had very similar dolphin occurrences as the undecorated upsweeps (Fig. 8) and could thus be the same signature whistle(s) from the same individual(s).

Similarly, stepping a whistle could be another form of embellishment with both stepped and unstepped whistles of the same contour belonging to the same individual(s). Stepped whistles were rare (4% of all whistles recorded) and sample size was too small to determine if stepped whistles came from the same (group of) individuals as their unstepped versions. It is interesting to note that the occurrences of the three stepped whistle types were more similar to each other than to any other whistle type (Fig. 9); perhaps, the encounters with stepped whistles had something else in common (e.g., some environmental parameters or activity state). While some whistle types occurred with steps all the way through, other whistle types were embellished with a step only at the end, which raises the question whether different information is conveyed in these cases and whether different behavioural states result in different modifications of common whistle contours.

The most commonly recorded behavioural state in the Inner Harbour was foraging [18]. Research suggests that during foraging, the number of whistles increases in order to recruit more dolphins or to enhance group coordination for successful foraging [40]. This might explain why all whistle types recorded were emitted in bouts at some stage, and hence qualify as signature whistles. This might also explain the large number of embellishments (and specifically, added frequency modulations) as such elements have been associated with excitement and foraging success in other cetacean populations [41,42].

The bottlenose dolphins of the Swan-Canning River System form strong associations, which means that individuals are not normally seen alone, but rather in groups. Strongest associations exist between mothers and their calves or juveniles. The present study included sightings of six mother-calf pairs (i.e., Moon and her calf Night, Panuni and Cruze, Pirulli and Soul, Two-Rakes and Zari, Resource and Product, and Tupac and Gizmo), with the latter two pairs always seen together. Thus the probabilities of recording a particular whistle type tended to be similar for mothers and their offspring. Other studies have reported that bottlenose dolphin calves produce individually distinctive whistles by the age of 1-2 years, and that male calves tend to produce signature whistles similar to those of their mothers whilst female calves produce more distinct whistles [43]. Thus, as these calves become independent juveniles (and eventually adults), it will be informative to compare how the probability of recording a particular whistle type in their presence may change.

Similarly, male bottlenose dolphins can also form very strong social bonds known as 'alliances'. Over time, the distinctiveness of individual repertoires can decrease as males display a convergence in their whistles [44]. The present study included males frequently seen together (Group 1: Arrow, Bottomslice, and Hii; Group 2: Extreme, Kwillena Lookalike, and Print). However, a larger, longer-term dataset would be required to more fully investigate the influence of male associations on whistle structure and occurrence in the Swan-Canning dolphins.

Otherwise, group size and composition are dynamic properties of dolphin societies and thus change over time and space, including with behaviour [45]. For example, dolphins might disperse throughout the Swan-Canning River System in small groups, but rejoin for foraging. In our 5-h dataset of simultaneous visual and acoustic observations, some individuals of the Swan-Canning River community were never encountered, some were only encountered once, and others were encountered repeatedly—albeit in different groups. A larger sample size is therefore needed to match signature whistles with photo-ID over all possible permutations of grouping.

While to this end, the present study only managed to assign probabilities for the co-occurrence of individual dolphins and signature whistles, this is the first vital step in the development of a complete catalogue that would ultimately allow effective passive acoustic monitoring of this inherently vulnerable dolphin community. We note that Arrow and Soul, who were part of this study, have not been seen since 2017, and that Highnitch died from entanglement in fishing line in August 2018. Most recently, in 2019, Zari and Tupac died of cetacean morbillivirus[1].

Dedicated simultaneous visual and acoustic observations should be carried out in future and at additional seasons and locations within the Swan-Canning River System. There is a successful citizen science dolphin watch program, Dolphin Watch (https://www.riverguardians.com/projects/dolphin-watch) in the Swan-Canning Rivers, where the public submits observations of dolphins encountered. Combined with passive acoustic monitoring, a more complete and ongoing assessment of this dolphin community's distribution, behaviour, associations, and ultimately conservation status can be undertaken.

Conclusion

[1] https://www.riverguardians.com/projects/dolphin-watch

While passive acoustic monitoring is a useful tool for conservation management, its benefits are even greater if sounds can be matched to individuals. Dolphin signature whistles provide this link. The development of a photo-ID catalogue is often an early step in conservation research. The challenge is matching the photo-ID catalogue with a library of signature whistles, because wild dolphins rarely occur in isolation, but instead, multiple individuals are photographed together and whistle simultaneously. Based on the simultaneous collection of photo-ID and acoustic recordings during a number of encounters with different groupings of dolphins, we developed a Bayesian statistical approach for assigning probabilities of signature whistles to individual dolphins. Two hierarchical cluster trees (one for the photo-ID data and one for the signature whistles) highlighted the particular groupings of dolphins and whistles that require future sampling effort, to ultimately achieve a unique match between photo-ID and signature whistles. We believe this approach will be useful not just for the ~~rapidly declining~~ Swan River dolphin community, but more generally.

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The following author contribution statements refer to the authors by their initials.

Supervised all fieldwork: CPSK.
Collected the visual and acoustic data: 2013 (RNW), 2014 (SAM), 2017 (CPSK).
Transcribed fieldwork logs: SW.
Extracted whistles from recordings: RNW, SW, CE.
Measured whistle features: SW, RNW, CE.
Classified the whistles used in this article: CE, SW, RNW.
Led the project to match whistles with photographs: CE.
Identified dolphins in photographs: SW, CPSK.
Undertook the statistical analyses: CE, CPSK, SW.
Wrote the manuscript: CE, SW, CPSK, SAM, RNW.
All authors approved submission of the manuscript.

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