

Discriminating between the vocalizations of Indo-Pacific humpback and Australian snubfin dolphins in Queensland, Australia

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Australian snubfin and Indo-Pacific humpback dolphins co-occur throughout most of their range in coastal waters of tropical Australia. Little is known of their ecology or acoustic repertoires. Vocalizations from humpback and snubfin dolphins were recorded in two locations along the Queensland coast during 2008 and 2010 to describe their vocalizations and evaluate the acoustic differences between these two species. Broad vocalization types were categorized qualitatively. Both species produced click trains burst pulses and whistles. Principal component analysis of the nine acoustic variables extracted from the whistles produced nine principal components that were input into discriminant function analyses to classify 96% of humpback dolphin whistles and about 78% of snubfin dolphin calls correctly. Results indicate clear acoustic differences between the vocal whistle repertoires of these two species. A stepwise routine identified two principal components as significantly distinguishable between whistles of each species: frequency parameters and frequency trend ratio. The capacity to identify these species using acoustic monitoring techniques has the potential to provide information on presence/absence, habitat use and relative abundance for each species. © 2014 Acoustical Society of America. [<http://dx.doi.org/10.1121/1.4884772>]

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I. INTRODUCTION

Sound is very important to cetaceans for navigation, communication, and foraging (Tyack, 2008). Study of the acoustic repertoires of cetaceans is thus critical for understanding their communication systems and social interactions (Janik and Slater, 1998) and for population monitoring (di Sciara and Gordon, 1997). Despite the important role of acoustics in many aspects of cetacean behavioral ecology, the acoustic behavior of most species of odontocetes (toothed whales) remains inadequately studied, as the vocalizations of many of these cetaceans remain unknown (Janik, 2009).

Sounds are generally described based on general features of their spectral composition and structure (a process described as qualitative, as it does not include quantitative analysis of acoustic measurements) (Popper, 1980). In

addition to extensively studied species such as bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*), quantitative analysis on vocalizations of free-ranging delphinid species include studies of spinner dolphins (*Stenella longirostris*) (Norris *et al.*, 1994), spotted dolphins (*Stenella frontalis*) (Pryor and Kang-Shallenberger, 1991; Herzing, 1996), Hector's dolphins (*Cephalorhynchus hectori*) (Dawson and Thorpe, 1990; Slooten, 1994), and the Tucuxi (*Sotalia fluviatili*) (Monteiro-Filho and Monteiro, 2001; Erber and Simão, 2004). Nonetheless, quantitative descriptions are still lacking for many species of odontocetes (Rendell *et al.*, 1999).

The ability of an individual to recognize conspecifics is probably crucial for communication and reproduction for the many species of odontocetes that have complex social structures and rich vocal repertoires (Janik, 2009). Quantitative studies of the acoustic repertoires of odontocetes have shown measurable differences in whistle production within and between species (Rendell *et al.*, 1999). Several hypotheses have been proposed to explain interspecific whistle variation.

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Divergence in the vocalizations of sympatric species has been suggested as an evolutionary mechanism to maintain reproductive isolation as a result of selection pressures against hybridization (Rendell *et al.*, 1999). An animal's adaptation to its environment may also play a role in geographic variation of whistle characteristics within a species (Ding *et al.*, 1995). Considering that there are 72 species of odontocetes, relatively few studies have addressed the topic (Steiner, 1981; Schultz and Corkeron, 1994; Matthews *et al.*, 1999; Rendell *et al.*, 1999; Mellinger and Clark, 2000; Oswald *et al.*, 2003).

In Australian coastal waters, Indo-Pacific humpback dolphins (*Sousa chinensis*, hereafter referred to as humpback dolphins) and Australian snubfin dolphins (*Orcaella heinsohni*, hereafter referred to as snubfin dolphins) occur in sympatry throughout most of their ranges (Corkeron *et al.*, 1997; Parra *et al.*, 2002; Parra *et al.*, 2004). Phylogenetic analyses of mitochondrial and nuclear DNA suggest that Australian populations of humpback dolphins are genetically distinct from those found in China and Indonesia and may indeed be different species (Frère *et al.*, 2011; Mendez *et al.*, 2013). The Australian snubfin dolphin was described only recently as a new species endemic to the waters of Australia, and potentially New Guinea and the Solomon Islands (Beasley *et al.*, 2005).

Due to their coastal distribution and apparently small and fragmented populations, snubfin and humpback dolphins are subject to anthropogenic threats such as coastal development, incidental catches in gillnets and shark nets, pollution, overfishing of prey resources, and vessel traffic (Parra *et al.*, 2004, 2006). Knowledge of the acoustic repertoires of these species could improve the capacity to distinguish them acoustically, allowing the use of automated passive acoustic monitoring to provide valuable information about their occurrence, relative abundance and fine scale habitat use in high-risk areas, such as regions subject to port developments (Cagnazzi *et al.*, 2013) or where they may be impacted by bycatch from gillnets (Rojas-Bracho *et al.*, 2009). Knowledge of the acoustic repertoires of these species is not yet adequate for this approach to be developed.

The few studies available on the vocalizations of humpback dolphins are mainly descriptive and qualitative including observations of underwater sounds in the Indus Delta region (Zbinden *et al.*, 1977), a description of the clicks from a population near Hong Kong (Goold and Jefferson, 2004), and qualitative descriptions of the repertoires of populations in Hong Kong waters (Sims *et al.*, 2012) and Australia (Smith, 2000; Van Parijs and Corkeron, 2001). Apart from a limited comparison of humpback dolphin whistles with those of bottlenose dolphins in Moreton Bay, Australia (Schultz and Corkeron, 1994) there are no other quantitative studies on the vocalizations of humpback dolphins in the wild. This lack of acoustic information is even more evident for the snubfin dolphin, for which there is only one qualitative study (Van Parijs *et al.*, 2000).

In this study, we examined the vocalizations of two geographically separated populations of humpback and snubfin dolphins along the east coast of Queensland to: (1) briefly

describe their sounds qualitatively, and (2) quantitatively elucidate patterns in the variation of whistle characteristics between these two species. We demonstrate that interspecific variation between the whistles of Australian snubfin and humpback dolphins is evident.

II. METHODS

A. Data collection—Study site and target species

Acoustic recordings of each species were obtained at two locations along the east coast of Queensland. Recordings of each species were made in the absence of the other species to avoid confounding the acoustic sampling with mixed species recording. Vocalizations of humpback dolphins were collected in Moreton Bay, off North Stradbroke Island (27° 23' S, 153° 26' E; Fig. 1), Queensland, Australia, between February and April 2008 (18 field days). Snubfin dolphin sounds were recorded at the mouth of the Fitzroy River (23° 31' S, 150° 53' E; Fig. 1) in Keppel Bay, central Queensland, between July and August of 2010 (seven field days). Both of these areas are characterized by habitat features that are often preferred by these two species: shallow coastal waters in the vicinity of a river mouth. For both humpback and snubfin dolphins, foraging was the most commonly observed behavior in these areas (Cagnazzi, 2010; Berg Soto, 2012).

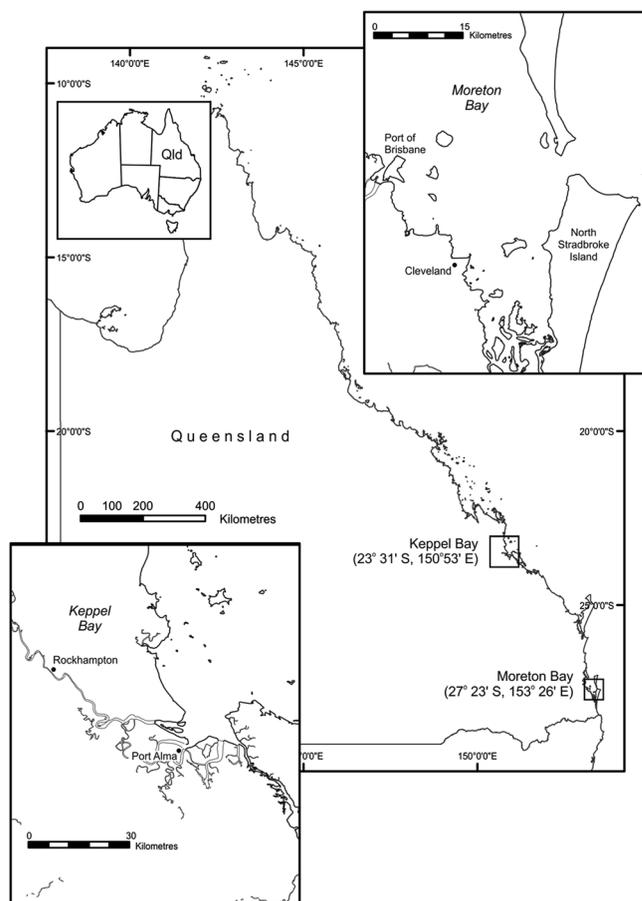


FIG. 1. Map of Queensland and our studies site: Keppel Bay (snubfin dolphins recorded) and Moreton Bay (humpback dolphins recorded).

B. Acoustic recordings

Acoustic recordings were made from small boats (4–6 m long) during calm sea conditions (Beaufort <3), at distances of 20–150 m from a dolphin school, in waters 3 to 10 m deep, during daytime (i.e., from 6 a.m. to 5 p.m.), during high and low tide. A school was defined as either: (1) a solitary animal, or (2) any aggregation of dolphins where a member was within 10 m of any other member and where over 50% of the animals elicited the same behavioral state (Van Parijs *et al.*, 2002). When dolphins were sighted, the boat was maneuvered slowly ahead of them to a distance of approximately 100 m, before shutting off the engine and drifting to reduce background noise.

Dolphin recordings were obtained from a single High Tech Inc. hydrophone (model HTI-96-MIN, frequency response: 5 Hz–30 kHz \pm 1.0 dB, with an in-built +40 dB pre-amplifier giving resultant sensitivity of -165 dB re 1 V/ μ Pa). The hydrophone was lowered from the side of the vessel into the water to a depth of approximately 3 m. Dolphin vocalizations were recorded onto Scandisk Ultra compact flash memory cards, as “.wav” files using a Micro Track (M-Audio 24/96 digital recorder) at a sampling rate of 44.1 kHz on a single channel to optimize data storage space. Analysis of recordings was limited to a maximum frequency of 22 kHz by the recording sampling rate. Although humpback dolphins are known to produce whistles with maximum frequency around 30 kHz (Sims *et al.*, 2012), we believe our limited recording capacity did not affect the results of our study as none of the fundamental waveforms from the analyzed whistles were cut off in the spectrograms. In addition, the ability to discern whistles between species using a lower sampling rate may prove more effective and economic for the development of future automated acoustic buoy systems. Acoustic recordings of dolphin schools were obtained at different times of the day, at different locations within the study site, to minimize the likelihood of re-sampling the same group.

C. Qualitative analysis—Spectrographic measurements and exploratory statistics

Recordings were analyzed as spectrograms [512 point fast Fourier transform (FFT), 22 kHz bandwidth] using Raven v1.3, Cornell University Bioacoustics Laboratory (Charif *et al.*, 2007). Only recordings with good signal-to-noise ratio were included, on the basis of aural and visual inspection of the sound and spectrogram (Rendell *et al.*, 1999). Consequently, sounds that were selected for analysis were clear sounds not obscured by another noise and of good signal-to-noise ratio so that unambiguous quantitative measures could be achieved.

Vocalizations were divided into three acoustic categories: click trains, burst pulses, and whistles (narrowband, frequency-modulated sounds). Initial qualitative categorization of the vocalizations was undertaken using a double blind, independent observer method. The vocalizations were originally categorized by a primary observer (A. Berg Soto) based on aural and visual inspection of the sounds and methodology by Van Parijs and Corkeron (2001). The initial

categorization of vocalizations was validated using a blind, independent observer. The independent observer (J.N. Smith), who had experience in the acoustics of coastal dolphins, was provided with a subsample of the catalogue, consisting of 61 snubfin (about 4% of total the recorded material) and 74 humpback dolphin (over 7% of the total recorded material) sound files. Sound files of whistles, burst pulses and clicks were randomly sorted and re-labeled based on an arbitrary consecutive numbering system for each species. The second observer had no information about the vocalization types, recording context or dolphin identity. The same acoustic software (Raven, Version 1.3) and spectrogram parameters used in the original classification of the vocalizations were used by the second observer. The re-classified vocalizations were then compared with the original classification to determine the number of common vocalization types classified by both observers (Rehn *et al.*, 2010).

Five primary acoustic variables were measured for each whistle: (1) start frequency (Hz); (2) end frequency (Hz); (3) minimum frequency (Hz); (4) maximum frequency (Hz); and (5) duration (s) (Steiner, 1981; Ding *et al.*, 1995; Rendell *et al.*, 1999; Van Parijs and Corkeron, 2001). Four additional values were determined from each whistle: (1) number of harmonics (Corkeron and Van Parijs, 2001; Van Parijs and Corkeron, 2001), (2) number of inflections (number of reversals in sign of the slope) (Rendell *et al.*, 1999; Oswald *et al.*, 2003; Dunlop *et al.*, 2007), (3) ratio of start to end frequency (frequency trend ratio), and (4) ratio of maximum to minimum frequency (frequency range ratio) (Dunlop *et al.*, 2007). Ratios of frequencies were calculated rather than their differences as ratios better match the way in which mammals perceive frequency differences acoustically (Richardson *et al.*, 1995). These measurements were not extracted from burst pulses, as some frequency parameters are difficult to obtain due to the nature of these sounds.

D. Quantitative analysis

We used SPSS version 19 to conduct a series of quantitative tests on the vocalizations of humpback and snubfin dolphins.

1. Auto-correlation tests

To minimize the risk of obtaining vocalizations from the same dolphins and using repeated whistle samplings of the same individuals in our analysis (i.e., pseudo-replication; Hurlbert, 1984), we investigated the auto-correlation structure of the data. This test was performed for each species using different units of analysis: (1) individual recordings, (2) encounters, and (3) field days. Median values were calculated for the nine acoustic measures for whistle types identified for these units of analysis. Units of analysis that produced positive results for auto-correlation or partial auto-correlation were discarded from further analysis. The unit of analysis that minimized the risk of pseudo-replication in the data obtained from humpback dolphins was field days. To maintain consistency we used the same units of analysis for further statistical tests of the snubfin dolphin data as well.

2. Principal component analysis

A principal component analysis was performed on the correlation matrix of our standardized variables. The principal component analysis was forced to output all possible components ($n = 9$) required to explain 100% of the variance. This approach produced nine principal components that could be then used in a stepwise methodology in the discriminant function analysis, in order to select those groups of variables that were significant in discerning between whistles of both species. Although the first principles components usually explain most of the variance in the data, they are not necessarily the best for discrimination (McLachlan, 1992; Mallet *et al.*, 1996). Thus, we considered all nine components (equal to our number of variables) from the analysis to explore all possible discriminating components. Acoustic values which had factor loadings with any main component extracted greater than -0.5 and less than 0.5 , were not considered to be highly correlated (Field, 2000).

3. Discriminant function analysis

Discriminant function analysis was used to classify species based on the parameters of their whistles (Oswald *et al.*, 2003). Stepwise discriminant function analyses classified whistles to predetermined groups based on linear functions derived from the principal components used and considered only those that were significant in discerning between groups. This process determined the probability of sounds being correctly classified to each of the two species and showed us which variables are more important for this process. Only cross-validated results were considered. Here, each case is classified by the functions derived from all cases except that case, so the cross-validated classification rate is a more accurate measure of the predictive classification ability of the model.

We used groups of acoustic variables that behaved similarly, obtained through principal component analysis, as individual variables in the discriminant function analysis, rather than using the median frequency measurements obtained from whistles identified at the level of the independent units of analysis (converted to a logarithmic scale; Dunlop *et al.*, 2007). This was performed, as single variables may go undetected when a stepwise routine is performed on the raw data. It is very common for multivariate methods to analyze principal components instead of the raw variables (Johnson and Wichern, 2002, page 426).

As the sample sizes of whistles were different for humpback dolphins ($n = 49$) and snubfin dolphins ($n = 18$) at the level of the units of analysis chosen to minimize pseudo-replication (field days), the percentages for each species were then compared to the probability of randomly selecting a whistle from each species, according to their respective relative frequencies in the total data set. Thus a better-than-chance correct classification for humpback dolphin whistles would need to be higher than 73%, and for snubfin dolphin whistles, higher than 27% (Table III).

Once the significant main components that differentiated between the whistles of both species were identified, further discriminant function analyses were performed to identify which minimum combination of components

produced the best total cross-validated, correct classification percentage. After the best combination of significantly discerning main components was determined, we produced a graph of principal component scores from these selected components (Fig. 3).

III. RESULTS

A. Qualitative description

A total of 1024 clear vocalization samples from humpback dolphins was collected across 18 field days over 12.2 h of recordings from 46 dolphin schools (mean school size = 2, range 1–10). For snubfin dolphins, we used 1558 clear vocalizations from 4 h of recordings conducted over seven field days from 20 different schools (mean school size = 2, range = 1–5). The larger number of high quality vocalizations recorded for Australian snubfin dolphins was partly a result of the lower levels of underwater noise in Keppel Bay than in Moreton Bay, where humpback dolphins were recorded. Other possible explanations for these differences include species differences, variation in source levels, animal proximity to hydrophone, and propagation conditions of the study site, all of which are unknown.

The revision of the initial catalogue by the independent observer resulted in a smaller set of vocalizations. Vocalizations for which the two observers disagreed were not considered further, reducing the number of vocalizations categorized to about 80% of the original catalogue. Mean, standard deviation, and range were calculated for each of the final sound types identified: click trains, burst pulses, and whistles. Burst pulses and whistles were observed as discrete phenomena and not as points on a continuum, as described false killer whales (*Pseudorca crassidens*) vocalizations (Murray *et al.*, 1988) The following is a comparative qualitative description of the main sound types recorded for each species.

1. Click trains

There are several standard ways of measuring the duration and bandwidth of odontocete clicks that have been developed for beaked whale echolocation studies (e.g., Zimmer *et al.*, 2005; Johnson *et al.*, 2006). We decided to report clicks in a similar manner to that used in previous studies of snubfin and humpback dolphins in Australia (Van Parijs and Corkeron, 2001), to enable comparisons with an existing baseline. Thus, we considered each click train as a unit of constituent clicks and provided acoustic measures obtained from spectrograms and waveforms [Fig. 2(a)] (Van Parijs and Corkeron, 2001).

Broadband clicks were recorded as “click trains” (a series of clicks in quick succession) for both humpback ($n = 64$ click trains recorded) and snubfin ($n = 1446$ click trains recorded) dolphins [Fig. 2(a)]. The highest value of the minimum frequency of humpback dolphins’ click trains (mean \pm standard deviation = 4 ± 3 kHz) was 10.7 kHz, while the highest minimum frequency for snubfin dolphins’ click trains (10.2 ± 4.5 kHz) was 17.4 kHz (Table I). The

Humpback sounds

Snubfin sounds

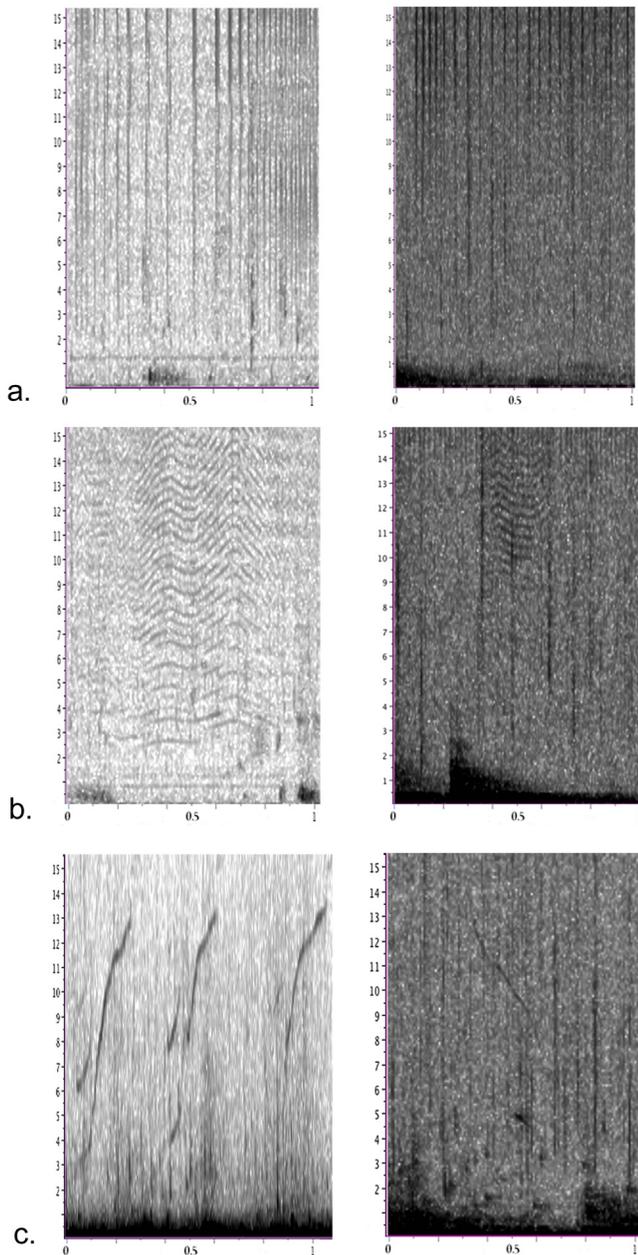


FIG. 2. (Color online) Sample spectrograms (x axis=seconds, y axis =kHz) of (a) click trains, (b), burst pulses, and (c) whistles from humpback and snubfin dolphins recorded in Queensland. Spectrograms were generated using a FFT of 512.

maximum frequency for clicks elicited by both species extended above 22 kHz (the limit of our analyzed frequency bandwidth). The duration of humpback dolphin click trains (2.79 ± 2.66 s) was significantly longer ($t = 2.151$; $p = 0.032$) compared with snubfin dolphins (1.53 ± 18.42 s) (Table I).

2. Burst pulses

Both humpback and snubfin dolphins produced burst pulses [Fig. 2(b)]. We recorded 143 burst pulses from humpbacks and 77 from snubfin dolphins. These burst pulses consisted of either tightly packed sidebands or sparse undulating

sidebands extending above 22 kHz [Fig. 2(b)]. The average duration of burst pulses was 0.86 ± 0.84 s for humpback dolphins, and 0.41 ± 0.42 s for snubfin dolphins (Table I). Some of these burst pulses were very short in duration (0.07 s for both species), while others were much longer (4.6 s for humpback dolphins) (Table I). The mean minimum frequency (repetition rate tone) value for humpback dolphins was 5.8 ± 3 kHz; snubfin dolphins 7.6 ± 4 kHz (Table I).

3. Whistles

Both species showed a diverse range of unique narrow band, frequency modulated sounds, commonly referred to as “whistles” (Popper, 1980) [Fig. 2(c)]. Whistles recorded for humpback dolphins ($n = 742$), varied in frequency and duration, as well as the number of inflections. Not all samples of whistles recorded exhibited harmonics. Less variation was found in whistles recorded from snubfin dolphins ($n = 34$). Over half of these whistles exhibited harmonics, which could be a result of lower noise levels in these recordings. However, very few snubfin whistles had more than one harmonic.

Whistles of humpback dolphins ranged in duration from very short emissions lasting 0.3 s to longer whistles of 4.6 s. Snubfin dolphin whistles ranged in duration from 0.08 to 0.45 s (Table I). The mean lowest frequency calculated for humpback and snubfin groups were 6.35 ± 2 and 4 ± 2 kHz, respectively, and the mean highest frequencies were 12.3 ± 4 and 6.5 ± 3 kHz, respectively (Table I), suggesting that snubfin dolphins may produced whistles of lower frequency than humpback dolphins. Although the fundamental frequency of dolphin whistles can reach maximum frequencies over 22 kHz, such whistles were not observed within our sampled recordings.

B. Quantitative comparisons

1. Auto-correlation analyses

Temporally spaced auto-correlation analyses on the whistle data collected for humpback dolphins ($n = 739$) showed that there was autocorrelation in most acoustic variables when the unit analyzed was: (1) the individual recording ($n = 739$) and (2) the encounter ($n = 64$), but not across days ($n = 49$) (95% confidence level over 25 lags). The corresponding analysis for snubfin dolphins ($n = 33$) did not detect significant auto-correlation at any of the three units of analysis. However, we also analyzed the snubfin dolphin data at the day level ($n = 18$) to be consistent with humpback dolphin data.

2. Principal component analysis

Nine principal components were produced from the principal component analysis that accounted for 100% of the variation of the sounds of both species combined (Table II). Component 1 (37.2% of variance) was loaded positively with start and end frequency, as well as maximum and minimum frequency, representing the frequency characteristics of the whistles. Component 2 (14.9% of variance), 3 (13% of variance), and 4 (11.7% of variance) were highly correlated to trend frequency ratio, range frequency ratio and duration,

TABLE I. Mean, standard deviation and range for click trains, burst pulses, and whistles recorded from humpback and snubfin dolphins in Queensland.

Species	Humpback dolphins			Snubfin dolphins		
	Vocalization	Clicks	Burst pulses	Whistles	Clicks	Burst pulses
Sample size	64	143	742	1446	77	34
Maximum Frequency	>22 kHz	>22 kHz	12.25 ± 4.12 kHz 4.18 – 21.78 kHz	>22 kHz	>22 kHz	6.47 ± 2.89 kHz 1.54–12.92 kHz
Minimum Frequency	3.98 ± 2.56 kHz 0.15–10.7 kHz	5.77 ± 3.19 kHz 0.91–16.3 kHz	6.35 ± 1.96 kHz 1.66–16.2 kHz	10.23 ± 4.5 kHz 0.33–17.37 kHz	7.64 ± 3.65 kHz 1.38–15.38 kHz	4 ± 1.95 kHz 0.61–9.46 kHz
Duration	2.79 ± 2.66 s 0.21–15.3 s	0.86 ± 0.84 s 0.07–4.6 s	0.25 ± 0.2 s 0.03–1.26 s	1.53 ± 18.42 s 0.11–701 s	0.41 ± 0.42 s 0.07–2.15 s	0.23 ± 0.08 s 0.08–0.45 s
Number of inflections	-	-	0.85 ± 0.88 0–7	-	-	0.66 ± 1.41 0–7
Number of harmonics	-	-	0.5 ± 0.6 0–5	-	-	0.8 ± 0.83 0–3

respectively. The last two acoustic variables, number of inflections and number of harmonics, were highly correlated with Principal Components 5 and 6, respectively (11.2% each). The remaining three components were weakly correlated with all acoustic variables, and together explained only 0.8% of the variance (Table II).

3. Discriminant function analysis—Stepwise methods

The first component entered in the discriminant function analysis model through a stepwise methodology was Component 2 (frequency trend ratio), with a total classification accuracy of 80.6%. The corresponding values were 85.7% for humpback and 66.7% for snubfin whistles (Table III). The second component added was Component 1 (frequency parameters), with a total correct classification of 91%. Using these two components, classification accuracy was 95.9% and 77.8% for humpback and snubfin dolphin whistles, respectively (Table III). The third component added in the analysis was Component 6 (number of harmonics), which resulted in 86.6% total classification accuracy, and 89.8% correct classification for humpback dolphins; snubfin dolphin classification remain the same as with the previous two components (Table III). The final component

selected in the model was Component 9 (no clear loading), which produced a 91% total classification, 98% for humpback dolphins and 72.2% for snubfin dolphins (Table III).

The stopping criterion for the stepwise routine allowed four components to enter the model. The first two Components (2 and 1) produced a similar total classification accuracy to that obtained using all four components selected through the stepwise methodology (91%). To simplify the model, we chose the minimum number of components (2 and 1) to create a principal component graph (Fig. 3) and visually represent the distinction between whistles of different species. Based on this, and considering the larger number of humpback dolphin whistles in the analysis, the ability to classify humpback whistles correctly improved 23% from chance alone, while that of snubfin dolphin whistle improved 51% (Table III). The principal component graph shows separation between humpback and snubfin whistles, mainly along the y axis (Component 2—frequency trend ratio).

IV. DISCUSSION

This study documents the vocalizations of both humpback and snubfin dolphins (Fig. 2) and provides a framework for future, more comprehensive studies on the whistles of

TABLE II. Rotated factor loadings (Varimax) for each acoustic variable considered in the principal component analysis of whistles of both humpback and snubfin dolphins ($n = 67$) for all nine principal components extracted. Values in bold had loadings greater than 0.5 or less than -0.5. in at least one of the principal factors (Field, 2000).

	Component								
	1	2	3	4	5	6	7	8	9
Duration	0.006	-0.034	0.245	0.968	0.041	0.014	-0.004	0.004	0.000
Start freq	0.934	0.223	-0.122	-0.034	0.067	-0.072	-0.129	-0.188	-0.015
End freq	0.834	-0.452	0.251	0.043	-0.049	-0.094	-0.045	0.111	0.096
Trend ratio	-0.143	0.972	-0.146	-0.036	-0.032	0.101	-0.013	-0.008	0.003
Min freq	0.850	-0.119	-0.407	-0.080	0.090	-0.126	0.257	0.030	-0.006
Max freq	0.873	-0.302	0.323	0.101	-0.072	-0.085	0.018	0.129	-0.051
Range ratio	0.019	-0.200	0.924	0.306	-0.112	0.010	-0.003	0.013	0.002
No. inflections	0.026	-0.025	-0.094	0.036	0.980	0.165	0.003	-0.004	0.000
No. harmonics	-0.149	0.102	0.014	0.014	0.172	0.968	-0.005	-0.001	0.000
% of variance	37%	15%	13%	12%	11%	11%	0.6%	0.1%	0.07%
Cumulative %	37%	52%	65%	77%	88%	99%	99%	99%	100%

TABLE III. Correct classification percentages for all humpback dolphins and snubfin dolphins' whistles. Rows represent different combinations of significantly discernible components identified through a stepwise routine.

Combinations	Total cross-validated correct classification	Correct cross-validated classification for humpback dolphins' whistles	Correct cross-validated classification for snubfin dolphins' whistles
Random chance alone	n/a	73%	27%
Component 2	80.6%	85.7%	66.7%
Component 2 and 1	91%	95.9%	77.8%
Component 2, 1, and 6	86.6%	89.8%	77.8%
Components 2, 1, 6, and 9	91%	98%	72.2%

these two species. Discriminant analyses using the two most significantly discernible components extracted through principal component analysis (basic frequency parameters and frequency trend ratio), correctly classified 96% of humpback dolphin calls and 78% of snubfin dolphin whistles.

As with other acoustic studies of cetaceans in which underwater caller identification was not discerned, it is likely that our recordings often included multiple measurements on the same individual (Schultz and Corkeron, 1994; Rendell *et al.*, 1999; Oswald *et al.*, 2003). Thus, our analysis has some inherent limitations that may reduce the robustness of our interspecific comparisons. Pseudo-replication can produce reduced variance, leading to statistical tests prone to type 1 error; however we used auto-correlation analysis to address this problem. Our other acoustic measurements of the whistles were not as reliable as the first two components selected in the stepwise methodology. For instance, harmonics are potentially misleading, as only fundamentals less than 10 kHz will display harmonics below 20 kHz, which was our analytical upper frequency limit. In addition, as harmonics are weaker than their fundamental frequencies, their

presence will be dependent on dolphin proximity to the hydrophone and how loud the animals vocalized. Thus, we concur with other studies that have found harmonics an unreliable quantitative measure.

Few other quantitative acoustic studies of cetaceans have reported correct classifications as high as we obtained: e.g., humpback whale social sounds (89.4% correct classification; Dunlop *et al.*, 2007), Atlantic spotted dolphins (61%), long-finned pilot whales (68%), and Atlantic white-sided (80%) (Steiner, 1981), short beaked (47%), and long beaked common dolphin (40.9%), and spotted (37.5%), striped (29.9%), and spinner dolphins (45.8%) (Oswald *et al.*, 2003). The main difference between these studies and ours is that we supplied the discriminant techniques with a set of uncorrelated summary indices (principal components) that typically describes groups of correlated variables, whereas these other studies used raw individual variables in their discriminant procedure. It is possible that their discriminant approach used in the earlier studies lost potentially useful and unique information embedded in correlated raw variables with consequential reduction in classification accuracy.

These groups of variables (i.e., trend frequency ratio and overall frequency parameters) could play an important role when using acoustic monitoring to estimate the distribution, abundance, and habitat use of different species. Possible contributions to these interspecific differences include: (1) interspecific differences (e.g., genetic, physiological), (2) differences in sound propagation between the different environments, (3) dolphin school sizes and dynamics, and (4) behavior. The environmental conditions defining the habitat used by a dolphin school, such as bathymetry and vessel noise can affect propagation and greatly influence the signal to noise ratio at any given receiver (Sundaram *et al.*, 2005). Sims *et al.* (2012) considered site effects to be probable factors in the differences between the repertoires of humpback dolphin populations from Hong Kong and Australia, including the possibility of masking. As our recordings of humpback and snubfin dolphin vocalizations come from two different sites, this difference is a possible factor affecting the differences in the observed whistle repertoire between these two species reported here.

School size (i.e., single individuals vs multiple) and composition (i.e., age and sex represented in the school) can also affect the way in which each member of a school produces sounds (i.e., sound frequency and amplitude) while different behavioral states will affect the types of vocalizations produced and recorded (Petrella *et al.*, 2012).

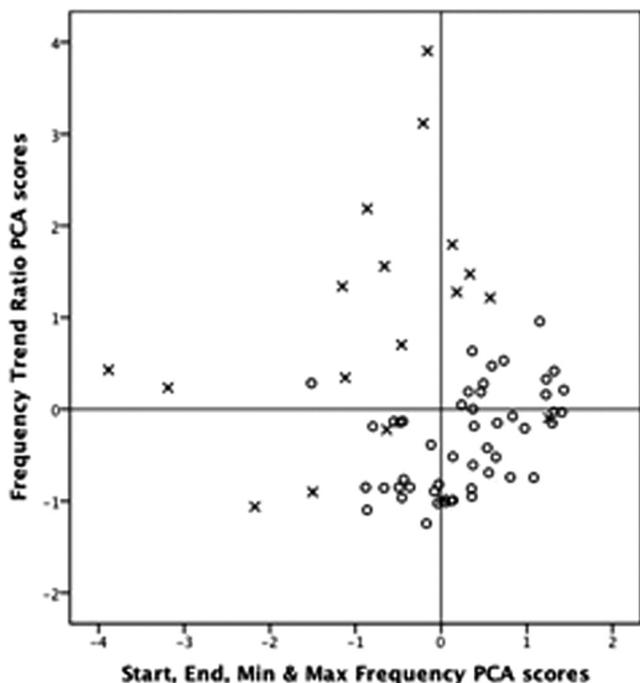


FIG. 3. Principal Component analysis plot of humpback dolphins (○) and snubfin dolphin whistles (x). X axis represent Component 1 (frequency parameters) and y axis represent Component 2 (frequency trend ratio).

Humpback and snubfin dolphins differ in their school sizes, social structure, and habitat patterns (Parra, 2006; Parra *et al.*, 2011). Thus, these differences may drive the apparent interspecific differences in the acoustic repertoires. Although it remains unclear how such factors contributed to the observed differences between our study and those of others, further comparative studies across different habitats and populations, coupled with behavioral observations should provide further insights into the factors underlying these interspecific differences in acoustic repertoires.

The acoustic repertoires described here are not an exhaustive catalogue of both species, but rather a spatial and temporal snapshot of the vocalizations of two specific populations. Individual and population differences may magnify or suppress interspecific differences. Future research should combine genetic and acoustic studies across the range of snubfin and humpback dolphins to test whether vocal divergence is correlated with genetic and/or environmental divergence.

Given their inconspicuous behavior and low densities (Parra *et al.*, 2006), the capacity to identify snubfin and humpback dolphins acoustically should improve our ability to conduct presence/absence or relative abundance studies at the species level using towed arrays (e.g., during vessel surveys) or fully automated static, passive acoustic monitoring in combination with visual surveys. As the knowledge of the distribution of these species in Australia remains incomplete especially in remote areas, passive acoustic monitoring of small populations may provide a cost effective approach to identifying the presence of these species. This approach often becomes especially important in areas in which there is a potential effect of anthropogenic threats, such as gillnetting, port development, and human coastal expansion. Examples include the study of relative abundance of Maui's dolphins in Manakau and Kaipara Harbors in New Zealand (Rayment *et al.*, 2011), as well as for the vaquita (*Phocoena sinus*) in the Gulf of Santa Clara, Mexico, where researchers have established the benefits of acoustic surveys over visual survey techniques (Rojas-Bracho *et al.*, 2009). Further research on intra- and interspecific variation of whistles among different populations of coastal dolphins in Australia will enhance our capacity to use passive acoustic monitoring at various spatial scales to detect these species.

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