

Signature whistles in free-ranging populations of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*

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ABSTRACT

Common bottlenose dolphins (*Tursiops truncatus*) use individually distinctive signature whistles which are highly stereotyped and function as contact calls. Here we investigate whether Indo-Pacific bottlenose dolphins (*T. aduncus*) use signature whistles. The frequency trace of whistle contours recorded from three genetically distinct free-ranging populations was extracted and sorted into whistle types of similar shape using automated categorization. A signature whistle identification method based on the temporal patterns in signature whistle sequences of *T. truncatus* was used to identify signature whistle types (SWTs). We then compared the degree of variability in SWTs for several whistle parameters to determine which parameters are likely to encode identity information. Additional recordings from two temporarily isolated *T. aduncus* made during natural entrapment events in 2008 and 2009 were analyzed for the occurrence of SWTs. All populations were found to produce SWTs; 34 SWTs were identified from recordings of free-ranging *T. aduncus* and one SWT was prevalent in each recording of the two temporarily isolated individuals. Of the parameters considered, mean frequency and maximum frequency were the least variable and therefore most likely to reflect identity information encoded in frequency modulation patterns. Our results suggest that signature whistles are commonly used by *T. aduncus*.

Key words: Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, categorization, identity, signature whistle.

Individuals of many long-lived species form stable associations, lasting years and even decades. In these instances, maintenance of associations usually generates a

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selective pressure for individual recognition (Wanker *et al.* 1998, Jouventin *et al.* 1999, Kazial *et al.* 2008). Many odontocetes live in a fluid fission-fusion society (Connor 2002, Markowitz *et al.* 2008) where individuals form temporary groups that frequently fuse into larger parties and split into smaller ones (Smolker *et al.* 1992, Connor *et al.* 2000). Nevertheless, throughout life, individual-specific social relationships are important (Tyack and Sayigh 1997) and stable associations form (Connor *et al.* 2000, Wells 2003, Möller *et al.* 2006).

Maintenance of relationships within a constantly changing social environment is likely to require a system of individual recognition (Sayigh *et al.* 1999). Options for transmitting identity information underwater are limited due to restricted visibility and a reduced sense of olfaction (Kishida *et al.* 2007). However, acoustic signals travel particularly well through water and most cetaceans are reliant on sound generation for orientation, foraging, and social interactions (Janik 2009). Thus it is the most likely channel in which to encode and transmit identity information.

Individual distinctiveness is enhanced when differences between individuals are large and variation within individuals is minimal (Boughman and Moss 2003). Common bottlenose dolphins (*Tursiops truncatus*) use vocal production learning (reviewed in Janik and Slater 1997) during the development of their recognition call—the signature whistle, generating large degrees of interindividual distinctiveness (Janik 2009). Vocal learning refers to instances where the vocalizations themselves are modified as a result of experience with those of other individuals (Janik and Slater 1997, Janik 2009). Individuals develop their signature whistles through experience with their acoustic environment (Miksis *et al.* 2002, Fripp *et al.* 2005), generating a unique whistle contour with high levels of individual distinctiveness which is independent of general voice features (Janik *et al.* 2006). Identity information is encoded in the distinct frequency contour of these learned stereotyped signature whistles (Janik *et al.* 2006). Each animal has only one signature whistle and its frequency modulation pattern remains stable over decades (Sayigh *et al.* 1990), facilitating maintenance of long term associations and group cohesion within their fluid social structure (Scott *et al.* 1990, Janik and Slater 1998). Signature whistles range between 1 and 27.3 kHz in frequency and last between 0.10 and 4.11 s (Buckstaff 2004, Esch *et al.* 2009b). They can be produced as a single element, or as connected and disconnected multi-looped forms (Esch *et al.* 2009b) and they are often produced in bouts containing repetitions of the same whistle type (Janik *et al.* 2013).

In separation contexts, signature whistles are the predominant whistle type produced by *T. truncatus*, comprising up to 100% of the whistles produced when animals are in isolation (Caldwell *et al.* 1990). Individuals emit the same signature during brief capture-release contexts and when in undisturbed, freely interacting contexts, demonstrating that they are not artefacts of stressful circumstances (Cook *et al.* 2004). Signature whistles play a key role in communication between groups (Quick and Janik 2012) and are likely to facilitate reunions in mother-calf pairs (Smolker *et al.* 1993).

Signature whistles have been documented in over 143 captive *T. truncatus* as well as free-ranging animals (Caldwell *et al.* 1990; Sayigh *et al.* 1990, 1999, 2007; Janik and Slater 1998). However, with the exception of bottlenose dolphins (*Tursiops* sp.) residing in Shark Bay, Australia (Smolker *et al.* 1993), little attention has been paid to whether or not congeneric species use signature whistles. Furthermore, vocal production learning, the process by which signature whistles develop in *T. truncatus* (Sayigh *et al.* 1990, Miksis *et al.* 2002, Fripp *et al.* 2005), has yet to be conclusively demonstrated in other bottlenose dolphin species. Confusion surrounding the taxo-

onomic status of *Tursiops* over recent decades (e.g., Ross and Cockcroft 1990, Wang *et al.* 1999, Natoli *et al.* 2004, Charlton-Robb *et al.* 2011), combined with the challenging task of studying vocal communication in free-ranging animals, may partly explain why this topic has received little attention.

Key similarities in the social organization, behavior, and ecology of *T. aduncus* and the coastal form of *T. truncatus*, combined with their genetic relatedness suggest that *T. aduncus* may also use signature whistles. Coastal populations of both species are often small (less than 300 individuals) and resident, as demonstrated by the site fidelity of identifiable individuals (Möller and Harcourt 1998, Wilson *et al.* 1999, Kogi *et al.* 2004, Stensland *et al.* 2006, Currey *et al.* 2008, but see Reisinger and Karczmarski 2010). A fission-fusion social system is common to both species, with individuals of either sex having preferential associations (Connor *et al.* 2000; Möller *et al.* 2001, 2006; Wiszniewski *et al.* 2009a). Both have extended periods of maternal care, including several years with elevated rates of association between mothers and calves during lactation (Connor *et al.* 2000, Kogi *et al.* 2004).

Here we study the temporal production of stereotyped whistles in wild *T. aduncus* and two temporarily isolated individuals to look for evidence of signature whistles in this species. Signature whistles in *T. truncatus* were discovered using the same methods (Caldwell and Caldwell 1965, Caldwell *et al.* 1990, Janik *et al.* 2013). Therefore, repeated stereotyped whistle production by *T. aduncus* would be strong evidence for a similar signaling system.

MATERIALS AND METHODS

Study Populations

Acoustic recordings of *T. aduncus* were collected from three wild, free-ranging populations inhabiting the coastal waters of Plettenberg Bay, South Africa (34°1'S, 23°25'E), Mikura Island, Japan (33°52'N, 139°36'E), and Jervis Bay, southeast Australia (35°07'S, 150°42'E) and from two temporarily isolated females in Prospect Lake, Ballina, eastern Australia (28°50'52''S, 153°34'49''E) (details of data collection are given in Table 1). Molecular analysis has confirmed the status of each population as *T. aduncus* (Möller and Beheregaray 2001, Kakuda *et al.* 2002, Natoli *et al.* 2004, Wiszniewski *et al.* 2009b) with significant levels of genetic differentiation apparent between populations (Wiszniewski *et al.* 2009b, Gridley 2011). Acoustic data were collected during focal follows (Altmann 1974) of groups of dolphins, from Plettenberg Bay, Mikura Island, and Jervis Bay. Samples from Prospect Lake, Ballina, were made opportunistically in 2008 and 2009 during a rescue event where relocation of two different mother and calf groups was required after the dolphins became entrapped in the man-made lake. During both of these rescue events, the mother-calf pairs became separated. In addition to the neonate calf in 2009, a subadult female was also temporarily captured in the lake and relocated. Recordings analyzed in this paper from these rescue events only include the periods where the mothers were freely swimming in the lake while separated from the calves and the subadult in 2009. During separation, the calves and the subadult were restrained in slings held by rescuers with the dorsal surfaces held above the water. In previous studies of *T. truncatus*, this kind of situation elicited high rates of signature whistle production (Sayigh *et al.* 1990, 2007). Each adult female had ventral speckling which is common in adults of *T. aduncus* but not *T. truncatus* (Hale *et al.* 2000, Amir *et al.* 2005) and could be

Table 1. Details of acoustic data collection from three wild free-ranging populations of Indo-Pacific bottlenose dolphins (*T. aduncus*) and two temporarily entrapped animals.

| Population (recording year) | Method and depth (m) | Hydrophone model | Recording medium | Sampling rate | Frequency response | Reference |
|-----------------------------|--|--|---|---|--|--|
| Plettenberg Bay (2009) | (a) Towed from boat (2 m) (b) Stationary from boat (2.5 m) | (a) HTI-96-MIN (b) Magrec HP/30 General Purpose | (a) Edirol UA-25 sound card to PC (b) Edirol R1 | (a) 96 kHz (b) 44.1 kHz | (a) 2 Hz to 30 kHz (± 1 dB) (b) 200 Hz to 15 kHz (± 1.5 dB) | This study |
| Mikura Island (2000) | Snorkeler with modified underwater video recording system | Purpose built hydrophone connected to SONY video audio input | Adapted Sony DCR-TRV900 camcorder in underwater housing | 44.1 kHz | 1 to 20 kHz (flat) | Dudzinski <i>et al.</i> (1995) Morisaka <i>et al.</i> (2005a) |
| Jervis Bay (2001–2003) | (a) Towed from boat using electric motor (2–5 m) (b) Stationary from boat (2–5 m) | HTI-96-MIN | TCD-D100 DAT recorder | (a and b) 44.1 kHz and 48 kHz (some recordings filtered above 17 kHz) | 5 Hz to 30 kHz (± 1 dB) | Lemon <i>et al.</i> (2006) |
| Ballina (2008 and 2009) | Deployed in lake during natural entrapment event (0.3–0.5 m) | Aquaeq C100-27 | H4 Zoom Recorder | 44.1 kHz | 7 Hz to 22 kHz (flat) | This study |

individually identified using photo-identification of dorsal fin markings (Würsig and Würsig 1977). Both were known long term (for >5 yr prior to entrapment) residents in a population of *T. aduncus* that used the coastal waters (≤ 6 km from the coast) and estuaries in the Ballina area (Hawkins and Gartside 2008).

Acoustic Analyses

Acoustic analyses focused on the identification of repeated stereotyped whistles as found in free-ranging (Janik *et al.* 2013) or isolated (Caldwell and Caldwell 1965, Sayigh *et al.* 2007) *T. truncatus*. For this, we categorized whistles into types and looked for either a bout delivery pattern as found in free-ranging *T. truncatus* (Janik *et al.* 2013) or an individually-specific whistle type used almost exclusively by isolated individuals (Caldwell and Caldwell 1965, Sayigh *et al.* 2007).

We use the term “contour” to describe a narrow band tonal signal with at least part of the fundamental frequency above 3 kHz. This distinguishes contours from other narrowband sounds produced by bottlenose dolphins (van der Woude 2009, Simard *et al.* 2012). Only contours longer than 0.1 s were used in this analysis (Lilly and Miller 1961, Janik *et al.* 2013) and harmonics other than the fundamental were not considered. A whistle is defined as a unit of one continuous contour (either single element or connected multiloop whistle) or two or more repeated contours separated by a period of silence less than 0.25 s in duration (disconnected multiloop whistle) (Esch *et al.* 2009b). Dolphins may also produce signature whistles as two or more disconnected loops without a repeated loop structure (Esch *et al.* 2009b). To be considered as one whistle unit these loops have to occur in the same sequence within 0.25 s of each other at least 80% of the time. The term “whistle type” is used to describe all whistles of a particular frequency modulation pattern as determined by automated categorization (see below). The term signature whistle type (SWT) is used to describe whistle types that showed individual distinctiveness in isolated animals (Caldwell and Caldwell 1965, Sayigh *et al.* 2007) or the temporal delivery pattern used by *T. truncatus* whereby signature whistles are produced in sequences separated by inter-whistle intervals (IWIs) of 1–10 s (Janik *et al.* 2013).

Signature whistles are often produced in repetitions of the same whistle type and in a single encounter the same SWTs may be repeated many times with few other whistles recorded at the same time. To maximize the chances of sampling whistles from different free-ranging individuals we subsampled the acoustic data from Plettenberg Bay and Jervis Bay. Files were divided into short recording sections and analysis initiated from the first high quality (quality 2 or 3, see below) contour following a random start point. Only sections containing five or more extractable contours were used and the average section length was 5 min 34 s (\pm SD 4 min 41 s). This approach ensured that a similar sample size was used across populations and prevented single recordings from being over sampled thereby reducing the likelihood that the same stereotyped whistles were extracted many times. This was not necessary for Mikura as all recordings from this population were short (under 10 min in duration) or Ballina as we used all available recordings of isolated individuals (see below).

Categorization and SIGID

In the first step, contours were extracted as a series of frequency measurements at 5 ms intervals along the fundamental frequency. For this, contours from recordings of free-ranging *T. aduncus* were first visualized in the spectrogram display of Adobe

Audition v2.0 (Hanning window, FFT size 512). Each was visually assessed and graded based on the signal-to-noise ratio (SNR) (1: signal is faint and barely visible on the spectrogram, 2: signal is clear and unambiguous, 3: signal is prominent and dominates). Extractable contours were those graded as 2 or 3, had a clear overall shape, were unmasked and not cut off by the frequency bandwidth of the recording system. The fundamental frequency of each contour was automatically extracted in MATLAB v 6.5.1 using a supervised peak function which detects and traces the peak frequency of contours within a user defined area (display settings: FFT size 2048, 512 frame length, 87.5% overlap and a Hanning window) (Deecke and Janik 2006). The user could then edit the extracted contour to best fit the underlying contour in cases of simultaneous echolocation clicks, whistles or other sources of noise. Extracted contours were saved as a series of frequency points at 5 ms time resolution.

Signature whistle types were identified in each free-ranging population through contour categorization and bout analysis (SIGID, Janik *et al.* 2013, see below for details). Extracted contours were classified into categories using ARTwarp (Deecke and Janik 2006), an unsupervised neural network algorithm which incorporates dynamic time warping (Buck and Tyack 1993). There are two key parameters which can be adjusted to fine tune the categorization process: the warping function and the vigilance parameter (hereafter VP). Dynamic time warping allows the input contour to be “sped up” or “slowed down” in parts by a factor, termed the warping function. The VP is the level of similarity which an input contour must have with the reference contour after dynamic time warping to be classified in this category (Deecke and Janik 2006). A set of reference contours, which represent each category, are created during categorization. If the input contour does not match any of the reference contours by an amount greater than the VP then it becomes a reference contour for a new category. Following Janik *et al.* (2013) each recording section was categorized separately using a VP of 91% and warping function of 3 (therefore any two contours whose length differs by a factor of 3 or more are given a similarity rating of zero). The maximum number of iterations for each contour running through the ARTwarp neural network before final categorization was capped at 200, the learning rate of the neural network was 0.1 and the maximum number of categories was set to the total number of contours categorized per recording (see Deecke and Janik 2006 for further details). According to these settings, each contour could theoretically be placed into its own unique category.

Following categorization, the intercontour intervals (ICIs) of all extracted contours within the same category were calculated as the time from the contour start point to the end of the preceding contour and from the contour end point to the start of the following contour. If a contour overlapped the preceding contour in the same category, the overlapping contour was removed from consideration and the ICIs recalculated. Contours that were categorized together and separated by a period of silence up to 0.25 s or contours which occurred in the same sequence within 0.25 s of each other at least 80% of the time were classified as disconnected multilooped whistles. Repeatedly emitted whistles were those where the IWI to the preceding or following whistle was between 1 and 10 s of another in the same category (Janik *et al.* 2013), using the start time of the first loop and end time of the last loop in disconnected multilooped whistles.

Janik *et al.* (2013) looked at whistle types containing four or more whistles and calculated the proportion of whistles repeated within 1–10 s of each other. They found that if the proportion of whistles occurring within 1–10 s of another of the same type was 75% or higher, it was a signature whistle. They termed this approach

to identifying signature whistles SIGID. As it is the temporal production of whistles that underlies whether a whistle is likely to be a signature whistle, this criteria can also be applied on a whistle by whistle basis (Janik *et al.* 2013) by searching recordings for series of whistles of the same type produced within 1–10 s (Quick and Janik 2012). We followed this approach to identify SWTs from recordings of *T. aduncus* by analyzing the repeated whistle types for sequences of whistles produced within 1–10 s. As we are applying this to a different species we used a more stringent criterion than suggested by Janik *et al.* (2013) in that we only considered whistle types containing five or more whistles from the same recording section. Therefore, for any whistle type there must be at least one point in time where whistles are produced in a sequence with a minimum of four out of five whistles produced within 1–10 s. If a whistle type fulfilled these criteria it was considered to be a SWT. Contours from categories that did not meet these criteria were classified as nonSWTs (NSWT).

Finally cross-comparison of SWTs was conducted to determine whether the same SWT was present in more than one recording section. This was necessary because two or more recording sections could be analyzed from the same encounter with the same individuals present and also because signature whistles remain stable for time periods spanning decades (Sayigh *et al.* 1990). The reference contours of SWTs from different recording sections were run through ARTwarp at a warping function of two, and VP of 91%. A lower warping function was used here, since average contours of the same signature whistle in different encounters should not differ by much in their contour. If the reference contours grouped together, the composing whistles were grouped together and counted as one unique SWT.

Variability in Signature Whistle Type Parameters from Free-ranging T. aduncus

Certain whistle parameters may be more likely to encode identity information than others. We investigated the variation in SWT parameters for each population by calculating the coefficient of variation [$CV = 100 \times (\text{standard deviation}/\text{mean})$] for each whistle type and generating an average (CV_i) of these for the following seven standard whistle parameters (following those outlined by Oswald *et al.* 2003, Morisaka *et al.* 2005b); start, end, minimum and maximum frequency, the frequency range, mean frequency (average of all the frequency points at 5 ms resolution making up the contour), and duration (s). The frequency and duration parameters were automatically measured from extracted whistles using purpose written MATLAB script.

Recordings of Isolated T. aduncus from Ballina, eastern Australia

All available contours from the recordings of two entrapped isolated *T. aduncus* were independently visually categorized by three experienced judges (the authors: TG, VMJ, and EH) for the occurrence of whistle types. Whistle contours from a subsection of each recording were extracted ($n = 10$) and automatically categorized in ARTwarp using the same settings as described above and with a warping function of three.

RESULTS

Signature whistle types were identified in all free-ranging populations as well as recordings of the two temporarily isolated individuals.

Table 2. Summary of acoustic data used to identify signature whistle types (SWTs). Only recording sections containing five or more extracted contours were included in this analysis. To remove replicates, SWTs were finalized after cross comparison of reference contours between recording sections using ARTwarp categorization with a warping function of 2.

| Population | Recording days | No. of sections analyzed | No. of contours extracted | No. of ARTwarp categories | Mean (\pm SD) no. of whistles per SWT category | No. SWT identified |
|-----------------|-----------------|--------------------------|---------------------------|---------------------------|---|--------------------|
| Plettenberg Bay | 10 | 16 | 511 | 137 | 14 (10.7) | 12 |
| Mikura | 6 | 24 | 685 | 163 | 24 (22.9) | 12 |
| Jervis Bay | 10 ^a | 21 | 438 | 89 | 26 (21.9) | 10 |

^aThe number of recording days in Jervis Bay is a minimum as recordings from several days were occasionally stored on the same Digital Audio Tape (DAT).

Signature Whistle Types in Free-ranging *T. aduncus*

In total, more than 17 h of acoustic recordings of free-ranging *T. aduncus* were considered for analysis. After subsampling, over 3,652 contours were identified, of which 1% were cut off by the frequency bandwidth of the recording system. In total 1,634 contours were extracted from 61 recording sections (4 hr 25 min) made over >26 d (Table 2). Of these, 818 contours (50%) were identified as either a continuous SWT or a constituent loop of a disconnected SWT, 805 (49%) were classified as NSWTs and 11 (1%) overlapped another contour in the same category and were removed from analysis. In total, 34 SWTs were identified. This included 12 from Plettenberg Bay, 12 from Mikura Island, and 10 from Jervis Bay (see Fig. 1 for examples). Of these 34 SWTs, 15 were identified in two or more recording sections.

Variability in Signature Whistle Type Parameters

The number of whistles in each SWT ranged between 5 and 77, with mean values of 14 (\pm SD 10.7), 24 (\pm SD 22.9), and 26 (\pm SD 21.9) whistles per SWT for Plettenberg Bay, Mikura Island, and Jervis Bay, respectively. The variation in SWT parameters was lowest for mean frequency and maximum frequency (range CV_i = 6.3–8.2 and 6.4–11.2, respectively) and generally high for frequency range and duration (range CV_i = 20.0–30.3 and 15.9–35.8, respectively), although there was population variation in this (Fig. 2).

Signature Whistle Types in Isolated *T. aduncus* from Ballina, eastern Australia

The contours from 1 hr 26 min of recording from two isolated *T. aduncus* were visually categorized (12 min from animal a, 1 hr 14 min from animal b). On each occasion a single stereotyped whistle type was prevalent and produced repeatedly, comprising 100% ($n = 395$) and 87% ($n = 368$) of the whistles from recordings of animal a and b respectively (Fig. 3). The extracted whistle contours from each subsection were categorized together by ARTwarp with a high similarity rating (97%–99%). Stereotyped whistles were produced in bouts containing sequences of five or more whistles produced at IWI of 1–10 s, *i.e.*, both whistle a and b were SWTs. The

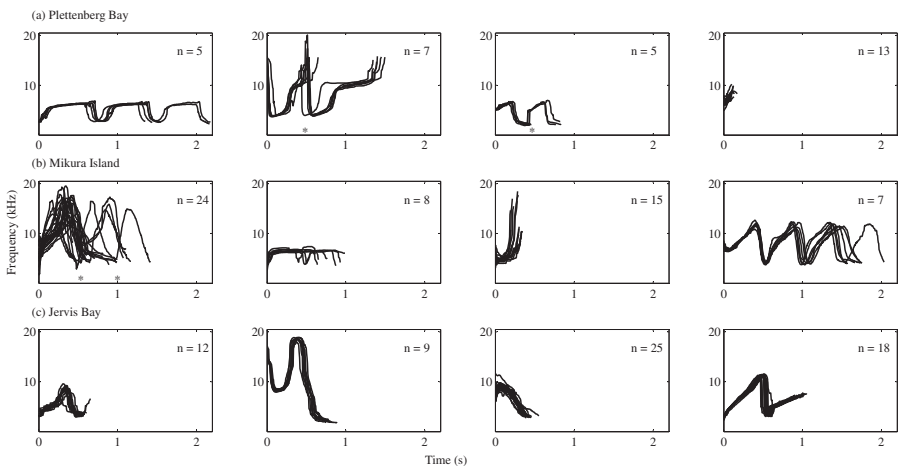


Figure 1. Representative signature whistle types (SWTs) identified from three free-ranging populations of *T. aduncus* through contour categorization in ARTwarp and bout analysis (SIGID, Janik *et al.* 2013). Disconnected multilooped SWTs include a period of silence 0.03–0.25 s long. This silent period (not plotted) occurs at the position of an inflection point, marked with an asterisk (*) on three of the plots.

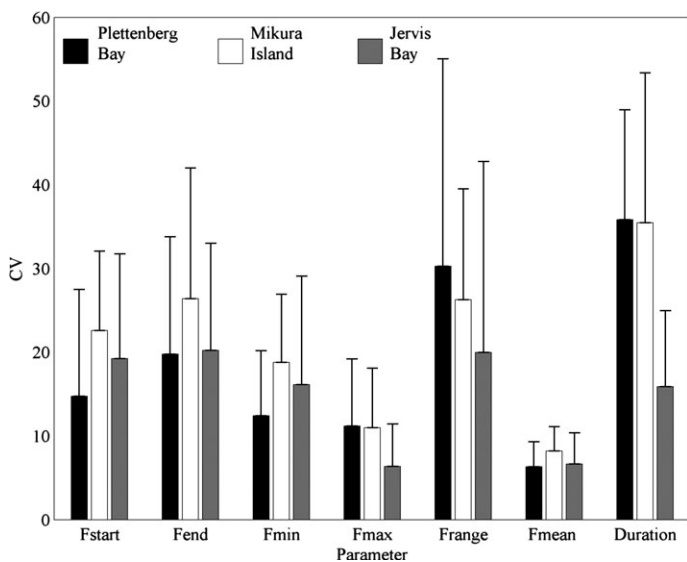


Figure 2. Mean (\pm SD) coefficient of variation in signature whistle type parameters for three populations of *T. aduncus*. Frequency (kHz) denoted by F.

context at the time of recording (isolation and separation from calf), the stereotyped call nature and the temporal pattern of whistle production, which mirrors that of *T. truncatus*, shows that these are signature whistles.

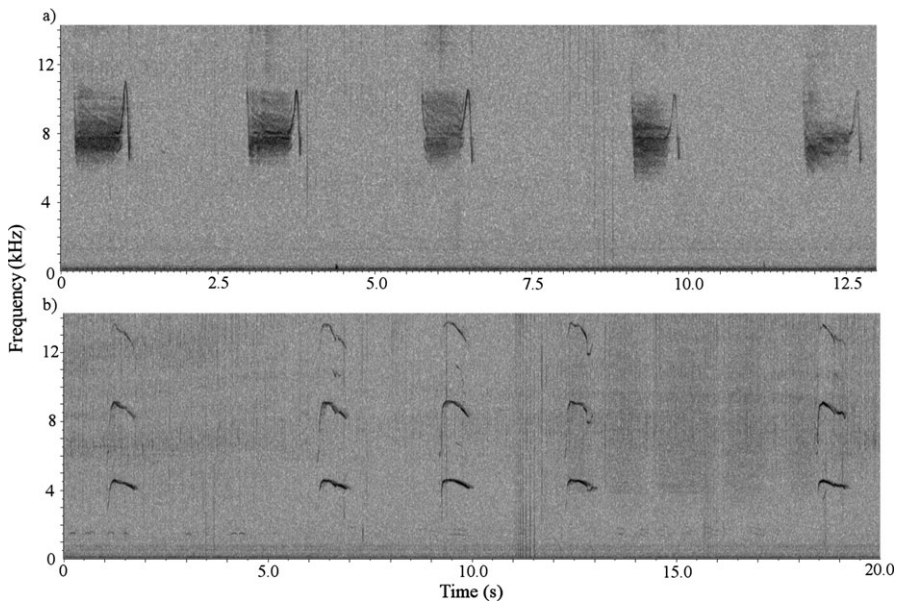


Figure 3. Spectrogram of signature whistle types from recordings of two different adult *T. aduncus* during temporary isolation and separation from their calf. Both animals were recorded in Prospect Lake, Ballina (eastern Australia) in 2008 (a) and 2009 (b). Note different scale to x axis on (a) and (b).

DISCUSSION

This study has demonstrated clear stereotyped categories in the whistle repertoires of *T. aduncus* and provides evidence that this species is using signature whistles. In total, 34 SWTs were identified in recordings from three geographically separated and genetically distinct populations of free-ranging *T. aduncus* and a further two SWTs were identified from recordings of known isolated individuals. The identification of SWTs in recordings of both freely-ranging and isolated *T. aduncus* from several populations provides good evidence that these call types have functional importance in the vocal repertoire of *T. aduncus*.

Previous studies have used temporary capture (Cook *et al.* 2004, Watwood *et al.* 2005), localization (Janik and Slater 1998) or tagging (Shapiro 2006) to assign signature calls to individuals. When captures are risky for animals, or when logistical and financial reasons do not allow for captures, reliable identification of signature whistles is challenging. While we cannot be certain that each SWT identified from the three free-ranging populations is produced by a different individual, the pattern and timing of contour occurrence (*i.e.*, repeatedly emitted whistles produced at intervals of 1–10 s), mirrors that of *T. truncatus* producing individually distinctive signature whistles in freely interacting contexts (Janik *et al.* 2013) and thus provides evidence that each SWT was emitted by a different individual. Although dolphins can copy each other's signature whistles (Tyack 1986, Janik and Slater 1998), in the wild matching is rare and mostly involves two animals each producing just one whistle (Janik 2000). Therefore, whistle matching is unlikely to have influenced our results, particularly as we removed overlapping contours of the same type from the analysis.

Considering what we know of signature whistle production in *T. truncatus* and how it varies with behavioral context (Cook *et al.* 2004, Esch *et al.* 2009a), it is not surprising that signature whistles were recorded in the presence of individuals entrapped in Prospect Lake, Ballina, when mothers were separated from their calves and the subadult. The high proportion of SWTs produced (100% and 87%) is in accordance with the proportions of signature whistles reported by Caldwell *et al.* (1990) for isolated individuals. A second whistle type was apparent at the start of the recording of animal b in 2009. This may be the SWT of the subadult which was being stabilized in a sling at the start of this recording or perhaps a second whistle type produced by animal b, however, without acoustic localization it is not possible to be sure. Across the three free-ranging populations, the average number of contours categorized into SWTs by ARTwarp (50%) was comparable to the value of 52% of whistles identified by Cook *et al.* (2004) when investigating rates of signature whistle production by free-ranging *T. truncatus*. The predominance of SWTs in both isolated and free-ranging contexts demonstrates the importance of this category in the vocal repertoire of *T. aduncus*.

Frequency range and duration had comparatively high degrees of variation within SWTs (Fig. 2). Signals used to express motivational state are likely to be highly variable (Falls 1982) and previous research has demonstrated that the number and duration of loops are affected by behavioral context (Esch *et al.* 2009a). Maturation may also play a role, with older animals producing longer whistles (Caldwell *et al.* 1990). Therefore it seems that whistle duration, which is often though not exclusively, a function of the number of repeated loops in a SWT (Caldwell *et al.* 1990, Gridley 2011), is a poor encoder of identity information in *T. aduncus*. Mean frequency was the least variable SWT parameter for all populations. This is not surprising considering that the main carrier of identity information in *T. truncatus* is the overall frequency modulation pattern of the whistle (Janik *et al.* 2006) and as SWTs are stereotyped this would be well reflected by the mean frequency parameter.

In general, whistles of *T. aduncus* are shorter than *T. truncatus* (Gridley *et al.* 2012) and it is therefore possible that the signature whistles of *T. aduncus* are also shorter in duration. Of the SWTs identified from the free-ranging populations, five were relatively short in duration (around 0.25 s or less). These short whistles were mostly up-sweeps and unlike the majority of SWT identified had similar frequency modulation patterns and frequency characteristics across populations. These short SWTs may be too simplistic in nature to accurately convey identity information and they may instead be chirps (short whistles less than 0.25 s in duration, Richards *et al.* 1984) which can also be produced in repeated emissions (Janik *et al.* 2013). However, further investigation is necessary to determine the function of these short whistle types.

Additional research is required to understand the function of SWTs in *T. aduncus* and establish whether they fulfill the same role as signature whistles in *T. truncatus*. Tagging studies (Johnson and Tyack 2003) or temporary captures (Sayigh *et al.* 1999, Janik *et al.* 2006) would help to confirm individual variation in whistles. Detailed captive studies, particularly those in controlled conditions involving newborn calves would help to understand signature whistle ontogeny (Caldwell and Caldwell 1979), signature whistle stability through time, and would be useful in determining whether *T. aduncus* are capable of vocal production learning.

Categorization in ARTwarp offers a fast and consistent way to divide repertoires and can be widely applied to help understand whistle communication in a range of species. Observations of stereotyped whistles in several delphinid species (Caldwell and Caldwell 1968, Caldwell *et al.* 1973, Van Parijs and Corkeron 2001, de

Figueiredo and Simao 2009) pose a case for a broader use of signature whistles which could be investigated using automated categorization in ARTwarp and the SIGID method.

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LITERATURE CITED

- Altmann, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49:227–267.
- Amir, O. A., N. S. Jiddawi and P. Berggren. 2005. The occurrence and distribution of dolphins in Zanzibar, Tanzania, with comments on differences between two species of *Tursiops*. *Western Indian Ocean Journal of Marine Science* 4:85–93.
- Boughman, J. W., and C. F. Moss. 2003. Social sounds: Vocal learning and development of mammal and bird calls. Pages 138–224 in A. M. Simmons, A. N. Popper and R. R. Fay, eds. *Acoustic communication*. Springer-Verlag, New York, NY.
- Buck, J. R., and P. L. Tyack. 1993. A quantitative measure of similarity for *Tursiops truncatus* signature whistles. *Journal of the Acoustical Society of America* 94:2497–2506.
- Buckstaff, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 20:709–725.
- Caldwell, M. C., and D. K. Caldwell. 1965. Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature* 207:434–435.
- Caldwell, M. C., and D. K. Caldwell. 1968. Vocalization of native captive dolphins in small groups. *Science* 159:1121–1123.
- Caldwell, M. C., and D. K. Caldwell. 1979. The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*)—ontogeny. Pages 369–401 in H. E. Winn, ed. *Behaviour of marine animals*. Plenum Press, New York, NY.
- Caldwell, M. C., D. K. Caldwell and J. F. Miller. 1973. Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon*. *Cetology* 16:1–21.
- Caldwell, M. C., D. K. Caldwell and P. L. Tyack. 1990. Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. Pages 199–234 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Charlton-Robb, K., L.-A. Gershwin, R. Thompson, J. Austin, K. Owen and S. Mckechnie. 2011. A new dolphin species, the burrunan dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters. *Plos One* 6:E24047.
- Connor, R. C. 2002. Ecology of group living and social behaviour. Pages 353–370 in A. R. Hoelzel, ed. *Marine mammal biology: An evolutionary approach*. Blackwell, Oxford, U.K.
- Connor, R. C., R. S. Wells, J. Mann and A. . 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91–126 in J. Mann, R. C. Connor, P. L.

- Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago, IL.
- Cook, M. L. H., L. S. Sayigh, J. E. Blum and R. S. Wells. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society of London Series B-Biological Sciences 271:1043–1049.
- Currey, R. J. C., L. E. Rowe, S. M. Dawson and E. Slooten. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. New Zealand Journal of Marine and Freshwater Research 42:439–449.
- de Figueiredo, L. D. and S. M. Simão. 2009. Possible occurrence of signature whistles in a population of *Sotalia guianensis* (Cetacea, Delphinidae) living in Sepetiba Bay, Brazil. Journal of the Acoustical Society of America 126:1563–1569.
- Deecke, V. B., and V. M. Janik. 2006. Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. Journal of the Acoustical Society of America 119:645–653.
- Dudzinski, K. M., C. W. Clark and B. Würsig. 1995. A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. Aquatic Mammals 21:187–193.
- Esch, H. C., L. S. Sayigh, J. E. Blum and R. S. Wells. 2009a. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). Journal of Mammalogy 90:638–650.
- Esch, H. C., L. S. Sayigh and R. S. Wells. 2009b. Quantifying parameters of bottlenose dolphin signature whistles. Marine Mammal Science 25:976–986.
- Falls, J. B. 1982. Individual recognition by sounds in birds. Pages 237–278 in D. E. Kroodsmas and E. H. Miller, eds. Acoustic communication in birds. Academic Press, New York, NY.
- Fripp, D., C. Owen, E. Quintana-Rizzo, A. Shapiro, et al. 2005. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. Animal Cognition 8:17–26.
- Gridley, T. 2011. Geographic and species variation in bottlenose dolphin (*Tursiops* spp.) signature whistle types. Ph.D. thesis, University of St Andrews, St Andrews, U.K. 224 pp.
- Gridley, T., P. Berggren, V. G. Cockcroft and V. M. Janik. 2012. Whistle vocalizations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting the south-west Indian Ocean. Journal of the Acoustical Society of America 132:4032–4040.
- Hale, P. T., A. S. Barreto and G. J. B. Ross. 2000. Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans. Aquatic Mammals 26:101–110.
- Hawkins, E. R., and D. F. Gartside. 2008. Social and behavioural characteristics of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in northern New South Wales, Australia. Australian Mammalogy 30:71–82.
- Janik, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355–1357.
- Janik, V. M. 2009. Acoustic communication in delphinids. Advances in the Study of Behavior 40:123–157.
- Janik, V. M., and P. J. B. Slater. 1997. Vocal learning in mammals. Advances in the Study of Behavior 26:59–99.
- Janik, V. M., and P. J. B. Slater. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56:829–838.
- Janik, V. M., L. S. Sayigh and R. S. Wells. 2006. Signature whistle shape conveys identity information to bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America 103:8293–8297.
- Janik, V. M., S. L. King, L. S. Sayigh and R. S. Wells. 2013. Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 29:109–122.
- Johnson, M. P., and P. L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3–12.

- Jouventin, P., T. Aubin and T. Lengagne. 1999. Finding a parent in a king penguin colony: The acoustic system of individual recognition. *Animal Behaviour* 57:1175–1183.
- Kakuda, T., Y. Tajima, K. Arai, K. Kogi, T. Hishii and T. K. Yamada. 2002. On the resident “bottlenose dolphins” from Mikura water. *Memoirs of the National Science Museum, Tokyo* 38:255–272.
- Kazial, K. A., T. L. Kenny and S. C. Burnett. 2008. Little brown bats (*Myotis lucifugus*) recognize individual identity of conspecifics using sonar calls. *Ethology* 114:469–478.
- Kishida, T., S. Kubota, Y. Shirayama and H. Fukami. 2007. The olfactory receptor gene repertoires in secondary-adapted marine vertebrates: Evidence for reduction of the functional proportions in cetaceans. *Biology Letters* 3:428–430.
- Kogi, K., T. Hishii, A. Imamura, T. Iwatani and K. M. Dudzinski. 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science* 20:510–526.
- Lemon, M., T. P. Lynch, D. H. Cato and R. G. Harcourt. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. *Biological Conservation* 127:363–372.
- Lilly, J. C., and A. M. Miller. 1961. Sounds emitted by the bottlenose dolphin. *Science* 133:1689–1693.
- Markowitz, T. M., W. J. Markowitz and L. M. Morton. 2008. Mating habits of New Zealand dusky dolphins. Pages 151–176 in B. Würsig and M. Würsig, eds. *The dusky dolphin: Master acrobat off different shores*. Elsevier, London, U.K.
- Miksis, J. L., P. L. Tyack and J. R. Buck. 2002. Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *Journal of the Acoustical Society of America* 112:728–739.
- Möller, L. M. and L. B. Beheregaray. 2001. Coastal bottlenose dolphins from southeastern Australia are *Tursiops aduncus* according to sequences of the mitochondrial DNA control region. *Marine Mammal Science* 17:249–263.
- Möller, L. M., and R. G. Harcourt. 1998. Social dynamics and activity patterns of bottlenose dolphins, *Tursiops truncatus*, in Jervis Bay, southeastern Australia. *Proceedings of the Linnean Society of New South Wales* 120:181–189.
- Möller, L. M., L. B. Beheregaray, R. G. Harcourt and M. Krutzen. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:1941–1947.
- Möller, L. M., L. B. Beheregaray, S. J. Allen and R. G. Harcourt. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behavioral Ecology and Sociobiology* 61:109–117.
- Morisaka, T., M. Shinohara, F. Nakahara and T. Akamatsu. 2005a. Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations. *Journal of Mammalogy* 86:541–546.
- Morisaka, T., M. Shinohara, F. Nakahara and T. Akamatsu. 2005b. Geographic variations in the whistles among three Indo-Pacific bottlenose dolphin *Tursiops aduncus* populations in Japan. *Fisheries Science* 71:568–576.
- Natoli, A., V. M. Peddemors and A. R. Hoelzel. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *Journal of Evolutionary Biology* 17:363–375.
- Oswald, J. N., J. Barlow and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. *Marine Mammal Science* 19:20–37.
- Quick, N. J., and V. M. Janik. 2012. Bottlenose dolphins exchange signature whistles when meeting at sea. *Proceedings of the Royal Society B* 279:2539–2545.
- Reisinger, R. R., and L. Karczmarski. 2010. Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. *Marine Mammal Science* 26:86–97.

- Richards, D. G., J. P. Wolz and L. M. Herman. 1984. Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Physiology* 98:10–28.
- Ross, G. J. B., and V. G. Cockcroft. 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). Pages 101–128 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Sayigh, L. S., P. L. Tyack, R. S. Wells and M. D. Scott. 1990. Signature whistles of free-ranging bottlenose-dolphins *Tursiops truncatus*: Stability and mother offspring comparisons. *Behavioral Ecology and Sociobiology* 26:247–260.
- Sayigh, L. S., P. L. Tyack, R. S. Wells, A. R. Solow, M. D. Scott and A. B. Irvine. 1999. Individual recognition in wild bottlenose dolphins: A field test using playback experiments. *Animal Behaviour* 57:41–50.
- Sayigh, L. S., H. C. Esch, R. S. Wells and V. M. Janik. 2007. Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour* 74:1631–1642.
- Scott, M. D., R. S. Wells and A. B. Irvine. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. Pages 235–244 in S. Leatherwood and R. Reeves, eds. *The Bottlenose dolphin recent progress in research*. Academic Press, San Diego, CA.
- Shapiro, A. D. 2006. Preliminary evidence for signature vocalizations among free-ranging narwhals (*Monodon monoceros*). *Journal of the Acoustical Society of America* 120:1695–1705.
- Simard, P., N. Lace, S. Gowans, E. Quintana-Rizzo, S. A. II Kuczaj, R. S. Wells and D. A. Mann. 2012. Low frequency narrow-band calls in bottlenose dolphins (*Tursiops truncatus*): Signal properties, function, and conservation implications. *Journal of the Acoustical Society of America* 130:3068–3076.
- Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex-differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123:38–69.
- Smolker, R. A., J. Mann and B. B. Smuts. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology* 33:393–402.
- Stensland, E., I. Carlen, A. Sarnblad, A. Bignert and P. Berggren. 2006. Population size, distribution, and behavior of Indo-Pacific bottlenose (*Tursiops aduncus*) and humpback (*Sousa chinensis*) dolphins off the south coast of Zanzibar. *Marine Mammal Science* 22:667–682.
- Tyack, P. L. 1986. Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry or signature whistles? *Behavioral Ecology and Sociobiology* 18:251–257.
- Tyack, P. L., and L. S. Sayigh. 1997. Vocal learning in cetaceans. Pages 208–233 in C. T. Snowdon and M. Lausberger, eds. *Social influences on vocal development*. Cambridge University Press, Cambridge, U.K.
- van der Woude, S. E. 2009. Bottlenose dolphins (*Tursiops truncatus*) moan as low in frequency as baleen whales. *Journal of the Acoustical Society of America* 126:1552–1562.
- Van Parijs, S. M., and P. J. Corkeron. 2001. Evidence for signature whistle production by a Pacific humpback dolphin, *Sousa chinensis*. *Marine Mammal Science* 17:944–949.
- Wang, J. Y., L. S. Chou and B. N. White. 1999. Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus: *Tursiops*) in Chinese waters. *Molecular Ecology* 8:1603–1612.
- Wanker, R., J. Apcin, B. Jennerjahn and B. Waibel. 1998. Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): Evidence for individual vocal recognition. *Behavioral Ecology and Sociobiology* 43:197–202.
- Watwood, S. L., E. C. G. Owen, P. L. Tyack and R. S. Wells. 2005. Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour* 69:1373–1386.
- Wells, R. S. 2003. Dolphin social complexity: Lessons from long-term study and life history. Pages 32–56 in F. B. M. De Waal and P. L. Tyack, eds. *Animal social complexity*:

Intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA.

- Wilson, B., P. S. Hammond and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Wiszniewski, J., S. J. Allen and L. M. Moller. 2009a. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour* 77:1449–1457.
- Wiszniewski, J., L. B. Beheregaray, S. J. Allen and L. M. Möller. 2009b. Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. *Conservation Genetics* 11:1405–1419.
- Würsig, B., and M. Würsig. 1977. Photographic determination of group-size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198:755–756.