SIGNATURE WHISTLE STABILITY IN WILD FEMALE ATLANTIC SPOTTED DOLPHINS, STENELLA FRONTALIS

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Signature Whistle Stability in Wild Female Atlantic Spotted Dolphins, *Stenella frontalis*

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ABSTRACT

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Previous qualitative assessment indicated that signature whistles of temporarily captured, free-ranging dolphins remain stable over periods of 2-12 years. This study reports on the stability of signature whistle parameters in wild female Atlantic spotted dolphins in the Bahamas over five or more years and between changes in age class. Signature whistles from seven female dolphins were pooled into blocks of 'early' and 'late' years for the time assessment. Signature whistles from five females were pooled by age class for the second analysis. Duration, minimum frequency, maximum frequency, and change in frequency were measured from spectrograms of whistles for statistical analysis. No significant changes were found in any of the signature whistle parameters either between early and late periods of time or with a change in age class.

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Introduction

Numerous studies have been conducted to identify, classify and determine the social significance of dolphin signature whistles (Sayigh *et al.* 1990, Herzing 1996, Tyack 1997, Sayigh *et al.* 1998, Smolker & Pepper 1999, Janik 2000). However, few studies have focused on the stability of dolphin signature whistles, partly due to difficulties in access to the same individuals over a long period of time. Initial qualitative studies on temporarily captured, free-ranging bottlenose dolphin (*Tursiops truncatus*) signature whistles indicate that these vocalizations remained stable over periods of 2 – 12 years (Sayigh *et al.* 1990). This study aims to quantitatively assess signature whistle stability of wild female Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. The whistles used in this study were collected by the Wild Dolphin Project from free-ranging dolphins in the Bahamas from 1985 to 2002.

Dolphin Acoustics

Dolphin acoustics are generally classified into two functional categories. One includes broadband (up to 130 kHz) clicks used for echolocation (Au & Herzing 2003). The clicks are broadband 'pulsed' sounds which aid in navigation and location of prey. A second functional category includes frequency modulated whistles and burst-pulsed sounds used for communication (Buck & Tyack 1993, Herzing 2000). Burst-pulsed sounds are the most common sounds used in delphinid communication. They are aurally labeled as squawks, barks, and trills, but are currently being redefined with broadband analysis. The whistles used in spotted

dolphin communication are characterized by frequency modulation (4-18 kHz) over time, lasting .5-8s in duration (Herzing 1996, 2000).

Lammers and Au (2003) have shown that whistles produced by dolphins are directional, contrary to previous beliefs that whistles are omnidirectional. The results of this study suggest that in addition to conveying signaler identity and position, directional whistles, specifically harmonic information, may also facilitate in the coordination of movements by conveying direction of travel. Lammers and Au (2003) report that the harmonic structure of whistles provides a cue that listening dolphins could interpret to assess the signaler's direction of travel. Nearby listeners will not always receive the same signal equally; it will depend on their position relative to the signaler. The directionality of whistles can also lead to an explanation of 'partials' or 'deleted' whistles often found in a dolphin's repertoire (Caldwell & Caldwell 1979, McCowan & Reiss 1995). 'Partials' may actually be the beginning of a second whistle or multiple parts of the same whistle. Should a dolphin change its orientation relative to the hydrophone during whistle production, the signal may be cut off, leaving only a partial whistle.

Most research to date has focused on classifying whistles based on the whistle's contour. 'Contour' is defined as the relative change in frequency over time, which constitutes the general "shape" of the whistle (Caldwell *et al.* 1973, Sayigh *et al.* 1990, McCowan 1995). The contour of the whistle may contain distinctive characteristics which individualize each dolphin's whistle. These whistles often vary with respect to features such as duration, number of loops, and position in the frequency band, while still retaining their overall contours (Caldwell & Caldwell

1979, Buck & Tyack 1993, Janik *et al.* 1994, McCowan 1995, Tyack 1997). While we, as humans, classify whistles based on contour, it is unknown what criteria dolphins use when analyzing or classifying whistles.

Signature Whistle Hypothesis

The most common vocalization used during mother-calf reunions and for maintaining contact is the signature whistle, which is believed to convey individual identification. Caldwell & Caldwell (1965) defined a signature whistle as an individually distinctive sound that occupies more than 90% of the total whistle vocabulary of any one dolphin. Signature whistles are hypothesized to broadcast the individual identity of the sender to members of its social group, which would facilitate mother-calf reunions, courtship and mating, alloparental care and group cohesion (Sayigh *et al.* 1990, Smolker *et al.* 1993, Tyack 1997, Herzing 2000).

Several studies have demonstrated that dolphins possess abilities that would be required to produce and use signature whistles as suggested by the signature whistle hypothesis. These studies show that: 1) inter-individual variability is much higher than intra-individual variability of whistle parameters; 2) dolphins are able to discriminate among computer-generated whistle-like sounds; 3) dolphins have the capacity to associate arbitrary sounds with arbitrary objects; and 4) female dolphins orient more strongly to the signature whistles produced by kin than those produced by familiar animals (as summarized in Sayigh *et al.* 1998). These abilities would be necessary to label and recognize a signature whistle as belonging to a specific dolphin for the purpose of identification.

Mothers and calves are known to separate and reunite frequently; this pattern can give some insight into signature whistle use in maintaining contact in a society with fluid patterns of association. When mothers and their calves separate, infants are more likely to produce whistles first; signature whistles used in this context may function to elicit some sort of cooperation from the mother (Smolker *et al.* 1993). The mother may approach the infant, wait for the infant to catch up, or whistle, thereby revealing her location. The use of signature whistles by these infants so early in development suggests that both the mother and the calf can recognize one another's whistle. This study provides some insight into whistle use by mothers and calves; however, more work is clearly needed to determine the function of signature whistle use by other members within dolphin societies.

There is much debate over the significance of signature whistles in a dolphin's repertoire. Some results conflict with the signature whistle hypothesis and suggest that the hypothesis is incomplete, or that signature whistles may play a less predominant role in a dolphin's whistle repertoire. It is important to keep in mind that many of these studies have been conducted in limited contexts (captivity), involving few dolphins. To resolve these problems will require more research with additional or expanded contexts and sample sizes.

McCowan (1995) states that the most predominant whistle type produced by any one dolphin is a shared contact call, findings which are inconsistent with the signature whistle hypothesis. She claims this whistle type is a contact call which identifies a social group, rather than a signature whistle that identifies specific individuals. However, these conflicting results may be attributed to differences in

methods of data collection and analysis. McCowan (1995) designed a contour similarity technique for assigning whistles to categories by normalizing the duration of each whistle. However, to date, there is no evidence that suggests dolphins normalize whistles with regard to duration.

In a review of this and other classification techniques, Janik (1999) compared the classification of bottlenose dolphin (*Tursiops truncatus*) signature whistles by human observers to the performance of three computer methods (including McCowan's 1995 method). The results of the study showed that none of the computer methods were capable of reliably identifying the signature whistles as well as human observers. Janik (1999) states one possible explanation for the superior performance by the human observers is that the overall shape of the contour was assessed, while the computer methods assessed the similarity over the whole contour weighing each part equally. As previously stated, it is unknown what criteria dolphins use to classify whistles, and this needs to be determined before one can create a program to accurately categorize signature whistles.

Signature Whistle Stability

The social structure of wild dolphins is described as fission-fusion, one in which stable associations between individuals are intermixed with fluid patterns of association between many different individuals (Smolker *et al.* 1993, Sayigh *et al.* 1995, Tyack 1997). While the overall composition of the group may change, there are associations between individuals that remain stable. It would, therefore seem advantageous for dolphins to use signature whistles for individual or group

identification, as proposed by the signature whistle hypothesis. If whistles remained stable over the life of the dolphin, this would facilitate maintaining relationships over time by conveying individual identity.

Sayigh *et al.* (1990) analyzed signature whistles recorded over 14 years from stable groups of bottlenose dolphins from Sarasota, Florida in a temporary capture setting. Their results, obtained by visually comparing spectrograms of whistles collected from female dolphins over 11 years, indicated that the signature whistles remained stable. Differences in whistle contour that were observed from one year to the next did not exceed differences within a single recording session. Caldwell *et al.* (1990) also reported stable signature whistles in both female and male captive bottlenose dolphins up to 18 years. However, data collected by Smolker and Pepper (1999) and Watwood *et al.* (2004) indicate that wild male dolphins in an alliance converge on a shared whistle type, rather than each male maintaining their own individual signature whistle.

Selective pressures can act very differently on each sex, and this may, in part, explain the contrasting results between males and females in signature whistle stability assessments. The theory of sexual selection states that traits which enhance an individual's ability to compete for or attract mates will be selected for (Alcock 1998). Males may gain an advantage, such as access to females, by forming an alliance. Once a male is a member of an alliance, it may no longer be necessary to be individually identified, or perhaps there is greater advantage in being identified as part of a particular group rather than being identified as an individual. This apparent difference in signature whistle use by males and females does not invalidate the

signature whistle hypothesis, as the signal is still used for identification; only in males it identifies a group rather than an individual. These contrasting results indicate that gender- or association-specific differences in signature whistle use by dolphins must be examined.

Study Population

The whistles I used in this study were collected from free-ranging Atlantic spotted dolphins in the Bahamas from 1985 to 2002. This community of habituated dolphins is accessible to underwater observation, allowing for data to be collected under natural conditions in many behavioral contexts (Herzing 1996). These resident dolphins inhabit an offshore, shallow sandbank and its adjacent deep waters off Grand Bahama Island. Spotted dolphins (n = 212) have been individually identified by photographs and video of dorsal fins, flukes and constellations of spots. Sex was determined by observing the genital region of each individual. Each dolphin's age was determined by observing the development of its spots. As the dolphins mature, their color changes chronologically as follows: two-toned (0-3 years), speckled (4-8 years), mottled (9-15 years) and fused (15+ years) (Herzing 1997).

Whistle Definition

There is no universal agreement on the definition of a whistle. Dolphins produce continuous sinusoidal-like whistles as well as multi-loop whistles. The basic component of both types of whistles is a loop. Continuous whistles are those in which loops are connected end-to-end creating a continuous repeating pattern of

loops (Figure 1a). Multi-loop whistles are those in which loops follow each other closely separated by a constant silent interval, creating a repeating pattern (Figure 1b). Some researchers propose that continuous and multi-loop whistles should be regarded as a single whistle (Tyack 1997, Janik & Slater 1998). Others suggest that continuous and multi-loop whistles should be broken down into individual whistle loops for analysis (Janik 1999, Smolker & Pepper 1999). The number of loops found in both types of whistles may vary with behavioral or emotional state. In my study, the unit of measurement was a single loop (see Figure 1).

Methods and Analysis

Field Methods

Underwater video and sound data were collected using a variety of video cameras (Sony CCDV9 8mm, Yashica KV 1 Hi 8mm). Labcore 76 hydrophone flat to 22 kHz (± 3 db) with a sensitivity of -192 dB re 1 μ Pa were used for simultaneous sound input (Herzing 1996). Each daily sample was logged to record the identity of the dolphins present, the behavioral context, and the vocalizations recorded during each encounter.

Sample Size

The initial criterion for choosing female dolphins required that signature whistles be recorded over an eight year period. Seven female dolphins fulfilled this criterion: Flying A, Heaven, Little Gash (LG), Little Hali (LH), Luna, Venus and Whitepatches (WP). After a preliminary inspection, some whistles and/or years were

omitted from this study. This was due to either an inability to make a positive identification on the dolphin vocalizing or the whistle was of low quality for analysis. However, dolphins that produced many whistles in the remaining years (even if less than eight years) were included. Table 1 shows the span of years and total numbers of whistles recorded for each of the seven dolphins included in this study. Males from this population were not analyzed because I was unable to obtain enough vocalizations for analysis.

Data Collection

I digitized each signature whistle from the audio portion of the recorded video tapes using a digital signal processor (MacDSP 1.8b4) with a sampling rate of 62.50 kHz and stored on a Macintosh IIci computer. The video log and markers of signature whistles from the counter were used to locate whistles. Positive identifications of each dolphin were made by observing dorsal fins, flukes and spots. Identification of the vocalizing dolphin was made when a visible bubble stream was emitted and when the dolphin was alone or in close proximity of the recording equipment during production of the whistle (McCowan & Reiss 1995, Herzing 1996).

Spectrograms of each signature whistle were created and measured using Canary 1.2 acoustic measurement software. Measurements of four parameters, duration, minimum frequency, maximum frequency and change in frequency, were taken from the fundamental frequency of each loop using manual cursors (Figure 2). Duration was measured by aligning the left cursor with the start of a loop (left-most edge) and the right cursor with the end of the loop (right-most edge or point at which

the pattern started to repeat itself) (Figure 3). Minimum frequency was measured by aligning the bottom cursor with the lowest point (on the frequency scale) of the loop (Figure 4a). Similarly, maximum frequency was measured by aligning the top cursor with the highest point (on the frequency scale) of that loop (Figure 4b). Change in frequency was measured by subtracting the minimum frequency from the maximum frequency of a single loop (Figure 4c).

Whistle Analysis and Statistics

Years in which whistles were recorded were pooled into blocks of 'early' and 'late' years to get a large enough sample size to evaluate a change in whistle parameters over time. Table 2 shows the whistle sample size and pooling of years for the seven dolphins used in the time assessment. The blocks of 'early' and 'late' years were determined for each dolphin by the 'clumping' observed from the gaps between years in which whistles were recorded.

Years were also pooled by age class to evaluate a change in whistle parameters with maturation from a younger age class to an older one (Table 3). Specific age classes varied for each dolphin, and any change in age class was examined (T→S, n = 2; S→M, n = 2; M→F, n = 1). For example, Heaven matured from two-tone to speckled, while LG matured from speckled to mottled. Two dolphins (Flying A [mottled] and Luna [fused]) were not included in this analysis, as they were classified as the same age class during observations.

Tests for normality (Kolmogorov-Smirnov) showed that the whistles of the seven female dolphins were not normally distributed for any of the parameters

(duration: $d = 0.171$, $p < .01$; minimum frequency: $d = 0.051$, $p < .01$; maximum frequency: $d = 0.098$, $p < .01$; and change in frequency: $d = 0.048$, $p < .01$). Therefore, a nonparametric pair wise test (Wilcoxon Matched Pairs Test) was run for both the time and age assessments.

Wilcoxon matched pairs tests were used to test the following null hypotheses (H_0): Time: female Atlantic spotted dolphin signature whistle parameters (duration, minimum frequency, maximum frequency and change in frequency) do not change over time when pooled into blocks of early and late years. Age: female Atlantic spotted dolphin signature whistle parameters (duration, minimum frequency, maximum frequency and change in frequency) do not change with the maturation from a younger to an older age class. Statistica 4.1 (copyright StatSoft, Inc. 1991-94) was used to run the statistical analyses.

Results

No significant change was found in signature whistle parameters over time (Wilcoxon duration: $Z = 1.690$, $p = .09$; minimum frequency: $Z = 0.676$, $p = .50$; maximum frequency: $Z = 0.169$, $p = .87$; change in frequency: $Z = 0.676$, $p = .50$). The Wilcoxon also showed no significant change in signature whistle parameters with a change in age class (duration: $Z = 0.674$, $p = .50$; minimum frequency: $Z = 0.135$, $p = .89$; maximum frequency: $Z = 0.135$, $p = .89$; change in frequency: $Z = 0.135$, $p = .89$).

Discussion

Summary of Results

The results of this study indicate that wild female Atlantic spotted dolphin signature whistles in the Bahamas do not change with regard to duration, minimum frequency, maximum frequency or change in frequency either over a period of five or more years or with maturation (as indicated by a change in age class).

Signature Whistle Stability Over Time

The results presented in this quantitative investigation are consistent with qualitative studies which found that signature whistles remained stable throughout a dolphin's lifetime (Caldwell *et al.* 1990, Sayigh *et al.* 1990). The importance of this stability becomes evident when one examines the environment and society in which dolphins live. They inhabit an aquatic environment which favors long distance communication by acoustic rather than visual or chemical cues, as in terrestrial species. The use of whistles allows for communication in an acoustic medium.

Dolphin societies have been described as fission-fusion, in which dolphins maintain stable bonds between few individuals, while randomly associating with many other individuals (Smolker *et al.* 1993, Sayigh *et al.* 1995, Tyack 1997). Signature whistles which remain stable over a dolphin's lifetime would aid individual and kin recognition in this type of society. Stable signature whistles may also facilitate in associating past histories (interactions) with certain individuals (Connor & Norris 1982). This makes maintaining relationships with many members of a social group possible.

One such relationship in which individual identification is crucial is between mothers and dependent calves. Female dolphins invest great maternal care in their offspring; the calf depends upon its mother for protection and to learn to hunt and forage. It is essential that mothers and calves be able to identify each other, especially during separations. In a study on sex difference in signature whistle production, Sayigh *et al.* (1995) found that female calves developed signature whistles that were different from their mothers. Given that female dolphins are known to display high maternal investment and females in the Sarasota population are known to associate frequently with related females, selective pressures should act on females to develop signature whistles which would facilitate in the care of their offspring. Therefore, it would be beneficial for females to develop a signature whistle distinct from members of its social group. This distinction would make it easy for a calf to find its mother in a group of related females. Although stability over time was not assessed in this study on sex difference in signature whistle production, maintaining a distinct whistle throughout a female's lifetime should allow for continued identification within a group of related females.

Sayigh *et al.* (1995) also found that male calves tend to develop signature whistles similar to their mothers. This difference in signature whistle development between males and females was attributed to the different roles each sex plays within dolphin societies. Once independent, male calves tend to leave their maternal group, and eventually form an alliance with one or two other males (Sayigh *et al.* 1995, Watwood *et al.* 2004). Sayigh *et al.* (1995) state that male dolphins may benefit by developing a stable signature whistle similar to that of their mothers, possibly to

maintain kinship bonds or reduce the chances of inbreeding. Results from Smolker and Pepper (1999) and Watwood *et al.* (2004) challenge this reasoning: they found that males converged upon a shared whistle type with the formation of a male alliance. This suggests that due to differing selective pressures upon males, they may benefit by being identified as part of an alliance, rather than as an individual.

Evolutionary theory indicates that a species' social environment can be a powerful force for evolutionary change (Alcock 1998). This may provide some insight on the differences in signature whistle use between male and female dolphins. Once independent from their mothers, males form an alliance with one or two other males. Selective pressures have favored this alliance formation, a change in the social environment which has led to the convergence of a shared whistle type. Males in an alliance may benefit by gaining access to females. They may achieve this advantage by being identified as part of a particular group, rather than being identified as an individual. Conversely, females are shown to maintain a stable signature whistle over time. These contrasting results indicate that gender- or association-specific differences in signature whistle use by dolphins must be examined.

Signature Whistle Stability With Age Class

I show that signature whistle parameters of wild female Atlantic spotted dolphins in the Bahamas do not change with a change in age class. This finding may indicate that the age classes that we, as humans, have implemented to categorize dolphins are not an appropriate measure of a biologically significant event for

measuring signature whistle use. Perhaps other measures of maturation or status would better describe a biologically significant event in which changes in signature whistles might occur. Coefficients of association (COA) and reproductive status are two such measures that may affect signature whistle production and use. Therefore, pooling whistles based on COAs or reproductive status may reveal association-specific uses for signature whistles.

COAs are a measure of the amount of time each individual spends with members of its social group. Examining the COAs of a population will reveal changes in associations between individuals. Some of these changes in association will occur with changes in reproductive status. Females are known to associate with other females of the same status (i.e. females and their dependent calves will associate together in nursery groups) (Reynolds *et al.* 2000, Watwood *et al.* 2004). Examining signature whistle use by females as they change associations among other females of the same reproductive status may also support association-specific uses for signature whistles. The COAs of a population will show changes in association with the formation of a male alliance. Smolker and Pepper (1999) and Watwood *et al.* (2004) observed signature whistle convergence in the males of an alliance, indicating that examining other biologically significant events may reveal gender- or association-specific differences in whistle use by dolphins.

Whistle Development

Caldwell and Caldwell (1979) reported captive infants whistling within a few days of birth, and observed stereotyped signature whistle development over the first

year of life. Young calves were also observed by Smolker *et al.* (1993) using signature whistles to initiate reunions with their mothers after being separated, suggesting whistle development at a young age. While I did not focus on signature whistle development in calves, the results indicate that the signature whistles of the two-toned calves (Heaven and LH) were fully developed at the time of recording (see Table 1 for age classes). These findings are consistent with previous reports that dolphin signature whistles are formed at an early age, and do not change with development or ontogeny.

Studies have shown that the local acoustic environment can have an impact on captive infant signature whistle development. Caldwell and Caldwell (1979) found one captive infant developed a signature whistle similar to a white-sided dolphin held in the same tank, while another infant, held alone with its mother, quickly developed a signature whistle similar to its mother. Tyack (1997) reported one instance in which signature whistles recorded from a stranded bottlenose calf after a five month period (at 6-7 months old) in captivity were 'quite different' from recordings at the time of stranding (at 1-2 months old). The calf stranded without its mother, and was kept in a tank with a nulliparous adult female. The infant's signature whistle had become similar to the signature whistle of the foster mother over a five month period. Because the calf stranded without its mother, it was impossible to tell how similar or different the calf's original whistle was to its mother's whistle. Due mostly to difficulties in repeated access to infants and their mothers in the wild, little is known about whistle development or the environmental influences (social milieu and network of individuals) on signature whistle development in wild dolphins.

The sample size and methods used in this study are consistent with, if not expanded upon, past and current studies on dolphin signature whistles. Three main aspects of dolphin whistle research are addressed: recording setting, sample size and method of contour analysis.

There are generally three settings in which dolphin signature whistles are collected: in captivity, while temporarily captured, and in the wild. Given that each of these settings has advantages and disadvantages, the most appropriate one must be adopted for a particular investigation. Many studies have been conducted which examined signature whistle production and use by captive dolphins (Caldwell *et al.* 1973, Tyack 1986, Janik *et al.* 1994, Janik 1999). This setting may provide many researchers with a practical platform for conducting observational and experimental studies (access to the same dolphins over time, extensive life history information, etc...).

There are, however, limitations associated with studies conducted in a captive setting, some of which may still be unknown. It is unknown to what degree influences from captivity alter signature whistle production and use as compared to wild dolphins. Questions arise, such as how do influences from poolmates affect whistle development? How do the acoustic properties of the tank affect whistle use? Are signature whistles produced in captivity representative of those produced and used in the wild?

Many studies conducted on captive dolphins only analyze those signature whistles produced while the dolphin is isolated from its poolmates, either voluntarily

or forced (Caldwell *et al.* 1973, Janik *et al.* 1994, Janik 1999). By isolating calves and controlling the local acoustic environment, many questions associated with signature whistle development can be addressed. For instance, can the signature whistle be shaped by controlling the acoustic input to the calf? How are signature whistles formed, is it by adopting the last part of the signal it hears first, as seen in some bird species? Isolation is one method used to positively identify a vocalizing dolphin; however it further limits the context in which these whistles are studied.

A second setting in which many signature whistles have been collected is the temporary capture of free-ranging bottlenose dolphins in Sarasota, Florida (Sayigh *et al.* 1990, Buck & Tyack 1993, Sayigh *et al.* 1995, 1998). This setting allows for continued intimate access to the dolphins and the development of a large catalog of individuals and dataset. However, this method is unnatural for dolphins, and it is unknown how the stress of the capture affects the dolphins and their whistle production. Are the signature whistles produced during the temporary capture representative of those whistles produced in a natural setting in the wild? Suction-cup hydrophones, which are placed directly on the head of the captured dolphin, are commonly used to record vocalizations (Sayigh *et al.* 1990, Buck & Tyack 1993, Sayigh *et al.* 1995). While these hydrophones ensure a positive identification of the vocalizer and a clean signal, the question arises of what added stress they are causing the dolphin.

Studies conducted on signature whistle production and use in wild dolphins will have the advantage of recording in a 'natural' setting across many behavioral contexts (assuming habituation to human presence). Research on wild dolphins has

its limitations as well. For much of the world, the animals are only accessible by following them in a boat, therefore only observing behaviors and interactions occurring at the surface (Smolker *et al.* 1993, Janik 2000).

This study examined data collected on wild Atlantic spotted dolphins in the Bahamas. Data collected from the Wild Dolphin Project is unique in that the environment is one which allows for underwater observation and recording of dolphins that have been habituated to the presence of humans for the past 20 years. This long term, intimate access to the animals has facilitated creating an extensive catalog of known individuals and a dataset including both behavioral and acoustic recordings. While this context of data collection is ideal for describing what happens under natural conditions, it is unable to dissect the underlying mechanisms, which requires experimentation.

Sample size, in both the number of dolphins and whistles used, varies greatly in the literature. The sample sizes of dolphins used to record signature whistles ranges from less than five (Caldwell *et al.* 1973, Tyack 1986, Buck & Tyack 1993, Janik *et al.* 1994, Janik 1999), to more than 20 (Sayigh *et al.* 1995, 1998). Sample sizes of signature whistles used for analysis also vary in the literature, from less than 100 (Tyack 1986, Buck & Tyack 1993, Janik 1999) to more than 1000 total (Caldwell *et al.* 1973, Sayigh *et al.* 1990, Janik *et al.* 1994, Janik 2000). Reported time spans of signature whistle collection vary from days (Tyack 1986, Janik 2000) to many years (Sayigh *et al.* 1990, 1995, 1998).

The pooling of whistles to obtain a large enough sample size for analysis is common in the literature. Some studies pool whistles recorded over a period of

months (Caldwell *et al.* 1973, Janik *et al.* 1994, Janik 1999), while others pool over years (Caldwell *et al.* 1993, Sayigh *et al.* 1990, 1995). The methods used in this analysis, including sample size and pooling of whistles, are similar to these previous studies examining dolphin signature whistles.

Yet another aspect that varies in dolphin whistle research is the method of contour analysis. Many studies use visual inspection of frequency contours by humans to qualitatively categorize signature whistles (Tyack 1986, Sayigh *et al.* 1990, Janik *et al.* 1994, Sayigh *et al.* 1995, Janik 2000). Other studies use computer techniques to obtain quantitative comparisons of signature whistle contours (Buck & Tyack 1993, Janik *et al.* 1994). In a review of four classification techniques, Janik (1999) found that visual inspection by human observers was superior to three computer methods. He also cautions that an appropriate computer method can not be developed until it is known what criteria dolphins use to classify and identify signature whistles. This study involved measuring parameters from each contour for statistical analysis to determine stability.

'Signature' Calls of Other Species

The results presented in this paper are consistent with observations on 'signature' call use by some species in many aspects, yet are contradicting in other aspects. Numerous studies have shown the presence of individually distinctive calls in the repertoire of many species (birds: Bailey 1978, Mathevon *et al.* 2003, White 1971; primates: Cheney *et al.* 1996, Rukstalis *et al.* 2003, Symmes *et al.* 1979; cetaceans: Caldwell & Caldwell (1965); pinnipeds: Campbell *et al.* 2002).

Differences in 'signature' call use can, in some cases, be attributed to the selective pressures upon differing societies.

Some species are known to produce individually distinctive calls upon returning to their offspring or nest sites. Female Steller sea lions (*Eumetopias jubatus*) emit individually distinctive contact calls to locate their pups in a crowded rookery (Campbell *et al.* 2002). Gulls (*Larus ridibundus* and *Larus genei*) identify themselves to their chicks by producing long calls (Mathevon *et al.* 2003). White (1971) found that gannets (*Sula bassana*) also emit 'landing calls' to identify themselves upon returning to the nest. These species live in competitive and sometimes antagonistic societies where they would benefit by being able to convey individual identity.

Individually distinctive call use in some species to maintain contact is similar to signature whistle use by an infant dolphin to reunite with its mother. Symmes *et al.* (1979) report squirrel monkeys (*Saimiri sciureus*) use individually distinctive isolation peeps (IP) when visually separated from troop members. Bailey (1978) found the bobwhite quail (*Colinus virginianus*) also produces an individually distinctive separation call when an individual is separated from its group.

Symmes et al. (1979) also found IPs were stable over 'reasonably extended time periods' and persisted through different seasons, ages and membership in different social groupings. This stability over time and age is consistent with the results presented in this paper. In an examination of changes in social environments, Rukstalis *et al.* (2003) found that captive marmoset (*Callithrix kuhlii*) phee calls, which possess signature-like features, are altered with a change in social context.

These findings are similar to those observed during male alliance formation in bottlenose dolphins, and support the need for further analysis to determine gender and association effects on signature whistles.

Future Research

There are limitations of this study which indicate a need for future investigations. The current study addresses signature whistle stability in female Atlantic spotted dolphins in the Bahamas only; the signature whistles of males were not analyzed. Smolker and Pepper (1999) and Watwood *et al.* (2004) found males which formed an alliance all converged on a shared whistle type. This change in whistle type after alliance formation is not consistent the results presented in this paper, and indicates that signature whistle use may vary by gender or should be examined in accordance with changing relationships over time. Clearly, much more research is needed in order to determine the function and use of signature whistles by all members in dolphin societies.

Another limitation to the current study is the small sample sizes, and the resulting pooling of data to obtain larger sample sizes. The pooling of data was necessary to obtain a large enough sample size for analysis; however, this results in a dilution of the data. Larger datasets will allow for year by year analyses, the assessment of significant biological events and changes in specific age classes on signature whistle production and use. Due mostly to difficulties in repeated access to infants and their mothers in the wild, little is known about whistle development or the environmental influences on signature whistle development in wild dolphins. Future

investigations with larger, longer time-based datasets can address some of these limitations and expand on the current study.

Applications

The results from research into the classification of signature whistles may have many applications to understanding the communication system of dolphins. It is possible that more information than whistler identity is present in the whistles, especially given the narrowband nature of these samples. If the classified whistles were analyzed with behavioral data collected simultaneously, the social context of whistles produced could be evaluated. If a correlation between whistle type and behavior can be identified, vocalizations may be used to provide information about behavioral processes. As many researchers have noted, in order for research into dolphin communication to progress, an important step is to have a quantitative measure of similarity between signature whistle contours, which would provide an objective and easily repeatable basis for comparisons, especially when dealing with a long-lived and socially complex mammal society (Buck & Tyack 1993).

References

Alcock, J. (1998). Animal behavior: an evolutionary approach. 6th edition. Massachusetts: Sinauer Associates, Inc. p. 439.

Au, W. W. L. & Herzing, D. L. (2003). Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*). *Journal of the Acoustical Society of America, 113 (1)*: 598-604.

Bailey, K. (1978). The structure and variation of the separation call of the bobwhite quail (*Colinus virginianus*, Odontophorinae). *Animal Behaviour, 26*: 296-303.

Buck, J. R. & Tyack, P. L. (1993). A quantitative measure of similarity for *Tursiops truncatus* signature whistles. *Journal of the Acoustical Society of America, 94 (5)*: 2497-2506.

Caldwell, D. K. & Caldwell, M. C. (1965). Individualized whistle contours in bottlenose dolphins (*Tursiops truncates*). *Science, 207*: 434-435.

Caldwell, M. C. & Caldwell, D. K. (1979). "The whistle of the Atlantic bottlenose dolphin (Tursiops truncates)-ontogeny." In: Behavior of Marine Animals, Vol 3: Cetaceans. Winn, H. E. & Olla, B. L. (eds). New York: Plenum Press. p. 369-401.

Caldwell, M. C., Caldwell, D. K. & Miller, J. F. (1973). Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagidon*. *Cetology 16*: 1-21.

Caldwell, M. C., Caldwell, D. K. & Tyack, P. L. (1990). "Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin." In: The Bottlenose Dolphin. Leatherwood, S. & Reeves, R. R. (eds). San Diego: Academic Press, Inc. p. 199-234.

Campbell, G. S., Gisiner, R. C., Helweg, D. A. & Milette, L. L. (2002). Acoustic identification of female Steller sea lions (*Eumetopias jubatus*). *Journal of the Acoustical Society of America, 111 (6)*: 2920-2928.

Cheney, D. L., Seyfarth, R. M. & Palombit, R. (1996). The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour, 52*: 507-518.

Connor, R. C. & Norris, K. S. (1982). Are dolphins reciprocal altruists? *American Naturalist, 119 (3)*: 358-374.

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis,* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals, 22 (2)*: 61-79.

Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): age classes, color phases, and female reproduction. *Marine Mammal Science, 13 (4)*: 576-595.

Herzing, D. L. (2000). "Acoustics and Social Behavior of Wild Dolphins: Implications for a Sound Society." In: Hearing By Whales and Dolphins. Au, W. W. L., Popper, A. N. & Fay, R. R. (eds). New York: Springer. p. 225-272.

Janik, V. M. (1999). Pitfalls in the categorization of behavior: a comparison of dolphin whistle classification methods. *Animal Behavior, 57*: 133-143.

Janik, V. M. (2000). Whistle matching in wild Bottlenose dolphins (*Tursiops truncatus*). *Science, 289*: 1355-1357.

Janik, V. M., Dehnhardt, & Todt. (1994). Signature whistle variations in bottlenose dolphins. *Behavioral Ecology and Sociobiology, 35 (4)*: 243-248.

Janik, V. M. & Slater, P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behavior, 56*: 829-838.

Lammers, M. O. & Au, W. W. L. (2003). Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): a signal feature to cue direction of movement? *Marine Mammal Science 19 (2)*: 249-264.

Mathevon, N., Charrier, I. & Jouventin, P. (2003). Potential for individual recognition in acoustic signals: a comparative study of two gulls with different nesting patterns. *C. R. Biologies, 326*: 329-337.

McCowan, B. (1995). A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Turisops turncatus*). *Ethology, 100*: 177-193.

McCowan, B. & Reiss, D. (1995). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins: a re-evaluation of the signature whistle hypothesis. *Ethology, 100 (3)*: 194-209.

McCowan, B. & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. *Animal Behavior, 62*: 1151-1162.

Reynolds, J. E., Wells, R. S. & Eide, S. D. (2000). The Bottlenose Dolphin: Biology and Conservation. University Press of Florida: Gainesville.

Rukstalis, M., Fite, J. E. & French, J. A. (2003). Social change affects vocal structure in a Callitrichid primate. *Ethology, 109*: 327-340.

Sayigh, L. S. et al. (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. et al. (1995). Sex differences in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology 36*: 171-177.

Sayigh, L. S. et al. (1998). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour, 57*: 41-50.

Smolker, R. A, Mann, J. & Smuts, B. B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology, 33*: 393-402.

Smolker, R. A. & Pepper, J. W. (1999). Whistle convergence among allied male bottlenose dolphins. *Ethology, 105 (7)*: 595-617.

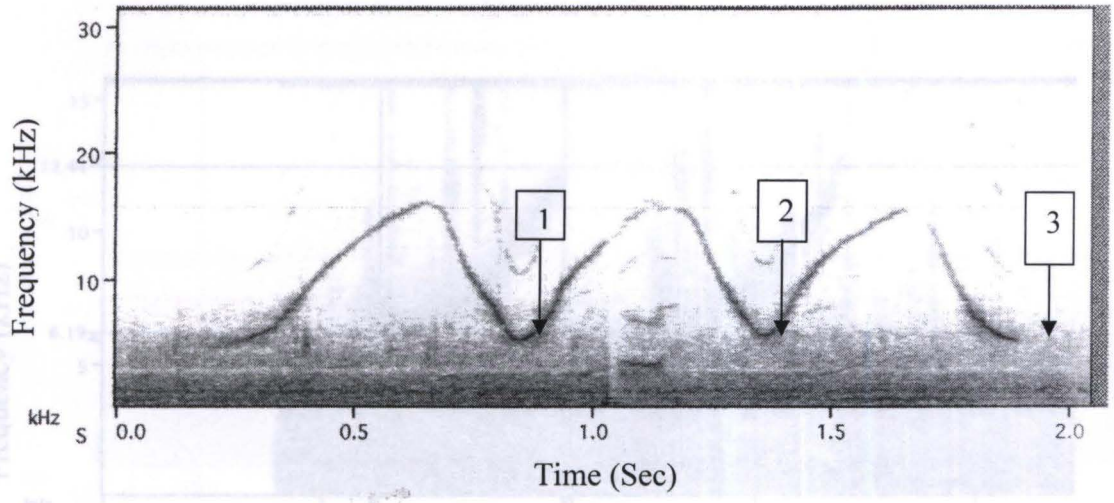
Symmes, D., Newman, J. D., Talmage-Riggs, G. & Lieblich, A. K. (1979). Individuality and stability of isolation peeps in squirrel monkeys. *Animal Behaviour, 27 (4)*: 1142-1152.

Tyack, P. L. (1997). Development and social functions of signature whistles in Bottlenose dolphins *Tursiops truncatus*. *Bioacoustics, 8*: 21-46.

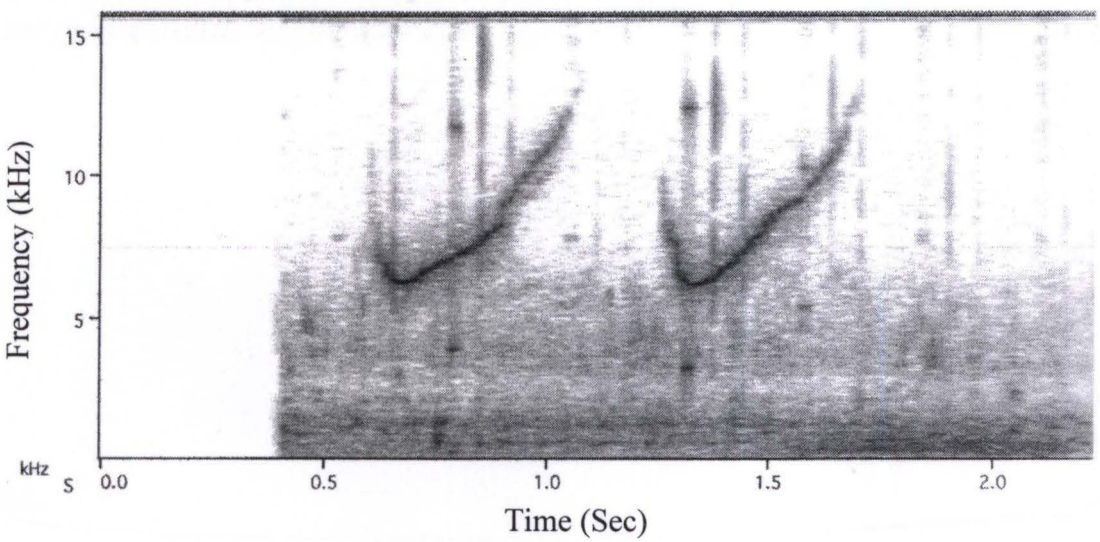
Watwood, S. L., Tyack, P. L. & Wells, R. S. (2004). Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology 55*: 531-543.

White, S. J. (1971). Selective responsiveness by the gannet (*Sula bassana*) to played-back calls. *Animal Behaviour, 19*: 125-131.

Figure 1. Whistle definitions.

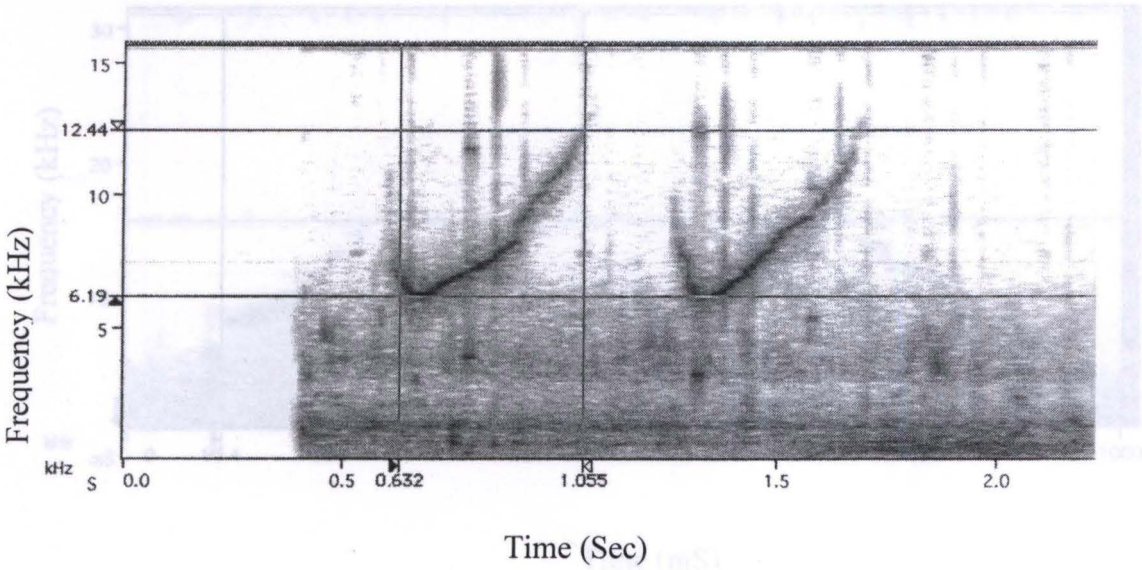


a. Spectrogram of Luna's signature whistle illustrating a continuous whistle type composed of three loops. The end of one loop is defined as the point in which the pattern starts to repeat itself (1, 2 and 3).



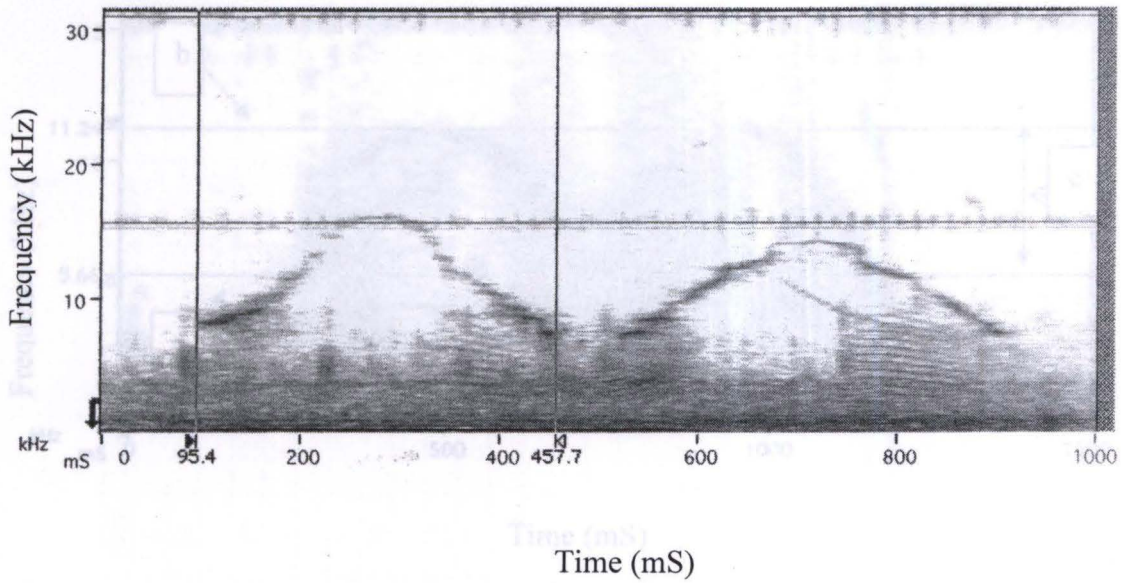
b. Spectrogram of WP's signature whistle illustrating a multi-loop whistle type composed of two loops. The loops are separated by a silent interval, but follow each other closely creating a repeating pattern.

Figure 2. Parameter measurement using manual cursors.



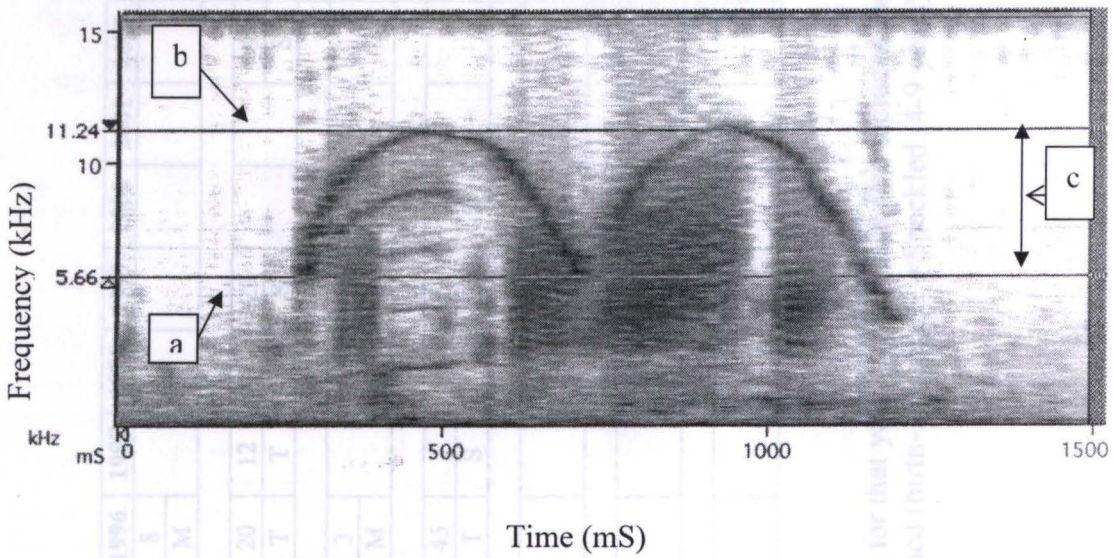
Spectrogram of WP's signature whistles showing the manual cursors (solid lines) used to determine duration (vertical cursors) and frequency measurements (horizontal cursors) of each loop.

Figure 3. Duration measurement using manual cursors.



Spectrogram of Heaven's signature whistles showing the manual cursors (solid vertical lines) used to measure duration. The left cursor is aligned with the start (left-most edge) of the loop and the right cursor is aligned with the end (right-most edge or the point at which the pattern starts to repeat itself) of the loop.

Figure 4. Frequency measurements using manual cursors.



Spectrogram of LH's signature whistles showing the manual cursors (solid horizontal lines) used for frequency measurements. The bottom cursor is aligned with the lowest point of the loop to measure minimum frequency (a). Similarly, the top cursor is aligned with the highest point of the loop to measure maximum frequency (b). Change in frequency (c) is defined as the difference between the minimum and the maximum frequency of a single loop.

Table 1. Number of whistles per year studied.

Animal	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Flying A						27 M		79 M		8 M						
Heaven									31 T	20 T	12 T		29 S			9 S
Little Gash	22 S		11 S	15 M				3 M	10 M	3 M						
Little Hali							19 T			45 T	3 S		5 S	1 S		
Luna				14 F	5 F	26 F	10 F	80 F	5 F							
Venus						66 S	8 S	45 M	56 M					10 M	17 M	
White Patches				10 M			8 M	8 M	8 F							

The numbers in each column represent the total number of whistles for that year. Age class is also included for each year the dolphin was studied, and is described as: T = Two toned (birth-3 years); S = Speckled (4-9 years); M = Mottled (10-16 years); F = Fused (16 + years).

Table 2. Whistle sample size and pooling of years in the time analysis.

Name	Early Years				Total	Late Years				Total		Total
Flying A			1992			1994		1996				
			M			M		M				
			27		27	79		8		87		114
Heaven	1995	1996	1997			1999			2002			
	T	T	T			S			S			
	31	20	12		63	29			9	38		101
LG	1987		1989	1990			1994	1995	1996			
	S		S	M			M	M	M			
	22		11	15	48		3	10	3	16		64
LH	1993			1996		1997		1999	2000			
	T			T		S		S	S			
	19			45	64	3		5	2	10		74
Luna		1990	1991	1992		1993	1994	1995				
		F	F	F		F	F	F				
		14	5	26	45	10	80	5		95		140
Venus	1992	1993	1994	1995				2000	2001			
	S	S	M	M				M	M			
	66	8	45	56	175			10	17	27		202
WP		1990				1993	1994	1995				
		M				M	M	F				
		10			10	8	8	8		24		34

The years are pooled into blocks of early and late years for the time analysis. The numbers in each column represent the total number of whistles for that year. Total number of whistles for each block of years is also included. Age class is also included for each year the dolphin was studied, and is described as: T = Two toned (birth-3 years); S = Speckled (4-9 years); M = Mottled (10-16 years); F = Fused (16 + years).

Table 3. Whistle sample size and pooling of years in the age analysis.

Name	Younger Years				Total	Older Years				Total		Total
Heaven	1995	1996	1997			1999			2002			
	T	T	T			S			S			
	31	20	12		63	29			9	38		101
LG	1987		1989			1990	1994	1995	1996			
	S		S			M	M	M	M			
	22		11		33	15	3	10	3	31		64
LH	1993			1996		1997		1999	2000			
	T			T		S		S	S			
	19			45	64	3		5	2	10		74
Venus	1992	1993				1994	1995	2000	2001			
	S	S				M	M	M	M			
	66	8			74	45	56	10	17	128		202
WP		1990	1993	1994		1995						
		M	M	M		F						
		10	8	8	26	8				8		34

The years are pooled based on age class for the age analysis. The numbers in each column represent the total number of whistles for that year. Total number of whistles for each block of years is also included. Age class is also included for each year the dolphin was studied, and is described as: T = Two toned (birth-3 years); S = Speckled (4-9 years); M = Mottled (10-16 years); F = Fused (16 + years).