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Time of Day and Social Change Affect Underwater Sound Production by Bottlenose Dolphins (*Tursiops truncatus*) at the Brookfield Zoo

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Abstract

This study investigated diel changes in ambient noise levels and the number of whistles produced by bottlenose dolphins (*Tursiops truncatus*) at the Brookfield Zoo in Brookfield, Illinois. Automated, continuous 24-h underwater recordings were made from 1 January to 31 March 2008. The number of whistles, types of whistles, and background noise level were examined for each hour. Nine distinct frequency contours were identified, named, and analyzed for minimum frequency, maximum frequency, peak frequency, and duration.

Since all pumps and filters at the Seven Seas Exhibit of Brookfield Zoo were housed in a separate building isolated from the dolphins' pools, background noise was relatively low and consistent throughout the day (95 to 98 dB re: 1 µPa). However, when the zoo staff used a scrubber to clean the pool walls, the background noise was higher and fluctuated (up to 112 dB re: 1 µPa). The dolphins whistled significantly less during these scrubbing periods.

The dolphins exhibited a distinct diel pattern in whistle production. Increased whistle production coincided with increased interactions with humans during feeding/training sessions; the number of whistles peaked in the late afternoon (~1600 h) and then quickly tapered off throughout the night.

The investigation began with eight dolphins; however, the death of one young male and the transport of two adult males to another facility left five dolphins: two adult females and two juvenile females along with an unrelated young male. These changes provided an opportunity to explore how social change affected whistle production.

After the two adult males were transported out of the facility, two of the distinct whistle types disappeared, suggesting that each of the two dolphins had a unique whistle type. The results of this investigation highlight the usefulness of passive recording for monitoring ambient noise, as well as for documenting the activity pattern and social interactions of captive bottlenose dolphins.

Key Words: diel pattern, whistle, background noise, ambient noise, bottlenose dolphin, *Tursiops truncatus*

Introduction

The number of whale-watching boats, swim-with-dolphin programs, eco-tours, recreational vessels, and commercial shipping has greatly increased worldwide (Scarpaci et al., 2000), and the associated anthropogenic noise with these activities may affect marine mammal behavior and sound production (Richardson et al., 1995; Southall et al., 2007). However, research investigating the effects of human activity on free-ranging or captive populations of cetaceans is lagging.

There is evidence that delphinids alter their sound production patterns in the presence of some human activities. For example, whistle production by free-ranging bottlenose dolphins (*Tursiops truncatus*) significantly increased in the presence of one commercial swim-with-dolphin program in Australia, regardless of dolphins' behavioral state (e.g., traveling, feeding, or social) prior to the arrival of the vessel transporting the swimmers (Scarpaci et al., 2000). The behavior and sound production of captive cetaceans also can be affected by human activities. The captive environment can exclude the opportunity for cooperative foraging, increase the prevalence of sounds produced above the water surface, and even modify the social structure of a group compared to free-ranging cetaceans (Defran & Pryor, 1980; Galhardo et al., 1996). Underwater acoustic behavior may also change in a captive environment. At the L'Oceanográfic in Valencia, Spain, Castellote & Fossa (2006) observed a persistent decrease in acoustic activity of beluga whales (*Delphinapterus leucas*) after long air transportation from South America to their new facility. The same belugas also decreased underwater sound production when four harbor seals (*Phoca vitulina*) were introduced to their pool.

Sound production by captive dolphins and whales often occurs in conjunction with human activity such as feeding, training sessions, or public presentations. Beluga whales at the New York Aquarium became more acoustically active during feedings (Fish & Mowbray, 1962). Captive bottlenose dolphins at three aquaria in Japan were most acoustically active during the day when human caretakers were present (Sekiguchi & Kohshima, 2003). The 16 captive bottlenose dolphins at these Japanese facilities also increased swim speed, respiration rate, and production of clicks and whistles in the afternoon (1200 to 1600 h) when humans were present, but decreased these behaviors at night (2400 to 0300 h) when humans were absent.

Over a month period, Tanchez (2003) made automated hourly underwater recordings for 5 min/h and documented the diel pattern of three types of underwater sounds (i.e., whistles, tonal calls, and noisy calls) produced by five captive beluga whales at John G. Shedd Aquarium. The highest number of underwater sounds per hour from belugas was produced during the hours when caretakers and visitors were present at the aquarium (0900 to 1800 h). All types of underwater sounds produced by the belugas increased significantly during feeding, and most sound types increased significantly when enrichment was provided and in the presence of humans. In addition, the presence of artificial and ambient light over the pools significantly increased the use of some sound types by the whales. For all sound types, the number of sounds per hour declined sharply after 1800 h when the aquarium was closed to the public and staff members left.

During the same month-long period and using the same methods as Tanchez (2003), Brickman (2003) documented the number of underwater sounds produced per hour by five Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) housed in a pool adjacent to the beluga pool at the Shedd Aquarium. These dolphins produced five underwater sound types, and the usage pattern of sound was nearly identical to that of belugas—that is, the number of sound types was highest when humans were present, during training and feeding sessions, and lowest when the aquarium was closed to the public. Collectively, these studies indicate that monitoring the number of underwater vocalizations over the course of a 24-h period is a good method for examining activity patterns in odontocetes.

The bottlenose dolphin is the species of odontocete most commonly kept in captivity (Galhardo et al., 1996). It is important to learn how captivity can affect these animals. Methods of non-invasive monitoring could be useful for improving the quality of life for captive dolphins. Passive recording of underwater sound production on a regular basis is one such method that could be used to assess the activity patterns, social interactions, health, and well-being of dolphins kept in captive environments. Through these passive recordings, animal care staff could acquire typical baseline rates and types of sound production across time, and then note any changes to this baseline pattern, which could indicate a need for closer examination of the captive population.

The present study conducted at the Brookfield Zoo used an automated, continuous acoustic recorder to investigate the diel patterns in ambient pool noise and the number and types of underwater sounds produced by a group of eight bottlenose dolphins. The initial objectives were to (1) describe any diel pattern in the number and types of whistles produced by dolphins; (2) characterize the hourly background noise levels in the pools; and (3) determine if the number, types, or acoustic properties of whistles were correlated with changes in background noise.

During the study, there was an unexpected death of one young male; and later, two adult males were transported to another facility. This provided the unique opportunity to address how social change affected the number, types, diel usage pattern, and acoustic properties of whistles. Because the number of dolphins changed from eight to five over the study period, these recordings provided the opportunity to examine possible signature whistles (individually unique and stable frequency contours) that allow individual dolphins to broadcast their identity to other dolphins.

Materials and Methods

Facility

This study was conducted at the Seven Seas Dolphinarium at the Brookfield Zoo in Brookfield, Illinois. Pool depths, configuration, and water volumes are shown in Figure 1. The bottlenose dolphins were housed in a series of four interconnected pools of different sizes. These four pools were connected by underwater channels and wire-mesh gates, which were used to physically separate the dolphins, but their acoustic environment was shared.

Bottlenose Dolphins at Brookfield Zoo

At the beginning of the study, Seven Seas was home to eight bottlenose dolphins, consisting of

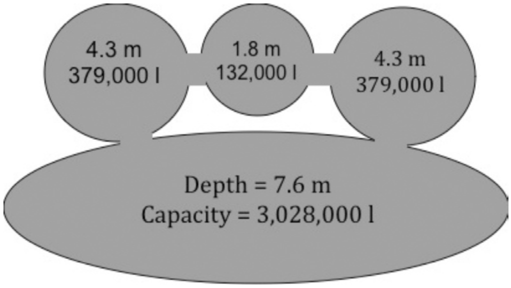

Figure 1. Diagram of the Seven Seas' bottlenose dolphin pools at Brookfield Zoo; these four pools were connected by underwater channels. Wire-mesh gates could be used to physically separate the dolphins, but the acoustic environment was shared.

two groups separated by gates among the four pools. The location of the groups was switched throughout the day, so all groups occupied the large pool during some portion of the day.

The first group consisted of two adult males: Lucky (approximately 34 y old) and Hastings (approximately 33 y of age). The second group, or family group, consisted of four females and two young males: (1) Tapeko, female, approximately 26 y old; (2) Kaylee, female, 14 y old, Tapeko's daughter; (3) Noelani, female, 4 y old, Tapeko's daughter; (4) Micco, male, 6 y old, Kaylee's son; (5) Jett, male, 6 y old, unrelated to the others; and (6) Allison, female, 2 y old, Tapeko's daughter.

On 13 January 2008, the young male, Micco, died unexpectedly, leaving the group with one less dolphin. On 10 March 2008, the two adult males, Lucky and Hastings, were transported from the Seven Seas to another facility in preparation for an upcoming renovation of the Brookfield Zoo pools. This left Seven Seas with a group of five dolphins (two adult females and two juvenile females, along with an unrelated young male) that had been together before Lucky and Hastings left.

Recording Equipment and Procedures

A calibrated Ithaco 605 hydrophone, with a linear frequency response from 100 Hz to 100 kHz ± 3 dB, was placed in one of the interconnected pools to record the dolphins' underwater sound production and background noise (see Figure 1). A 30-GBtye Apple iPod™ with a Belkin Tune Talk Stereo adaptor served as the recorder. The signal from the hydrophone was input to the Belkin Tune Talk adaptor. Because of the limitations of the iPod software and the Belkin adaptor, the effective frequency response of the entire recording system was only linear up to 22 kHz. However, using this limited frequency range facilitated making long recordings and the ability to operate the system on batteries overnight. The recording system was stored in a small, plastic, waterproof box on the edge of a pool and could be easily transported to a different pool when the dolphin groups were switched among pools. The hydrophone was always placed in an empty pool, separate from the dolphins, as a precaution against the dolphins tampering with the equipment (Figure 1).

Underwater sounds were recorded continuously, 24 h a day, for 15 randomly selected days from 1 January to 31 March 2008. The study was divided into three phases: Phase 1 – recordings of eight dolphins housed in two groups, Phase 2 – recordings of seven dolphins, housed in two groups, and Phase 3 – recordings of the five dolphins housed together in one group. Recordings were made for 4 d in Phase 1, 4 d in Phase 2, and 7 d in Phase 3. It was not possible to get an equal number of recordings due to the unexpected changes in the dolphin group composition.

Sound Analyses

Recordings were transferred from the iPod onto an Apple MacBook laptop as .wav files for analysis. Recordings were examined using spectrograms and power spectrums with *Raven Pro 1.3* (Cornell Bioacoustics Research Program, Ithaca, NY, USA) or *Audacity* (GNU General Public License) software. Displays of the sounds were viewed on the laptop while listening to the sounds.

To measure absolute sound levels in dB re: 1 μPa, the hydrophone (which itself was previously calibrated) was calibrated with the *Raven* software, using an acoustic test signal with a known frequency and amplitude. This acoustic test signal allows for the calculation of a calibration constant that was then used to convert the software's output values to absolute sound levels in decibels. The first minute of each hourly recording was analyzed for background noise level, the number of dolphin sounds, and the types of dolphin sounds. The background noise for the hourly sample was determined by averaging the power spectrum over a 22-kHz bandwidth for a period of 1 min. Spectrographic analysis was used to determine the total number of dolphin whistles and the number of different whistle types. A single whistle was defined as a narrow-band signal with a particular frequency contour and was separated from another contour (whether the same shape or different) by an audible gap of time. Whistle types were determined by listening to and observing spectrograms for distinctive whistle frequency contours that were repeated throughout the recordings. It was not possible to identify the dolphin producing each whistle type because the recordings included the entire group, and there was no concurrent video footage.

The authors identified nine whistle types and named them based on the appearance of their contour on the spectrogram (spectrograms of each whistle type are provided in Figure 4). The whistle type descriptions (and names) follow: signal increasing gradually in frequency over time (UpSweep), constant frequency signal (CF), frequency-modulated upsweep signal (FM), constant frequency followed by a downsweep (CF-FMsweep), signal shaped like an upside-down letter "U" (InvtU-loop), signal shaped like the letter "U" (U-loop), initial InvtU-loop followed by a distinct downsweep (Staff), U-loop followed by a distinct upsweep (Hook), and upsweep followed by a downsweep (Up-down). Whistles that did not match any of these types were classified as "Other."

The number of whistles of each type was counted for each hourly minute-long sample; however, to analyze the acoustic properties of the nine sound types, a random sample of 20 of each sound type was spectrographically analyzed for minimum frequency, maximum frequency, the frequency at the peak amplitude, and duration. All spectrograms were analyzed with an upper frequency scale of 22 kHz.

Two-way contingency table analyses at the $\alpha = 0.05$ level of significance were conducted and α levels were adjusted for multiple comparisons with the Bonferroni correction. Two-way contingency tables can be used to test independence of two categorical variables (e.g., whistle type and phase) within a single population (the dolphins). A series of two-way contingency tables was used to examine the relationship between (1) the mean number of whistles/min sample by hour of the day and by the phase of the study and (2) the mean usage of each whistle type/min sample by hour of the day and by phase of the study.

While analyzing recordings, the only large background noise fluctuation was observed when the Seven Seas staff entered the water and scrubbed the pool walls using a battery-operated scrubber. Scrubbing occurred daily for approximately 1 h to remove algae on the pool walls, and SCUBA divers were submerged while holding the scrubber against the pool walls or bottom. During pool cleaning, all of the dolphins were gated into other pools so that they would not interfere with the person using the scrubbing equipment. During these events, the hydrophone was placed as far from the scrubber and as close to the dolphins as possible to most accurately record the dolphins' acoustic environment. To compare whistle production rate during scrubbing noise vs without scrubbing, a Wilcoxon signed-rank test was used. This test compared the total number of whistles during a 1-min sample with scrubbing to the total number of whistles during a 1-min sample at the same hour of another day randomly selected during the same phase without scrubbing for all eight periods of scrubbing recorded during the study. For example, if the scrubbing was done at 1200 h during Phase 1, the number of whistles during 1 min of scrubbing was compared to the number of whistles during 1 min at 1200 h during another day in Phase 1 without scrubbing.

Results

Background Noise

All pumps and filters at Seven Seas were housed in a separate building isolated from the dolphin pools; therefore, background noise was relatively low and consistent throughout the day. Background noise was consistent over a 24-h period (except during scrubbing), and it ranged from 95 to 98 dB re: 1 µPa (n = 350-min samples).

However, a higher amplitude background noise was measured when the Seven Seas staff scrubbed the pools. Noise from the scrubber (~112 dB re: 1 µPa) was approximately 42 dB re: 1 µPa higher than the typical background noise and broadband in nature (n = 10-min samples). No whistles were recorded during scrubbing sessions. A Wilcoxon signed ranks test was used to compare whistle production rate during scrubbing (0 whistles detected) and without scrubbing activity (mean = 11.7 whistles/min, SD = 6.02, $n = 10$). Test results were significant (W = -45, df = 9, $p < 0.005$), indicating that the bottlenose dolphin whistle rate was lower during scrubbing.

Diel Underwater Sound Patterns and Changes in Whistle Rate Across Phases

The total number of whistles counted was 2,451, collected from a total of 360 hourly samples (24 samples from 15 d). The total number of underwater whistles/min in a given hour produced by bottlenose dolphins at Seven Seas ranged from 0 to 109. Dolphin sound activity increased throughout the day, peaked in the late afternoon (~1600 h), and then quickly tapered off throughout the night (Figure 2).

The mean number of underwater whistles/min by bottlenose dolphins during Phase 1 (eight dolphins, separated into two groups) ranged from 0 to 80 (mean = 17.6; SD = 24.1); for Phase 2 (seven dolphins; two groups), it ranged from 0 to 66 (mean = 11.02; SD = 16.6); and for Phase 3 (five dolphins; one group), it ranged from 0 to 109 (mean = 10.1; SD = 15.8). As the total number of dolphins recorded declined, the mean number of whistles/min significantly decreased ($\chi^2 = 800$, df = 44, $p = 0$). However, even with these decreases, the basic diel pattern of the number of whistles peaking in late afternoon was retained across the three phases of the study (Figure 3).

Whistle Types
Nine distinct types of underwater whistles were observed during Phase 1, eight types during Phase 2, and six types during Phase 3. Spectrograms for each whistle type are in Figure 4, and descriptive statistics of frequency at maximum amplitude (peak frequency), minimum frequency, maximum frequency, and duration are in Table 1, along with the average number of each whistle type/min in each phase. These whistle types ranged from a minimum frequency of 2.530 kHz (CF-FMsweep) to a maximum frequency of 19.702 kHz (Up-down). Peak frequency ranged from 5.491 kHz (U-loop) to 10.967 kHz (Staff). Whistle duration ranged from 0.173 s (Hook) to 0.808 s (CF-FMsweep). All whistle types were recorded during all three phases with the following exceptions: U-loop and Staff occurred only during the first two phases, and Up-down was recorded only during Phase 1.

A two-way contingency analysis indicated there were significant hourly differences in the mean usage of whistle types/min sample

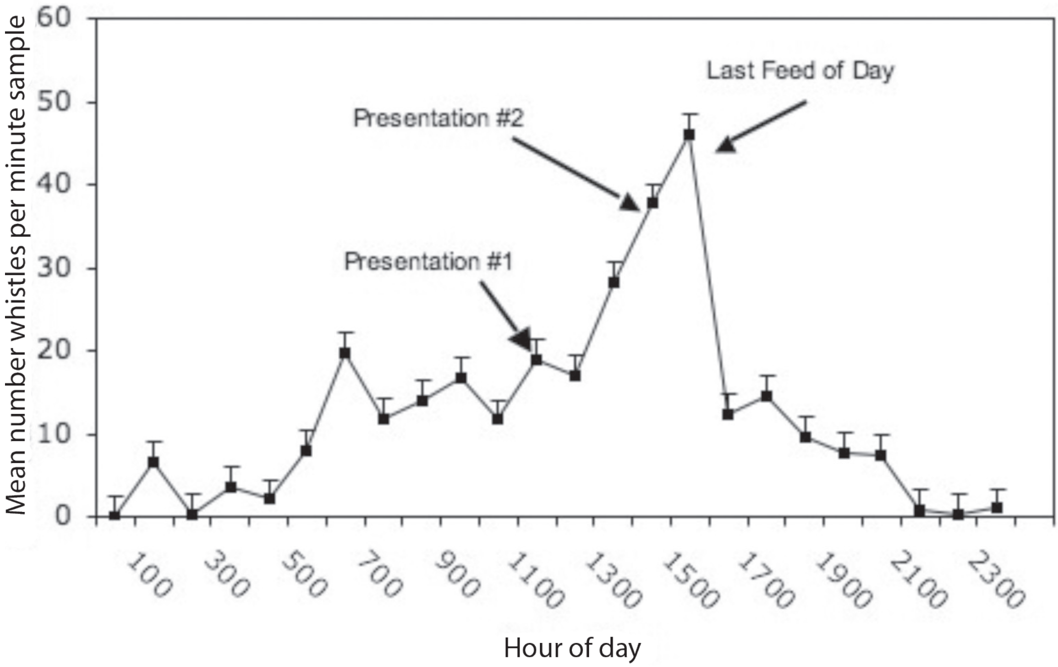

Figure 2. Diel patterns of the mean number of underwater whistles per hourly minute sample (± SD) produced by bottlenose dolphins at the Seven Seas Exhibit at Brookfield Zoo from 1 January to 31 March 2008; the two daily presentations and the last feeding/training session of the day are designated with arrows.

Table 1. Mean peak frequency, minimum frequency, maximum frequency, and duration of 20 samples of each whistle type from bottlenose dolphins at Brookfield Zoo; mean number of whistles per minute of each whistle type is also given by phase.

Whistle	Frequency (kHz)			Time (msec)	Mean number of whistles/min		
Type	Peak	Minimum	Maximum	Duration	Phase 1	Phase 2	Phase 3
UpSweep	9.031	5.644	15.958	243.3	4.80	2.64	2.61
Hook	8.795	6.416	15.049	172.8	2.96	3.17	2.37
InvtU-loop	10.672	4.344	11.207	433.0	1.48	0.53	1.18
CF	10.837	10.234	10.973	235.5	3.28	2.83	1.15
FM	8.997	6.334	13.673	357.3	1.06	0.53	0.46
CF-FMsweep	7.919	2.530	8.091	807.7	0.28	0.02	0.41
U-loop	5.491	5.475	8.376	286.7	2.34	0.60	0.00
Staff	10.967	5.609	11.361	387.0	0.42	0.70	0.00
Up-down	6.576	3.891	19.702	654.1	0.64	0.00	0.00

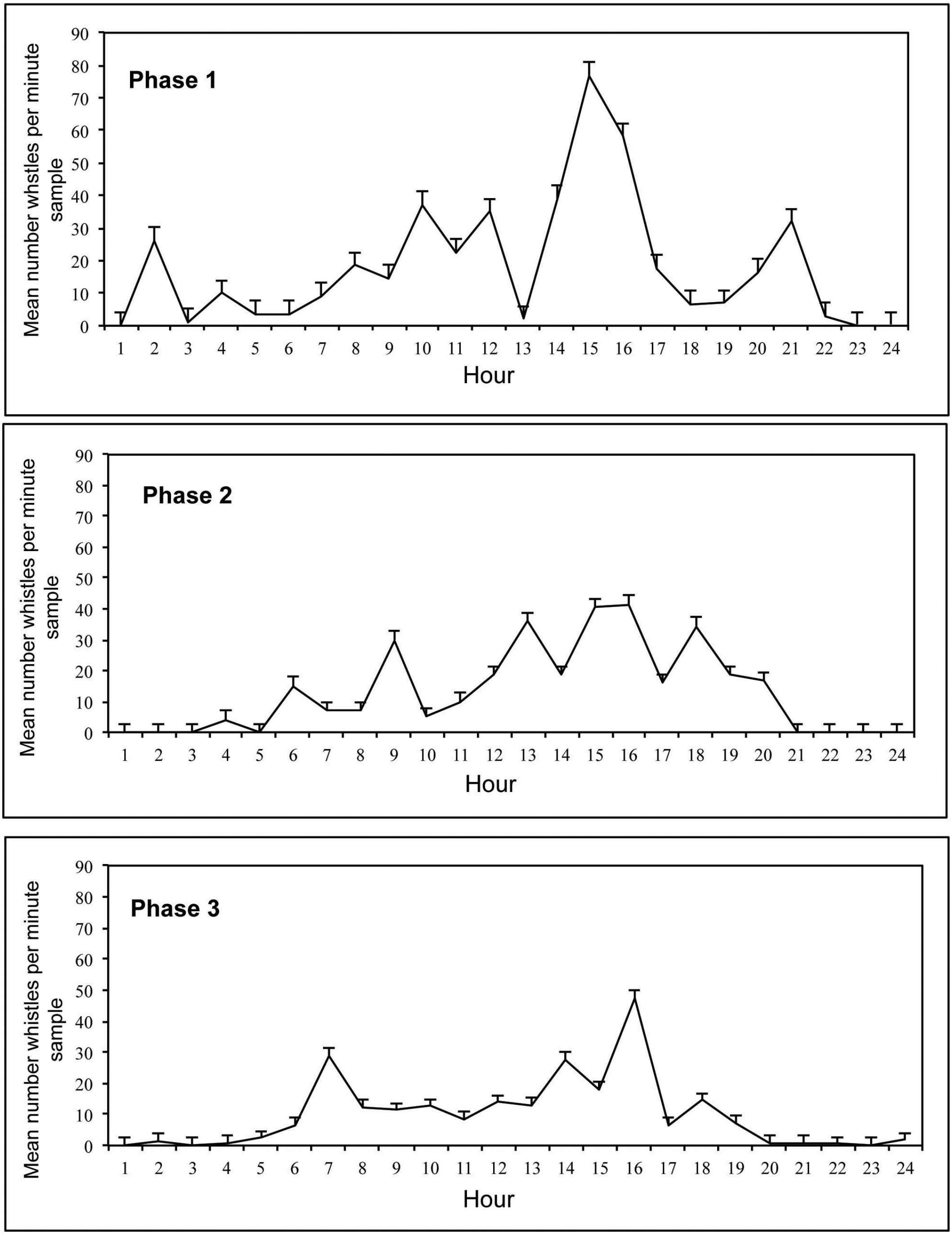

Figure 3. Diel patterns of the mean number of underwater whistles/min (± SD) by bottlenose dolphins at Brookfield Zoo by phases of the study; Phase 1 consisted of eight dolphins in two groups, Phase 2 consisted of seven dolphins in two groups, and Phase 3 consisted of five dolphins in one group.

over the entire study (χ^2 = 1,357, df = 176, p = 0.00; n = 2,451 total whistles). When examined across phases, there were significant differences (χ^2 = 377, df = 16, p = 0.00) in usage of different

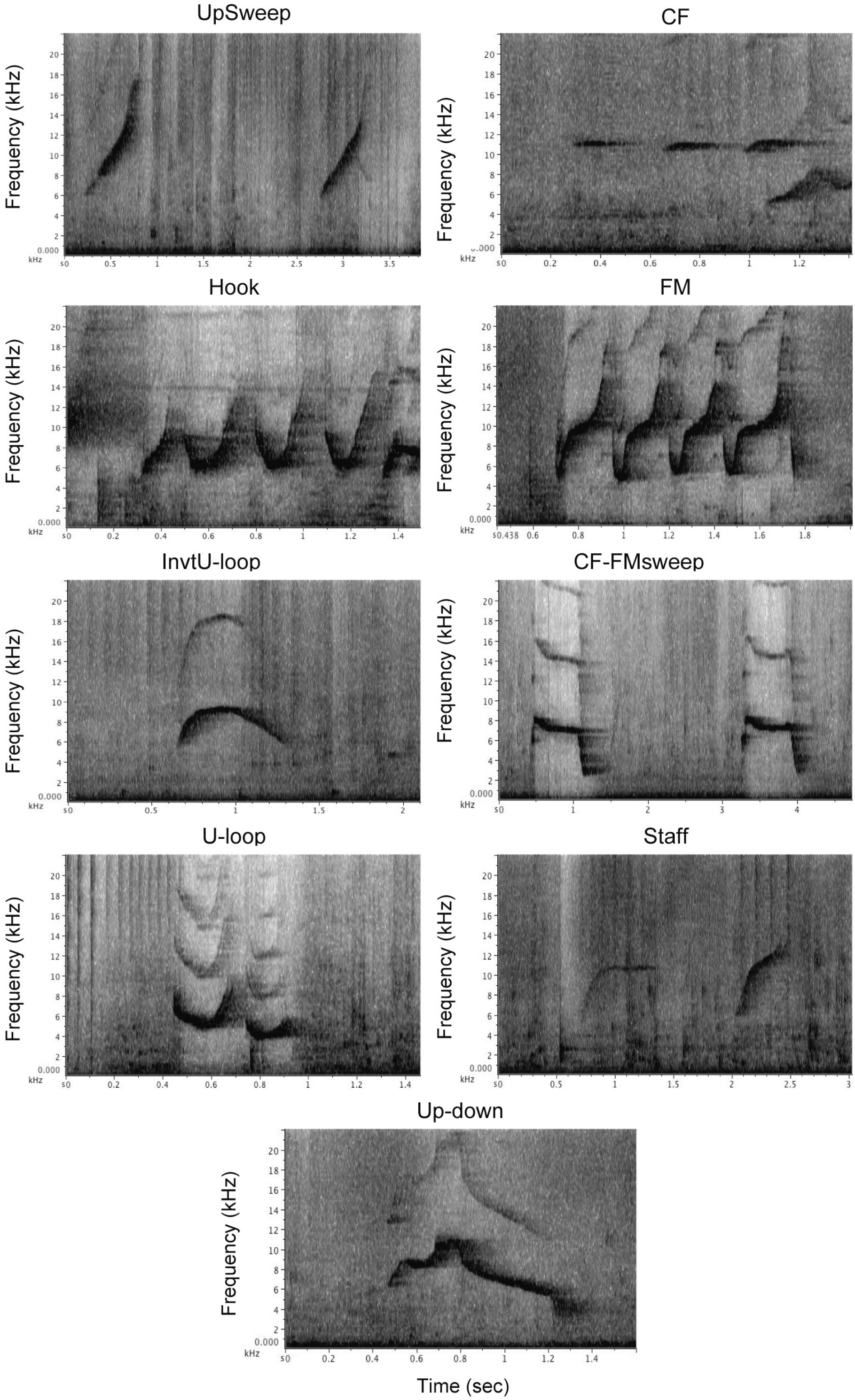

Figure 4. Spectrograms of nine underwater whistle types collected from bottlenose dolphins at Brookfield Zoo from 1 January to 31 March 2008

whistle types among phases. In addition, the mean usage of each whistle type was significantly different by hour within a phase. For example, the mean usage of UpSweep was significantly different for each hour by phase ($\chi^2 = 222$, df = 38, $p = 0.00$). All other results were as follows: Hook ($\chi^2 = 488$, df = 30, $p = 0.00$), InvtU-loop ($\chi^2 = 100$, df = 28, $p = 0.00$), CF ($\chi^2 = 325$, df = 40, $p = 0.00$), FM ($\chi^2 = 91$, df = 24, $p = 0.00$), CF-FMsweep ($\chi^2 = 122$, df = 20, $p = 0.00$), U-loop ($\chi^2 = 76$, df = 13, $p = 0.00$), and Staff ($\chi^2 = 28$, df = 11, $p = 0.00$). Up-down whistles were not included in the analysis because they did not occur in all phases.

The majority of whistle types followed the diel pattern of peak production in the afternoon. The one exception was the CF whistle type, which was produced most commonly during Phase 1 around 0200 h.

Discussion

Background Noise

There was very low background noise in the Seven Seas pools at the Brookfield Zoo, likely due to the effective design of the facility—all filtering equipment is isolated in a separate building so mechanical noise does not propagate well into the dolphin pools. This design provided a consistently quiet environment for the dolphins living at the Seven Seas. This noise level in the facility is comparable to the noise level of an air conditioner 6 m away (Richardson et al., 1995).

The only exception to this quiet environment was when the scrubber was used to clean algae off the walls of the pools. The scrubber sounds were predominantly below 6 kHz and were on average 42 dB re: 1 µPa higher in amplitude than the typical

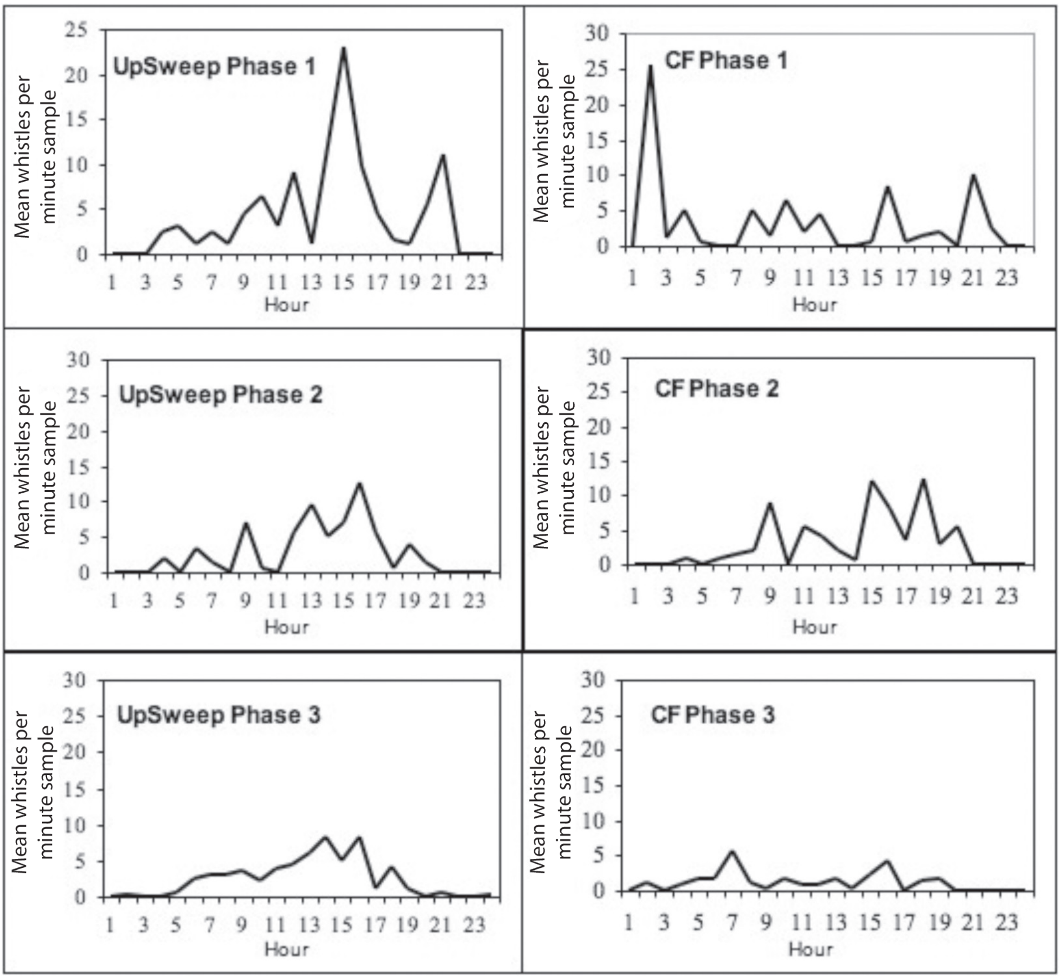

Figure 5. Diel patterns of UpSweep and CF whistle types across the three phases of the study; Phase 1 consisted of eight dolphins in two groups, Phase 2 consisted of seven dolphins in two groups, and Phase 3 consisted of five dolphins in one group.

background noise in the pools. Dolphins produced no whistles during scrubbing. However, at approximately 112 dB re: 1 µPa, the scrubber is not likely to cause any physiological damage, such as a temporary threshold shift, which begins in bottlenose dolphins at ~195 dB re: 1 µPa (Finneran et al., 2005). The scrubber noise level is comparable to a heavy truck moving at 64 km/h at 15 m away or to a kitchen blender (Richardson et al., 1995). It is more likely that the scrubber noise masked communication among dolphins, and they ceased calling until the scrubbing was over.

It is possible that very faint whistles were masked by the scrubbing noise and, therefore, not seen or heard in the recordings. However, the authors were careful to listen closely to all scrubber recordings for any narrow-band, frequency-modulated sounds that would contrast with the broadband scrubber noise. In addition, most of the energy produced by the scrubber was below approximately 6 kHz, while many of the recorded whistles extended well above that frequency (Table 1). Another possibility for failing to detect whistles during scrubbing sessions is that whistles produced by the dolphins were higher in frequency than the capability of the recording system. However, the fundamental component of dolphin whistles most often falls between 5 and 15 kHz (Herman & Tavolga, 1980), so this possibility seems unlikely.

Scrubbing is necessary to provide a clean environment for the dolphins, and it usually occurred for less than 1 h/d. However, it may be possible for the staff at the Seven Seas to explore quieter scrubber models.

Diel Underwater Whistle Patterns

Similar to other studies on diel variation in underwater sound production by odontocetes in captive environments (Fish & Mowbray, 1962; Brickman, 2003; Sekiguchi & Kohshima, 2003; Tanchez, 2003), bottlenose dolphins at the Brookfield Zoo were most acoustically active during the day when the facility was open to the public and the staff was present. Increased whistle production coincided with increased interactions with humans such as during feeding, presentations, and training. Whistle production peaked around 1600 h, coinciding with the last feeding and training session of the day. Other peaks coincided with the two daily dolphin presentations open to the public (1130 h and 1430 h), during which time the dolphins also received food. This diel pattern is unique to captive dolphins. In populations of free-ranging bottlenose dolphins, foraging behavior, when dolphins are often most acoustically active, is correlated with tidal state, not time of day (Gregory & Rowden, 2001).

As the number of dolphins across the three phases of the study decreased from eight to seven and then to five, the mean number of whistles/min also decreased, which was expected because there were fewer dolphins to whistle. However, decreases in dolphin number did not change the diel pattern. When considered individually, every whistle type followed a similar diel pattern, with the exception of the CF whistle type, which in Phase 1 was produced most commonly at 0200 h. The hourly usage of every whistle type changed significantly over the three phases, even though the diel pattern remained consistent.

Social changes are likely to have an effect on sound production, although without knowing the whistler's identity, it was difficult to discern the exact effects. Staff and U-Loop whistle types completely disappeared from the repertoire during Phase 3, while the number of CF and UpSweep whistles appeared to steadily decrease across all three phases. A decrease in the overall number of whistles was expected because there were fewer dolphins in the pools. However, because one whole social group was removed (the two adult males), the number of some whistles types may have decreased during the last phase because there were no longer two physically separated groups.

Whistle Types

The signature whistle hypothesis suggests that individual dolphins broadcast their identity to other dolphins through the use of individually unique, stable frequency contours (Caldwell & Caldwell, 1965, 1968, 1972, 1979; Caldwell et al., 1990; Harley, 2008). The whistle types in the current study resemble signature whistles in two ways: (1) each whistle type maintained a distinctive contour pattern or shape throughout the study and (2) the number of whistle types decreased as the number of dolphins present decreased, suggesting that a whistle type may have been unique to a specific dolphin. For example, after the death of one dolphin, the Up-down whistle type disappeared from the repertoire, suggesting it was used exclusively by that young male. In addition, after the removal of two adult males, the Staff and U-Loop whistle types disappeared, indicating they were used exclusively by the two adult males moved from the facility.

However, because the whistler's identity was unavailable, it is impossible to determine with certainty whether each dolphin was in fact producing one predominant whistle type. In addition, there was always one more whistle type observed than the number of dolphins (nine whistle types during Phase 1 with eight dolphins, eight whistle types during Phase 2 with seven dolphins, and six whistle types during Phase 3 with five dolphins). This evidence points to distinctive and stable contours, but without information on the whistler's identity or location, the context of these whistles is unknown.

To add to the difficulty of studying signature whistles, bottlenose dolphins, which commonly associate with each other, may produce each other's signature whistle (Tyack, 1986, 1993). Whether dolphins at the Brookfield Zoo were imitating each other's signature whistles could not be determined in this study.

Signature whistles are produced most often in contexts of isolation, in cases wherein dolphins in one social group are out of visual contact with other dolphins (Sayigh et al., 1990; Janik & Slater, 1998). Because the bottlenose dolphins at the Seven Seas were separated physically into different pools with gates and yet remained in acoustic contact, signature whistles could have been used to maintain cohesion across pools. When the two mature males were removed (Phase 3), the rest of the dolphins were now in one group and never were separated by a gate. Certain individuals from this group, however, still voluntarily swam into an open, unoccupied pool and then were visually isolated from the others, a situation in which use of signature whistles might occur.

Future Research

The bottlenose dolphins at the Brookfield Zoo provided a unique opportunity to investigate the types and usage of underwater whistles in a changing social group. The development of signature whistles is influenced by whistles of other dolphins in the community (Buck & Tyack, 1993; Fripp et al., 2005). Signature whistles of male calves appear to be more similar to their mothers' whistles than whistles of female calves (Sayigh et al., 1995), which is adaptive in free-ranging dolphins because female offspring are more likely to have a long-term association with their mother than male offspring (Wells, 2003). Because there are mother-offspring relationships in the Brookfield Zoo bottlenose dolphin group, the development of signature whistles could be easily investigated. Perhaps Micco's signature whistle was similar to Kaylee's signature whistle, or perhaps Tapeko's daughters (Allison, Kaylee, and Noelani) had very different signature whistles from their mother. Unfortunately, the identity of the various whistling dolphins could not be verified to test these ideas.

The most useful improvement to this study would be the ability to discriminate the whistler's identity. This could either be done with concurrent acoustic recording and video footage or through the physical isolation of one dolphin in a pool for recordings. With this knowledge, the predominant whistle of each dolphin (if there is one) could be identified and measured in different contexts.

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