Patterns of dolphin sound production and ovulation

Sue E. Moore1 and Sam H. Ridgway2

1SAIC, Maritime Services Division, 3990 Old Town Avenue, Suite 105A, San Diego, CA 92110, USA
2NCCOSC Research and Development (NRaD), Code 35, San Diego, CA 92152, USA

Abstract
The total number of sounds (whistles and pulsed sounds) produced by two female common dolphins and two female bottlenose dolphins, housed in separate enclosures, were counted over one 24-hour period roughly every 2-weeks from December 1979 through January 1981. Progesterone levels from each of the four dolphins were measured from blood samples drawn just before or soon after the sound counts. Moon phase, day length and water temperature were collated with bioacoustic and hormone data throughout the experiment. Peaks in progesterone level indicative of ovulation occurred in one of the common dolphins and in both bottlenose dolphins. The common dolphin exhibited nine progesterone peaks; four >10 ng/ml occurred in late spring and summer, with five lesser peaks (3.5–8.2 ng/ml) throughout the balance of the year. Both bottlenose dolphins ovulated in late April and mid-May, indicated by progesterone levels between 3.4–5.9 ng/ml; one of the females ovulated again in June and July, evidenced by progesterone levels between 3.1–4.4 ng/ml. Sound production was negatively correlated with progesterone levels in both species, although the relationship was statistically significant (r = −0.58, P < 0.01) only between number of pulsed sounds and progesterone level in one of the Tursiops females. Total sound production fell to its lowest level, and the whistle component was highest, during springtime progesterone peaks by both bottlenose dolphins. Sound production from the common dolphins fell off dramatically after the first five sampling periods, as the same female continued to ovulate through summer and early autumn. Both species exhibited progesterone peaks on study date 28/29 April 1980, when day length at 13.45 hours was increasing at a rate of about 2 minutes/day. The last progesterone peak occurred on 23/24 October and on 10/11 June for the common and bottlenose dolphins, respectively. Progesterone level was significantly associated with moon phase for the common (F = 4.42, P = 0.047) but not for the bottlenose dolphins. Six of nine progesterone peaks exhibited by the Delphinus female occurred on the full moon, including all four peaks >10 ng/ml. There was some diurnal pattern to sound production in both species, with fewest calls counted between hours 2300–0700 and 1000–1100 for common dolphins and between 0000–0400 for bottlenose dolphins. Sound production generally increased during feedings and decreased immediately afterwards. Conversely, sound production sometimes increased with no apparent instigation. The unaccounted influence of external factors undermine strong inferences regarding diurnal sound production patterns.

Introduction
Common dolphins (Delphinus delphis) and bottlenose dolphins (Tursiops truncatus) are ubiquitous species in temperate and tropical waters (Leatherwood & Reeves, 1983). Bottlenose dolphins are perhaps the best-studied cetaceans due to their penchant for coastal habitats and ability to thrive at marine parks and oceanariums. Indeed, bottlenose dolphins have served as the ‘template species’ for much of the scientific literature on cetacean physiology, sensory and bioacoustic capabilities (e.g., Leatherwood & Reeves, 1990; Au, 1993). Conversely, common dolphins are a pelagic species and have not adapted so readily to oceanariums. Consequently, there are comparatively few reports on their bioacoustic, physiologic and sensory capabilities (e.g., Moore & Ridgway, 1995; Hui, 1979, 1981; Caldwell & Caldwell, 1968).

Sound production is described for both common and bottlenose dolphins (reviewed in Thomson & Richardson, 1995). Sounds produced by both species fall into three general categories: (1) very short high-frequency echolocation clicks; (2) broadband pulsed sounds, including buzzes, cries and barks; and (3) narrowband whistles, including a variety of tonal sounds. Echolocation clicks are often inaudible to humans because they are highly directional and usually peak at frequencies about 20 kHz. However, clicks are broadband, so the frequency component below 20 kHz can be heard.
when the dolphin is oriented toward the hydrophone. Conversely, pulsed sounds and whistles typically contain most of their energy below 20 kHz and are clearly audible to humans. Powell (1966) quantified vocal activity in bottlenose dolphins over a 15 day period during summer. Sound production was greatest between 0500 and 0800 and lowest between 2300 and 0200. Switching feedings from daytime to nighttime greatly affected vocal activity periodicity. Klinowska (1986) did not mention other studies of seasonal or diurnal sound production in dolphins in her review of diurnal rhythms in cetacea.

Female common dolphins attain sexual maturity at about 3 years of age, with a calving interval of 2.6 years for animals in the eastern tropical Pacific (Perrin & Reilly, 1984). Female bottlenose dolphins start reproductive cycles at 5 to 10 years of age (Sergeant et al., 1975). Individuals tend to be seasonally polyestrous with multiple estrus cycles at roughly 24–36 day intervals, interspersed with periods of anestrus. Spontaneous ovulation, indicated by peaks in serum progesterone level of >3 ng/ml, is described for both common and bottlenose dolphins (Kirby & Ridgway, 1984).

At NRAD, bottlenose dolphin breeding and births were concentrated in spring in San Diego, California, and in autumn in Kaneohe, Hawaii, during a reproduction study conducted from 1981–84 (Schroeder, 1990).

In late 1979, we entered into research to evaluate sound production as an indicator of health and reproductive status in dolphins. Sounds produced by two female common dolphins and two female bottlenose dolphins were tallied each hour of a continuous 24, and collated with progesterone levels measured from blood samples drawn just before or soon after each 24-hour study as possible and analyzed (radioimmunoassay) for serum progesterone levels (see Kirby & Ridgway, 1984). Progesterone was the ‘ovulation indicator’, with serum levels greater than 3 ng/ml considered indicative of ovulation. Environmental features collated with sound counts and progesterone levels included: (1) moon phase; (2) total hours of daylight (i.e., sunrise to sunset); and (3) water temperature. Bi-monthly study dates, chosen to coincide with new and full moon phases, afforded adequate sampling for ovulation events. Standard parametric statistical analyses (Zar, 1984) were applied to the collated data set using STATISTICA software.

Methods
Two adult female common dolphins (04 and 05) and two adult female bottlenose dolphins (497 and 455) maintained at the Naval Ocean Systems Center (NOSC; now NRAD), San Diego marine mammal facility from 1979 through 1981 were the subjects of this study. The dolphin pairs were housed in separate enclosures (9 m diameter × 1.8 m deep) at the NOSC facility. The enclosures were supplied with fresh filtered seawater at ambient temperature. Each enclosure was equipped with a calibrated LC-10 hydrophone with a Celeesco LG-1364 line driver and 40 dB preamplifier positioned at mid-tank depth. The acoustic signal was filtered by an Ithaco Model 4302 filter set at 3.15 kHz hi-pass, with 24 dB/octave rolloff and 20 dB amplification, and output through standard stereo speakers.

Sound production was tallied for each hour of a 24-hour sample by counting each whistle and each pulsed sound as one sound event. Because pulsed sounds are not as discrete as whistles, a pulsed sound ‘event’ was arbitrarily agreed upon by observers as a ‘buzz’ or ‘creak’, usually lasting from 1 to 5 s. For example, a series of 100 dolphin clicks lasting 2 s and audible as a ‘buzz’ was tallied as one sound. Sounds were recorded on tape only during periods of high production rates. Tape recordings were made on an Ampex Model FR 1300 instrumentation recorder set at 39 cm/s (15 ips). Recording system bandwidth was 3.15–75 kHz ± 2 dB. A continuous polygraph hard copy record was made to augment sound counts. All totals include only those sounds perceptible to the human observer.

Blood samples were drawn from the dolphins just before or as soon after each 24-hour study as possible and analyzed (radioimmunoassay) for serum progesterone levels (see Kirby & Ridgway, 1984). Progesterone was the ‘ovulation indicator’, with serum levels greater than 3 ng/ml considered indicative of ovulation. Environmental features collated with sound counts and progesterone levels included: (1) moon phase; (2) total hours of daylight (i.e., sunrise to sunset); and (3) water temperature. Bi-monthly study dates, chosen to coincide with new and full moon phases, afforded adequate sampling for ovulation events. Standard parametric statistical analyses (Zar, 1984) were applied to the collated data set using STATISTICA software.

Results
Sound production over a 24-hour period was tallied on 27 dates between 3/4 December 1979 and 6/7 January 1981 (Table 1). Sampling periods fell on 14 new, 12 full and one quarter moon. Hours of daylight varied from 9.67 to 14.28, and water temperature from 13.89 to 20.56°C. Overall, 88 944 sounds were tallied from the Delphinae, 8% of them whistles (7052 whistles and 81 892 pulsed sounds); 436 971 sounds were counted from the Tursiops, 23% of them whistles (98 538 whistles and 338 433 pulsed sounds). Although collected, Tursiops data for the first two sampling periods were omitted.
from analyses because the dolphin pair consisted of a male and female. Notably, the *Tursiops* females produced nearly five times more sounds than the *Delphinus* females, even with two fewer sampling periods and reduction in sampling to 17 hours on 14 April 1980 due to equipment problems. O n e *Delphinus* females, and both *Tursiops* females, exhibited progesterone levels >3 ng/ml during the course of the study. Both species exhibited progesterone peaks on study date 28/29 April when day length at 13.45 hours was increasing at a rate of about 2 minutes/day. While the *Tursiops* females exhibited progesterone peaks only in spring and early summer, levels for the *Delphinus* female peaked throughout summer and early fall. Correlation of sound production with progesterone levels and environmental indices is described below.

**Common dolphins**

Common dolphin sound production was comparatively high from December through mid-February, fell off then re-bounded somewhat in April and May, then fell to very low values for the remainder of the experiment (Table 1; Fig. 1). Over 80% of all whistles tallied (5682 of 7052) were from the first five sampling periods, with fewer than 25 whistles counted during 11 of the last 22 sampling periods. Whistles averaged 5% of each sound sample (range: 0.3–21%). Female #04 exhibited nine progesterone peaks during the study: four >10 ng/ml during spring and summer, and five between 3.52–8.19 ng/ml during the balance of the year. Female #04 was the dominant animal of the two, always preceding the other animal at the feeding station. The subordinate female #05 never exhibited progesterone levels >1 ng/ml during the study, although levels of 0.834 and 0.955 ng/ml were obtained from the last two serum samples of the series.

Sound production was negatively correlated with progesterone levels in both common dolphins, but the relationships were not statistically significant (Fig. 2). The strongest negative correlation was
Figure 1. Total number of pulses and whistles tallied during each sampling period, and associated progesterone levels for the Delphinus females over the course of the study.
between the number of pulsed sounds and progesterone level in animal #05 ($r = -0.32$, $P < 0.20$). Progesterone levels in animal #04 were positively correlated with day length (see Fig. 2). Pulsed sounds and whistles were negatively correlated with day length and water temperature, with significant
associations between pulses and water temperature and between pulses, whistles and day length. There was a significant relationship between moon phase and progesterone level for female #04 (F=4.42, P<0.10) while the two progesterone peaks in female #497 fell on a full and new moon phase, respectively (F=0.02, P<0.90). There was no obvious dominance pattern between the two Tursiops females.

**Diurnal patterns of sound production**
Cumulative hourly counts depict some diurnal pattern to sound production in both species (Fig. 5). The Delphinus females produced pulsed sounds throughout the day, with somewhat lower occurrence between 2300–0700 and 1000–1100 hours. Pulsed sound counts were relatively high between 1200–2200. A sharp peak in pulsed sounds at 0800–0900 coincided with the morning feeding, with the aforementioned drop off of sound production immediately thereafter. Delphinus whistle production was uniformly low throughout the nighttime, but displayed some bi-modality between 0600–1800. Whistle counts peaked between 0800–0900 and 1300–1500, both periods generally coincident with feedings. Sound production patterns displayed by the Tursiops were strongly diurnal with minimum counts from 0000–0400. Like the common dolphins, whistles produced by Tursiops showed bi-modality between 0600–1800, with a drop in whistle production between 1000–1100, after the morning feeding. Unlike common dolphins, Tursiops continued to whistle at night with a small peak in production at 2000.

**Discussion**
Sound production in both Delphinus and Tursiops varied broadly over the study period. While the number of calls tallied from the female common dolphins fell off dramatically after the initial five sampling periods, the bottlenose dolphin females called at comparatively high rates throughout the study except during the spring/summer period associated with peaks in progesterone. Sound production was negatively correlated with progesterone levels in both species, but the only significant relationship was between number of pulsed calls and progesterone level for one of the Tursiops females. Notably, the sound sample with fewest calls (but the highest percentage of whistles) coincided with the first progesterone peak noted among the bottlenose dolphins. Sound production was also negatively correlated with day length and water temperature in both species, with the strongest relationships displayed by common dolphins. While peaks in progesterone were positively associated with full moon phases in one of the common dolphins, no relationship was found for either bottlenose dolphin female.

Overall, bottlenose dolphin sound production was nearly five times greater than that of the common dolphins, and whistles comprised a larger component of each sound sample. Reasons for these differences may lie in the dissimilar behavioral ecology of the two species (Leatherwood & Reeves, 1983). Common dolphins are pelagic cetaceans that often travel in herds numbering hundreds of animals, which break into small feeding groups in the late afternoon to feed on fishes and squid associated with the deep scattering layer. Conversely, bottlenose dolphins are neritic cetaceans that usually travel in groups of 10–25 animals and eat a wide variety of fishes and invertebrates. Although the function of the pulsed sounds and whistles produced by both species remains unknown, communication requirements may
Figure 3. Total number of pulses and whistles tallied during each sampling period, and associated progesterone levels for the *Tursiops* females over the course of the study.
Correspond to differences between the species in social organization and trophic dynamics.

Can sound production aid in assessment of reproductive condition in dolphins? Although statistical relationships were somewhat ambiguous, overall results presented here suggest that it can. The drop in sound production, especially pulsed calls, by the Tursiops females just prior to the first

Figure 4. Correlations of pulse sound and whistle counts with hours of daylight, water temperature and progesterone levels for Tursiops females #497 and #455. Statistical significance: *P<0.05; **P<0.01.
Figure 5. Cumulative hourly counts of pulses and whistles for *Delphinus* and *Tursiops* females. Note difference in scale between histograms.
progesterone peak was dramatic. Similarly, peaks in progesterone were generally dissociated with sound production by the *Delphinus* females. One must consider the latency of the progesterone rise after ovulation and the coarseness of the bi-weekly sampling regime employed here. Further, a progesterone assay alone is not specific enough about ovulation date to detail the sound–ovulation association. Since this experiment, daily urine analysis has become a more practical method to determine ovulation pattern in cetaceans (Walker et al., 1988). Analysis of urine samples can provide a much finer measure of hormonal pattern than we were able to achieve. Results presented here suggest that a detailed study of dolphin sound production, especially whistles in *Tursiops*, may elucidate sound–ovulation associations that could be useful in assessment of reproductive condition in dolphins.

**Acknowledgements**

This study could not have been completed without the assistance of several talented individuals. We thank Vicky Kirby (formerly, San Diego Zoological Society) for progesterone analysis and for helping in some of the all-night sound counts; Donald Carder (NRaD) and Frank Shipp (NRaD) for help with electronics; and Janet Clarke (SAIC) for database management. This research was conducted under NMFS/NOSC Marine Mammal Research Permit No. 12.

**References**


