Aquatic Mammals 1996, **22.3**, 175–184

Patterns of dolphin sound production and ovulation

Sue E. Moore[1] and Sam H. Ridgway[2]

[1]*SAIC, Maritime Services Division, 3990 Old Town Avenue, Suite 105A, San Diego, CA 92110, USA*
[2]*NCCOSC 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 acoustic sampling. Because none of the four dolphins became ill during the sampling period, the research became focused on sound production and ovulatory pattern of the females. Preliminary results for bottlenose dolphins were summarized in Ridgway (1983), but without quantification. Whistles produced by the common dolphins were described in Moore & Ridgway (1995), but without reference to reproductive condition, or extant environmental parameters. Here we present a quantitative account of sound production for both species, with reference to reproductive status and simple environmental indices.

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 Celesco 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 *Delphinus*, 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

Table 1. Summary data for 24-hour sound production–progesterone level study. Date indicates day on which study was initiated. Progesterone level in pg/ml. *Tursiops* data for 3 and 18 December 1979 were omitted due to male+female pair; *Tursiops* call counts for 14 April 1980 are for 17 hours only (*) due to equipment malfunction; ***=no data

				Sound production				Progesterone level			
				Delphinus		*Tursiops*		*Delphinus*		*Tursiops*	
Date	Moon 0–new 1–full	Daylight hours	Water °C	Whistles	Pulses	Whistles	Pulses	#04	#05	#497	#455
3 Dec 1979	1	9.93	***	1914	12 513	***	***	2.56	0.67	***	***
18 Dec 1979	0	9.67	***	774	6747	***	***	7.81	0.39	***	***
9 Jan 1980	0.5	10.00	13.89	1367	6746	6793	14 105	0.47	0.41	0.13	0.21
17 Jan 1980	0	10.27	14.44	914	11 599	4497	18 846	0.36	0.36	***	***
1 Feb 1980	1	10.62	15.55	713	9566	6436	16 207	0.47	0.09	***	***
15 Feb 1980	0	11.03	14.44	24	3817	5401	19 593	0.74	0.06	0.13	0.24
29 Feb 1980	1	11.47	14.99	31	2400	4693	22 429	0.30	0.46	0.05	0.34
17 Mar 1980	0	12.07	14.99	5	809	3328	11 671	6.24	0.60	0.18	0.29
31 Mar 1980	1	12.53	16.11	195	3366	4198	24 693	0.65	0.46	0.03	0.09
14 Apr 1980	0	12.92	16.11	24	1401	1842(*)	3828(*)	1.27	0.64	0.08	0.12
28 Apr 1980	1	13.45	14.99	40	4909	2327	1275	13.68	0.40	4.01	0.08
14 May 1980	0	13.82	15.55	39	4228	1682	3918	1.40	0.16	3.35	5.93
3 Jun 1980	1	14.20	16.67	67	2051	3358	9216	10.36	0.47	0.50	1.24
12 Jun 1980	0	14.28	15.55	16	897	3787	23 237	0.54	0.23	0.17	3.10
27 Jun 1980	1	14.28	17.78	1	366	6498	21 128	15.51	0.33	0.14	0.11
10 Jul 1980	0	14.17	18.33	12	684	2971	13 064	0.42	0.66	0.16	4.41
27 Jul 1980	1	13.85	17.78	64	1061	2395	19 190	13.33	0.48	0.20	0.23
11 Aug 1980	0	13.55	18.87	4	837	3051	11 152	3.52	0.61	0.20	0.11
25 Aug 1980	1	13.05	20.00	5	563	5815	13 636	4.49	0.44	0.07	0.12
9 Sep 1980	0	12.60	20.56	86	644	4528	10 414	1.20	0.36	***	0.15
23 Sep 1980	1	12.10	20.00	35	634	3943	9911	0.77	0.14	0.08	0.19
7 Oct 1980	0	11.65	17.22	5	216	5507	12 252	0.72	0.20	0.10	0.14
23 Oct 1980	1	11.07	16.67	503	1844	4891	15 023	8.19	0.21	0.08	0.12
6 Nov 1980	0	10.62	16.67	18	882	3267	10 792	***	***	0.08	0.10
20 Nov 1980	1	10.33	16.67	102	1266	1716	9183	1.32	0.83	0.12	0.15
7 Dec 1980	0	9.92	15.00	70	962	4010	13 785	0.89	0.96	0.17	0.21
6 Jan 1981	0	9.98	15.00	24	884	1622	9885	***	***	***	***

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.

One of the *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

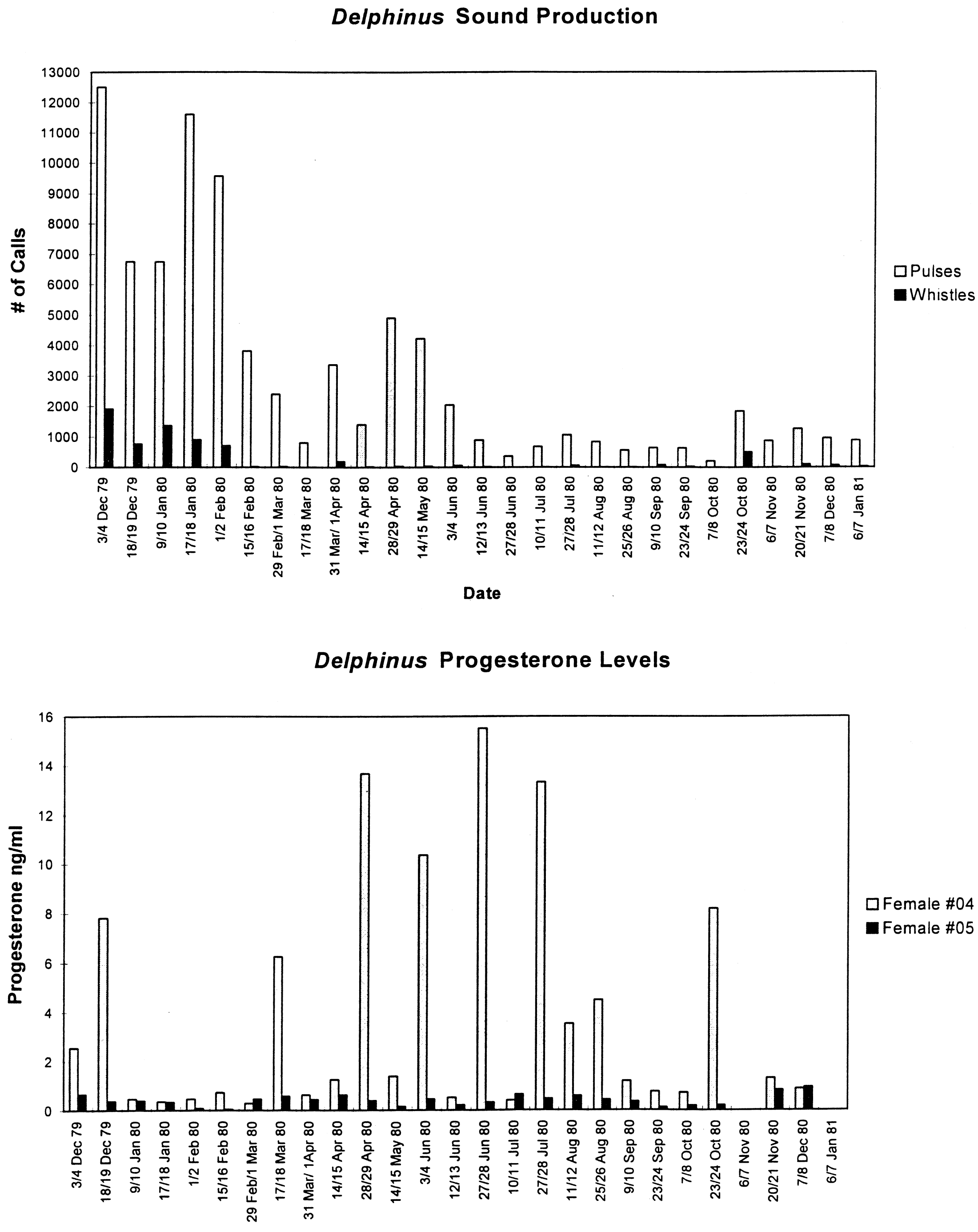
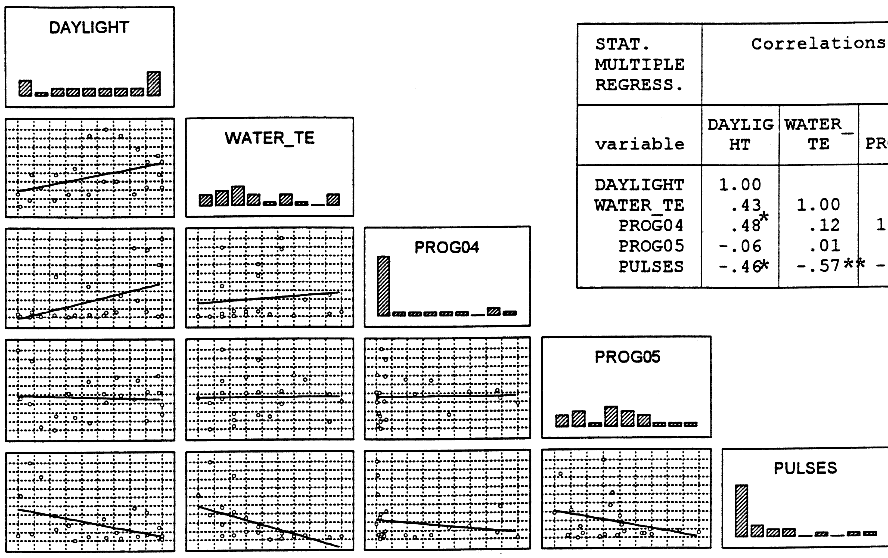


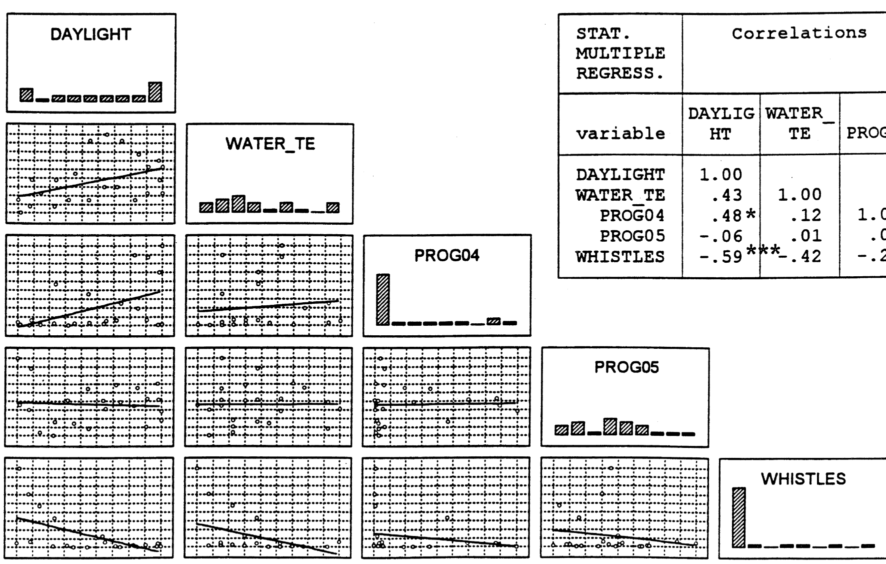
Figure 1. Total number of pulses and whistles tallied during each sampling period, and associated progesterone levels for the *Delphinus* females over the course of the study.

***Delphinus* Pulses**



STAT. MULTIPLE REGRESS.	Correlations				
variable	DAYLIGHT	WATER_TE	PROG04	PROG05	PULSES
DAYLIGHT	1.00				
WATER_TE	.43	1.00			
PROG04	.48*	.12	1.00		
PROG05	-.06	.01	.01	1.00	
PULSES	-.46*	-.57**	-.20	-.32	1.00

***Delphinus* Whistles**



STAT. MULTIPLE REGRESS.	Correlations				
variable	DAYLIGHT	WATER_TE	PROG04	PROG05	WHISTLES
DAYLIGHT	1.00				
WATER_TE	.43	1.00			
PROG04	.48*	.12	1.00		
PROG05	-.06	.01	.01	1.00	
WHISTLES	-.59***	-.42	-.21	-.18	1.00

Figure 2. Correlations of pulse sound and whistle counts with hours of daylight, water temperature and progesterone levels for *Delphinus* females #04 and #05. Statistical significance: *$P<0.05$; **$P<0.01$; ***$P<0.005$.

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 ($F=4.42$, $P=0.047$), but not for female #05 ($F=0.03$, $P=0.855$). Six of the nine progesterone peaks exhibited by female #04 fell on full moon phases, including the four >10 ng/ml measures.

Bottlenose dolphins

Bottlenose dolphin sound production was relatively high during all sampling periods except those from mid-April to early June (Table 1; Fig. 3). Whistles averaged 25% of each sound sample (range: 11–33%), except for the 28/29 April 1980 period when whistles constituted nearly 65% (2327 of 3602) of the sounds counted. Both bottlenose females exhibited progesterone peaks: female #497 ovulated the end of April and again in mid-May; female #455 exhibited four progesterone peaks, three between mid-May and mid-June and one in mid-July. Progesterone levels in both females was uniformly low the balance of the year.

Sound production was negatively correlated with progesterone levels in both bottlenose dolphins; however, the relationship was statistically significant only between counts of pulsed sounds and progesterone level in female #497 (Fig. 4). Of note, sound counts when both females were ovulating, between mid-April and mid-May, were less than half those recorded during any other sampling period. Indeed, the lowest sound count on 28/29 April coincided with the first ovulation event by female #497, and contained a component of whistles twice that of any other sound sample. Progesterone levels in female #455 were positively associated with day length. Pulsed calls and whistles were negatively correlated with day length and water temperature, but statistical relationships were not significant. Moon phase did not seem to strongly influence ovulation events in either bottlenose female. The three ovulations noted in female #455 occurred on new moon phases ($F=2.93$, $P<0.10$) 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

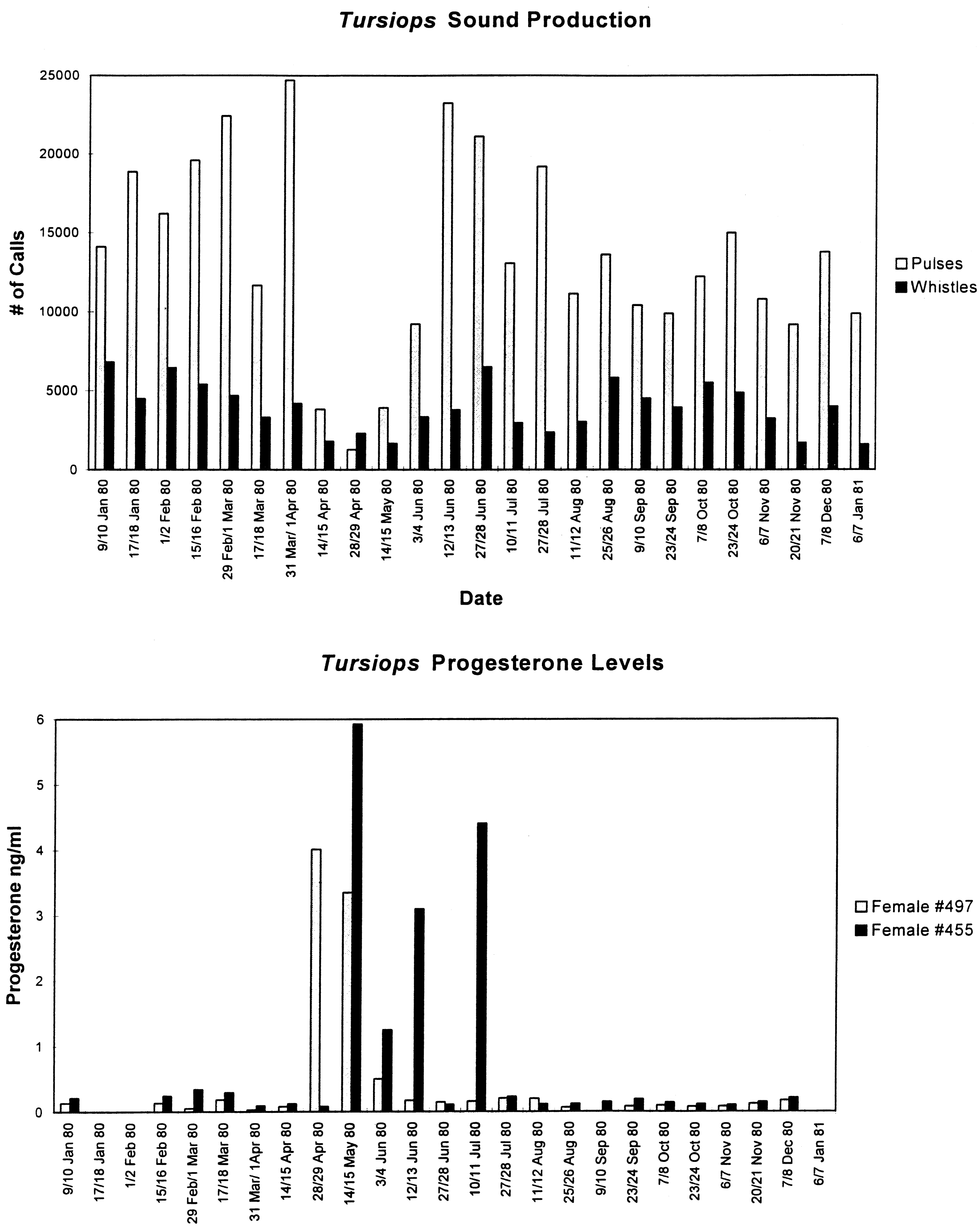
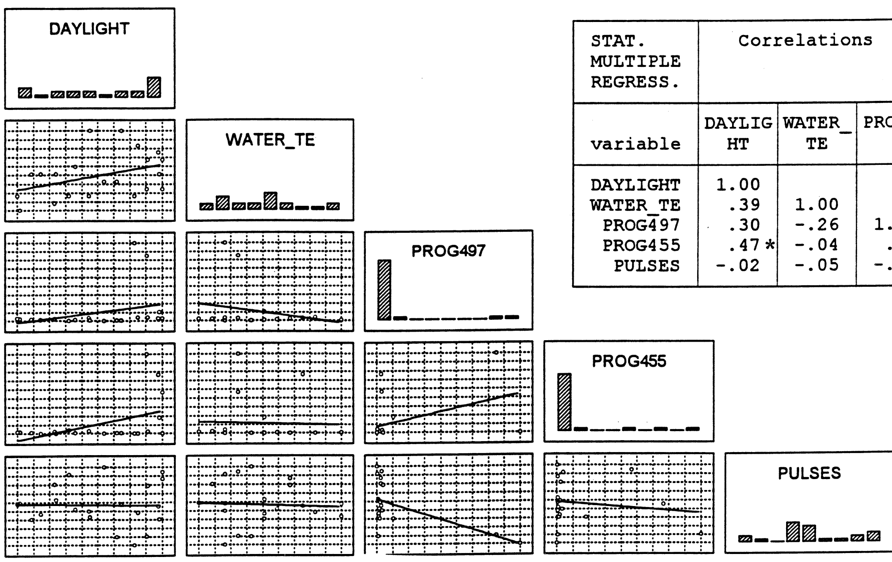


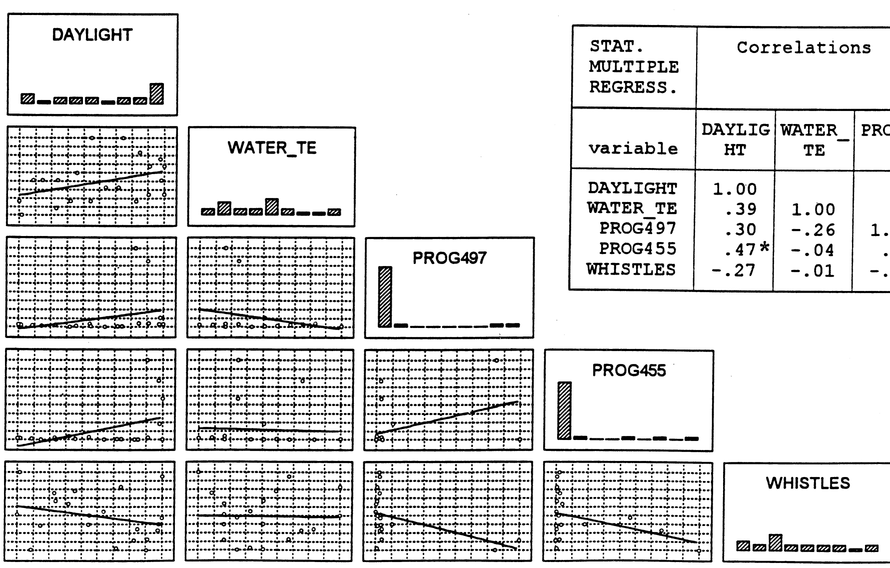
Figure 3. Total number of pulses and whistles tallied during each sampling period, and associated progesterone levels for the *Tursiops* females over the course of the study.

***Tursiops* Pulses**



STAT. MULTIPLE REGRESS.	Correlations				
variable	DAYLIG HT	WATER_ TE	PROG49 7	PROG45 5	PULSES
DAYLIGHT	1.00				
WATER_TE	.39	1.00			
PROG497	.30	-.26	1.00		
PROG455	.47*	-.04	.40	1.00	
PULSES	-.02	-.05	-.58**	-.15	1.00

***Tursiops* Whistles**

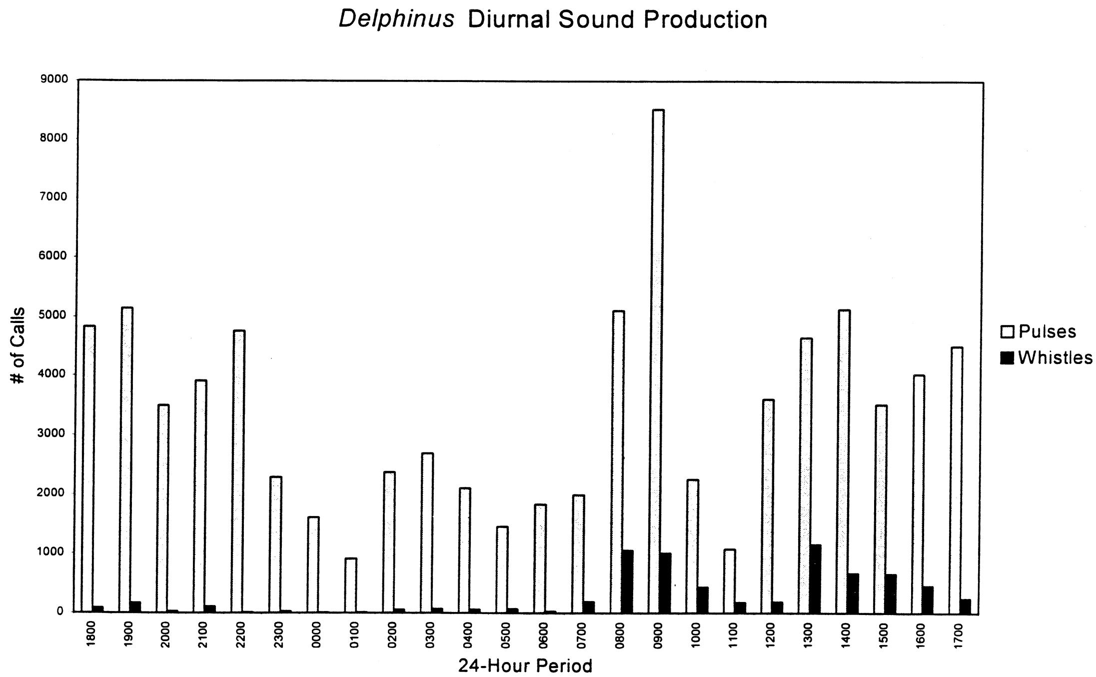


STAT. MULTIPLE REGRESS.	Correlations				
variable	DAYLIG HT	WATER_ TE	PROG49 7	PROG45 5	WHISTL ES
DAYLIGHT	1.00				
WATER_TE	.39	1.00			
PROG497	.30	-.26	1.00		
PROG455	.47*	-.04	.40	1.00	
WHISTLES	-.27	-.01	-.42	-.35	1.00

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: $*P<0.05$; $**P<0.01$.

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



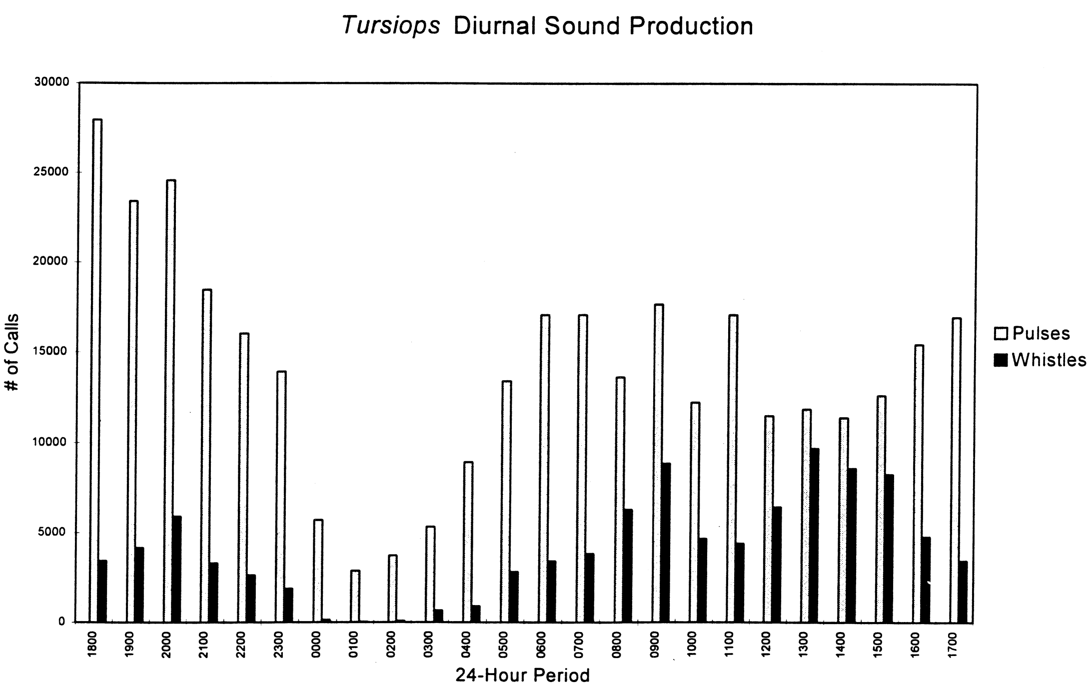


Figure 5. Cumulative hourly counts of pulses and whistles for *Delphinus* and *Tursiops* females. Note difference in scale between histograms.

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

Au, W. W. L. (1993) *The Sonar of Dolphins*. Springer-Verlag, New York, NY.

Caldwell, M. C. & Caldwell, D. K. (1968) Vocalization of naive captive dolphins in small groups. *Science* **159,** 1121–1123.

Hui, C. A. (1979) Correlates of maturity in the common dolphin, *Delphinus delphis. Fishery Bulletin* **77**(1), 295–300.

Hui, C. A. (1981) Seawater consumption and water flux in the common dolphin *Delphinus delphis. Physiological Zoology* **54,** 430–440.

Kirby, V. L. & Ridgway, S. H. (1984) Hormonal evidence of spontaneous ovulation in captive dolphins, *Tursiops truncatus* and *Delphinus delphis*. In *Reproduction in Whales, Dolphins and Porpoises* (eds W. F. Perrin, R. L. Brownell Jr. and D. P. DeMartin) pp. 459–464. Report of the International Whaling Commission, Special Issue 6, Cambridge, UK.

Klinowska, M. (1986) Diurnal rhythms in cetacea—a review. In *Behaviour of Whales in Relation to Management* (ed. G. P. Donovan) pp. 75–88. Report of the International Whaling Commission, Special Issue 8, Cambridge, UK.

Leatherwood, S. & Reeves, R. R. (1983) *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books, San Francisco, CA.

Leatherwood, S. & Reeves, R. R. (eds) (1990) *The Bottlenose Dolphin*. Academic Press, Inc., San Diego, CA.

Moore, S. E. & Ridgway, S. H. (1995) Whistles produced by common dolphins from the Southern California bight. *Aquatic Mammals* **21**(1), 55–63.

Perrin, W. F. & Reilly, S. B. (1984) Reproductive parameters of dolphins and small whales of the Family Delphinidae. In *Reproduction in Whales, Dolphins and Porpoises* (eds W. F. Perrin, R. L. Brownell Jr. and D. P. DeMartin) pp. 97–133. Report of the International Whaling Commission, Special Issue 6, Cambridge, UK.

Powell, B. A. (1966) Periodicity of vocal activity of captive Atlantic bottlenose dolphin: *Tursiops truncatus. Bulletin Southern California Academy of Sciences* **65**(4), 237–244.

Ridgway, S. H. (1983) Dolphin hearing and sound production in health and illness. In: *Hearing and Other Senses: Presentations in Honor of E. G. Wever* (eds R. R. Fay and G. Gourevitch) pp. 247–296. The Amphora Press, Groton, CT.

Schroeder, J. P. (1990) Breeding bottlenose dolphins in captivity. In: *The Bottlenose Dolphin* (eds S. Leatherwood and R. R. Reeves) pp. 435–446. Academic Press, Inc., San Diego, CA.

Sergeant, D. E., Caldwell, D. K. & Caldwell, M. C. (1975) Age, growth and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. *Journal Fisheries Research Board Canada* **30,** 1009–1011.

Thomson, D. H. & Richardson, W. J. (1995) Marine mammal sounds. In: *Marine Mammals and Noise* (eds W. J. Richardson, C. R. Greene Jr., C. I. Malme and D. H. Thomson) pp. 159–204. Academic Press, Inc., San Diego, CA.

Walker, L. A., Cornell, L., Dahl, K. D., Czekala, N. M., Dargen, C. M., Joseph, B., Hsueh, A. J. W. and Lasley, B. L. (1988) Urinary concentrations of ovarian steroid hormone metabolites and bioactive follicle-stimulating hormone in killer whales (*Orcinus orca*) during ovarian cycles and pregnancy. *Biology of Reproduction* **39,** 1013–1020.

Zar, J. H. (1984) *Biostatistical Analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ.