

ASPECTS OF UNDERWATER SOUND COMMUNICATION IN FLORIDA MANATEES (*TRICHECHUS MANATUS LATIROSTRIS*)

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We recorded underwater vocalizations of captive and wild Florida manatees (*Trichechus manatus latirostris*) to assess variability in acoustic structure of their sounds and to test hypotheses regarding the importance of specific acoustic traits in individual distinctiveness and in certain behavioral contexts. Manatees use vocalizations to maintain contact when in groups. The highest rates of vocalizing occur during antiphonal calling between females and calves. Vocalizations are complex, single-note calls with multiple harmonics, frequency modulations, nonharmonically related overtones, and other nonlinear elements. We measured 6 acoustic variables and found that individuals varied significantly in fundamental frequency, emphasized band, frequency range, and call contour (the overall pattern of complexity in frequency modulation). These traits did not vary within individuals on different dates or when manatees were alarmed and fleeing. Individual fundamental frequencies ranged from 1.75 to 3.90 kHz, and were negatively correlated with body size. Little sound energy occurred above 18 kHz in 502 call notes of 6 captive manatees sampled with a recording oscilloscope. Presence of harmonics and call duration differed by date and manatees emitted longer calls when fleeing disturbance. Call duration varied from 118 to 643 ms (geometric mean = 271 ms, 95% confidence limits = 264, 279 ms) in a sample of 479 vocalizations we recorded from 14 individuals. The maximum call duration recorded over the entire study was 900 ms. Females and calves responded only to each others' vocalizations when rejoining a group after brief separations, strongly suggesting individual recognition by sound. Structural complexity in the calls of manatees is similar to that in other sirenians, and may reflect their auditory capabilities and the unique physical properties of sound in shallow water.

Key words: communication, Florida, manatees, Sirenia, *Trichechus manatus latirostris*, vocalizations

The order Sirenia was named after the sirens of Greek mythology, mermaids who lured sailors to their death in shipwrecks by their singing. Despite this etymology, the range of complexity and significance of vocalizations in the communication and behavior of manatees has not been well established. Florida manatees (*Trichechus manatus latirostris*) were 1st documented to produce underwater vocalizations more than 40 years ago (Schevill and Watkins 1965). This was followed by limited analyses of sounds of 1 or 2 captive Amazonian manatees (*Trichechus inunguis*) and Caribbean manatees (*Trichechus manatus manatus*—Evans and Herald 1970; Sonoda and Takemura 1973). Observations of manatee behavior in conjunction with recording vocalizations were made by Hartman (1979) without spectrographic analysis, and by Reynolds (1981), who

also provided descriptive information on fundamental frequencies and calling rates of a female and calf separated by a floodgate. Hartman (1979) qualitatively described Florida manatee call notes with terms such as squeaks, chirps, and grunts, and described the contexts in which vocalizations were heard. Hartman (1979) hypothesized that aspects of manatee sounds may vary with motivational state, and may be individually distinctive and allow individual recognition.

There is renewed interest in the study of vocalizations of Florida manatees (Nowacek et al. 2003; Phillips et al. 2004), prompted in part to develop acoustic detection or warning technology to reduce accidental collisions between manatees and boats (Gerstein 2002; Niezrecki et al. 2003; Yan et al. 2005). However, interpretation of the properties of manatee vocalizations in the context of communicative function has been hampered in these studies by the inability to determine individual variation in the structure of manatee sounds and to observe the behavior of wild manatees while they are vocalizing. Our study conditions allowed us to circumvent some of these problems, and we provide a descriptive summary of

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aspects of manatee communication sounds based on larger samples of calls than gathered heretofore, and to test Hartman's hypotheses of individual distinctiveness and motivation-dependent variability in call structure. We interpret our findings in relation to recent advances in knowledge of Florida manatee auditory perception (Gerstein 2002; Gerstein et al. 1999) and the structure and use of sound in dugongs (*Dugong dugon*—Anderson and Barclay 1995) and Amazonian manatees (Sousa-Lima et al. 2002).

MATERIALS AND METHODS

Study area.—We recorded manatees in the field at Blue Spring State Park (28°56'50"N, 81°20'23"W) and the contiguous St. Johns River, Florida. Blue Spring is a 650-m-long, 20- to 30-m-wide, clear artesian spring 240 km south of the mouth of the dark, tannin-stained St. Johns River. The greatest depth is about 5 m. Florida manatees occur in marine, brackish, and freshwater habitats (Deutsch et al. 2003; Hartman 1979). However, the freshwater spring provides very favorable acoustic conditions for recording underwater sound because there is no interfering noise from snapping shrimp (*Alpheus heterochaelis*) typically found in marine settings. The bottom is soft mud, sand, and detritus. Water temperature is constant at 22.5°C. Manatees aggregate in Blue Spring during winter months to avoid the cooler St. Johns River, their typical habitat in warmer seasons. Individual manatees at Blue Spring are recognizable by unique scar patterns often visible from above the clear spring water. More detailed descriptions of this study area, attributes of the manatee population using it, and techniques for identifying individual manatees are available in Langtimm et al. (1998) and O'Shea and Hartley (1995). At Blue Spring, we observed manatees from banks and overhanging trees on shore and simultaneously recorded vocalizations. Some individuals also were radiotagged (O'Shea and Langtimm 1995) and tracked by boat in the St. Johns River, where additional observations and recordings were made. Field observations and recordings were all made by TJO, on 116 days between January 1980 and February 1984 and on 5 days from 1986 to 1988.

Before recording wild manatees, we also recorded captive manatees at SeaWorld of Orlando, Florida, on 6 dates in 1980–1981. The objectives of these sessions were to characterize the expected ranges of variation in temporal, frequency, and relative intensity attributes of manatee vocalizations; to obtain samples from known individuals to supplement recordings of wild manatees; and to judge the adequacy of our recording equipment. Manatees at SeaWorld were held communally in a circular cement tank with an adjoining isolation tank separated by a movable wooden barrier. We recorded calls of 6 individuals when they were held in short-term isolation in this adjoining tank. Research on captive and wild manatees was authorized under Federal Fish and Wildlife permit PRT-684532 and followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). This study was conducted before establishment of institutional animal care and use committees.

Recording and spectral analysis.—All sounds were recorded on Ampex 6.3-mm × 183-m × 1.5-mil polyester Number 632 professional audiotape (Ampex Corporation, Redwood City, California) using a Uher 4400 Report Stereo IC reel-to-reel stereo tape recorder (Uher Informatik, Braunschweig, Germany) at a tape speed of 19 cm/s, coupled with United States Navy Model H-56 hydrophones (Underwater Sound Reference Division, Naval Undersea Warfare Center, Newport, Rhode Island). The tape recorder was calibrated using pure tones at the United States Navy Underwater

Sound Reference Detachment in Orlando, Florida. Tape recorder sensitivity was flat over the range 0.1–19.0 kHz. Each H-56 hydrophone was calibrated before and after the study. Hydrophone sensitivity was flat over the frequency ranges of vocalizations and the tape recorder sensitivity. Details of hydrophone calibration methods appear in Groves (1974). The 2nd track of the stereo tape recorder was used for simultaneous voice annotation. We also recorded sounds of captive manatees using a Nicolet Model 1170 real-time recording oscilloscope (Nicolet Biomedical, Madison, Wisconsin) to verify that the acoustic energy for communication was contained within the range of frequency sensitivity of our field equipment. Oscilloscope recordings were made over short (20- to 80-ms) segments of each call near the midpoint (130-ms delay from onset) of the duration. In 1986 and 1987, a small number of sounds was recorded or monitored through a Gould Model CH-17u hydrophone (Gould Electronics, Eastlake, Ohio), which we calibrated at the Navy Underwater Sound Reference Detachment as flat over the range 0.1–10 kHz and ±3 dB re 1 volt/μPa over the range 10–20 kHz. Representative sounds have been digitized and deposited in archival collections at the Macaulay Library of Natural Sounds, Cornell University, and with the Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission.

In the field we distinguished individual manatees as sound sources in 3 ways while simultaneously recording and observing them through polarized sunglasses. We used behavioral cues and perceived loudness in relation to distance from the hydrophone to judge sources of sound. (For example, a female manatee resting below the hydrophone initiated vocalizing and was answered by her infant 25 m away, and the infant then swam to rejoin its mother; perceived loudness of the cries from the stationary adult female did not change, whereas those from the calf increased as it swam closer to the hydrophone.) In 1983 and 1984 we also used a 2-hydrophone array and relied on human perception to localize directionality of sound by time- and phase-delay properties. Two H-56 hydrophones were suspended 1 m below the water surface at Blue Spring separated by a distance that was a multiple of the observer's interaural distance, corrected for the wavelength of sound in water. The hydrophones were interfaced with the stereo channels of the tape recorder to stereo headphones, while a stereo mixer allowed simultaneous voice annotation of manatee behavioral observations on 1 track. Tests with known sound sources while the observer was blindfolded showed accurate left–right localization, but no ability to discern front and rear sources. Used in conjunction with behavioral cues from manatees under observation, the dual hydrophone array increased our ability to attribute sounds to specific individuals, particularly at times when small groups (2–5 animals) were present albeit widely scattered in relation to the position of the hydrophones. We also made recordings and observations of manatees in the St. Johns River by locating radiotagged individuals and following them in a 5.2-m boat (Boston Whaler Inc., Edgewater, Florida) and suspending a hydrophone 1 m below the surface of the water using a 3-m pole extended from the gunwale of the boat when anchored near focal animals. All observations were made opportunistically. Manatees were present at Blue Spring irregularly, and rain, surface ripples from wind, and glare from the sun frequently made simultaneous observation and recording impossible. At both Blue Spring and in the St. Johns River we monitored sounds of manatees during various activities to provide simple descriptive summaries of vocalization rates. These observations were limited to times when numbers of manatees present and activities were unambiguous. Definitions of activity categories (feeding, resting, traveling, nursing, and cavorting) are given in Hartman (1979) and Bengtson and Fitzgerald (1985). We counted numbers of calls during 10-min

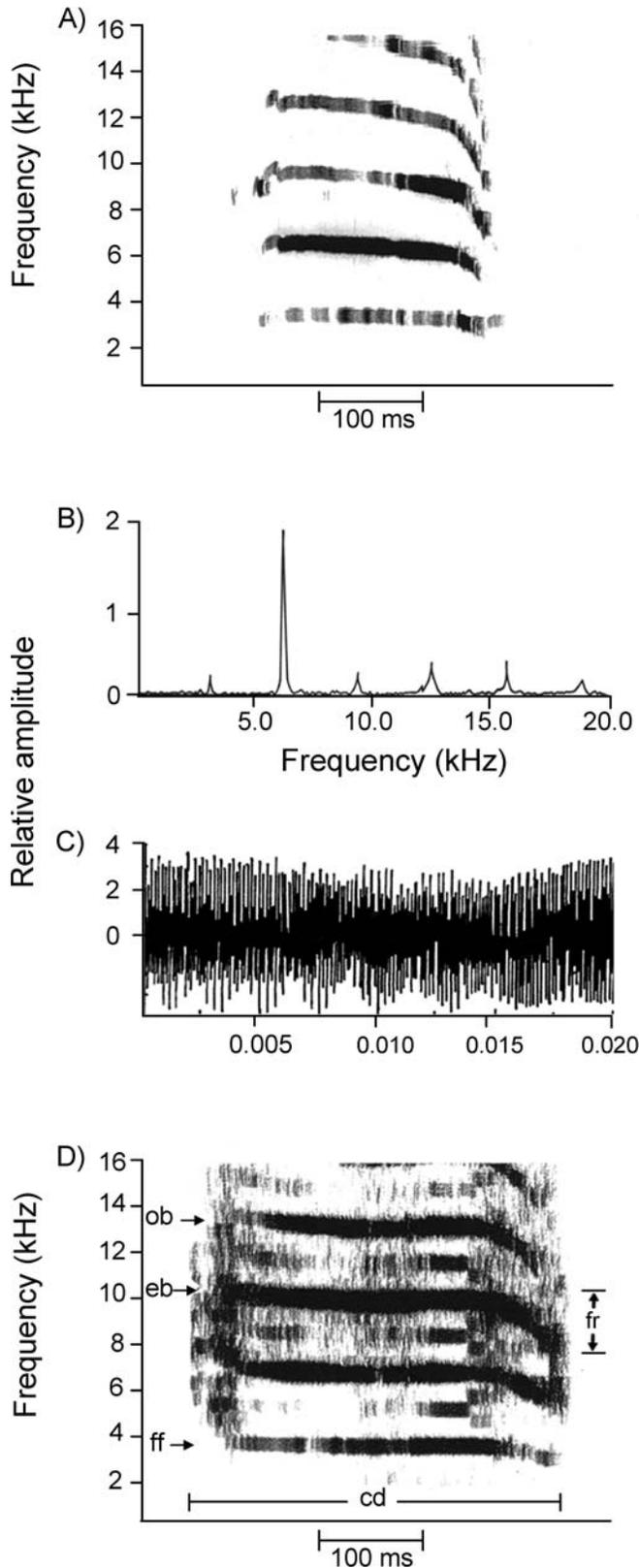


FIG. 1.—A) A wide band-width spectrogram of a call of a 1-year-old female Florida manatee (*Trichechus manatus latirostris*); B) frequency and relative amplitude plot of a 20-ms sample taken at the middle segment in the duration of the same call; C) time (s) and relative amplitude plots of the same segment; D) example of variables measured on a spectrogram display of a second 1-year-old female

sampling periods of resting manatees and approximately 2-min periods during other activities.

We used 3 techniques for spectrographic analyses. In cases where series of exchanges of calls between manatees were recorded (described as duets by Hartman [1979]) we made copies of these series of vocalizations at 19 cm/s with a 2nd Uher recorder. The copies were analyzed using real-time printouts produced by a Princeton Applied Research (PAR) Model 4512 FFT Real Time Spectrum Analyzer (PAR, Princeton, New Jersey) at the Rockefeller University Field Research Center for Ethology and Ecology, Millbrook, New York. The printouts were used to make descriptive measurements of time between calls and other characteristics of antiphonal calling. They also were used to select calls for which we produced more detailed spectrograms from the original recordings. These spectrograms were produced using a Kay Elemetrics 7029A Sona-graph (Kay Elemetrics Co., Pine Brook, New Jersey) at the wide-band filter setting or a Multigon Model 4600 Uniscan II spectrum analyzer with real-time spectrum display (Multigon Industries, Yonkers, New York). The Multigon Model 4600 displays digitized input from the tape recorder in the frequency-by-time format of a spectrogram, and provides cursors for measuring time and frequency on the screen display. We used this output to quantify acoustic variables for 479 calls from 14 individuals (9 wild and 5 captive manatees) used in the statistical analyses.

Call measurements and statistical analyses.—Manatee calls are single-note sounds with multiple harmonics and overtones (Schevill and Watkins 1965; Fig. 1). We measured 3 metric and 3 categorical variables of manatee calls. The categorical variables were emphasized band (the frequency band with greatest sound energy in a harmonic series; Fig. 1), number of other bands (the number of frequency bands in a harmonic series having at least 50% of the relative amplitude of the emphasized band, contributing to the subjective “fuzziness” of the sound of a call such that the fewer the other bands, the purer the tone; Fig. 1), and call contour (the overall temporal pattern of modulation of the emphasized band was classified in 1 of 6 categories; Fig. 2). The 3 metric variables measured for each call were duration (ms), fundamental frequency (kHz), and frequency range (kHz). Fundamental frequency was the lowest frequency band in a harmonic series; because some calls were frequency modulated, we measured the frequency of the lowest band at equally spaced time intervals throughout the call, and used the average value of those frequency measurements as the fundamental frequency. Some vocalizations included 2 or more different fundamental frequency bands, each with its own harmonic series (e.g., Figs. 1d and 2h). Vocalizations with such bands are described as containing overtones by Schevill and Watkins (1965), and these additional frequency bands are considered nonlinear elements by Mann et al. (2006). When 1 harmonic series was emphasized for at least 75% of the call duration, we measured the frequency of the fundamental of that series as the fundamental frequency of the call. When 2 or more series received approximately equal sound energy, we recorded a missing value. Frequency range was the range of frequencies in the emphasized band. This variable includes frequency modulation of 1 band, and switching between bands in different harmonic series. We tested the hypotheses that fundamental frequency

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Florida manatee. Explanation of symbols: eb = emphasized band; ob = other band (harmonic of the fundamental frequency); cd = call duration; ff = fundamental frequency; fr = frequency range (see “Materials and Methods” for further definitions). Note the presence of subharmonics (bands not harmonically related to the fundamental frequency) in D.

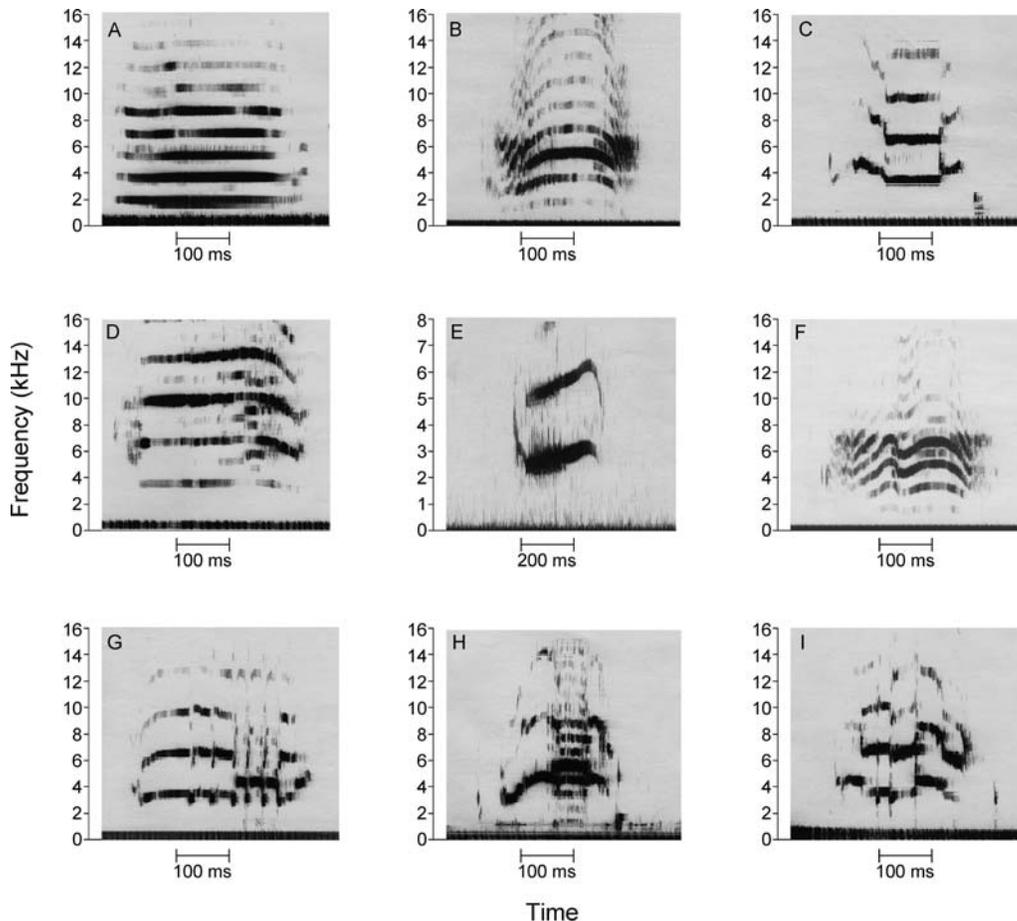


FIG. 2.—Contour categories for Florida manatee (*Trichechus manatus latirostris*) calls. A) Flat, unmodulated; B) hill-shaped (begins at low frequency, rises, then descends in frequency); C) U-shaped (begins at high frequency, descends, then rises); D) decreasing in frequency; E) increasing in frequency; F–I) complex modulations.

and mean range of the fundamental frequency were related to manatee body size (Sousa-Lima et al. 2002) using a Spearman rank correlation coefficient (Conover 1980). Body size was measured as total body length on captured manatees (O'Shea et al. 1985) within 1–5 months of recording dates on wild calves, 4–15 months on captive and wild adults, and 2–10 months on captive calves.

In addition to providing descriptive summary statistics of acoustic properties of manatee vocalizations (geometric means [GMs] and their 95% confidence limits [CL]), our primary objective was to test the hypothesis that certain call variables were individually distinctive. However, manatee vocalizations may represent graded communication signals, in which acoustic properties of calls could show variation at different times depending on context and the motivational state of the signaler. Therefore, observations based on multiple calls recorded from 1 manatee within a single sampling period may not be statistically independent. We investigated this potential problem by sampling 5 manatees (all wild calves) for which we had measurements of at least 15 calls on each of 2 or more days. We treated calls within an observation period as independent, and compared values of the 6 measured variables among days for each individual to determine the most repeatable among-measurement dates within individuals. Treating calls within an observation date as independent may be inappropriate if call parameters change throughout an observation period. However, we detected no significant serial autocorrelation among calls within an observation period for any of the metric variables (we

examined all call sequences containing 20 or more calls in a row). We also compared variables of calls from an adult female and calf manatee recorded in the St. Johns River when they were foraging and resting under normal conditions, and again when they were fleeing after being startled by disturbance from inadvertent noise by humans on the deck of our boat. This comparison was made to ascertain if changes in call variables could be discerned under these situations with clearly different motivational states.

We tested the distribution patterns of the metric variables against the assumption of normality to determine the appropriateness of parametric statistical approaches to hypothesis testing. Call duration was the only metric variable that was approximately normally distributed (after log transformation). Lack of normality in other variables rendered them inappropriate for application of discriminant function analysis to investigate distinctiveness among individuals based on multiple variables. Instead we consider this an exploratory analysis, and tested each variable of interest independently for distinctiveness among individuals. We performed a nested analysis of variance on call duration using individuals and days within individuals as factors, and calculated variance components for each factor. Fundamental frequency and frequency range were compared among days within each individual using the Kruskal–Wallis or Mann–Whitney test (Conover 1980). For the categorical variables we tested each individual for lack of independence between observation day and category level. We decided to err on the side of identifying characteristics

of calls variable among dates, within individuals (i.e., minimize type II error). We therefore tested each variable at the significance level $P = 0.10$. We evaluated each individual test at $\alpha = 0.02$ (0.10/5) to account for 5 tests on each variable. The variables call duration and other bands (presence of harmonics) showed substantial differences among days within individuals and were not analyzed further (see "Results"). For the remaining 4 variables we concluded that the different calls recorded from an individual can be treated as a sample of independent observations, and tested hypotheses explaining differences in these variables among individuals and between 2 age classes (adults and calves). The individual-by-category matrices for categorical variables contained rows with multiple sampling zeroes, making the data inappropriate for testing using the linear models approach (Grizzle et al. 1969). We therefore 1st tested for differences among all individuals using the Kruskal–Wallis test for metric variables and likelihood ratios (χ^2) for categorical variables. Then we tested separately for differences between age classes as follows: we created ordered categorical variables for fundamental frequency (<2,000 Hz, 2,001–2,500 Hz, 2,501–3,000 Hz, 3,001–3,500 Hz, 3,501–4,000 Hz, and >4,000 Hz) and frequency range (<750 Hz, 750–1,250 Hz, 1,251–2,000 Hz, and >2,000 Hz). For each of the 4 categorical variables (fundamental frequency, frequency range, emphasized band, and call contour) we performed the following analysis: for each age class we adjusted the cell frequencies in the individual by category matrix so that the row sum frequencies for all individuals were identical and equal to the row sum of the individual that originally had the smallest row sum. Then we summed all observations in each column of the matrix and tested for independence between the distributions of column sums in the 2 age classes. We adjusted data from all manatees in each age class to identical row sums to ensure that all individuals contributed equally to the distribution for that age class. We adjusted all row sums to the smallest original value because chi-square sample statistics depend on the total sample size and we chose to use the most conservative test.

RESULTS

Spectral characteristics of vocalizations.—We recorded more than 13,000 manatee calls. In addition to the Unigon screen displays measured for variables entered into the statistical analyses, we examined 1,428 Kay and 3,659 PAR spectrograms of these calls to subjectively ascertain overall variability in acoustic properties. Florida manatee vocalizations exhibit complex structural variability in temporal, frequency, and relative amplitude characteristics (Fig. 2). Call notes can be nearly purely tonal, but often include multiple harmonics ranging up to about 16 kHz. Fundamental frequencies of calls were as low as 600 Hz. Geometric mean fundamental frequencies of the 14 individuals varied from 1.75 kHz (95% $CL = 1.74, 1.77$ kHz) to 3.90 kHz (95% $CL = 3.67, 4.15$ kHz). In many cases the fundamental frequency contained less sound energy than higher harmonics (Figs. 2b, 2d, and 2f). Relative amplitudes of 502 call notes recorded directly on the oscilloscope from 6 captive manatees showed that almost all of the sound energy was contained in harmonics less than 18 kHz; we assumed this also to be true for wild manatees but could not judge this fully because of the 19-kHz upper frequency limits of sensitivity of the field tape recorder. In cases where harmonics had greater intensity than the fundamental frequency, these were usually the 1st or 2nd harmonic. Sound durations were variable. The 479 call notes recorded from known manatees

varied in duration from 118 to 643 ms ($GM = 271$ ms, 95% $CL = 264, 279$ ms). The longest sound recorded was 900 ms.

In addition to multiple harmonics, calls varied in frequency modulation, sometimes with complex rising and descending frequencies within notes, resulting in more complex shapes to spectrograms (Fig. 2). Nonlinear elements (for definitions see Wilden et al. [1998] and Mann et al. [2006]) occurred in calls, including subharmonics (Figs. 1d, 2a, and 2d), bifurcations from tonal harmonics to chaotic elements (Fig. 2b), frequency jumps (Figs. 2g and 2i), and biphonation (Fig. 2h). These frequency shifts and nonlinear elements resulted in distinctive subjective qualities to some call notes as perceived by the human ear, such as harshness, raspiness, or short trill-like sounds.

Geometric mean fundamental frequencies of individual manatees were negatively correlated with total body length ($r_s = -0.8, n = 11$ manatees for which we recorded 22–45 calls each, $df. = 9, t = -4.0, P = 0.003$). Geometric mean ranges of fundamental frequencies had a weaker negative rank correlation with total body length ($r_s = -0.64, n = 11, df. = 9, t = -2.7, P = 0.04$). Larger manatees had lower fundamental frequencies that tended to span a narrower range than smaller manatees.

One female was recorded on 2 occasions 1 year apart while it was a suckling calf. The fundamental frequency did not change appreciably ($GM = 3.54$ kHz, $CL = 3.34, 3.75$ kHz in 1981 compared to $GM = 3.53$ kHz, $CL = 3.36, 3.71$ kHz in 1982) despite growth over the 1-year period. This wild calf had a unique call contour with a trill-like quality distinctive to the human ear when 1st recorded in 1980. This distinctive quality was maintained when she was recorded or heard again in subsequent years up to 1987, despite her having reached adult size and sexual maturity, and including antiphonal calls made with her own calf. A small sample of calls ($n = 9$) recorded in 1987 showed individual features similar to those recorded in earlier years, with overlapping confidence intervals and no major change in fundamental frequency ($GM = 3.58$ kHz, $CL = 3.22, 3.99$ kHz in 1987). We also recorded vocalizations of a wild adult female in 1981 and again in 1987. In 1981 she emphasized the 1st harmonic at $GM = 2.20$ kHz ($CL = 2.12, 2.29$ kHz, $n = 27$). In 1987 she also emphasized the 1st harmonic in 14 of the 15 call notes recorded, at a similar frequency ($GM = 2.30$ kHz, $CL = 2.24, 2.37$ kHz), and had similar nonharmonically related bands and a distinctive contour. These observations suggest the hypothesis that some acoustic traits peculiar to individuals may remain constant over long periods.

Variability in call properties by individual, date, and motivational state.—Four acoustic elements varied among individuals: fundamental frequency, call contour, emphasized band, and frequency range. Fundamental frequency, call contour, and frequency range changed little between recording dates or when manatees were recorded while fleeing. The 14 individuals differed in distribution of fundamental frequency (Kruskal–Wallis test statistic = 372.4, $df. = 13, P < 0.001$). Several individuals had fundamental frequencies that showed little or no overlap with others in the same age category. In addition, adult females usually had lower fundamental frequencies than their calves ($\chi^2 = 81.7, df. = 2, P < 0.001$;

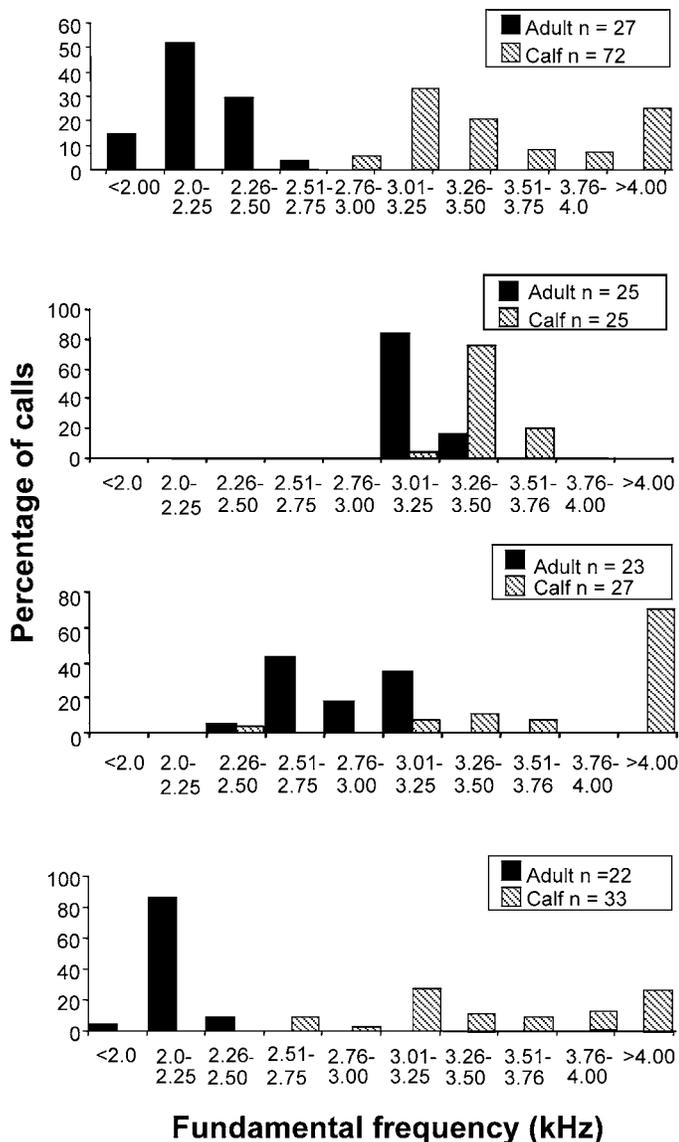


FIG. 3.—Distribution of fundamental frequency categories of calls of 4 adult female Florida manatees (*Trichechus manatus latirostris*) and their nursing calves.

Fig. 3) but one calf consistently had a lower fundamental frequency than its mother. Fundamental frequency shifted between dates for only 1 of the 5 calves recorded on more than 1 date (Mann–Whitney test statistic = 218.5, $n_1, n_2 = 17, 16$, $P < 0.001$). The shift in fundamental frequency for this individual was minor (130 Hz in recordings made 12 days apart) and likely not biologically significant. There were no detectable differences between the fundamental frequency of calls of the adult female when fleeing versus when undisturbed (Mann–Whitney test statistic = 105, $n_1, n_2 = 7, 16$, $P = 0.004$). We could not measure fundamental frequency for enough calls made by her calf when fleeing to conduct a similar comparison.

Individual manatees differed in the distribution of call contours ($\chi^2_{65} = 547.8$, $P < 0.001$, $n = 14$ manatees and 479 calls), and adult females also differed from calves in this

property ($\chi^2_5 = 91.1$, $P < 0.001$, $n = 225$ calf calls and 110 adult female calls). In general, adult females produced mostly flat, unmodulated calls (Fig. 2a), whereas calls of calves were mostly hill-shaped or descending (Figs. 2b and 2d). In 1 of 5 calves, distribution of call contour was dependent on observation date ($\chi^2 = 28.6$, $d.f. = 15$, $P = 0.10$). However, contingency tables were sparse because certain contours (e.g., Figs. 2c, and 2e–i) were rarely observed; small expected frequencies bias chi-square statistics upward (Brown 1981), suggesting that evidence that call contour is dependent on observation date may be weak.

Distributions of emphasized bands and frequency ranges also differed among individuals. Most manatees emphasized the 1st or 2nd bands in a harmonic series, but 2 individuals (both calves) emphasized the 3rd band or higher ($\chi^2 = 538.3$, $d.f. = 26$, $P < 0.001$, $n = 14$ manatees and 459 calls). Calves generally emphasized higher bands than adult females ($\chi^2 = 45.5$, $d.f. = 2$, $P < 0.001$). Individual manatees also differed significantly in distribution of frequency range (Kruskal–Wallis statistic = 227.3, $d.f. = 13$, $P < 0.001$). The distribution of calls among the 4 categories of frequency range also differed between adult females and calves ($\chi^2 = 63.8$, $d.f. = 3$, $P < 0.001$), with calves generally showing more strongly modulated calls covering a greater frequency range. None of the 5 wild calves recorded on >1 date exhibited a significant difference among dates in distribution of emphasized bands or distribution of frequency range. Vocalizations of the adult female and calf recorded when fleeing and when undisturbed showed no change in distribution of frequency range (Mann–Whitney test statistic = 109.5, $n = 7, 26$, $P = 0.41$ for the adult female; Mann–Whitney test statistic = 80.0, $n = 4, 27$, $P = 0.11$ for the calf), but both showed complete shifts in emphasized bands ($\chi^2 = 23.0$, $d.f. = 1$, $P < 0.001$, $n = 23$ calls for the adult female, $\chi^2 = 25.5$, $d.f. = 1$, $P < 0.001$, $n = 31$ calls for the calf).

Two acoustic properties varied considerably among dates and perhaps with motivational state: call duration and the presence of harmonics. The presence of harmonics differed significantly in distribution among dates for 3 of the 5 individuals sampled (Table 1). Although we observed substantial variation among the 14 individuals in call duration, variation among observation periods within individuals accounted for only 16% of the total variation in call duration ($P = 0.0001$, $F = 10.8$, $d.f. = 7$; Table 2). This component of variance (among dates within individuals) was one-third the magnitude of the among-individuals component. In addition, when the adult female and calf were frightened and vocalized while fleeing, their calls were substantially longer than when they were unstressed (Fig. 4). On another date, a 2nd female–calf pair was recorded a few minutes before their passing within 5 m of a 2-m-long alligator (*Alligator mississippiensis*) in clear water. As the alligator dove below the surface the calls of the calf became noticeably longer in duration ($GM = 190$ ms, $CL = 180, 200$ ms before, $n = 39$; $GM = 400$ ms, $CL = 360, 450$ ms after, $n = 22$). Manatee call duration appears to be an acoustic trait that may vary according to multiple factors, including motivational state such as alarm.

TABLE 1.—Distribution of the number of harmonics (other bands) present in calls of individual Florida manatee (*Trichechus manatus latirostris*) calves recorded on separate observation dates. Significance of likelihood ratio chi-square tests adjusted for multiple comparisons to 0.02 for each individual test (0.10 experimentwise error).

Individual	Date	No. calls	No. harmonics in calls					χ^2	d.f.	P
			0	1	2	3	4			
1	13 March 1981	19	2	17	0	0	0	25.2	9	0.003
	8 April 1981	26	2	14	9	1	0			
	24 February 1982	20	2	10	5	3	0			
	25 February 1982	19	1	6	9	3	0			
2	23 February 1981	25	0	0	2	7	8	13.1	3	0.004
	12 March 1981	20	0	0	5	10	5			
3	12 February 1983	21	0	1	8	3	4	17.6	4	0.002
	16 February 1983	14	0	0	2	11	1			
4	31 January 1984	17	0	0	6	4	5	2.7	4	0.610
	12 February 1984	16	0	1	5	6	3			
5	5 February 1982	21	2	5	11	3	0	4.8	3	0.186
	25 February 1982	18	1	9	4	4	0			

Variability in vocalization rates and evidence for individual recognition.—Rates of calling varied with activity, size, and group composition. The highest rates of vocalizations were made by cow-calf pairs. Resting manatees seldom vocalized. No vocalizations occurred in nine 10-min samples timed on solitary, resting manatees (6 males and 3 females). Six 10-min samples of resting groups of 2–6 manatees of both sexes yielded only 2 intervals with any calls, with rates of 0.4 calls/min in a group of 5 and 0.7 calls/min in a group of 6. Ten 10-min samples of 5 different resting cow-calf pairs yielded 6 silent intervals and 4 with rates of 0.1, 0.1, 0.6, and 0.6 calls/min. Solitary manatees were typically silent during other activities. No calls were made during 5 observations of solitary females feeding in three 10-min bouts and two 2-min bouts; 10 separate observations of traveling solitary manatees (averaging 1.9 ± 0.2 SE min per observation) also yielded no calls. In contrast, 5 observations of 2 separate cow-calf pairs feeding on vegetation during intervals of 2–10 min had rates of 2.2 ± 1.0 calls/min, and 7 observations (averaging 2.3 ± 0.2 min) of 4 separate cow-calf pairs while traveling all included vocalizations, ranging from 0.5 to 22.0 calls/min. Manatees traveling in small groups that did not include cows with calves also vocalized, but at seemingly lower rates (0–6.5 calls/min in three 2-min observations of groups of 2 or 3). We did not observe marked differences in call rates of manatees in clear water in comparison with rates in water of low visibility, but were unable to gather sufficient observations to evaluate this statistically. However, vocalization rates seemed higher during activities that involved more intense social behavior. For example, a group of 5 manatees (3 adult males and 2 subadult females) observed in five 2-min intervals of cavorting averaged 6.3 ± 1.7 calls/min (range 0.5–10 calls/min). Three cow-calf pairs observed during five 2-min intervals during or immediately before or after suckling averaged 10.4 ± 2.5 calls/min (range 4.6–20 calls/min).

Evidence for individual recognition was provided by observations of wild cow-calf pairs that rejoined after moving

TABLE 2.—Nested random-effects analysis of variance for log call duration of individual Florida manatees (*Trichechus manatus latirostris*). Dates within individuals are based on samples with at least 15 calls recorded per individual on each of >1 date. Calls were recorded on 2 dates for 4 individuals, and on 4 dates for 1 manatee.

Source	d.f.	SS	F	P	Variance component	%
Individual	4	6.60	83.8	0.0001	0.032	52
Date	7	1.48	10.8	0.0001	0.010	16
Error	224	4.41			0.020	32

apart in the presence of other manatees. We observed 43 such instances involving 9 cow-calf pairs separated by distances ranging from 2 to >40 m. In each case movement toward rejoining was preceded by calls made by either the cow or calf, and calling by both continued at least until the pair made physical contact. No other manatees made obvious responses to the cow or calf during these events. Intervals between calls in such episodes were short, calling rates were high, and calves called more often than did mothers (Table 3). In 1 pair observed rejoining on multiple occasions the geometric mean intervals between calf calls were about 3 s, whereas intervals between cow calls were longer and more variable (Table 3). Calves often responded quickly to calls of their mothers with an answering call, often after a latency of only about 1 s (Table 3).

Vocalizations also were made by adult males. Calls were recorded from at least 11 different adult males. Acoustic characteristics seemed comparable to those of calls made by females, but too few vocalizations were recorded from known individuals for statistical comparison. Thirty-nine calls re-

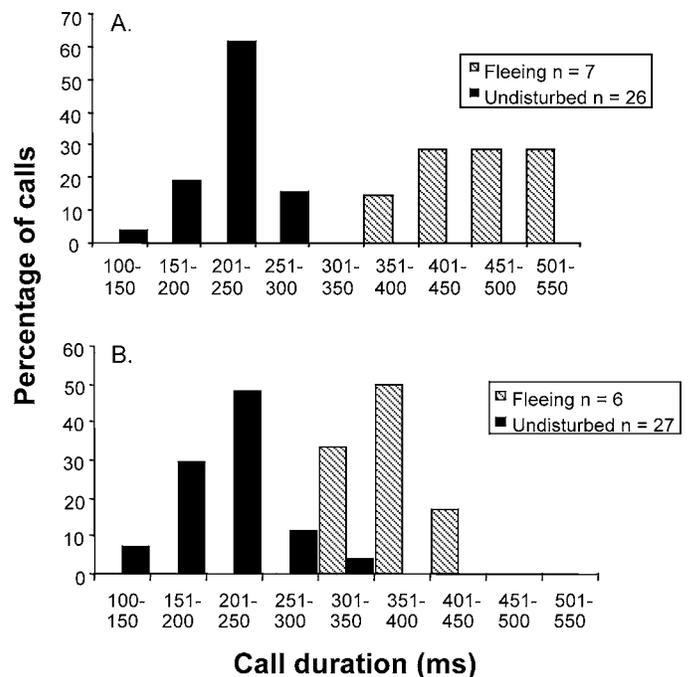


FIG. 4.—Distribution of call durations of A) an adult female Florida manatee (*Trichechus manatus latirostris*) and B) her nursing calf when undisturbed and while fleeing from sudden noises on the boat.

TABLE 3.—Descriptive summary statistics on temporal aspects of antiphonal calling between a wild adult female (cow) Florida manatee (*Trichechus manatus latirostris*) and her dependent calf on multiple occasions when the pair were rejoining after separation. Abbreviations: NR = not recorded; *GM* = geometric mean; *CL* = 95% confidence limits.

Date	Recording duration (s)	No. calf calls	No. cow calls	Calf call intervals (s)			Cow call intervals (s)			Latency cow call to calf call (s)		
				<i>GM</i>	<i>CL</i>	Range	<i>GM</i>	<i>CL</i>	Range	<i>GM</i>	<i>CL</i>	Range
4 February 1981	292	75	25	2.9	2.5, 3.3	0.5–27	5.7	3.4, 9.7	0.8–112	1.2	1.7, 2.7	0.0–8.3
4 February 1981	202	45	13	3.4	2.7, 4.2	0.6–19	18.6	9.8, 35.2	1.4–50	0.7	0.3, 1.6	0.1–9.5
13 March 1981	286	74	14	3.1	2.8, 3.5	0.9–11	12.5	4.8, 32.6	0.8–81	0.7	0.4, 1.2	0.2–6.3
26 March 1981	176	46	18	3.0	2.6, 3.6	1.5–13	8.4	6.7, 10.5	4.7–19	1.3	0.8, 2.1	0.3–5.7
8 April 1981	145	38	NR	3.1	2.6, 3.7	1.2–10		NR			NR	
24 February 1982	117	36	9	2.7	2.4, 3.1	1.4–6.5	9.1	6.7, 12.3	5.6–16	1.1	0.4, 2.9	0.3–5.2
25 February 1982	124	32	9	3.1	2.6, 3.6	1.5–13	7.8	4.9, 12.3	3.1–14	1.0	0.5, 2.0	0.3–5.0
25 February 1982	222	37	21	4.0	3.1, 5.2	1.2–31	7.7	5.3, 11.0	1.5–33	0.8	0.5, 1.2	0.3–6.5

recorded from 1 adult male in captivity (not included in the individual statistical analyses) ranged from 146 to 363 ms in duration (*GM* = 286 ms, *CL* = 267, 307 ms). The geometric mean fundamental frequency of this male was 3.34 kHz (*CL* = 3.28, 3.40 kHz), the 1st harmonic was emphasized in 72% of the calls (fundamental in 22%, 2nd in 6%), and frequency modulations and biphonations were sometimes present. Males were recorded vocalizing while cavorting in groups of 6–10, when disturbed from sleep, and in response to calls of other manatees when resting, feeding, or traveling.

DISCUSSION

Our data on fundamental frequencies of manatee vocalizations are similar to those already published (Schevill and Watkins 1965; Sonoda and Takemura 1973) and more recent recordings made without knowledge of individual identity or clear indications of context (Nowacek et al. 2003; Phillips et al. 2004). However, Florida manatee communication sounds have additional structural complexities that are perhaps best understood through comparisons with their auditory perceptual capabilities and the physics of sound propagation in shallow water. Although previous studies of auditory evoked potentials (Bullock et al. 1982) and anatomically based predictions (Ketten et al. 1992) suggest the best hearing sensitivity was at lower frequencies, a more recent study of audition in captive manatees (Gerstein 2002; Gerstein et al. 1999) produced reliable behavioral audiograms indicating a frequency range of best hearing (within 9 dB of maximum sensitivity) from 6 to 20 kHz, and peak sensitivity at 16 kHz. Manatees have general hearing capability over a frequency range of 0.4–46 kHz, but frequencies outside the 6- to 20-kHz range required marked increases in sound pressure levels for detection, and sensitivity dropped precipitously below 2 kHz. Studies of other animals show that auditory sensitivity is often tuned to frequencies used for communication (Owings and Morton 1998). This poses the question of why the frequencies of best hearing of Florida manatees occur at frequencies different from typical fundamental frequencies (1.4–4.0 kHz) of vocalizations.

Florida manatees inhabit rivers, bays, estuaries, and near-shore habitats (Deutsch et al. 2003), at shallow depths typically ranging from 1 to 3 m (Hartman 1979). This places them near

the surface at most times. Underwater sounds produced close to the surface are subject to the physical limitations of the Lloyd Mirror Effect, whereby lower-frequency sounds (including fundamental frequencies of some individual manatee vocalizations) can be attenuated or canceled by release of sound pressure at the surface layer from long sound waves within a zone of about 0.5–2 m below the surface boundary (Gerstein 2002; Gerstein et al. 1999; Medwin 2005). We suggest that the multiple harmonic structure of vocalizations provides an adaptive redundancy that may help override the Lloyd Mirror Effect and ensure signal reception during communication at shallow depths. The inclusion of multiple harmonics with greatest emphasis (highest intensity) at harmonics higher than the fundamental will help circumvent the canceling out of lower frequencies (the Lloyd Mirror Effect is insubstantial at >2 kHz in waters about 1.5 m deep [Gerstein 2002]), and these higher harmonics coincide more closely with the range of auditory best frequencies reported by Gerstein et al. (1999). Higher-frequency sounds also are easier for manatees to localize because they produce larger interaural intensity differences (Mann et al. 2005). This localization ability drops off at frequencies below about 2 kHz (Gerstein 2002). Additionally, most manatee communication sounds are produced by females and their calves. Although we observed low fundamental frequencies for some females, the Lloyd Mirror Effect does not apply when the signaler and receiver are very close (Gerstein et al. 1999). This is typically the case between manatee cows and calves when traveling and resting (Hartman 1979; Reynolds 1981). Frequencies below 2.0 kHz also are more difficult for manatees to localize than higher frequencies (Gerstein 2002), but this is probably of lesser importance when manatee cows and calves are communicating at near-touching distances. Higher harmonics probably play a more important role in communication among adult manatees when at least one is near the surface (e.g., during breathing or feeding on floating vegetation) and when manatee cows and calves are separated by greater distances or are fleeing and in need of maintaining contact. Thus, we argue that a harmonic structure encompassing multiple frequencies allows both detection and localization over a range of distances in shallow water. Gerstein (1999) found that manatees perceive their own vocalizations at intensity levels below ambient noise. He suggested that this was due to a loudness summation effect

across the perceived auditory critical frequency bands of hearing sensitivity that are encompassed by the harmonics and frequency shifts typical of vocalizations we recorded. Our findings that the use of harmonics can vary among dates within individuals suggests that manatees can easily modify this aspect of the signal, perhaps to best accommodate prevailing conditions and motivational states. In addition to frequency characteristics, Gerstein (2002) reported that the ability to detect underwater sound sources was dependent on the duration of the signal, with shorter, more pulsed sounds above a lower limit of 200 ms (such as the 264- to 279-ms-duration calls we found to be typical) more easily detected at a given sound pressure level than longer sounds. Short duration sounds also may reduce mixing of the source signal with potential reflections.

Our findings support past speculation on the communicative function of Florida manatee sounds first made based on natural history observations without spectral analyses by Hartman (1979), and allow comparisons with vocalizations and communication for other species of sirenians. Most published work on acoustic characteristics of vocalizations in the Sirenia is based on studies of captive individuals and did not attempt to understand variability in call structure. This is true for Florida manatees (Schevill and Watkins 1965), Amazonian manatees (Evans and Herald 1970; Sonoda and Takemura 1973), and dugongs (Marsh et al. 1978; Nair and Lal Mohan 1975). Nonetheless these studies revealed aspects of the structure of single call notes that share basic similarities to those we describe for Florida manatees: short durations (typically 50–500 ms), fundamental frequencies of 1–8 kHz, multiple harmonics, highest intensity in harmonics other than the fundamental, frequency modulations, and the presence of what are now recognized as nonlinear elements (Mann et al. 2006), described previously as overtones, nonharmonic components, and intercalated frequencies (Schevill and Watkins 1965). This suggests similar adaptations for shallow-water communication and perhaps a similar sound-generating mechanism for all sirenians. To our knowledge, there have been no anatomical studies of potential sound-generating mechanisms in manatees since the descriptions of laryngeal anatomy by Hill (1945) and Murie (1872). Direct observations of vocalizing dugongs led to speculation that sounds may originate in the frontal area (Anderson and Barclay 1995). More intensive anatomical studies on possible sound-production mechanisms in sirenians would be timely given increased knowledge of their vocalizations and auditory perception.

Recent research has revealed that some sirenians employ elaborations in their use of these single-note calls. In western Australia, male dugongs produce complex sequences of calls that are probably vocal displays related to a shallow-water lek mating system (Anderson 2002; Anderson and Barclay 1995). However, individual call notes bear similar hallmarks to those of Florida manatees (Anderson and Barclay 1995). These dugongs also produced lower-frequency “bark” calls with chaotic elements suggested to be aggressive in motivation, unlike any of our observations in Florida. Vocalizations of African (*Trichechus senegalensis*) and Amazonian manatees have yet to be quantified based on field observations. However, captive Amazonian manatees produce vocalizations similar to

those of Florida manatees, and are individually distinctive (Sousa-Lima et al. 2002). Individual distinctiveness was thought to be of functional importance in Amazonian manatee mother–young recognition, as we observed in Florida manatees. We also found that the use of contact calls varied with behavior and that the highest rates of vocalization occurred between mothers and calves, consistent with other observations (Bengtson and Fitzgerald 1985; Hartman 1979; Reynolds 1981). Florida manatee cows and calves are clearly distinctive in fundamental frequency, frequency range, and call contour; repeated observations in the field showed that mothers and calves differentially responded to each others' vocalizations. In addition to these basic traits, it has been hypothesized that the existence of nonlinear elements in bird and mammal calls can have communication significance. These elements may confer information about individual identity and motivation, and are difficult for signal receivers to ignore (Fitch et al. 2002). Further research into the functional significance of these elements in sirenian vocalizations is desirable. Clearly, there is considerable selective advantage for individual recognition of females and young in species such as manatees, which have long periods of maternal investment and are likely to lose visual contact in dark or turbid water and at night (Hartman 1979; Sousa-Lima et al. 2002). Sousa-Lima et al. (2002) also reported that captive Amazonian manatees exhibit an inverse relationship between total body length and mean range of the fundamental frequency. They found no relationship between body size and fundamental frequency in Amazonian manatees, whereas we found this relationship to be the stronger of the 2 relationships with size that we investigated. Perhaps this is because our sample spanned a wider range of body sizes (155–353 cm total length compared to 100–211 cm in Amazonian manatees). Taken together these findings support the possibility that the anatomical sound-production mechanism of manatees also increases with growth in body size, resulting in sound emissions of greater wavelength and hence lower frequency.

In conclusion, our study of underwater sound communication in Florida manatees has revealed a simple pattern in social function based on signals that are sometimes complex in structure. Calls have some structural characteristics that appear to provide information on individual identity, basic motivational state, and perhaps size of the signaler; however, calls are primarily used to maintain contact between individuals, particularly females and juveniles. Social use of sounds is more limited than in dugongs (Anderson and Barclay 1995). However, certain complexities in attributes of single-note calls, such as variable use of harmonic structure, may be common among all species of Sirenia and are likely related to adaptation for sound propagation and audition in shallow water.

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